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OLFACTORY CONSCIOUSNESS ACROSS DISCIPLINES

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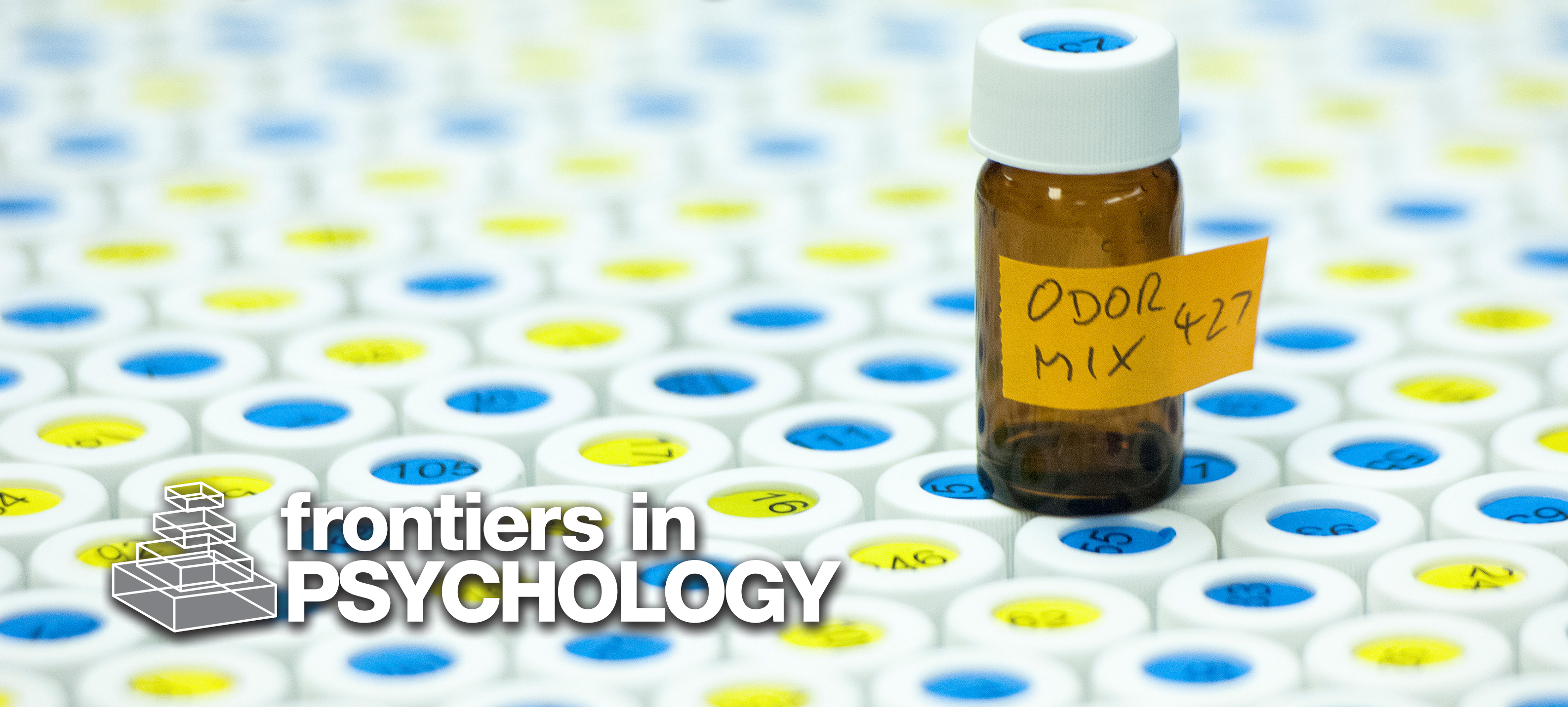

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OLFACTORY CONSCIOUSNESS ACROSS DISCIPLINES

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Vials containing different mixtures of odorants are used in psychophysical experiments that probe olfactory perception.
Credit: Zach Veilleux/The Rockefeller University

Our sense of smell pervasively influences our most common behaviors and daily experience, yet little is known about olfactory consciousness. Over the past decade and a half research in both the fields of Consciousness Studies and Olfaction has blossomed, however, olfactory consciousness has received little to no attention. The olfactory systems unique anatomy, functional organization, sensory processes, and perceptual experiences offers a fecund area for exploring all aspects of consciousness, as well as a external perspective for re-examining the assumptions of contemporary theories of consciousness. It has even been suggested that the olfactory system may represent the minimal neuroanatomy that is required for conscious processing.

Given the variegated nature of research on consciousness, we include original papers concerning the nature of olfactory consciousness. The scope of the special edition widely incorporates olfaction as it relates to Consciousness, Awareness, Attention, Phenomenal- or Access-Consciousness, and Qualia. Research concerning olfaction and cross-modal integration as it relates to conscious experience is also address.

As the initial foray into this uncharted area of research, we include contributions from across all disciplines contributing to cognitive neuroscience, including neurobiology, neurology, psychology, philosophy, linguistics, and computer sciences. It is our hope that this Research Topic will serve as the impetus for future interdisciplinary research on olfaction and consciousness.

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EDITORIAL
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Olfactory consciousness across disciplines

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Keywords: olfaction, smell, consciousness, theories of consciousness, perceptual consciousness

Although vision is the *de facto* model system of consciousness research, studying olfactory consciousness has its own advantages, as this collection of articles emphatically demonstrates. One advantage of olfaction is its computational and phenomenological simplicity, which facilitates the identification of basic principles. Other researchers study olfactory consciousness not because of its simplicity, but because of its unique features. Together, olfaction's simplicity and its distinctiveness make it an ideal system for testing theories of consciousness. In this research topic, the results of recent research into olfactory consciousness are presented.

SIMPLICITY OF OLFACTION

The relative simplicity of olfaction makes it a natural starting point for investigating perception. Olfaction has been used as a theoretical launchpad at least since 1764, when Reid wrote that "beginning with the simplest, and proceeding by very cautious steps to the most complex" (Reid, 1764) is the best strategy to understand the human mind. Following his own advice, Reid begins his *Inquiry into the Human Mind* with a chapter on olfaction. Quilty-Dunn's article explores Reid's account of odors as secondary qualities and argues for the relevance of Reid's theory for contemporary debates (Quilty-Dunn, 2013). The simplicity of the olfactory system is also what prompts Merrick and her colleagues to suggest in their review article that olfaction can be used as "the gateway to the neural correlates of consciousness" (Merrick et al., 2014).

Keller, in his contribution, takes advantage of the relative simplicity of the olfactory system in his attempt to identify the function of conscious information processing. Visual perception performs a myriad of functions. This versatility of vision makes the identification of the subset of vision's functions that require consciousness challenging. This problem, Keller argues, is much more tractable in olfaction, which is a specialized sense with circumscribed functions (Keller, 2014).

UNIQUE FEATURES OF OLFACTION

The many unique features that distinguish olfactory consciousness from other forms of perceptual consciousness are reviewed here with a focus on cognition by Stevenson and Attuquayefio (2013), and with a focus on neuroanatomy and neurodynamics by Merrick et al. (2014).

One striking feature of olfaction is the difficulty associated with olfactory imagery. It is easier to imagine seeing something than it is to imagine smelling it. Whether it is at all possible to voluntarily experiencing smells in the absence of the physical stimulus is the topic of ongoing research. Stevenson and Attuquayefio review the relevant literature and conclude that olfactory imagery is not possible (Stevenson and Attuquayefio, 2013). In contrast, Arshamian and Larsson argue that some individuals are capable of imagining smells (Arshamian and Larsson, 2014). Young (2014) sides with Arshamian and Larsson. According to Young, the fact that experiences during olfactory imagery have a qualitative character shows that olfactory awareness is always qualitatively conscious. In addition, he surveys evidence that olfactory sensory states can have a qualitative character in the absence of awareness.

Another peculiarity of olfaction is that it is unclear what, if anything, smells represent. Lycan, in his article, argues that olfaction does represent (Lycan, 2014). Lycan elaborates his previous proposal that a smell represents a miasma in the air (Lycan, 1996, 2000). In contrast, Batty, in her contribution, defends her proposal that there are no represented objects in olfaction (Batty, 2014). Instead, according to Batty, smells represent olfactory properties as occurring abstractly in our vicinity. Batty argues that, because there are no objects in olfaction, there can also be no object-failure, and therefore no olfactory illusions. A third view on the topic of olfactory objects is presented by Castro and Seeley (2014), who argue that the objects of olfactory perception are not objective physical entities, but affective categories.

The unique temporal structure of olfactory perception serves as the focus of Olofsson's review (Olofsson, 2014). Olfaction has a much lower temporal resolution than vision and audition. Olofsson reviews the literature on measurements of the time it takes subjects to respond to olfactory stimuli and proposes a cascade model of olfactory perception according to which we first detect an odor, then identify it, and finally determine odor valence and edibility.

THEORY TESTING IN OLFACTION

Some contributions to this research topic show that the simplicity of olfaction and its distinctiveness make it a useful system for testing theories of consciousness. Quality-space theory explains the nature of the mental qualities distinctive of perceptual states by appeal to their role in perceiving rather than by appeal to conscious subjective reports (Rosenthal, 2010). Here, Young and his coauthors show that quality-space theory, which is typically described in terms of color qualities, also applies to odor qualities (Young et al., 2014).

A second theory that is discussed here is the global workspace theory, according to which widespread broadcasting of information in the brain is necessary for consciousness (Baars, 2005). It has previously been suggested that the global workspace theory fails to explain conscious odor perception (Young, 2012). Here, Baars defends the global workspace theory against this suggestion and argues that the theory is applicable to olfactory consciousness (Baars, 2013). The widespread broadcasting of information that is central for the global workspace theory may be accomplished through synchronous gamma oscillations. Mori and colleagues review what is known about these oscillations in olfactory networks (Mori et al., 2013). They concluded that in olfaction the olfactory bulb plays the role that the thalamus plays for visual consciousness.

OUTLOOK

Olfactory Consciousness across Disciplines demonstrates that the simplicity and distinctiveness of olfactory consciousness make it an ideal system for theory testing. Theories of consciousness that aspire to be applicable to all modalities have to be consistent with these results. This research topic provides the resources for testing theories of consciousness in olfaction and offers some examples. We hope that this will enable and encourage a more systematic investigation of olfactory consciousness.

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Reid on olfaction and secondary qualities

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Thomas Reid is one of the primary early expositors of the "dual-component" theory of perception, according to which conscious perception constitutively involves a non-intentional sensation accompanied by a noninferential perceptual belief. In this paper, I will explore Reid's account of olfactory perception, and of odor as a secondary quality. Reid is often taken to endorse a broadly Lockean picture of secondary qualities, according to which they are simply dispositions to cause sensations. This picture creates problems, however, for Reid's account of how we perceive secondary qualities, including odors. Given Reid's insistence that we come to be aware of odors only by inferring a causal relation to obtain between them and our olfactory sensations, it seems that he cannot allow for direct, noninferential perceptual awareness of odors. Since his general account of perception invokes noninferential perceptual beliefs to explain perceptual awareness, it seems that Reid must either reject this general account for the case of olfactory perception (and supplant it with something else), or else deny that we ever actually perceive odors. I will attempt to reconcile these ideas by appeal to Reid's doctrine of "acquired perception," which involves the incorporation of learned conceptual representations into perceptual states via perceptual learning. Reidian acquired perception enables genuine olfactory perceptual acquaintance with odors despite the dependence of the semantic properties of the relevant representations on causal relations to sensations. In exploring these issues, I hope to illuminate several features of Reid's account of perception and demonstrate its interest to contemporary theorizing about conscious perception—especially olfaction—in the process. Reid's theory of olfaction remains a live, coherent option for present-day theorists.

Keywords: reid, olfaction, perceptual learning, sensation and perception, philosophy of perception

"OF SMELLING"

In a letter to Hugh Blair, dated 4 July 1762, David Hume commented on the manuscript of Thomas Reid's first major philosophical work, *An inquiry into the human mind on the principles of common sense* ('*IHM*'). Hume complimented its literary qualities, but noted that "there seems to be some Defect in Method" (*IHM* Appendix 1.1, 256). "For instance," Hume offered, "under the Article of Smelling, he gives you a Glimpse of all the Depths of his Philosophy" (*Ibid.*).

Reid took a thorough investigation of perception to be fundamental to a proper philosophical understanding of how the mind works. Besides the introduction and conclusion, each chapter of *IHM* is devoted to one of the five senses. Reasoning that it "is so difficult to unravel the operations of the human understanding" that we cannot expect to succeed except by "beginning with the simplest, and proceeding by very cautious steps to the most complex," Reid begins with a chapter on olfaction, "Of smelling" (*IHM* 2.1, 25). As Hume noted, the chapter is rich and disparate in its contents; it is larger than the chapters on gustation and audition combined, and is nearly as long as the chapter on tactition (the chapter on vision, perhaps unsurprisingly, dwarfs them all).

In this paper, I will explore Reid's theory of olfactory perception as a special—and especially pure—case of his theory of the perception of secondary qualities generally. His theory of secondary-quality perception, including olfaction, appears to have serious problems. My aim by the end of the paper is to provide an understanding of Reid's account of olfactory perception (and secondary-quality perception in general) that does justice to his general theory of perception and his notion of odors[1] and the other secondary qualities[2]. Hume's remark is apt;

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[1] The term "odor" is sometimes used to refer to qualities of external objects, and ptsometimes to refer to particular clouds of airborne particles or locations (see Batty, 2010a,b). Following what I take Reid's standard usage to be, I typically use the term to refer to qualities of objects; hopefully, not much hangs on this terminological point.

[2] Olfaction is of special interest in understanding Reid's account of secondary-quality perception, and not simply because Reid takes it to be the proper initial area of inquiry into perception. Vision and tactition involve perception of both primary and secondary qualities, and Reid says very little about gustation aside from likening it to olfaction. Gustation is also arguably wrapped up with tactition in a way that olfaction is not. Reid's discussion about audition, though useful in understanding his account of secondary-quality perception, is also largely about language and Reid's doctrine of natural signs. Olfaction is thus useful because, on Reid's account, it appears to be a sense purely dedicated to a particular kind of secondary quality. Furthermore, I will argue that Reidian olfactory perception is entirely acquired and in no part innate (see Two Solutions and Olfactory Perceptual Acquaintance), whereas this is false of vision and tactition and not obviously the case for audition—for example, Reid seems to believe in an innate faculty for the auditory perception of musical qualities (*IHM* 4.2, 50). Understanding Reid's account of olfactory perception is useful, therefore, because it is purely a matter of the acquired perception of a particular kind of secondary quality. Given its simplicity as well as Reid's special interest in it, olfaction is uniquely suited to provide an understanding of Reidian secondary-quality perception.

understanding Reid's theory of olfaction will require calling upon many other aspects of Reid's theory of perception and his general philosophy of mind.

The following discussion is historical in nature, but it will be valuable to many who are interested in olfactory perception, and the perception of secondary-qualities generally. As will be explained below, problems for Reid's account arise from the conjunction of two theses that many hold today: that perception is partly a matter of noninferential intentional awareness of qualities of external objects, and that odors are dispositions (or the bases of dispositions) to cause sensations. If the discussion below is correct, then these theses can be comfortably reconciled, which should be of interest to contemporary theorists. Furthermore, I will explore Reid's theory of "acquired" perception, which occurs when learned contents are incorporated into perceptual experience. This controversial idea is also part of contemporary philosophical discussion (see, for example, Churchland, 1979), and solving problems that arise for Reid's account will aid in understanding the nature of acquired perception. Finally, I will explain how Reidian olfactory perception accommodates both the qualitative and representational aspects of olfactory perceptual experience, while making minimal ontological commitments about the nature of odor. Clarifying and understanding Reid's theory of olfactory perception sheds light on all these contemporary issues, and provides a coherent and arguably attractive account of olfaction.

SETTING UP THE PROBLEM

PERCEPTION

Reid thinks the senses each deserve their own investigation, but he does have a general outline of how perception works, which Wolterstorff (2001) calls the Standard Schema. According to the schema, perception is a matter of having a sensation, which has no intentional content and is individuated by its felt quality, and then noninferentially forming a "conception and belief" of an external object and/or its properties, relations, and so on. Similar views of perception crop up quite frequently throughout the history of philosophy. The idea that perceptual awareness of outer objects is a matter of sensations giving rise to conceptual representations is perhaps most often identified with Kant. It was endorsed in the 20th century by Sellars (1956), and it (or something very close to it) is held by his various philosophical inheritors, e.g., Churchland (1979); Rosenthal (2005), and Coates (2007). Though Reid often receives credit for the origination of the view and the sharp sensation–perception distinction it licenses, A. D. Smith, who refers to the theory as the *dual-component view*, claims to find it earlier in the work of Malebranche, Digby, and sargeant (Smith, 2002, 284n17). Kuehn (1987) makes a strong historical case that the similarities between Reid and Kant are in fact due to a direct, as well as indirect, Reidian influence on Kant's thought.

It is crucial for Reid's general picture of perception that the intentional component of perception (the conception and belief)[3] make one immediately or directly aware of external objects and their properties. One of Reid's stated purposes in philosophy is to avoid succumbing to the theory of ideas, according to which (as Reid understands it) perceiving external objects is a matter of directly and noninferentially perceiving some mental entity—an idea, in Locke's and Berkeley's terminology, or an impression in Hume's—and positing a relation of some kind to obtain between the mental entity and some object in the world, or else leaving out the external world altogether. Reid took Berkeley and Hume to infer their radical epistemological and metaphysical conclusions from this premise, and thought their inferences valid. He saw this as a good sign that the premise was likely false, and tried to build another account of perception and knowledge that would explain the relevant phenomena equally well, and without what he saw as highly implausible conclusions[4].

Reid's account of perceptual intentionality is direct in two senses that are relevant to the ensuing discussion. First, the intentional component of perception is noninferential. It does not arise out of any process that could reasonably be called inference, and in that respect it constitutes a direct awareness of the object represented. Second, perceptual intentionality is, to borrow a phrase from Tyler Burge, "referentially non-derivative" (Burge, 2005, p. 30). That is, it does not refer to its object in virtue of referring to something else. In Acquired Acquaintance, I will place more restrictive conditions on perceptual awareness, but for now, these two ways in which, for Reid, the intentional component of perception is direct will suffice.

SECONDARY QUALITIES

One of the few things Reid agrees with Locke about is the legitimacy of the distinction between primary and secondary qualities. He does not agree, however, with Locke's way of drawing the distinction. For Locke, the mental states that stand for primary qualities "are resemblances of them," whereas ideas of secondary qualities "have no resemblance of them at all" (Locke, 1690, p. 2.8.15, 137). Reid, conversely, does not think mental states can ever resemble qualities of external objects, so neither primary nor secondary qualities resemble our sensations or perceptions of them (see *IHM* 5.8, 75; Van Cleve, 2011); to think otherwise, for Reid, is to make a basic category error that reveals deep philosophical confusion. For Reid, the distinction between primary and secondary qualities has to do, at least in part, with the kinds of understanding we have of different qualities of objects. With respect to the primary qualities, we have "a direct and distinct notion," but of secondary qualities "only a relative notion, which must, because it is only relative, be obscure" (*EIP* 2.17, 202). Our notions of secondary qualities are relative because such qualities "are conceived only as the unknown causes or occasions of certain sensations with which we are well acquainted" (*Ibid.*); because the causes are unknown, they are obscure to us. There is an interesting debate in the secondary literature on Reid as to whether his ontological account of secondary qualities has them as dispositions to cause

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[3] When I refer to the intentional component of perception, or to perceptual intentionality, I mean to refer to the conception–belief element of perceptual awareness. When I refer to perceptual awareness, I generally mean the complex of sensation and intentionality.

[4] See, e.g., the letter to the earl of Findlater and Seafield that opens *IHM* for Reid's announcement of his intentions in this regard (*IHM* Dedication, 3–6).

sensations or as the bases of those dispositions[5]. In either case, however, it is clear that we only really think there are secondary qualities at all in virtue of positing a causal relation to obtain between them and our sensations, and that our ordinary knowledge of them does not progress beyond that relative and obscure notion.

THE PROBLEM

Perhaps the problem is already clear. On the one hand, Reid says perceptual intentionality is not based on inference, and refers to its objects non-derivatively, i.e., not in virtue of referring to anything else. On the other hand, Reid says our notions of secondary qualities like odors are not direct, and are ostensibly based on our inferring there to be external qualities that cause our sensations. Our awareness of secondary qualities, such as it is, appears therefore to be both inferential and referentially dependent on sensations. There has been considerable controversy about whether Reidian sensations' mediating perceptual intentionality, as occurs even in the perception of primary qualities, renders Reid's general view of perception indirect in some Lockean sense[6]. I am not interested in that question here, however. Given that the very content of our notion of a secondary quality such as odor is dependent on an inference from awareness of sensations, for Reid, it seems impossible that we could ever actually perceive odors or any secondary qualities at all on his view. This is the conundrum. Van Cleve (in press) argues that the proposition that perception is immediate, the proposition that our notions of secondary qualities are relative and obscure, and the proposition that we can perceive secondary qualities, form an inconsistent triad.

TWO SOLUTIONS

ORIGINAL AND ACQUIRED PERCEPTION

I will sketch two possible solutions to the problem just raised, one that relies on nativism (which Reid generally endorsed), and one that relies on perceptual learning. First, it will be helpful to explain a crucial aspect of Reid's philosophy, namely, the distinction between *original* and *acquired* perception. As mentioned in the previous section, Reidian perception occurs when sensations give rise to noninferential intentional states that take external things as their objects. It is an open question to what extent the patterns of mental causation that relate sensations to perceptual intentional states are learned, and to what extent they are innate. Wilfrid Sellars, who seems to endorse the same broad view of perceptual awareness[7], argues that the very capacity to have intentional states is entirely learned, and so he would deny that the relevant causal connections between the sensory and intentional components of perception are innate to any extent (Sellars, 1956). Reid, on the other hand, endorses a strong form of nativism, according to which certain kinds of sensations give rise to certain kinds of intentional states due to the nature "of our constitution" (see, e.g., *IHM* 5.2, 56). Reid calls this sort of perception "original perception" (e.g., *IHM* 6.21, 177), and contrasts it with "acquired perception," which occurs when the causal connections between the sensory and the intentional components of perception are acquired through habituation (e.g., *IHM* 6.21, 177–178).

There are some uncontroversial examples of qualities that are perceived through original perception, but they are few in number, and are, somewhat surprisingly, mostly proprietary to tactition. They include tactile perception of texture, solidity, shape, motion, and what Reid calls "hardness," which is the propensity of a body to resist deformation in response to pressure (*IHM*, Chapter 5). They also include the visual perception of what Reid calls the "visible figures" of objects (*IHM* 6.22, 186), which are two-dimensional forms that operate according to a non-Euclidean spherical geometry (*IHM* 6.9)[8]. Uncontroversial examples of acquired perception include the visual perception of three-dimensional figure (which Reid calls "real figure," and also, because it is originally perceived only through tactition, "tangible figure"). They also include perceiving what are today called higher-level properties, or as Siegel (2011) calls them, "K-properties." According to Reid, of all our perceptual capacities, "the far greater part is *acquired*, and the fruit of experience" (*EIP* 2.21, 235; italics his).

> The farmer perceives by his eye, very nearly, the quantity of hay in a rick, or of corn in a heap. The sailor sees the burthen, the built, and the distance of a ship at sea, while she is a great way off. Every man accustomed to writing, distinguishes his acquaintance by their hand-writing, as he does by their faces. And the painter distinguishes in the works of his art, the style of all the great masters. In a word, acquired perception is very different in different persons, according to the diversity of the objects about which they are employed, and the application they bestow in observing them.
> (*IHM* 6.20, 172)

It is not obvious how olfactory perception fits into the original–acquired dichotomy. I will describe two ways of solving the problem of olfactory perception, one according to which olfactory perception is acquired, and another according to which odors are perceived originally. The acquired story is superior, though it will require some work to make sense of it.

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[5] The "base" view seems more popular. For articulations and defenses of that view, see (Lehrer, 1989; Wolterstorff, 2001; McKitrick, 2002); for the dispositional view, see Van Cleve (2011). For what it's worth, I think the base view is likely the correct interpretation of Reid, but since I am here only concerned with the perception of secondary qualities and not with their ontology, nothing hereafter should hang on it.

[6] See (Wolterstorff, 2001; Buras, 2002; Smith, 2002; Van Cleve, 2002, 2004). For defense of Reid's direct realism, see Copenhaver (2004), Quilty-Dunn (2013).

[7] See (Smith, 2002), Chapter 2, for an interesting critical discussion of Reid and Sellars, and of the similarities between the two.

[8] This led Reid to develop a fascinating and ingenious sketch of a non-Euclidean geometry in 1764 (*IHM* 6.9), several decades before such projects were incorporated into mainstream Western mathematics [Daniels (1974); see Yaffe (2002) for a thorough discussion]. It was not well-recognized as fascinating or ingenious at the time. Joseph Priestley, in his critical examination of Reid's *IHM*, remarked, "I do not remember to have seen a more egregious piece of solemn trifling than the chapter which our author calls the "Geometry of Visibles" (Priestley, 1775, p. 99–100).

ACQUIRED OLFACTORY PERCEPTION

By far the more popular solution in the secondary literature is to interpret Reid as saying that secondary qualities are perceived only via acquired perception. This approach is endorsed by, at least, Lehrer (1978), McKitrick (2002), Nichols (2007), Buras (2009). As McKitrick says, we "do not originally perceive secondary qualities, except as unknown causes of sensations. It is not a part of our original constitution that sensations produced by secondary qualities give us perceptions of those qualities as they are in themselves" (McKitrick, 2002, p. 493). On the contrary, according to this interpretation, our conception of secondary qualities is in the first instance a theoretical inference from our sensations to their causes. We can only come to perceive secondary qualities by incorporating this conception into occurrent perceptions. Since Reid says "our senses give us only a relative and indirect notion" of secondary qualities (*EIP* 2.17, 201), it seems natural to say that, in terms of original perception, we do not have any sort of direct perceptual awareness of odors. Acquired perception would thus be required to supplement our endowed perceptual capacities.

The problem with this route is that it does not seem immediately to avoid the crucial problem of the perception of secondary qualities. The problem, recall, is this: if our conception of secondary qualities is an inference from our sensations to some unknown outer cause, and if perceptual intentionality must be noninferential and referentially non-derivative, then we cannot perceive secondary qualities. McKitrick simply says that such perception is "mediated" by our awareness of sensations (McKitrick, 2002, p. 494; see also Nichols, 2007, p. 169)—but of course, by Reid's measure of what constitutes perception, such "perception" is not really perception. It is just an inference based on awareness of a mental entity, e.g., an olfactory sensation. According to Nichols, "our perceptual beliefs about primary qualities conform to a non—inferential theory" of perceptual knowledge, while those about secondary qualities do not (Nichols, 2007, p. 215).

There is a way out of this problem. It is crucial to distinguish between a given notion's referring to type A by means of reference to a relation to type B, and a token intentional state's referring to a token of A by means of a token of B. Less abstractly, there is a difference between our notion of a given type of odor, O, having the content, *The kind of property that causes sensations of type O**, and my occurrent awareness of the instance of O in my environment being referentially derivative of my awareness of my token sensation of O*[9]. These two ideas are doubly dissociable. On the one hand, my notion of rain is not referentially or inferentially dependent on my notion of a lawn chair cushion's being wet, but my occurrent belief that it rained might be based on an inference from the wetness of the cushion. On the other hand, and more importantly for the case of olfactory perception, my notion of what it is to be an odor of type O might be wholly dependent on O's bearing certain relations to sensations, but my occurrent perceptual belief that there is an instance of O before me need not be an inference from my awareness of a token O* sensation. This latter case is enabled by the possibility of acquired perception, whereby conceptions formed initially through inference or some other non-innate procedure can become noninferential constituents of perceptual intentional states. For instance, where I might once have thought there was a car in the street because I thought a car was the likely cause of my sensations, through perceptual learning, I gain the capacity to form, noninferentially, an auditory perception as of a car in the street[10], [11].

The case is confused with olfaction (and other secondary qualities) because the semantics of our conception of a given odor O involves a description of a relation it stands in to sensations. That seems to imply that becoming aware of O in perception is really just a matter of introspectively becoming aware of sensations and positing such a relation to obtain between *my present sensations* and some odor in the environment. But that simply does not follow. If sensations can noninferentially give rise to conceptions, then a sensation of type O* could noninferentially give rise to a conception of O; in that case, my awareness of O will not be an inference from O*. It will just also happen to be the case, given the vagaries of olfaction, that my notion of what O is depends on its relations to O*, and my acquisition of that notion *did* depend on inference from O* sensations.

The semantics of our conception of odor can be derivative from our awareness of sensations without making every instance of our perceptual awareness of odors being so derivative. The primary function of acquired perception, for Reid, is to enable inferential awareness to transform into noninferential perception. The particularly indirect and relative semantics of our conceptions of olfactory properties obscures this point in the case of olfactory perception, but there as elsewhere, our indirect conceptions can become incorporated into perceptual awareness, thus yielding direct perception of odors in the environment without being mediated by occurrent awareness of token sensations. Though the semantics of our conception of O is referentially derivative at the level of types—that is, our conception refers to odors of type O via referring to a relation that obtains between such odors and sensations of type O*—the token representation of O that figures in an acquired olfactory perception would be referentially non-derivative at the token level, since it does not refer to the token instance of O in the environment in virtue of referring to a token O* sensation. No token acquired perception, therefore, is referentially derivative of any token sensation, even if the type of which the perceptual representation is a token is referentially derivative of sensation-types.

The acquisition of our conceptions of odors would, in this story, be causally dependent on our already being able to form conceptions of objects, perhaps via original perceptions of their primary qualities. We may, in the first instance, be perceptually aware of objects by means of their primary qualities and

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[9] Following a somewhat standard notation, I use a letter to denote a type of quality of external objects, and the same letter followed by an asterisk to denote the type of sensation that corresponds to it.

[10] Of course, whether I need to have the sensations first is a separate question, and has no bearing on the inference/reference point. A token sensation can causally precede a perceptual intentional state without being referred to or rendering the intentional component of perception inferential; indeed, that is how Reidian perception typically functions.

[11] For a primer on the psychology of perceptual learning, see Kellman and Garrigan (2009).

also be aware of our olfactory sensations; we may then posit some unknown quality in the objects we perceive that is causally responsible for our olfactory sensations. Through a gradual trial-and-error learning process, we form fine-grained conceptions of odors, and through the process of perceptual learning, we become able to trigger these conceptions in acquired perceptions without undergoing any inference or making reference to our occurrent olfactory sensations. A passage where Reid discusses the acquisition of our conceptions of colors provides a helpful analog:

> By the constitution of nature, we are led to conceive this [color sensation] as a sign of something external. A thousand experiments for this purpose are made each day by children, even before they come to the use of reason. They look at things, they handle them, they put them in various positions, at different distances, and in different lights. The [sensations] of sight, by these means, become associated with, and readily to suggest, things external, and altogether unlike them. In particular, that [sensation] which we have called the appearance of color, suggests the conception and belief of some unknown quality, which occasions the idea; and it is to this quality, and not to the [sensation], that we give the name of color.
>
> (*IHM* 6.4, 86)

ORIGINAL OLFACTORY PERCEPTION?

One could argue that there is original perception of some secondary qualities. Van Cleve suggests that perhaps original perception of secondary qualities can be said to occur if it allows for the subject to locate the instance of the quality in space. As he observes, however, this would rule out olfaction if we "have no such innate ability to localize the causes of our olfactory sensations" (Van Cleve, in press).

Reid seems to say, however, that though olfaction and audition do not enable original localization, they still involve original perception:

> In smelling, and in hearing, we have a sensation or impression upon the mind, which, by our constitution, we conceive to be a sign of something external: but the position of this external thing, with regard to the organ of sense, is not presented to the mind along with the sensation.
>
> (*IHM* 6.8, 99)

Van Cleve suggests that we may "have an original perception to the effect that *some* quality exists that is causing our sensation or, more colloquially, that a certain scent is in the air,"[12] and that "one could even be said to have an objectual perception of the scent or quality itself, without knowing where it resides" (Van Cleve, in press)[13].

The question would immediately arise, of course, as to whether the awareness we come to form of the odor is actually just an inference from our awareness of the sensation. Reid seems to talk as though it is inferential when he says that the senses originally give us only a relative and indirect notion of odor. Perhaps, on the other hand, the account could work in the exact opposite direction from the acquired-perception account. That is, instead of saying we gain a notion of odor through inferences from sensations, and then incorporate it into perception through perceptual learning, yielding noninferential perceptual awareness of odors, we could say that we *begin* with such noninferential perceptual awareness of odors, and through exploring what our notion of an odor is, develop an indirect and relative notion. This story is undeveloped as it stands, but there is nothing internally inconsistent in it.

Nonetheless, the nativist story leaves the origin of our capacity to represent odors noninferentially unexplained, whereas the acquired-perception story explains it in terms of our inferentially taking there to be causes of our sensations and eventually coming to represent such causes noninferentially without referring to token sensations. Indeed, though the passage quoted above in this section does speak of "our constitution" and thus suggests original perception, it could be that Reid simply means we have a natural tendency to posit causes of our sensations, as he says children theorize about the causes of color sensations. The acquired account is preferable on the theoretical grounds that it enables a fuller explanation of how olfactory perception takes place, and there does not appear to be textual evidence that cuts unambiguously against it. Furthermore, Reid's criteria for positing innate psychological laws include the inability to explain the relevant psychological phenomena "by tradition, by education, or by experience" (*IHM* 5.2, 58). The mere existence of a coherent and explanatorily efficacious account of olfaction in terms of perceptual learning would thus suffice by Reid's own lights to make a nativist explanation unnecessary. There are serious (though surmountable) problems for the acquired account, however, to which I turn now.

ACQUIRED ACQUAINTANCE

ACQUIRED PERCEPTION NOT PERCEPTION?

One might be inclined to challenge the idea that acquired perception is actually *perception*. The argument arises because lots of cases that seem to fit the criteria for acquired perception do not seem like perception. For van Cleve, for example, one's awareness of the external environment should only be considered perceptual awareness if it involves "conception of the acquaintance variety" (Van Cleve, 2004, in press), which he argues acquired perception does not involve. As noted above, perception, according to Reid, involves "conception and belief." Conception is simply the intentionality-providing component of all intentional mental states; it may therefore be open to further debate whether it involves conceptual representation in something like the contemporary sense (Alston, 1989). Of course, Reid does always talk of conception in perception as paired with belief, perhaps suggesting that it is a form of intentional content that can figure in a belief (and thus, perhaps trivially, that it is conceptual in nature). However, he also talks of conception occurring by itself, in cases

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[12] Batty argues that olfaction represents odors (conceived of as particulars in the ambient environment, rather than qualities of objects) as being "here" [2010a, p. 524–525; see also Batty (2010b), Richardson (2013)].

[13] Lycan, similarly, says there is no analog of stereopsis in olfaction, despite the presence of two nostrils and olfactory bulbs, which is a mere "superfluity" (Lycan, 2000, 287n12). This is probably incorrect. Porter et al. (2007) found that the distance between the nostrils facilitates different odor sampling in each nostril; furthermore, they showed that scent-tracking in humans is significantly worse when odors are equally distributed between both nostrils.

of "simple apprehension," which for Reid is merely having a thing in mind, without predicating anything of it such that one's mental state is truth-evaluable (*EIP* 1.7, 65). It thus seems possible to construe different kinds of conception as involving different sorts of contents (Alston, 1989). One might, therefore, argue that what distinguishes perception from mere belief is the kind of conception or awareness involved, perhaps in terms of nonconceptual content (e.g., Copenhaver, 2010; Quilty-Dunn, 2013).

The immediate question is, what forms of awareness constitute acquaintance? Perhaps we can characterize perceptual acquaintance without taking a stand on the kind of content involved in the relevant state[14] . The term "acquaintance" evokes a heavy load of Russellian baggage—van Cleve says he means it "in something like Russell's sense" (Van Cleve, in press). In order to understand the proposal better, I will turn briefly to Russell's notion of acquaintance. Russell says, "I am acquainted with an object when I have a direct cognitive relation to that object, i.e., when I am directly aware of the object itself" (Russell, 1910, p. 108). For Russell, of course, the objects with which we are directly related must be sense-data, and cannot be ordinary outer objects. When discussing the perception of external objects and their qualities, then, we can put that assumption aside. Russell also attaches unique epistemic significance to acquaintance. When one is acquainted with an object, "no further knowledge of it itself is even theoretically possible" (Russell, 1912, Ch. 5, 32). Again, this aspect of Russellian acquaintance simply could not extend to the perception of external objects. While Reid would certainly say that knowledge of objects gained through perception occupies a special epistemic position, there is little reason to saddle Reid with the false view that perceptual knowledge is unimprovable, since we could always get a better view on an external object, and gain further, more accurate, and more complete knowledge of it and its properties. Relatedly, one could (along Russell's lines) endorse perceptual acquaintance as intrinsically veridical, and so if there is no object, there could not be perceptual acquaintance at all. This view in contemporary philosophy of perception is called *disjunctivism* (see, e.g., Burge, 2005; Martin, 2006; Brewer, 2011). It seems unlikely that Reid held such a view. First of all, Reidian perception is a complex of sensation and belief, which seems quite different from the nonrepresentational relation posited by disjunctivists. Second, there is no textual evidence to my knowledge that would license attributing disjunctivism to Reid. If an account of perceptual acquaintance can be constructed that does not involve a commitment to disjunctivism, it would therefore seem to be preferable.

Below, I will propose four conditions for perceptual acquaintance. I believe they capture the spirit of van Cleve's invocation of the Russellian notion, shorn of the baggage discharged in the previous paragraph. All four conditions can be applied to perceptual awareness of external objects (and not just sense-data), and indeed to Reidian acquired perception. These are not intended to be necessary or sufficient conditions. Rather, what follows is a sort of grab bag of properties that seem to mark many cases of perceptual acquaintance. The justification for appealing to these properties and not others is simply that they appear to characterize the cases that we would want to call perceptual acquaintance, and do not characterize cases that we wouldn't. The validity of these conditions should be judged on a case-by-case basis, to see whether they tend to apply where (and only where) we want them to.

CONDITIONS FOR PERCEPTUAL ACQUAINTANCE

First of all, acquaintance could be understood as involving *phenomenal immediacy*. By that I mean simply that our conscious awareness of the object is not preceded by a separate awareness of something else. This is presumably what Russell has in mind when he says one is "directly aware of the object itself" (Russell, 1910, p. 108). Since acquired perception involves noninferential perceptual beliefs that seem to the subject to be automatically activated and not to refer to their objects in virtue of referring to anything else, then the awareness they engender presents itself to the subject simply as an immediate awareness of a state of affairs in the environment.

Second, the relevant state could involve acquaintance if it is *psychologically noninferential*. This notion of acquaintance is similar to, though separate from, the point about phenomenal immediacy. Whereas that point has to do with whether the subject's conscious awareness of the object is manifestly derivative of her awareness of something else, psychological noninferentiality is simply a matter of the actual underlying psychological processes that give rise to the relevant intentional state. We can thus partially provide criteria for an intentional state's constituting acquaintance by stipulating that such states cannot arise through a psychological process of inference.

Third, acquaintance could be partially constituted by being *directly causally related* to the object. The object itself, and its qualities that are perceived, play a special and constitutive role in the causal process that brings about one's perceptual awareness. It is because the object is triangular that I represent it as triangular; I thus stand in a relation to it not merely of being accurately aware of its qualities, but also of its being responsible for my being so aware. Though one might take the acquaintance relation to be metaphysically thicker in some sense, it seems fair to say that the object's F-ness being directly causally responsible for one's veridical perception of its F-ness does justice to Russell's insistence on the acquaintance relation as one of "presentation" (Russell, 1910, p. 109). We can simply understand an object's presenting itself to us as a function of its causal efficacy in producing occurrent veridical perceptual awareness of it.

Fourth, acquaintance could be a matter of *sensory character*. This condition is a bit more difficult for Reid, who makes a sharp separation between the sensory component of perceptual awareness and the intentional component. Nonetheless, perceptual intentionality could be said to have a sensory character on a Reidian view insofar as the relevant intentional states are intimately tied to the qualitative character of sensations. Sensations and perceptual intentionality are, of course, metaphysically independent for Reid. There are still two important ways in which the qualitative character of sensations colors perceptual intentionality. On the one hand, sensations bear tight causal relations to

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[14] As has been noted (see, e.g., Byrne, 2005), the conceptual/nonconceptual distinction could apply to the kind of content or the kind of state involved. I hope here to avoid making any claims on either side.

the intentional components of perceptual awareness. Perceptual intentionality can thus be individuated from other forms of intentionality via its unique causal situation with respect to sensations. On the other hand, Reid often stresses that it is highly difficult, and perhaps sometimes impossible, introspectively to separate the relevant contributions to the felt character of a perceptual state. That is, from the first person, it is extremely unnatural and difficult to isolate the sensory component and the intentional component. Reidian perceptual experience presents itself to consciousness as a package deal, a unified sensory presentation of external objects and states of affairs. One might object to this last point that acquaintance is a first-order property of perception, and not a matter of the way in which one has a higher-order awareness of it. I do not see why this must be the case, however. There does not seem to be a principled reason to deny that an intentional state's constituting acquaintance could be partly a matter of its higher-order relational properties, i.e., the way in which it presents itself to consciousness and introspection[15] . Indeed, given that Russellian acquaintance is a function of the way in which the subject relates to her own mental states, it does not seem very revisionary to construe acquaintance in this way.

Something that may strike the reader about the above criteria for acquaintance is that they are all a function of extrinsic properties of perceptual intentionality, and not of its intrinsic properties. Phenomenal immediacy consists in the perceptual intentional state's not seeming to the subject to depend on awareness of something else; psychological noninferentiality is a matter of the state's not arising through an inferential process; direct causal relations to the object are straightforwardly extrinsic and relational; and sensory character is constituted both by the state's causal ties to sensations as well as its higher-order relational property of being typically phenomenally bound up with sensation, as far as consciousness and introspection are concerned. One may object that acquaintance should be wholly a matter of the intrinsic properties of a given state of awareness. It does not seem, however, that there is a principled reason to enforce such tight strictures on an account of what perceptual acquaintance consists in. Furthermore, it should be regarded as a rather considerable benefit that the extrinsic notions of acquaintance allow us to get some sort of independent theoretical traction on the idea of acquaintance, enabling us to get clearer on what we mean when we talk about being perceptually acquainted with objects and putting us in a better position to decide whether a particular case involves such acquaintance.

The above account is not intended to be complete. Nonetheless, the four proposed characteristics—actually five, considering that sensory character involves two different ways in which sensations leave their mark on perceptual intentionality—put us in a better position for understanding what acquaintance is, and for deciding on whether a given case constitutes acquaintance. To repeat, these conditions are not intended to be necessary and sufficient; it could be that none are necessary and none are individually sufficient, and that certain clusters are sufficient for acquaintance[16]. By way of vindicating these conditions, I will now argue that there are cases of acquired perception that fulfill them and that the cases that worry van Cleve (e.g., seeing his wife is home by virtue of seeing her keys on the table) do not. Perhaps some of Reid's examples of acquired perception don't involve perceptual acquaintance, but some do, and most importantly, acquired olfactory perception does.

The simplest attention to one's own experience, according to Reid, is sufficient to show that there are cases of acquired perception that are phenomenally immediate. Taking the example of a hearing the sound of a rolling coach as such, it would be very difficult (says Reid—and it seems hard to disagree) to deny that one's auditory awareness of the coach presents itself as unmediated by awareness of anything else (*IHM* 2.6, 38). It does not seem phenomenally to be the case that we first hear low-level auditory properties and then, in virtue of that perception, come separately to hear the sounds as emanating from horse feet. Reid says that we can hardly be convinced that our acquired perceptions are not innate (*EIP* 2.9). Indeed, with respect to the acquired perception of three-dimensional Euclidean figure, the primary reasons for positing a distinction between acquired and original visual perception are due to third-person conclusions about vision drawn from, among other things, facts about how painters simulate perceptions of three-dimensional shape with two-dimensional figures, and from the perceptual reports of patients whose congenital cataracts are removed. Phenomenally speaking, acquired perception is just as immediate a form of awareness of external objects as original perception. This fact is, for Reid, largely responsible for why the distinction between acquired and original perception is not to be found in ordinary language (*EIP* 2.9).

Whether cases of acquired perception are psychologically noninferential is a harder question to answer. On the one hand, we might tempted to say no, because it seems to involve first having an original perception; e.g., we originally just see visible figure, and then seeing visible figure causes us to see "real" or "tangible" figure. One could thus cast the psychological move from one perception to the next as a form of inference. On the other hand, the grounds for so casting it are unclear. It is doubtful, or at the very least open to debate, that the mere existence of a causal transition between contentful states is sufficient to constitute inference (Boghossian, in press). Even if it were true, it still seems that classic worries about the inferentiality of perceptual awareness arise not from mere worries about causal state transitions, but rather from the worry that the states that arise later in the causal chain are dependent in some richer sense on the earlier states. That is, the worry that the perception of 3D figure is mediated by inference is really a worry that perception of 3D figure is somehow derivative of perception of 2D figure; that

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[15] Consciousness, for Reid, as a mental operation, is noninferential higher-order awareness. For discussion of whether Reid thought that higher-order views offered the right theory of what it is for a state to be conscious —which is a separate question—see Copenhaver (2007). This is not the place, however, to offer an interpretation of Reid's theory of consciousness (if he held one at all).

[16] For instance, given that the visual perception of shape does not constitutively involve sensation for Reid [though see Yaffe (2003a)], the points about sensory character might not apply. In the case of auditory perception of the size of a bell, on the other hand, the sensory character seems crucial to its constituting acquaintance.

our representation of 3D figure involves an inference according to some inferential scheme, *If there is 2D figure x, then there must be 3D figure y*. There is no reason to think perception of 3D figure by mature adults on Reid's account involves anything more robust than a brute-causal relation between perceptual states. In the absence of a reason to think that relation is inferential, and given its phenomenal immediacy, we can tentatively assume it to be noninferential[17].

Acquired perception also involves direct causal relations to the environment. It is well-known that spelling out the necessary and sufficient conditions for the kind of direct causal relations that are required for veridical perception is tricky, given the existence of deviant causal chains (Chisholm, 1957; Grice, 1961; Dretske, 1981, 2003; Searle, 1983; Burge, 2010). In the typical 3D perception case, however (assuming there is some proper causal story to tell), the object's having the 3D shape it does clearly plays the crucial causal role in bringing about the veridical perception of that shape. Similarly for the size of the bell one hears, or the horse's hooves, and so on for many standard cases of Reidian acquired perception.

Typically, acquired perceptions have sensory character, with the major (though arguable) exception of the visual perception of shape[18]. With respect to the higher-order notion of sensory character, the case for the introspective inextricability of the sensory and intentional components of perceptual experience appears to be just as strong for cases of acquired perception as for original perception. To create an example, hearing a voice as the voice of a particular friend seems phenomenally intertwined with the qualitative character of the auditory sensations involved; and similarly, of course, for hearing the sounds of the coach grinding the cobblestones, and so on.

It is less clear whether acquired perceptions occupy the same sort of tight causal relations to sensations as original perceptions. It is an open question whether or not acquired perceptions always causally depend on prior token original perceptions that causally mediate sensation and acquired perception. Here is a reason to think that they do not. Reid simply does not have much of an account of the process of perceptual learning and how it enables acquired perception to occur. What little he does say is essentially that there is a constantly reinforced habituation process. Given just that meager constraint on how perceptual learning takes place, then it seems possible not only that acquired perception could occur on the onset of original perception, but also that the sensations themselves could give rise to an acquired perception immediately and concurrently with original perception[19] .

Suppose a given array of sensation-types, S, is innately hooked up to a certain original perception-type, P, and that perceptual learning enables one to have a token of the acquired perception-type, A, upon having a token of P. Abstracting from problem cases, every time a token of A occurs, a token of P occurs first; and every time P occurs, S occurs first. Then (again, limiting to the typical cases), it follows that any habituation or conditioning process that reinforces a connection between P and A will also reinforce a connection between S and A. S could therefore, at some point, simply give rise to A directly. There may be theoretical reasons why this could not happen—something about the mechanism that gives rise to A could preclude mere sensations from being causally sufficient, for example—but such reasons do not fall out of Reid's account. In the absence of a reason to think it cannot happen, then, since the bare bones of Reid's account imply that S could cause A directly, it seems that we can tentatively say that Reidian acquired perception can hook up to sensation directly. Even if that were not the case, and the connection between S and A must always be mediated by P, it seems that one could still consider that mediated relation a kind of tight causal connection that is sufficient for A to have sensory character and thus to be different from mere thought. Of course many thoughts have causal connections to sensations, but not the reliable causal structure of S—>P, P—>A. Acquired perceptions thus typically have sensory character in both the causal and higher-order senses.

TESTING THE CONDITIONS

The above has hopefully sufficed to show that acquired perception fulfills the four (or five) conditions I have laid out for perceptual acquaintance. *Maybe so*, one might reply, *but then so much the worse for those conditions*. The reply may be that the conditions specified for perceptual acquaintance are too liberal, and that is the only reason why acquired perception looks like a species of perceptual acquaintance. Van Cleve's (2004, in press) helpful challenge to those who support the notion of acquired perception as perceptual acquaintance (e.g., Copenhaver, 2010) is to explain why his "seeing" that his wife is home by seeing her keys on the table does not fit the rubric for perception established by acquired perception. The spirit of the challenge is to show that construing acquired perception as a form of perceptual acquaintance doesn't just broaden the category of perception into triviality. This challenge is important because acquired perception has been invoked at crucial moments in the secondary literature on Reid to avoid Reid's theory of perception lapsing into incoherence or obvious falsity. For example, construing acquired perception as genuine perception is necessary to avoid saying that Reid's theory of the visual perception of the real shapes of objects amounts to indirect realism (Copenhaver, 2010; Quilty-Dunn, 2013), which is inconsistent with his fervent arguments against the idea that perception is indirect.

Fair enough, then: does van Cleve's example satisfy all the above conditions? It does not satisfy phenomenal immediacy. If van Cleve sees his wife's keys and "sees that" she is home, then it seems obvious that he can phenomenally distinguish two distinct acts of awareness and the asymmetric dependence relation that holds between them. One is aware of the set of keys, and aware

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[17] In Quilty-Dunn (2013), I argued that the perception of 3D figure could be considered immediate noninferential perception if it was the sort of awareness that is proprietary to perception (and not mere thought), echoing (Van Cleve, 2004). This was vague and unexplored; the notion of perceptual acquaintance outlined here should provide a clearer and more substantive account of what makes a certain form of awareness count as *perceptual* awareness.

[18] See Yaffe (2003a), Falkenstein and Grandi (2003), Yaffe (2003b) for an extended discussion of whether the visual perception of shape constitutively involves sensation.

[19] See Goldstone (1998) for an overview of various mechanisms of perceptual learning that could underwrite such a process.

that one's wife is home; furthermore, one is aware that the latter awareness is based on the former. Perhaps van Cleve would question that description of the phenomenology, but I find it difficult to see how it could be incorrect. If that's right, then the "perception" is not phenomenally immediate.

His awareness is also psychologically inferential. Unless the phenomenology is radically inadequate, then the inference drawn from the presence of the keys to van Cleve's wife being home is not only present but manifest in the experience. It also seems like the most obvious psychological interpretation of the situation is that he perceives the keys, thinks that if the keys are there then his wife is home, and draws the inference that his wife is home. In the absence of a reason to think otherwise, it seems from the first-person and third-person points of view that the case clearly involves inference.

Van Cleve's awareness of his wife is also not directly causally related to her. There is a causal connection between her and van Cleve's perception (viz., she put the keys there and they caused his perception) but it is not the kind that is unique to perception. This point relies on there being an account of the right kind of causal relation, which I cannot provide here. For one, however, when we are talking about visual perception, it could be argued that the direct causal relation must be carried out primarily through the medium of ambient light. There is no direct connection via ambient light between van Cleve and his wife, so it seems fair to say he is not visually acquainted with her[20]. By contrast, there is a direct connection through light between van Cleve and the 3D shape of the keys, so he may be visually acquainted with their 3D shape[21].

Finally, van Cleve's intentional state directed toward his wife does not have sensory character. Focusing first on the higher-order notion, one could very likely pull apart the sensory qualitative character and the intentional state from the first-person with ease. The visual sensations would likely not seem inextricably wrapped up with one's awareness of a person who is absent from one's field of vision. Regarding the causal notion, the issue is a bit more difficult. On the one hand, there is a kind of causal connection between the sensations and van Cleve's awareness of his wife's being home. On the other hand, it seems that it is not the same kind that obtains between, for example, my auditory sensations, and my awareness of the C-minor chord in the song I hear. What exactly this difference consists in is hard to say, but that there is a difference in kind seems clear. Perhaps it consists in the subject's history of perceptual learning. If one studies music for years, one develops a very close causal tie between certain auditory sensation-types and awareness of certain musical properties; there does not seem to be a similar close causal tie, learned through normal processes of perceptual learning, for seeing one's wife to be home upon seeing her keys on the table.

Furthermore, with respect to ordinary acquired perception, I argued above that it seems open that the causal connection between sensations and acquired perceptions could come to obtain without being mediated by original perceptions. One might protest, for whatever reason, that this never actually happens. Even so, there is a difference between ordinary cases of acquired perception and the case with the keys on the table, which is that in the latter case, it seems impossible that it could happen. It is very difficult to see how the mere sensations could simply give rise to van Cleve's awareness of wife. It seems more natural to say that they give rise to such awareness only by first giving rise to an awareness of the keys themselves, leading to an inference that his wife is home.

If this discussion has been correct, then typical cases of Reidian acquired perception satisfy all the conditions laid out for perceptual acquaintance, and van Cleve's seeing that his wife is home by seeing her keys on the table satisfies none of them (certainly not all of them, in any case). These conditions thus fulfill the desiderata of enabling acquired perception to constitute perceptual acquaintance while ruling out the case of the keys on the table, i.e., avoiding triviality. It should be fair to appeal to them, then, in deciding whether acquired olfactory perception of the secondary quality of odor is possible. All we need to ask is whether acquired olfactory perception satisfies most or all of the conditions for perceptual acquaintance.

OLFACTORY PERCEPTUAL ACQUAINTANCE

It is important to keep in mind the important characteristics of acquired olfactory perception mentioned in Two Solutions. The olfactory conceptions that form constituent elements of acquired olfactory perception are, in terms of their semantic properties, relative notions of whatever quality is causally responsible for generating certain types of sensations. Nonetheless, though that is Reid's semantic account of such conceptions, when they figure in an occurrent olfactory perception, they need not represent the odor by explicitly appealing to its relation to the occurrent sensation. There is a principled difference between, on the one hand, representing one's occurrent olfactory sensation O* followed by representing there to be a causal relation between it and some external quality O, and on the other hand, having O* and then simply representing external quality O, without the latter representation being mediated by representing O* and without explicitly representing the relation between the tokens of O and O*.

Both ways of becoming aware of O do involve relations to O*, because both are caused by O*, and because the perceiver's notion of O is a notion of some external quality that bears a certain causal relation to sensations of type O*. But the first kind of awareness involves inferring there to be some quality O that causes *this*

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[20] Perhaps there could be visual perception, with the same sensory qualitative character and perceptual contents, via a distinct medium (e.g., using a prosthetic eye that relies on sonar, or to borrow from Daniels, 1974, sensitivity to gravitational fields). These issues present a thorny set of problems. Nonetheless, in the case we are considering, there is nothing to replace the ambient light, so such problems should not arise.

[21] Copenhaver claims that a certain amount of "practical engagement" with a perceptible property that is "prevalent in one's environment" (Copenhaver, 2010, p. 305) can facilitate acquired perception. This condition is problematic, however, since it is compatible with the case currently being examined becoming, through the right sort of practical engagement, an instance of perceptual acquaintance (Ibid.). It seems to me that it is impossible to be perceptually acquainted with someone who is not in one's field of vision. The condition of a causal connection via a proprietary causal medium—e.g., ambient light—suffices to rule out such a case. In any case, practical engagement is arguably successful in giving rise to acquired perception only insofar as it facilitates the right kind of perceptual learning, which might be facilitated through non-practical modes of interaction with the relevant perceptible property.

token O* sensation; the second kind simply involves representing there to be O, and the notion of O happens to be a notion of the kind of thing that causes sensations of type O*. The second kind of awareness does not involve an occurrently mediated form of awareness. It is both phenomenally immediate and psychologically noninferential, thus satisfying those two conditions for perceptual acquaintance.

The acquired olfactory perception of O also stands in a direct causal relation to the instance of O itself in the environment. There is particularly good reason to say so if, as suggested in the previous section, the crucial causal connection for a given sensory modality involves the medium that is proprietary to that modality. Certainly typical olfactory perception will involve such a connection to the olfactory qualities of external objects. Reid describes the medium of olfaction as involving "effluvia" (i.e., airborne particles) emanating from objects, so olfactory perceptual states are causally related to olfactory qualities of external objects via that medium.

Olfactory sensations are also quite intimately bound up with the intentionality of olfactory perception, and thus imbue that intentionality with sensory character in both senses mentioned in the previous section. As far as our ordinary consciousness and even reflective introspective awareness of olfactory perception is concerned, for Reid, we do not separate the qualitative character of the sensations from the perception of the external olfactory quality. According to at least the early Reid in *IHM*, our terms for the qualitative aspects of odors are better understood to refer to the qualitative characters of olfactory sensations than to external olfactory properties, so closely are olfactory sensation and perceptual intentionality bound up in consciousness and introspection (*IHM* 2.2, 27). With respect to the causal construal of sensory character, acquired olfactory perceptual states are closely keyed to olfactory sensations. This condition is only met once adequate perceptual learning has taken place, but once it has, then the relevant acquired perceptions are caused directly by the sensations[22].

By all the standards set above for perceptual acquaintance, acquired olfactory perception plainly constitutes such acquaintance.

CONCLUSION

I have tried to resolve the tension between Reid's theory of perception and his account of our conception of odors. It has long been noted in the secondary literature that acquired perception is required, but problems still lingered. Two points are really central to preserving the coherence of Reid's theory. First, it is necessary to make clear the distinction between the semantics of our conceptions of odors involving relations to sensation, and our occurrent perceptual awareness of them being subjectively predicated on relations to occurrent sensations. Second, it is necessary to argue that some instances of acquired perception, including olfactory perception, do constitute perceptual acquaintance such as to block van Cleve's negative arguments.

According to the resulting interpretation, our notions of odors are based on inferring their causal relations to our sensations, but they can be perceived noninferentially through acquired perceptual acquaintance. Reid's theory of olfactory perception is therefore coherent, and for contemporary philosophers, perhaps attractive. A Reidian account allows one to explain the qualitative character of olfactory experience in terms of perceptual sensation, and to explain the intentional or representational aspect of such experience without having to adopt anything more robust than a dispositional (or dispositional-base) account of odors. It also provides, given the interpretation advanced above, a relatively tidy explanation of the acquisition of our capacity to represent dispositional properties such as odors in perception.

There is an odd, and oddly popular, caricature of Reid prevalent among present-day philosophers. According to this caricature, Reid thinks that all phenomenal character in perception is due to nonintentional sensations, and that the intentional component of perception involves no phenomenal character at all. Clare Batty, for instance, writes, "If we take it that Reidian sensations are one and the same as what we now think of as experiences, then Reid himself also held that olfactory experiences are purely sensational" (Batty, 2010a, p. 520; see also Siegel, 2011, p. 21; Smith, 2002, p. 70). If the terms of the present-day debate were explained to him, it seems far more likely that Reid would say perceptual experience is not merely a matter of sensation but also of the intentional component of perception—which, I have argued, constitutes perceptual acquaintance. It would be hard for him to deny, for example, that visual perceptual intentionality affects the way things *look* to the subject, which seems sufficient for its affecting visual phenomenology. By the same token, representing there to be a certain odor in an object or in the environment will affect the way things seem to the subject in her olfactory perceptual experience.

Reid's account of olfaction thus allows for both a representational account of our experiences of odors as properties of objects or environments, and also for an account of the qualitative character of olfactory perceptual experience, while requiring no more substantial an ontological commitment than to dispositional properties (or their bases). Reid's account is also consistent with a representational account that locates odors in the object (which is how he sometimes talks), or with one that "locates" them simply as immanent in one's immediate environment (see *IHM* 6.8, 99; see Batty, 2010a for discussion of the relative merits of these views).

Finally, one need not be wedded to Reid's dual-component (sensation and belief) view of perception to make use of his account. One could instead say that our notion of odor is relative to our notion of the qualitative properties of olfactory experiences (without regarding those properties to be instantiated in states called sensations) and that the intentional or representational contents of those experiences can come to incorporate acquired representations of odors as dispositions or dispositional bases, without supposing the intentional/representational component to involve belief, as Reid does. Anyone who endorses a distinction between the qualitative and intentional aspects of perceptual states might thus be able to employ Reidian ideas—which should be a particularly attractive option for theorists who also take odors and other secondary qualities to be dispositional

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[22] In fact, the issue about whether the causal connection between sensation and acquired perception must be mediated by an original perception does not even arise on the interpretation advanced here, according to which there is no original perception in olfaction.

properties. A Reidian theory of olfactory perception should, for all these reasons, be considered a live option in contemporary debates on olfaction and secondary qualities generally.

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The evolutionary function of conscious information processing is revealed by its task-dependency in the olfactory system

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Although many responses to odorous stimuli are mediated without olfactory information being consciously processed, some olfactory behaviors require conscious information processing. I will here contrast situations in which olfactory information is processed consciously to situations in which it is processed non-consciously. This contrastive analysis reveals that conscious information processing is required when an organism is faced with tasks in which there are many behavioral options available. I therefore propose that it is the evolutionary function of conscious information processing to guide behaviors in situations in which the organism has to choose between many possible responses.

Keywords: olfaction, consciousness, evolution, task-dependency, information processing

Brains continuously process information. Sometimes this information processing is conscious, which means that there is *something it is like for the organism to process the information*, to borrow an expression from the philosopher Thomas Nagel (1974). In contrast, most information is processed non-consciously and there is nothing it is like for the organism to process the information, just like there is nothing it is like for the organism to filter blood in the kidney. In this paper I will contrast conscious and non-conscious processes in the olfactory system to identify the evolutionary function of conscious information processing.

The approach presented here differs in two important aspects from similar approaches. First, this is not an analysis of the *function of consciousness* but of the *function of conscious information processing*. Conscious information processing is the subset of information processing that is accompanied by consciousness. An analogy can illustrate the importance of this seemingly subtle difference. The central nervous system can be divided into gray matter and white matter. One can speculate about the function of the “grayness” of gray matter, or one can investigate the function of gray matter without discussing the function of its “grayness.” The approach presented here is analogous to the second option. This means that whatever conclusion will be reached, it is consistent with consciousness having no function at all (Flanagan, 1997). A second important feature of the approach presented here is that I am interested in the *evolutionary function* of conscious information processing, whereas discussions of the function of consciousness often focus on the *current uses* of consciousness. To illustrate the importance of the distinction between evolutionary function and current uses, let’s consider wings. The evolutionary function of wings is flight. However, wings have many different current uses. Bees use wings to communicate. Some birds protect their young by taking them under their wings. Butterflies have patterns on their wings to scare or confuse predators. Male ostriches and birds of paradise use their wings during courtship displays and cranes use their wings to shade the water surface to better see their prey swimming underneath (Gazzaniga et al., 2009, p. 651).

I believe that the analysis of the evolutionary function of conscious information processing presented in this paper will provide an interesting contrast to the literature on the current uses of consciousness. My analysis will be presented in biological terms because determining evolutionary functions of evolved mechanisms is a common strategy in biology where “mechanism” and “evolution” are central concepts. I will introduce the strategy of determining evolutionary function through contrastive analysis in the first section of the paper. In the second section I will apply this strategy to conscious information processing in the olfactory system. The result of this analysis is that it is the function of conscious information processing in the olfactory system to guide behaviors in situations in which an organism is faced with tasks in which there are many different behavioral options to chose from. In the third section I will argue that many apparently competing proposals describe the processes in the brain at a different level and are therefore consistent with the results presented here. In the fourth section I will sketch how the task-dependency of conscious information processing relates to more general observations outside of the olfactory system.

CONTRASTIVE ANALYSIS OF EVOLUTIONARY FUNCTION

The evolutionary function of a biological mechanism is determined by its evolutionary history. At some point during our evolutionary history, an organism appeared that had the capacity to process information consciously in a certain brain structure. This capacity was inheritable, which means that the organism’s offspring also had the capacity. In addition, the organism with the capacity for conscious information processing had an adaptive advantage over organisms without this capacity. Conscious information processors therefore had more offspring (on average over time) than other organisms of the same species. If a capacity is heritable and results in an increased number of offspring, it will be selected for through evolution by natural selection (Lewontin, 1985). To identify the evolutionary function of conscious information processing, one has to identify the reason why the first conscious information processor had more offspring than its competitors.

From this characterization of evolutionary function it is clear that the evolutionary function of conscious information processing is not necessarily something that could not also be accomplished by non-conscious processes. As has been pointed out previously (Dretske, 1997), the lack of alternatives is not a requirement for evolutionary function. The function of a fish's fins is aquatic locomotion although many mammals, birds, insects, amphibians, jellyfish, and other creatures move in water without fins. This is important to point out because inquiries into the function of consciousness are often attempts to identify functions that can only be performed consciously. However, the lack of alternatives is not part of the concept of evolutionary function. It is also not reflected in the common usage of the word "function." That one can sit on rocks, benches, and toilets does not conflict with the proposal that it is the function of chairs to provide a surface to sit on. Similarly, that the first organism capable of conscious information processing had an advantage over organisms without that capability does not mean that this organism was capable of solving problems its competitors could not solve. The more likely scenario is that conscious information processing was more efficient than non-conscious information processing at solving certain problems. Evolutionary processes optimize efficiency. Efficient information processing is achieved by keeping the brain as small as possible. The metabolic rate in brain tissue is much higher than in other tissues, because the membrane potential of neurons has to be permanently sustained (Nieuwenhuys et al., 1998, p.11–14). In humans, around 20% of all energy is consumed by the brain, a ten times higher percentage than in other mammals like pigs and horses (Mink et al., 1981). Therefore, even if the problems that are solved in our brains by conscious information processing can be solved in a larger brain with non-conscious information processing, there is strong adaptive pressure to process information consciously.

The interesting question is, what the problems are that are more efficiently solved using conscious information processing. The fact that we still process much information non-consciously despite having the capacity to process information consciously suggests that conscious information processing is not simply a generally superior way of processing information. Instead, it is likely that different strategies are most efficient for different tasks. It is not uncommon that there is more than one information processing strategy for solving a problem. Often a strategy for exact calculations and an alternative strategy for estimations are available. In statistics there are for example two options to compute the *p*-value of a contingency table. One option is the Fisher's exact test and the other is the Chi-square test. As the name suggests, the Fisher's exact test results in the exact *p*-value. The Chi-square test, in contrast, is an approximation. The larger the sample size, the closer to the exact value is the Chi-square test approximation. In addition the number of calculations required to arrive at the exact value increases with the sample size. If one assigns a cost for calculations and a cost for potential inexactness of the *p*-value, then one can calculate the less costly strategy for determining the *p*-value for any sample size. For small sample sizes the Fisher's exact test is more efficient than the Chi-square test. However, because with increasing sample size the difference in calculation cost increases and the approximation approaches the exact value, there is a sample size above which the Chi-square test is more efficient. At very large sample sizes, the calculation cost of the Fisher's exact test is prohibitive.

Now let's imagine an evolved biological system whose fitness depends on calculating *p*-values of contingency tables. If there are variants that process the information for small sample sizes using a Fisher's exact test and for large sample sizes using a Chi-square test, these variants will have an evolutionary advantage over variants that always use the Chi-square test as well as over variants that always use the Fisher's exact test. The variants that can switch between the two computations cannot do anything that their competitors cannot do, but they do these things more efficiently. The evolutionary function of the Chi-square test performing mechanism would in this scenario be to calculate *p*-values for contingency tables when the sample size is large.

The methodology to identify the evolutionary function of a biological mechanism is contrastive analysis. Contrastive analysis compares situations in which the mechanism under study is employed to situations in which alternative mechanisms are employed. For fish's fins, this methodology would result in identifying aquatic locomotion as the fins' evolutionary function. Contrastive analysis requires generalizations over many cases and because evolution is an ongoing process the correlation between traits and functions is not expected to be perfect. The fact that some animals without fins are capable of aquatic locomotion does not mean that aquatic locomotion is not the function of fins. Furthermore, aquatic locomotion is the evolutionary function of fins even though a contrastive analysis is likely to uncover that sometimes fins are not used for aquatic locomotion but for walking over land, courtship displays, or temperature regulation. It is vey common for structures or mechanisms that evolved for one function to be further adapted for additional functions. The goal of contrastive analysis is to analyze current uses to identify the phylogenetically earliest function of a structure or mechanism. If the evidence shows that the first animals with fins used them for aquatic locomotion, then aquatic locomotion is the evolutionary function of fins.

To identify the evolutionary function of conscious information processing, situations in which information is processed consciously have to be compared to situations in which information is processed non-consciously. Numerous experimental designs have been developed for this purpose (Kim and Blake, 2005). One common strategy is to use two similar stimuli, only one of which is processed consciously. In vision, short visual displays are often contrasted with longer displays. Another often used paradigm is visual masking, in which a two-part stimulus that consists of a "target" and a "mask" is differently processed from a stimulus that consists only of the "target" (Breitmeyer, 2008). In olfaction, the processing of low concentrations of an odor can be compared to the processing of higher concentrations. Unfortunately, these experiments are very difficult to interpret because it is challenging to, for example, distinguish between the hypothesis that an odor at low concentration is not consciously processed *and therefore* cannot be named and the alternative hypothesis that the odor is not consciously processed *and also* cannot be named. For this reason, contrastive analysis of the processing of the same physical stimulus is preferable (Kim and Blake, 2005). The most common experimental design in which the same visual stimulus is processed differently involves visual competition (Blake and Logothetis, 2002). Examples of visual competition are ambiguous figures and binocular rivalry (Tong et al., 2006). Another situation in which the same visual stimulus is processed in different ways is when spatial attention is shifted (Cave and Bichot, 1999; Chun et al., 2011). Of special interest are covert shifts of visuospatial attention (as opposed to overt shifts which depend on eye movements; Wojciulik et al., 1998). These experimental designs are superior to those in which the processing of two different stimuli is compared, however, they do not contrast non-conscious with conscious information processing. Instead, they contrast conscious processing of one content with conscious processing of another content. For example the duck-rabbit, an ambiguous figure that can be perceived as a duck or as a rabbit, can be used to compare the conscious processing of the image of a duck with the conscious processing of the image of a rabbit.

The ideal situation for contrastive analysis is when both the stimulus and the content are the same, but processing is conscious in some situations and non-conscious in other situations. The sound of a clock ticking is sometimes processed consciously and sometimes processed non-consciously. One can become suddenly aware of it (Block, 1997). The same is true for the feel of one's clothes touching the skin. These are cases in which the same stimulus and the same content is sometimes processed consciously and sometimes non-consciously.

CONSCIOUSNESS IN THE OLFACTORY SYSTEM

The olfactory system is well suited for identifying the evolutionary function of conscious information processing because it is common that the same olfactory information is processed consciously in some situations and non-consciously in other situations. The olfactory system has the further advantage that it is anatomically and computationally relatively simple (Haberly, 2001; Lledo et al., 2005; Sela and Sobel, 2010). It has even been suggested that it represents the minimal neuroanatomy that is required for conscious information processing (Morsella et al., 2010). There is only a single synapse between the odor stimulus and the olfactory cortex and the pre-cortical processing in the olfactory bulb is understood in great detail (Shepherd et al., 2004; Hintiryan et al., 2012). Furthermore, the human olfactory system is an evolutionary conserved structure (Eisthen, 1997) that presumably has not changed significantly since it first evolved the capacity to process information consciously.

Despite the relative simplicity of information processing in the olfactory system and the evolutionary ancient neuroarchitecture underlying it, sometimes information about our olfactory environment is processed consciously. However, reflecting the relative simplicity of our olfactory system, olfactory phenomenology is very simple and lacks many of the complexities that hinder our understanding of conscious perception in the visual modality (Lycan, 2000; Köster, 2002; Stevenson, 2009a). Most prominently, the spatial structure of olfactory phenomenology is very impoverished. Subjects cannot discriminate between a stimulus in the left and right nostril (Radil and Wysocki, 1998; Frasnelli et al., 2008) and, despite the fact that olfactory experience can have a diachronic spatial structure, many philosophers think that olfactory perception does not represent the location or direction of olfactory stimuli (Lycan, 2000; Smith, 2002; Matthen, 2007; Peacocke, 2008; Batty, 2010). The phenomenological and biological simplicity of the human olfactory system and the fact that it is phylogenetically old and evolutionary conserved make it a good system for identifying the evolutionary function of conscious information processing by comparing situations in which olfactory information is processed consciously to situations in which it is not, which is the goal of this section of the paper.

Humans mostly use their sense of smell to evaluate food, ambient air, and potential mates (Stevenson, 2009b). Often, olfactory evaluation does not require conscious information processing. This is reflected by a variety of olfactory metaphors for situations in which we evaluate something but are not conscious of our reasons for the outcome of the evaluation: "smell a rat," "something smells fishy," "smell test," etc. That olfactory evaluation does not always require information to be processed consciously has also been demonstrated empirically. Social preferences, for example, have been shown to be influenced by odors that were not consciously processed by the subjects (Li et al., 2007). Similarly, an odor-specific effect has been shown on judgments of participants posing as job candidates (Cowley et al., 1977). Like evaluation of other people, evaluation of food often does not require conscious information processing. For example, sucrose solution is evaluated to be sweeter when an undetectably small amount of ethyl butyrate is added (Labbe et al., 2006). Similarly, odors at concentrations that are too low to be consciously processed can change the perceived odor quality when added to a mixture (Guadagni et al., 1963; Ito and Kubota, 2005). In all these cases, conscious information processing is not required for evaluation. However, there are also tasks in which conscious information processing is required. If the decision that has to be made is to either swallow or spit out a sip of wine, conscious processing is not required. However, if the task is to write a review of the wine's flavor, it is necessary to process the sensory information consciously.

Humans use their sense of smell predominantly for evaluation, however, this is a recent evolutionary development. In many other vertebrates odor-dependent navigation is the most prominent odor-guided behavior (Jacobs, 2012). In humans, odor-guided navigation does not play an important role, but there are still some examples of it. Infants, for example, use olfactory cues to orient toward their mother's breast (Varendi et al., 1994; Varendi and Porter, 2001). Under experimental condition, humans are also surprisingly good at following an odor trail (Porter et al., 2006). Navigating physical space based on olfactory cues does usually require conscious processing of the olfactory information. The only strategy available to locate the source of the gas leak in a building is through serial sampling and comparisons

[Unlike other species, humans to not have the capacity for directional smelling by comparing the olfactory input of the two nostrils (Radil and Wysocki, 1998; Frasnelli et al., 2008; Kleemann et al., 2009)]. To locate the gas leak, one has to sample the air by sniffing while walking from room to room. Through intensity comparisons, the location of the gas leak can be identified (Richardson, 2011). Throughout the entire process olfactory information is processed consciously and compared to stored conscious percepts of the smell in the other rooms. It seems unlikely that this task could be accomplished without conscious information processing. On the other hand, there is evidence that odor-dependent place preferences can be mediated without conscious information processing. It has been shown that people chose chairs in a dentist's waiting room depending on the odor the chairs were perfumed with (Kirk-Smith and Booth, 1980; Pause, 2004). In other studies, releasing an odor among the slot machines on the casino-floor of the Las Vegas Hilton increased how much was gambled in that area (presumably by increasing the time gamblers spent in the area; Hirsch, 1994). Perfuming a small pizzeria in the Brittany region of France with lavender increased the time patrons spend in the restaurant as well as the amount of money they spent (Guéguen and Petr, 2006). Many studies of the effect of ambient scents on behaviors do not control for all potential biases (Teller and Dennis, 2012) and subject numbers are usually low and replications rare. Each individual study has therefore to be interpreted with care. However, I think that taken together there is good evidence that we prefer to spend time in a pleasantly scented area than in an unpleasantly scented area, and that this preference can be mediated through non-conscious processing.

This brief overview over olfactory behaviors shows that olfactory information processing has two main functions in humans: navigation and evaluation. Contrastive analysis shows that for both functions there are situations in which they can be accomplished without conscious information processing and situations in which conscious information processing is required. We will swallow good wine and spit out wine that has turned into vinegar without the need to process the sensory information consciously. On the other hand, the very same sensory information has to be processed consciously when it is our task to write a review about the wine. Similarly, we will pick the seat in a room furthest away from an unpleasant smelling individual without the need for conscious information processing, but locating a gas leak requires conscious processing of the olfactory information. The difference between situations in which conscious processing of olfactory information is required and situations in which it is not required is therefore a difference in the tasks the organism is facing. Whether the sensory information has to be processed consciously or not depends on what the information is to be used for.

The salient difference between the tasks for which conscious information processing is required and the tasks for which it is not required is the number of behavioral options between which the organism has to choose to accomplish the task. In the case of spitting out or swallowing the wine, there are two options: spitting it out or swallowing it. In the case of writing a review about the wine, if the reviewer has a vocabulary of 10,000 words and the review is 100 words long, there are 6.5×10^{241} options. Similarly, in the case of having a place preference based on an odor, there are only two options: stay/go. However, in the case of attempting to identify the source of an odor there are as many options as there are paths in two-dimensional space. These examples show that the number of behavioral options increases in a combinatorial manner. There is a limited number of words and the task of writing a review consists of deciding between the many possible combinations of these words. Similarly, every navigation in space is a combination of many stay/go/turn decisions. It is tasks that require these combinations that require conscious information processing.

It may seem easy to find counterexamples that contradict this conclusion. We sometimes process the soothing lavender odor consciously when we are lying on the massage table in a spa and the only behavioral option that we consider is to do nothing. However, these apparent counterexamples are based on a confusion between evolutionary function and current use. That the crane uses its wing to shade the water surface to better see its prey is not in conflict with the proposal that the evolutionary function of wings is flight. Similarly, the current use of conscious information processing in a wide variety of situations does not contradict the proposal presented here. The result of the contrastive analysis is therefore that whether olfactory information is processed consciously or not depends on the task that the organism is facing. The stimulus has to be strong enough (very low concentrations of odors cannot be processed consciously) and the organism has to be in the right state (an organism in a coma cannot process information consciously), but when these requirements are met, whether information is or is not processed consciously depends on the task the organism is facing. In evaluation as well as in navigation, information is processed consciously when the organism is faced with many different behavioral options, but non-consciously when the choice is between few behaviors. Verbal communication and goal-directed navigation in physical space are combinatorial tasks with a very large number of options, which is why they require conscious information processing.

DESCRIPTIONS OF BRAIN PROCESSES AT DIFFERENT LEVELS OF HIERARCHY

I have developed a proposition about the function of conscious information processing that is consistent with the facts about consciousness in the olfactory system. The same facts are also consistent with a variety of other proposals. In this section of the paper I will discuss two of these alternative proposals and argue that they are not in conflict with the proposal presented here because they describe the processes in the brain at a different level of hierarchy.

Biological systems are hierarchically organized. Atoms make up molecules, which are the building blocks of cells. Cells combine to functional units that are called organs, and organisms are collections of organs. Organisms are parts of populations, which are parts of ecosystems. The collection of all ecosystems is the biosphere. Consequently, different processes can be described at different levels. There are textbooks of cognitive neuroscience and textbooks of molecular neuroscience. The topic of these textbooks is the same, but they address the topic at a different level of description. Statements at different levels of description cannot be in conflict. "Neurotransmitter release in neuron X leads to an increase in calcium level in neuron Y," "Neurotransmitter release in neuron X leads to firing of neuron Y," and "Neurotransmitter release in neuron X leads to avoidance behavior." are not competing hypothesis but descriptions of the same phenomenon at the molecular, cellular, and behavioral level.

For the purpose of this paper, the processes in the brain are described as information processing. This level of description is one level above the cellular or neural circuit level. Information processing in the brain is a consequence of neural activity in neural circuits that evolved for the purpose of processing information. This is the level at which much recent progress in the neurosciences has been made. The level of description above information processing is the level of cognitive processes. This is the level at which much recent progress in consciousness research has been made. There are therefore several proposals about consciousness at the level of cognitive processes, some of which are consistent with the data reviewed in this paper. However, these proposals are not in conflict with the proposal presented here. Instead, they are descriptions at a different level of the biological hierarchy.

One such proposal is that it is the function of *higher cognitive processes* to guide behaviors in situations in which there are many different behavioral options. A striking difference between the task of either drinking a wine or not and writing a wine review is that writing a review requires higher cognitive processes. Semantic symbols (words) have to be combined in ways that conform to the rules of syntax. Examples like this have lead some to believe that syntactic thought plays an important role in consciousness (Rolls, 2007). On the other hand, to locate an odor, physical space has to be represented and a multi-step path through it has to be planned. Examples like this have lead to proposals that phenomenal space is necessary for consciousness (Revonsuo, 2006, p. 170). Visually representing physical space and syntactic thought are very different cognitive processes. However, both can be considered "higher cognitive processes" and then the result of the contrastive analysis, at the level of cognitive processes, is that it is the function of higher cognitive processes to guide behaviors in situations in which there are many different behavioral options.

Another proposal at the level of cognitive processes that follows from the contrastive analysis presented here is that it is the function of *attention* to guide behaviors in situations in which there are many different behavioral options. A high level of attention is engaged when we are asked to report about the flavor of wine and when we try to locate a gas leak. Less attention is required to detect spoiled food one is about to swallow.

Both of these proposals, and maybe also others, are consistent with the results of the contrastive analysis presented here. However, they are descriptions of brain processes at the level of cognitive processes, and they are not in conflict with proposals at the level of information processing like the one presented here. Instead, these proposals raise the interesting question of the relationship between the information processing level and the cognitive system level. I have previously argued for a close connection between attention and conscious information processing in the olfactory system (Keller, 2011). However, this view is not universally shared, and in visual perception cases of consciousness in the absence of attention (van Boxtel et al., 2010) and attention in the absence of consciousness (Norman et al., 2013) have been described. The mapping of descriptions on the information processing level and the cognitive level therefore does not seem to neatly respect the borders of the categories that have been employed at the two different levels of description.

BEYOND OLFACTORY CONSCIOUSNESS

According to the proposal defended here, conscious information processing has been selected by evolutionary processes because it is more efficient than non-conscious information processing at solving tasks in which there are many behavioral options. It is plausible that in situations with few potential behaviors a simple algorithm that has been shaped by innate preferences and a combination of associative learning and generalizations is an efficient way of approaching the task. Such an algorithm would however not be an efficient way for approaching the task of writing a wine review because for this task it would be required to associate each possible flavor with one of the extremely large number of possible reviews. Instead, it may be that the most efficient way of writing a review, or of navigating toward a goal, is to simulate the responses before executing them. According to this theory, conscious information processing creates a simulation of the world in which behaviors can be tried out without actually being performed (Hesslow, 2002). A metaphor that has been used for this type of information processing has called it a "virtual reality arena of the mind" (Revonsuo, 2006). The metaphor of the "virtual reality arena of the mind" is similar to the influential metaphor of the "theater of the mind" (Baars, 1988, 2005). The key difference between a virtual reality arena and a theater is that the play in the virtual reality arena is interactive. Virtual reality arenas are computer-simulated interactive three-dimensional environments and if this metaphor is taken too literal, there is the danger of interpreting it as showing that phenomenal space is necessary for consciousness (Revonsuo, 2006, p. 170). However, navigation in physical space is only one type of task that has so many behavioral options that it is most efficiently solved by conscious information processing. Immersion in a virtual reality arena can simulate navigation in space, but it cannot simulate writing a wine review. A better metaphor that can be applied to all tasks that require conscious information processing, not only to navigation in physical space, is "menu for action," which has been suggested by Prinz (2012). Conscious information processing, according to Prinz, is, like the virtual reality arena, a precondition for decision rather than a mechanism for decision.

I have so far discussed only odor-guided behavior to provide support for the proposal that it is more efficient to process information consciously (and thereby create a menu for action), when there are many options. In situation with few options, I propose, it is more efficient to process information non-consciously. I have argued that odor-guided behaviors are a good model system for consciousness research. However, only a very small portion of behaviors are odor-guided. In the last section of this paper I will briefly discuss task-dependency of conscious processing of non-olfactory information. A comprehensive survey of non-olfactory information processing is beyond the scope of this paper, but the discussion of the non-olfactory cases will help clarify the proposal presented here.

The proposal that information is processed consciously when an organism is faced with many behavioral options explains why there are large differences in the frequency with which information is processed consciously between different modalities. There are almost always enough odor molecules in the air that we inhale to activate our olfactory system. However, we only rarely process this information consciously. In contrast, we usually process at least some visual information consciously. The reason for this difference between the modalities is that the behaviors that are visually guided are usually more complex than those that are odor-guided. Vision is the dominant sense in humans because it represents physical space more accurately than the other senses. Behaviors that depend on precise movements in physical space, like manipulation of objects and tool use, usually require choosing between a large number of behaviors and the visual information that guides these behaviors is therefore most efficiently processed consciously. In contrast, as pointed out above, olfaction mostly guides evaluative behaviors, which are usually associated with binary decisions like stay/go, spit/swallow, inhale/hold your breath, or approach/avoid.

Another feature of conscious information processing that is consistent with the dependency of conscious information processing on the number of behavioral options is that during skill acquisition information has to be processed consciously whereas during skill retrieval the same information can efficiently be processed non-consciously (Schneider et al., 1994; Floyer-Lea and Matthews, 2004). As someone learns to play a new song on the guitar, they have to process their finger positions and movements consciously. However, as they become more familiar with the song, the finger movements can increasingly be guided by non-conscious information processing. The reason for this change in how the information is processed is that familiarization with the song decreases the number of behavioral options. When a song is played from sheets for the first time, at every point during the song there is a very large number of combinations of notes and therefore finger movements that may follow. Once the song is familiar, at every point during the song, there is only one salient sequence of finger movements that follows. The potential behaviors are reduced from a very large number of combinations to one, which results in a difference in how the information is processed. The same reduction in the number of behavioral options is accountable for the difference between driving a route for the first time and driving it for the hundredth time. When driving a very familiar route in low traffic, not much sensory information is processed consciously. However, if suddenly a deer jumps onto the road in front of the car, information has to be processed consciously, because the deer makes it necessary to consider a wide variety of possible responses to avoid a collision. These examples illustrate that the relevant number is not the number of all possible behavioral options, but the number of task-relevant options. When pouring liquid in one's mouth with the goal of reducing thirst, the task-relevant options are to swallow it or to spit it out. Writing a review about the taste of the liquid is also an option, but it is not task-relevant. When a deer jumps in front of one's car, the number of task-relevant options suddenly increases and information is therefore processed consciously.

CONCLUSION

A contrastive analysis of situations in which olfactory information is processed consciously and situations in which it is processed non-consciously suggests that information is processed consciously only when an organism is faced with a task that requires considering many different behaviors. This appears to be the evolutionary function of conscious processing of olfactory information. Although task-dependency of conscious information processing is also widespread outside of the olfactory system, the proposal presented here has to be tested extensively outside of olfaction to see if it generalizes to conscious information processing in general. Regardless of the outcome of these tests, I hope that the analysis of the *evolutionary function of conscious information processing* presented in this paper will provide an interesting addition to the literature that is dominated by analyses of *current uses of consciousness*. Neuroscience has made remarkable progress in understanding brain processes at the level of neuronal circuits. Consciousness research has investigated consciousness mainly at the level of cognitive processes. An analysis at the level of information processing that lies between these two levels of hierarchy will hopefully help to bring these two fields together.

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The olfactory system as the gateway to the neural correlates of consciousness

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How consciousness is generated by the nervous system remains one of the greatest mysteries in science. Investigators from diverse fields have begun to unravel this puzzle by contrasting conscious and unconscious processes. In this way, it has been revealed that the two kinds of processes differ in terms of the underlying neural events and associated cognitive mechanisms. We propose that, for several reasons, the olfactory system provides a unique portal through which to examine this contrast. For this purpose, the olfactory system is beneficial in terms of its (a) neuroanatomical aspects, (b) phenomenological and cognitive/mechanistic properties, and (c) neurodynamic (e.g., brain oscillations) properties. In this review, we discuss how each of these properties and aspects of the olfactory system can illuminate the contrast between conscious and unconscious processing in the brain. We conclude by delineating the most fruitful avenues of research and by entertaining hypotheses that, in order for an olfactory content to be conscious, that content must participate in a network that is large-scale, both in terms of the neural systems involved and the scope of information integration.

Keywords: olfaction, consciousness, neural correlates of consciousness, conscious perception, olfactory consciousness

INTRODUCTION

How consciousness is generated by the nervous system remains one of the greatest mysteries in science (Crick and Koch, 2003; Roach, 2005): "No one has produced any plausible explanation as to how the experience of [anything]... could arise from the actions of the brain" (Crick and Koch, 2003, p. 119). Researchers from diverse fields have begun to unravel this puzzle by contrasting conscious and unconscious processes (Shallice, 1972; Logothetis and Schall, 1989; Crick and Koch, 1995; Kinsbourne, 1996; Wegner and Bargh, 1998; Grossberg, 1999; Di Lollo et al., 2000; Dehaene and Naccache, 2001; Baars, 2002, 2005; Gray, 2004; Libet, 2004; Laureys, 2005; Morsella, 2005; Merker, 2007; Doesburg et al., 2009; Damasio, 2010; Boly et al., 2011; Panagiotaropoulos et al., 2012). Through this contrastive approach, it has been revealed that the two kinds of processes differ in terms of the underlying neural events and associated cognitive mechanisms (see conclusions of this contrast in Godwin et al., 2013). (For discussion of the limitations of contrastive approaches, see Aru et al., 2012.) It has been proposed that, for several reasons, the olfactory system provides a unique portal through which to examine this contrast (Morsella et al., 2010; Keller, 2011). For this purpose, the olfactory system is beneficial in terms of its (a) neuroanatomical aspects, (b) phenomenological and cognitive/mechanistic properties, and (c) neurodynamic (e.g., brain oscillations) properties. In the three sections below, we discuss how each of these properties and aspects of the olfactory system can illuminate the contrast between conscious and unconscious processing in the brain.

NEUROANATOMY

When reverse engineering a complex phenomenon, it is best to focus on the simplest manifestation of that phenomenon. For example, when investigating the neural correlates of consciousness, it is more fruitful to focus on primitive states such as pain, the perception of a tone, or the smell of a rose than to focus on more elaborate and, in terms of cognitive processing, more multifaceted states, such as nostalgia and, say, an appreciation of the narrative structure of a novel. From this reductionistic standpoint, we propose that the best system for investigating the neuroanatomical correlates of consciousness is that of olfaction (Freeman, 2007a; Freeman and Quian Quiroga, 2013). To appreciate this proposal, it is necessary to first apprehend the neuroanatomy of olfaction. Hence, we now present a brief, selective review of the neuroanatomy of the olfactory system, with an emphasis on the regions most pertinent to the study of consciousness. (For a more thorough review of the olfactory system, see Neville and Haberly, 2004; Shepherd et al., 2004.)

Olfaction, perhaps the phylogenetically oldest sensory modality (Hosek and Freeman, 2001), is unique among sensory modalities in its anatomical organization (Price, 1990; Freeman, 2007a). Most notably, unlike other sensory modalities (e.g., vision, audition, or touch), bottom-up afference from the olfactory receptors bypasses the thalamic "first-order" relay neurons (Sherman and Guillery, 2006) and directly influences a region of the ipsilateral cortex (Shepherd and Greer, 1998; Tham et al., 2009), called the olfactory (piriform) cortex (Haberly, 1998; Mori et al., 1999; Neville and Haberly, 2004; Gottfried and Zald, 2005). Specifically, after sensory transduction in the olfactory epithelium of the nose, olfactory afference undergoes sophisticated processing in the olfactory bulb, a structure that can generate complex patterns of activation across neural populations, which are used for the encoding of odorants (Freeman, 1987; Xu et al., 2000). While historically the olfactory bulb was compared to the retina (Ramón y Cajal, 1909–1911), it has been proposed more recently that the primary function carried out by the bulb is similar to the primary function carried out by the first-order relay thalamus (e.g., the lateral geniculate nucleus) in other sensory modalities (e.g., vision): "both structures act as a bottleneck that is a target for various modulatory inputs, and this arrangement enables efficient control of information flow before cortical processing occurs" (Kay and Sherman, 2007, p. 47).

After processing in the bulb, olfactory afference is processed in the piriform (meaning, "pear-shaped") cortex. The piriform cortex is considered to be part of the "primary olfactory cortex," which also includes the olfactory tubercle, the periamygdaloid cortex, the lateral entorhinal cortex, the cortical portion of the amygdaloid nuclei, the ventral tenia teat, and the nucleus of the lateral olfactory tract (Carmichael et al., 1994; Tham et al., 2009). Piriform cortex is a phylogenetically old type of cortex, hence the namesake of this kind of cortex, *paleocortex*. Paleocortex contains only three cortical layers, which stands in contrast to neocortex, which contains six layers. (It is worth noting that the analogous cortical regions for the modalities of vision and audition consist, not of paleocortex, but of neocortex.) Interestingly, though paleocortex is less complex than neocortex, it still shares remarkable similarities with the neocortex, in terms of physiology, neurochemistry, and local circuitry (Haberly, 1998). Thus, by studying this possibly more simple form of cortex, one can learn a great deal about neocortex.

Despite the relative simplicity of the piriform cortex, it has been suggested that the anatomical connectivity of the posterior piriform may allow it to perform complex operations such as learning, memory retrieval, and other associative functions (Haberly, 1998). Indeed, a study of odor learning in humans revealed that learning-induced neural plasticity is observed in the posterior piriform cortex in a fashion similar to that found in a higher cortical region involved in olfaction, the orbitofrontal cortex (OFC; Li et al., 2006). The piriform cortex may also have a role in the seeming stability of odor perception through stimulus generalization (Barnes et al., 2008; Sela and Sobel, 2010). Ensembles of neurons in the piriform cortex respond similarly to a mix of odors and to the same mix of odors when one odor is removed, but they will respond differently if one of the odors is replaced by a novel odor (Barnes et al., 2008).

Two main output pathways carry odor information from the piriform cortex to other brain regions. The first output pathway targets subcortical limbic regions (e.g., the hypothalamus) that are involved in motivational, emotional, and homeostatic responses to odors. The second output stream from the piriform cortex targets neocortex (Tham et al., 2009). This output stream to the neocortex can be further broken down into two distinct pathways (Tanabe et al., 1975). The primary (direct) pathway projects from pyramidal cells in the piriform cortex directly to the OFC and is considered the chief pathway for odor information to be transmitted to neocortical areas (Yarita et al., 1980; Carmichael et al., 1994; Haberly, 1998). The secondary (indirect) pathway originates from a relatively small number of cells in the piriform cortex and projects to the OFC through the mediodorsal thalamic nucleus (MDNT). This pathway consists of only sparse fiber density (Price and Slotnick, 1983; Haberly, 1998; Ongür and Price, 2000; see also Poo and Isaacson, 2009).

As noted, the indirect pathway, involving the MDNT, has sparse fiber density compared to the direct monosynaptic pathway. Despite its sparse fiber density, there is evidence that this pathway may be involved in significant olfactory processing. For example, patients with damage to the MDNT show deficits in odor identification, discrimination, and hedonics (Potter and Butters, 1980; Sela et al., 2009). Furthermore, bilateral thalamic infarctions yield sudden, transient abnormalities in consciously experienced odor perception (Asai et al., 2008). There has also been an argument for the involvement of the MDNT in olfactory attention (Plailly et al., 2008). Based on these findings, one can tentatively conclude that the MDNT is neither necessary nor sufficient for conscious olfactory experience, but that it may play a role in olfactory identification, discrimination, and hedonics, as well as in the orienting of olfactory attention.

The OFC is the principal neocortical region for olfactory processing. It performs associative roles in olfactory information processing (Gottfried and Zald, 2005) and carries out multisensory integration (Rolls and Baylis, 1994). For example, it is in the OFC that inputs from gustation, olfaction, somatosensation, audition, and vision combine to create the multimodal perception of flavor (Rolls and Baylis, 1994; Shepherd, 2006). The OFC seems to play a particularly important role in primate cognition (Tanabe et al., 1975) and occupies a role in "central processing." It has been demonstrated that the magnitude of OFC activation (but not that of piriform cortex) predicts the degree of subsequent improvement in an olfactory judgment task (Li et al., 2006).

In summary, unlike most other sensory modalities, afferents from the olfactory sensory system (a) bypass the first-order, relay thalamus, (b) directly target the cortex ipsilaterally (Shepherd and Greer, 1998; Tham et al., 2009), which minimizes spread of circuitry, (c) involve a primary processing area that consists of paleocortex (which contains only half of the number of layers of neocortex), and (d) involve primarily only one brain region (the frontal cortex; Shepherd, 2007). The last observation stands in contrast to vision and audition, which often involve large-scale interactions between frontal cortex and parietal cortices, as in the case of the well-documented interactions between frontal-parietal cortex or frontal-occipital cortex. This summary reveals the relative simplicity of the anatomy of the olfactory system compared to that of other systems. In addition, it has been claimed that, because of its positioning within the cranium, the olfactory system features a privileged and accessible region (Shepherd and Greer, 1998). As Shepherd (2007) concludes, "In olfactory perception there is no 'back' of the brain; the primary neocortical receptive area is in the OFC, which is at the core of the prefrontal area. Thus, in olfaction, all of the sequences of processing that are necessary to get from the back to the front of the brain are compressed within the front of the brain itself. This reflects the evolutionary position of smell, with its privileged input to the highest centers of the frontal lobe throughout the evolution of the vertebrate brain. From this perspective, the basic architecture of the neural basis of consciousness in mammals, including primates, should be sought in the olfactory system, with adaptations for the other sensory pathways reflecting their relative importance in the different species" (p. 93).

IMPLICATIONS FOR CONSCIOUSNESS

We now discuss the conclusions that can be drawn regarding the neuroanatomy of olfactory consciousness. First, we discuss the role of the most peripheral anatomical structures: the olfactory epithelium and olfactory bulb. Regarding the latter, previous findings suggest that the olfactory bulb is unnecessary for endogenic olfactory consciousness (Mizobuchi et al., 1999; Henkin et al., 2000). (Again, the bulb has been described as being functionally equivalent to the first-order relay of the thalamus; Kay and Sherman, 2007; see also Murakami et al., 2005.) This observation is consistent with findings from research on the neural correlates of various kinds of conscious olfactory experiences, including olfactory perceptions, olfactory imagery, and olfactory hallucinations (Markert et al., 1993; Mizobuchi et al., 1999; Leopold, 2002). This research, which includes neuroimaging studies (Henkin et al., 2000), experiments involving direct stimulation of the brain (Penfield and Jasper, 1954), and lesion studies (Mizobuchi et al., 1999), suggests that endogenic, olfactory consciousness does not require the olfactory bulb. Perhaps most critically, it seems that patients with bilateral olfactory bulbectomies can still experience explicit, olfactory memories, suggesting that, under certain circumstances, these peripheral structures are not necessary for the instantiation of these kinds of conscious representations. However, the current literature lacks systematic, conclusive studies regarding this important clinical observation.

It is worth noting that Kallmann Syndrome, a genetic disorder in which the olfactory bulb and its tracts develop abnormally, is often characterized by complete anosmia or hyposmia (Madan et al., 2004; Fechner et al., 2008). Similarly, bifrontal craniotomies, a surgical procedure that removes the olfactory bulbs or olfactory nerves, have been performed on patients with severe phantosmias (e.g., olfactory hallucinations) and have yielded bilateral permanent anosmia (Markert et al., 1993). Excision of the olfactory epithelium has also been used as a treatment for severe phantosmias. In some cases, the procedure is not only effective in eliminating the phantosmias, but the patient has his/her olfactory ability restored after some time (Leopold, 2002). Based on these findings, one can conclude that, though there is some evidence that olfactory consciousness of some kind can persist despite the absence of the olfactory epithelium and olfactory bulb, more data are required before drawing strong conclusions regarding the necessary role of these peripheral structures in olfactory consciousness.

Second, we discuss the role of the thalamus. Although in olfaction the thalamus is not immediately influenced by the bottom-up afference (as is the case in other modalities), the MDNT does receive inputs from cortical regions that are involved in olfactory processing (Haberly, 1998). Hence, one should refrain from concluding that, in olfactory consciousness, thalamic processing is unnecessary. Nevertheless, because olfactory afferents bypass the relay thalamus, one can draw a more conservative conclusion: Consciousness of some sort does not require the first-order thalamic nuclei, at least for olfactory experiences and under several assumptions (Morsella et al., 2010).

It is likely that the MDNT plays a significant role in high-level olfactory processes, those above the processing of the early afferent signal. For example, as mentioned above, evidence suggests that this structure is important in olfactory discrimination (Eichenbaum et al., 1980; Slotnick and Risser, 1990; Tham et al., 2011), olfactory identification, and olfactory hedonics (Sela et al., 2009). The MDNT is also significant in more general cognitive processes, including attentional mechanisms (Tham et al., 2009, 2011), learning (Mitchell et al., 2007), and memory (Markowitsch, 1982). It is important to note that, pertinent to the topic at hand, no study we are aware of has documented a lack of basic conscious olfactory experience resulting from lesions of the MDNT (but see theorizing in Plailly et al., 2008). It seems that olfactory discrimination of some sort can survive following lesions of the MDNT (Slotnick and Kaneko, 1981; Slotnick and Risser, 1990).

In addition, it is important to consider that, regarding second-order thalamic relays such as the MDNT, these nuclei are similar in nature to first-order relays in terms of their circuitry (Sherman and Guillery, 2006). Thus, the circuitry of the MDNT is quite simplistic compared to, say, that of a cortical column. In addition, as mentioned above, the thalamus in olfactory processing involves only sparse fiber density. One might propose that such simplistic circuitry would be insufficient to instantiate a phenomenon as sophisticated as consciousness, but such a conclusion would be premature. To date, there is no strong theorizing regarding the kind of circuitry that the instantiation of consciousness would entail. Moreover, very little is known about all aspects of thalamic processing (see Morecraft et al., 1992). Hence, at this stage of understanding, one cannot rule out that thalamic processes are capable of constituting consciousness (see strong evidence for involvement of the thalamus in consciousness in Merker, 2007; Ward, 2011).

Regarding the paleocortex, it has been proposed that cortical involvement is required for consciousness of any kind (see various accounts in Godwin et al., 2013). Thus, lesions of the cortical regions involved in olfactory processing should result in the inability to have conscious olfactory experiences. According to Barr and Kiernan (1993), olfactory consciousness depends primarily on the piriform cortex. It is interesting to note that, if conscious olfactory experience can arise at the level of the piriform cortex, then this would be the only case in which a sensory system achieves conscious perception with little or no involvement of neocortical or thalamocortical circuits. However, according to Sela and Sobel (2010), and based on our own review of the literature, there are no documented cases of anosmia that have arisen due to focal lesions of the piriform cortex. Accordingly, in the animal literature, Staubli et al. (1987) showed that rats with ablations to the piriform cortex were still able to discriminate between simple odor cues (although not complex odor cues) in a comparable manner to control rats, suggesting that the piriform cortex may aid in more complex odor discrimination tasks but is unnecessary for the discrimination between simple odors. (Of course, one must be conservative when drawing conclusions about the conscious experience of these animals.)

Complementing these observations, the piriform cortex exhibits increases in odorant-induced activity at the onset of a new odor (Sobel et al., 2000; Poellinger et al., 2001). Although the time-course of this activation (from fMRI studies) varies from study to study [from 10 to 15 s (Poellinger et al., 2001) and 30 to 40 s (Sobel et al., 2000)], both the studies by Poellinger et al. (2001) and Sobel et al. (2000) indicate that accurate odor detection persists after activation in the piriform decreases to a baseline (or below baseline) level. Conversely, activation in the OFC does not decrease over odorant exposure (60 s; Poellinger et al., 2001). This difference in activation levels may represent the functional importance of olfactory tracts that bypass the piriform cortex and project directly from the bulb to the OFC (Shipley and Adamek, 1984).

Regarding the role of neocortex, Keller (2011) concludes, "There are reasons to assume that the phenomenal neural correlate of olfactory consciousness is found in the neocortical OFC" (p. 6; see additional evidence in Mizobuchi et al., 1999). In line with this proposal, Cicerone and Tanenbaum (1997) observed complete anosmia in a patient with a lesion to the left orbital gyrus of the frontal lobe, and Li et al. (2010) reported a comprehensive case study of a patient who experienced complete anosmia as a result of a right OFC lesion. Despite the patient's complete lack of conscious olfactory experience, neural activity and autonomic responses revealed a robust sense of *blind-smell* (unconscious olfactory processing that influences behavior; Sobel et al., 1999), a phenomenon we discuss below. This evidence suggests that, while many aspects of olfaction can occur unconsciously, the OFC is necessary for conscious olfactory experience. Independent of this research, and consistent with cortical accounts of consciousness, it has been proposed that the conscious aspects of odor discrimination depend primarily on the activities of the frontal and orbitofrontal cortices (Buck, 2000).

However, not all accounts implicate the neocortex in the generation of olfactory consciousness (e.g., Barr and Kiernan, 1993) and not all documented lesions of the OFC have resulted in anosmia. For instance, Zatorre and Jones-Gotman (1991) documented cases in which OFC lesions resulted in severe deficits, yet all patients demonstrated normal olfactory detection thresholds. Zatorre and Jones-Gotman (1991) conclude that the OFC is important in odor discrimination but not in conscious odor detection. Moreover, in the animal literature, rats with lesions of the OFC still perform normally on odor-identification tasks (Tait and Brown, 2007). Of course, only limited conclusions can be drawn because of the neuroanatomical differences in the OFC between the rat and humans (Uylings et al., 2003) and because of the difficulty of determining whether the animal is consciously experiencing a smell (e.g., the behavior of the animal could reflect a sort of blind smell).

In conclusion, although it is clear that the olfactory system is well suited system for the isolation of a neural correlate of consciousness, the current literature does not permit one to draw strong conclusions regarding the neuroanatomical regions that are critical for the generation of olfactory consciousness. Investigations on the neural correlates of phantosmias may further illuminate the circuits required for olfactory consciousness. But this is challenging research: It has proven difficult to identify the minimal region(s) whose stimulation is sufficient to induce olfactory hallucinations (Mizobuchi et al., 1999). It appears that, once more data are available, conclusions with greater certainty may soon be drawn, especially concerning the roles of the peripheral structures (the olfactory epithelium and bulb) and the MDNT in the generation of olfactory consciousness.

PHENOMENOLOGICAL AND COGNITIVE/MECHANISTIC PROPERTIES

There are phenomenological and cognitive/mechanistic properties that render the olfactory system a fruitful network in which to investigate the contrast between conscious and unconscious processing. Regarding the phenomenological properties, unlike what occurs with other sensory modalities, olfaction regularly yields no subjective experience of any kind when the system is understimulated, as when odorants are in very low concentrations or during sensory habituation to odorants. This "experiential nothingness" (Morsella et al., 2010) is more akin to the phenomenology of the blind spot than to what one experiences when visual stimulation is absent (darkness). It is important to note that, in the latter case, there still exists a conscious, visual experience (e.g., that of a black field). The experiential nothingness produced by an olfactory system yields no conscious contents of any kind to such an extent that, absent memory, one would not be able to know that one possessed an olfactory system. (For a comparison of olfactory consciousness to the phenomenon of *change blindness* in vision, see Sela and Sobel, 2010.)

As noted, this form of experiential nothingness can result from habituation or from an inadequate level of olfactory stimulation. In the latter case, subjects may be consciously unaware of the presence of an odorant (e.g., lavender) but still be influenced by the odorant unconsciously, as in the phenomenon of blind-smell (Sobel et al., 1999), the olfactory analog of *blindsight* (Weiskrantz, 1992), in which patients report to be blind but still exhibit visually guided behaviors. For example, in blindsight, a patient may self-report to be unable to see anything but may nonetheless walk around an obstacle placed in her path. In blind-smell, people can learn to associate certain odorants (e.g., lavender) with certain environments (e.g., a particular room), even though the concentration of odorants presented during learning was consciously imperceptible (Degel et al., 2001). That the subliminal odorant is influencing behavior is detectable in behavior and decision-making. The findings from research on blind-smell complement similar findings from investigations on subliminal visual perception (Pessiglione et al., 2007; see review in Hallett, 2007). Thus, the olfactory system features properties that render it ideal for experiments designed to contrast the neural correlates of sensory processes that are conscious (e.g., the smell of fresh bread) with those that lie in an experiential nothingness, as in the blind-smell of subliminal odorants.

Regarding habituation, though this phenomenon occurs in all sensory modalities, it may occur in a special manner for olfaction because of the absence of the possibility of voluntary re-access to an exposed odorant (Stevenson, 2009). For example, in haptic sensation, one may habituate to the feeling of wearing a wrist watch. Similar habituation can occur in olfaction: Upon entering a room, one may detect a smell for some time, before one habituates, and then the smell vanishes from consciousness. Although both sensory stimuli fade from consciousness, the feeling of one's watch can be experienced anew by voluntarily directing attention toward the watch. However, it seems that olfactory sensations cannot be re-accessed as easily through these attentional means (Köster, 2002). Regarding the experiential nothingness associated with olfaction, it is important to reiterate that research indicates that (a) accurate odor detection persists after activation in the piriform decreases to a baseline (or below baseline) level (Sobel et al., 2000; Poellinger et al., 2001), and (b) activation in the OFC does not decrease over odorant exposure (60 s; Poellinger et al., 2001).

We discussed three states associated with olfactory consciousness: (A) subliminal perception (**Figure 1**), which includes no conscious contents, (B) conscious detection of an odorant (**Figure 2**), which includes conscious contents and is indexed by self-report on the part of the subject, and (C) habituation (**Figure 3**), which, like subliminal perception, includes no conscious contents. When isolating the neural correlate of olfactory consciousness (NCC-O), one should seek regions that are active during B but not during A and C. It is important to note that the NCC-O of an odorant, as indexed by self-report, should not vary as a function of the organism's motivational or incentive state.

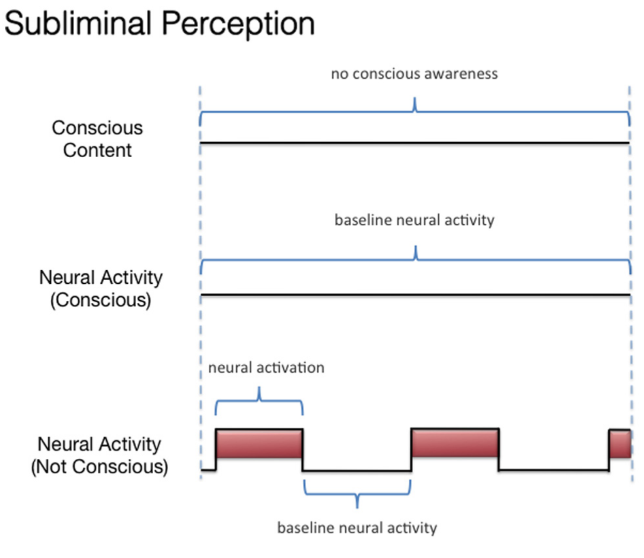

FIGURE 1 | Schematic representation of the relationship between the subjective events associated with subliminal perception of olfactory stimuli and hypothetical neural activity.

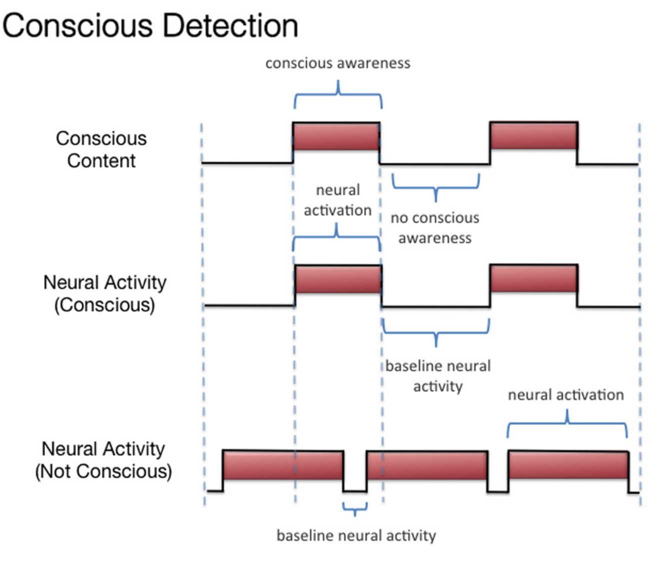

FIGURE 2 | Schematic representation of the relationship between the subjective events associated with conscious detection of olfactory stimuli and hypothetical neural activity.

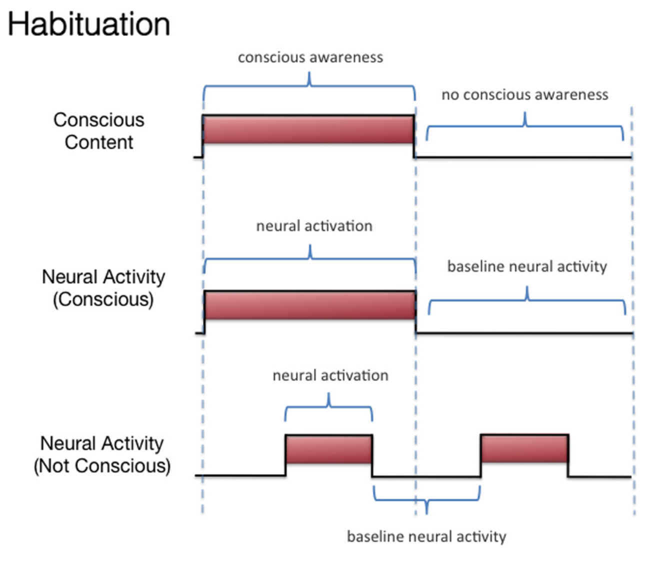

FIGURE 3 | Schematic representation of the relationship between hypothetical neural activity and the subjective events associated with habituation of olfactory stimuli.

Consider the example in which a master chef must detect whether the soups served in her restaurant are being cooked properly. The chef must compare the smell dimension of the dish to some standard in memory (e.g., perfect carrot soup). This conscious perception occurs in an invariable manner regardless of the chef's current emotional/incentive state. This is obvious when one observes in the chef a series of invariable judgments made when evaluating soups at different times. It would not be adaptive for the smell of token odorants (e.g., a soup) to be identified differently at different times, because of variables concerning the internal state of the organism. Of course, if the chef is hungry or sated, her entire conscious experience will be different when smelling the food item, but these motivational/incentive variables reflect other dimensions of conscious experience. Simply put, the smell of a banana, if experienced consciously by the organism, must be experienced in the same way when the organism is, say, hungry or sated. It is adaptive for there to be such an invariance and an independence between motivation and perception, as noted by Rolls et al. (1977) in their discussion of the limits of motivational influences over visual perception: "It would not be adaptive, for example, to become blind to the sight of food after we have eaten it to satiety" (p. 144). This is because food items are not used just for eating; they can also be used as, say, projectiles to throw at an entertainer.

Hence, the perception of the items should be invariant and not vary by emotional/incentive state. Our chef example reminds one of the multidimensional nature of conscious experiences and is reminiscent of the classic research regarding the multiple conscious dimensions of subjective pain (e.g., the sensorial and affective dimensions; Melzack and Casey, 1968). To give another example, no one who "grew to like olives," who at first did not like olives, ever thought that the first olive they ever tasted failed to represent subsequent olives, at least in terms of the flavor. When *growing to like* olives, something does change in one's conscious experience, but it is not the conscious perception of the olive flavor. This has implications for the study of the NCC-O: The NCC-O for a given odorant should vary as a function of whether there is (A) subliminal perception, (B) conscious detection of an odorant, or (C) habituation. However, it should not vary as a function of the organism being sated or hungry (**Figure 4**). It should be clarified, however, that it remains an empirical question whether the NCC-O of an odorant remains unchanging regardless of, say, the organism's current incentive/motivation state or the positive/negative contingencies associated with that odorant. There is evidence suggesting that the neural pattern underlying the representation of an odorant is changed slightly if that odorant is reinforced or unreinforced through conditioning (Freeman, 2007b; see also Keller, 2011).

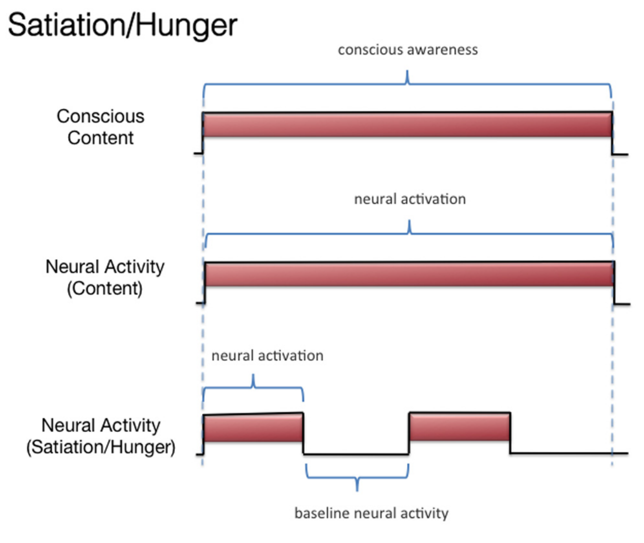

FIGURE 4 | Schematic representation of the relationship between subjective olfactory experience and hypothetical neural activity, under conditions of hunger and satiation.

Concerning habituation, its effects can be seen at the receptor level as well as at the level of the olfactory bulb (Wilson, 2009). Data concerning the functioning of the piriform cortex and OFC during habituation are less straightforward (Sobel et al., 2000; Poellinger et al., 2001; Wilson, 2009).

The olfactory system is a fruitful network in which to isolate the NCC-O also because of its cognitive/mechanistic properties. First, unlike in the visual modality, there are few sophisticated cognitive control functions that are usually coupled with olfactory processing. For example, there is no phenomenon in olfaction that is analogous to mental rotation, a form of high-level symbol manipulation. Thus, in olfaction, one is less likely to conflate the NCC-O with the neural correlates of high-level executive functions (see Aru et al., 2012), which is a recurring problem in the search for the visual NCC (see discussion in Panagiotaropoulos et al., 2013). In addition, because of the relative lack of control functions in olfaction, the subjective experience of the self-reporting subject is unlikely to be contaminated by introspections regarding, not olfactory experience, but cognitive effort or other aspects of control. In a similar vein, in vision and audition, mental images can be used to preserve information in working memory through active executive processes such as rehearsal (Baddeley, 2007), but olfactory images are difficult to couple with such executive operations (Stevenson, 2009). In fact, it has been demonstrated that participants report that olfactory images are more difficult to produce and less vivid in comparison to other forms of mental imagery (Betts, 1909; Brower, 1947; Lawless, 1997; Stevenson, 2009).

Second, olfactory experiences are less likely to occur in a self-generated, stochastic manner. Unlike in the case of vision and audition, in which visually rich daydreaming or "ear worms" (i.e., a song involuntarily repeating in one's head) can occur spontaneously during an experiment and contaminate visual and auditory dependent measures, respectively, there are little, if any, such self-generated olfactory experiences that could contaminate psychophysical measures. Last, the olfactory system is more segregated from the semantic system than is the most studied sensory system – vision. Many have argued that, in the case of vision, there are deep, inextricable relationships among perception, conceptualization, and semantic processing (Barsalou, 1999; Kosslyn et al., 2006). Such is not the case for olfaction. Thus, when isolating the NCC-O, one is less likely to include in it higher-level processes (e.g., semantic processes) that are associated with more than just simple olfactory (conscious) detection.

NEURODYNAMICS

For present purposes, it is fortunate that the olfactory system was one of the first systems in which the nature of oscillatory activity in the brain was investigated (e.g., Adrian, 1942). Before discussing research on the nature of this oscillatory activity, we will discuss the more general relationship between brain rhythms and consciousness.

It has been proposed that, to instantiate consciousness of any kind, the mode of interaction among regions is as important as the nature and loci of the regions activated (Ward, 2003; Buzsáki, 2006; Godwin et al., 2013). For example, the presence or lack of *interregional synchrony* leads to different behavioral, cognitive, and even consciously experienced outcomes (Ward, 2003; Hummel and Gerloff, 2005; Lewis et al., 2012). [See review of neuronal communication through "coherence" in Fries (2005)]. Regarding the neurodynamics underlying consciousness, the general view is that consciousness depends on "precise synchronization of oscillatory neuronal responses in the high frequency range (beta, gamma)" (Singer, 2011, p. 43). Singer (2011) adds, "brain states compatible with conscious processing should be characterized by a high degree of synchrony" (p. 43). Similar conclusions about the role of high frequencies in consciousness are found in the literature (e.g., Crick and Koch, 1990; Engel and Singer, 2001; Meador et al., 2002; Jung-Beeman et al., 2004; Doesburg et al., 2005; Aru and Bachmann, 2009; Doesburg et al., 2009; Uhlhaas et al., 2009; Hameroff, 2010; Wessel et al., 2012). Most recently, with the use of more sensitive technologies, the hypothesis was supported by Panagiotaropoulos et al. (2012), who examined activities of the lateral prefrontal cortex of the macaque. As revealed below, the olfactory system has the potential to provide additional evidence for these conclusions, such as those concerning the roles of gamma and beta frequencies in cognition. In addition, the relative simplicity of the neuroanatomical architecture of the system renders it a fruitful environment in which to investigate the neurodynamics of consciousness. (For a general review of the role of oscillations in cognition, see Sauseng and Klimesch, 2008; Wang, 2010; Siegel et al., 2012.)

Generally, the empirical evidence suggests that olfactory information may be encoded through oscillating neural assemblies (Adrian, 1942, 1950a,b; Freeman, 1975; Eeckman and Freeman, 1990; Gray, 1994; Laurent and Davidowitz, 1994; Kim et al., 2006). Different odorants elicit different, complex spatial patterns across spatially distributed neural ensembles of the olfactory bulb (Freeman, 1987; Laurent and Davidowitz, 1994; Xu et al., 2000). The elements comprising these dynamic patterns of activation are not static, but can evolve dynamically over time (Freeman, 1987; Laurent, 1996).

Classic research on the olfactory bulb, for example, illuminates the occurrence of organized, high frequency activity (gamma in the rat, ranging from 40 to 100 Hz; Adrian, 1942, 1950a,b; Kay and Beshel, 2010) during the perception of odorants. These high-frequency gamma "bursts" appear to be coordinated with respiration, which is associated with a slower oscillatory cycle (*theta* in the rat: 2–12 Hz; Eeckman and Freeman, 1990; Rojas-Líbano and Kay, 2008; Kay et al., 2009). [Concerning theta, Kay et al. (2009) state, "In the olfactory system, theta oscillations track the respiratory cycle and range in waking rodents from 2 to 12 Hz, with frequencies above 4 Hz defined usually as sniffing" (p. 9). See Schroeder and Lakatos (2009) for a treatment of the role of the respiratory cycle in oscillations.] Specifically, each phasic gamma burst begins shortly after inspiration, terminates during expiration, and can be modulated (via increases in frequency and duration) by the presence of an odorant (Eeckman and Freeman, 1990). Adrian (1942) associated the gamma burst with increased inter-cellular activity (including excitation and inhibition between neurons) within the olfactory bulb, a view that has been corroborated by subsequent research (Rall and Shepherd, 1968; Mori and Takagi, 1978; Gray, 1994; Lagier et al., 2004; Kay et al., 2009). [See Buzsáki and Wang (2012) for discussion of the origins of gamma oscillations.] If the lateral olfactory tract–axons of a subset of cells from the bulb that project to the piriform cortex (Haberly, 1998)–is severed or otherwise disrupted, gamma oscillations in the bulb persist (Gray and Skinner, 1988), but gamma no longer occurs in piriform cortex (Freeman, 1979; Haberly, 1998). This suggests that the mechanism involved in producing gamma oscillations resides within the olfactory bulb. (For a treatment of the interactions between the olfactory bulb and cortex, see Boyd et al., 2012; Oswald and Urban, 2012. For research on the role of gamma as a "temporal filter," see Litaudon et al., 2008.)

Further support for the aforementioned hypothesis that the olfactory bulb is the functional equivalent of the thalamus is provided by the study of oscillations in the olfactory system. Experiments have revealed that correlations between slow-wave (theta) activity in the olfactory bulb and piriform cortex resemble those found between the thalamus and neocortex (Fontanini et al., 2003; Fontanini and Bower, 2006). Importantly, local field potentials and intracellular membrane potentials in the piriform cortex are strongly correlated with the slow-wave oscillatory pattern of the olfactory bulb (Fontanini and Bower, 2006). A similar inter-relationship occurs between the thalamus and neocortex (Contreras and Steriade, 1995).

The functional role that gamma oscillations may play in olfaction and in sensory perception is still under debate, as is the nature of processing in the olfactory bulb (Gervais et al., 2007). Research suggests that the higher the *task demand* (e.g., fine discrimination of odors versus simple discrimination of odors), the higher the gamma amplitude will be in early perceptual processing (Beshel et al., 2007). For example, in the olfactory bulb of the rat, when fine odorant discriminations are required in a two-alternative choice task, there are high gamma amplitudes, independent of changes in the frequency bands of theta and beta (Beshel et al., 2007). Accordingly, disturbing gamma oscillations in invertebrates impairs the discrimination of similar odors (a high task demand), but does not impair the discrimination of dissimilar odors (a low task demand; Stopfer et al., 1997).

Gamma oscillations have been studied in the mammalian olfactory system since the time of Adrian. More recently, beta oscillations (∼15–30 Hz in the rat; Kay et al., 2009; Kay and Beshel, 2010) have attracted attention. These oscillations have been observed in response to volatile odorants and organic solvents, and are found in the olfactory bulb, piriform cortex, entorhinal cortex, and hippocampus (Zibrowski and Vanderwolf, 1997; Vanderwolf and Zibrowski, 2001). Unlike gamma oscillations, oscillations in the beta range require participation of (at least) the piriform cortex (Neville and Haberly, 2003). Surgical interruption of the lateral olfactory tract eliminates beta oscillations in the olfactory bulb (Neville and Haberly, 2003), whereas, as mentioned above, gamma oscillations can persist following such an interruption (Gray and Skinner, 1988).

It has been hypothesized that the reciprocal interactions between the bulb and piriform cortex engender local field potential oscillations in the beta range (Neville and Haberly, 2003). Beta oscillation episodes last longer than those of gamma oscillations, usually spanning 2–4 inhalation cycles in the rat. These oscillations are specific to a given odorant and reset when a new odorant is presented (Lowry and Kay, 2007). Beta oscillations in the olfactory bulb and anterior piriform cortex of the rat typically develop over the first three or four exposures to a particular odorant. In the piriform cortex of the rat, beta oscillations have also been shown to have a gradual enhancement or sensitization over repeated presentations of odorants, which, for certain odors, can last up to several days (e.g., Vanderwolf and Zibrowski, 2001). Beta coherence between the olfactory bulb and the hippocampus also accompanies odor learning in a go/no-go task (Martin et al., 2007). These oscillations have also been associated with certain types of odor learning (Martin et al., 2004; Kay et al., 2009) and odor discrimination. A study conducted by Kay and Beshel (2010) examined the phase of beta in the olfactory bulb and the anterior and posterior piriform cortices of the rat as the animal performed a two-alternative odor discrimination choice task. These investigators found that beta oscillations in the olfactory bulb drove or "entrained" both areas of the piriform, suggesting that beta oscillations may serve the purpose of transmitting olfactory information from the olfactory bulb to higher order, more cognitive areas. Accordingly, sensory research outside of olfaction has found evidence that beta may be involved in sensory gating (Hong et al., 2008) or in large-scale coupling for sensorimotor integration (Freeman, 2007b; Siegel et al., 2012). In addition, Kay et al. (2009) propose that, "beta oscillations are associated with motor models, favoring this oscillation as a good substrate for long-distance communication" (p. 7). Together, these studies suggest that beta oscillations may serve as a mechanism to link the olfactory system to various subcortical and cortical areas for cognitive processing (e.g., short-term perceptual learning and memory formation). Consistent with this interpretation, it has been proposed that, though gamma frequencies can be observed in processing at primary sensory areas, when the sensory information becomes part of a wider network which includes activations from other sensory modalities, then the frequencies are in the beta range (Freeman, 2007b). This occurs in olfaction (Freeman, 2007b). It remains unclear whether the higher frequency oscillations (e.g., those in the gamma range) play an essential role in the instantiation of conscious content (e.g., olfactory content *X*) or whether such a content can be instantiated independently by the more global (and slower) frequency ranges (e.g., beta). The neuroanatomical evidence reviewed above suggests that the central processes can instantiate the conscious representations of sensorial content without the peripheral structures. These facts remain puzzling.

Researchers have also examined the possible relationships among the different frequency bands (including *cross-frequency phase synchronization*; Sauseng and Klimesch, 2008) in the olfactory system. For example, Ravel et al. (2003) examined the relationship between gamma and beta oscillations by recording local field potentials in the olfactory bulb while rats performed an olfactory discrimination task. During this task, there was decreased power in the gamma band and increased power in the beta band (Ravel et al., 2003). The same pattern of activation was even more notable in well-trained rats, with gamma now being significantly decreased in both duration and amplitude, and beta power being amplified twofold during odor sampling (Ravel et al., 2003). As concluded by Kay and Beshel (2010), "Beta and gamma oscillations are not simply different frequencies but also show some opposing effects in the olfactory network" (p. 836). In addition, theta coherence (reflecting the strength of interaction between the olfactory bulb and piriform cortex) has been shown to increase parametrically to odorant volatility in awake rats but not in urethane-anesthetized rats (Lowry and Kay, 2007). Theta band coherence may facilitate beta oscillations, which, as mentioned above, may be a key mechanism for transmitting information across the olfactory system (Lowry and Kay, 2007; Kay and Beshel, 2010).

This brief survey into the neurodynamics of olfaction reveals that the relative simplicity of the neuroanatomical architecture of the olfactory system renders it a fruitful network in which to study brain oscillations (Freeman, 2007a; Schroeder and Lakatos, 2009). Examination of the long-studied oscillatory properties of the olfactory system corroborates what has been observed in other sensory modalities (cf., Fries, 2005; Sauseng and Klimesch, 2008; Singer, 2011; Siegel et al., 2012): (a) the synchronizations of high frequencies (e.g., gamma) in local (e.g., olfactory bulb) afferent processing (von Stein and Sarnthein, 2000; Bruns and Eckhorn, 2004; Kay and Beshel, 2010), especially when the process is challenging (e.g., fine discrimination versus simple discrimination; Kay and Beshel, 2010), and (b) the synchronization at a somewhat slower frequency range (e.g., beta or theta) for integration with a larger-scale cognitive network (Kay et al., 2009; Kay and Beshel, 2010), the next topic of discussion.

LARGE-SCALE NETWORK PROPERTIES

While it has been proposed that each of the sensory modules (e.g., for the perception of color, motion, and depth) can generate some form of conscious contents on its own (a "microconsciousness"; Zeki and Bartels, 1999), others have argued that, to become conscious, a content must become part of a broader, supra-modal network. More specifically, it has been proposed that, for olfactory perceptual information ("olfactory content," for short) to become a conscious content, it must interact with other, traditionally non-olfactory regions of the brain (Cooney and Gazzaniga, 2003). For example, olfactory contents may be transformed into conscious contents once they influence processes that are semantic-linguistic (Herz, 2003) or motor (Mainland and Sobel, 2006). These views are consistent with a consensus regarding the function of conscious processing more generally – that conscious processes integrate neural activities and information-processing structures that would otherwise be independent (Baars, 1988, 1998, 2005, 2013; Tononi and Edelman, 1988; Damasio, 1989; Freeman, 1991; Srinivasan et al., 1999; Zeki and Bartels, 1999; Edelman and Tononi, 2000; Dehaene and Naccache, 2001; Llinás and Ribary, 2001; Varela et al., 2001; Clark, 2002; Ortinski and Meador, 2004; Sergent and Dehaene, 2004; Morsella, 2005; Del Cul et al., 2007; Kriegel, 2007; Merker, 2007; Doesburg et al., 2009; Uhlhaas et al., 2009; Boly et al., 2011; Koch, 2012; Tallon-Baudry, 2012; Tononi, 2012). (See reviews of the integration consensus in Baars, 2002, 2013, and in Morsella, 2005.) Consistent with the integration consensus, Uhlhaas et al. (2009) specify that the earliest signature of conscious processing is, "the precise phase locking across a widely distributed cortical network" (p. 11). According to Freeman (2004), the conscious representations of information from different sources, such as from the different sensory modalities, must at some level be similar in form in order for the information from each of these modalities to be integrated with that of the other modalities, thereby forming a polysensory Gestalt of the world. In addition, the form must permit interaction between perceptual and motor systems (Freeman, 2004) if there is to be perception-to-action translations. It has been proposed that these perceptual Gestalts arise in consciousness in a discontinuous manner, with each conscious moment reflecting one snapshot of ongoing integration, resembling the still images of a motion picture, which, when presented one after the other, produce the illusion of continuous motion (Freeman, 2004, 2007b; Koch, 2004). (To learn about the level of representation that characterizes conscious contents, see Freeman, 2007a.)

Moreover, in both perception-based research and action-based research, conscious processing has been associated with more integration than unconscious processing, in terms of the information integration involved and in terms of the neural processes involved. For example, in action-based research, it has been documented that actions de-coupled from conscious processing [e.g., in blindsight, anarchic hand syndrome (Marchetti and Della Sala, 1998), automatisms, and other neurological disorders] reflect less integration than their conscious counterparts, as if the actions are not influenced by the kinds of information by which they should be influenced. Hence, the actions appear thoughtless, impulsive, and irrational.

One limitation of the integration consensus is that integration is a ubiquitous function in the nervous system, occurring for both conscious and unconscious processes. It seems that many kinds of information integration can occur unconsciously in the nervous system field. For example, in *afference binding* (Morsella and Bargh, 2011), integration occurs within sensory modalities (e.g., the binding of color to shape; Zeki and Bartels, 1999) and between sensory modalities, as in the case of the ventriloquist illusion (cf., McDonald and Ward, 2000; Watanabe and Shimojo, 2001) and in the McGurk effect (McGurk and MacDonald, 1976). (See list of unconsciously mediated intersensory illusions in Morsella, 2005, Table 1.) Unconscious integration of various kinds also occurs during motor control (the activation of muscle fibers through motor programs; James, 1890; Grossberg, 1999; Fecteau et al., 2001; Rossetti, 2001; Rosenbaum, 2002; Goodale and Milner, 2004; Johnson and Haggard, 2005; Heath et al., 2008; Liu et al., 2008), and during the control of smooth muscle (e.g., peristalsis and the pupillary reflex; Morsella et al., 2009b). Unconscious integrations also occur in the perception of the flavor of food, which involves the combining of information from multiple modalities (including haptic, gustatory, and olfactory; Shepherd, 2006), and in pain perception, in which there is, for example, interaction between sensory (lateral pain system) and affective components (medial pain system; Melzack and Casey, 1968; Nagasako et al., 2003).

Unconscious integration also occurs in *efference binding* (Haggard et al., 2002), which links perceptual processing to action/motor processing. Through this kind of stimulus-response binding, one can learn to press a button when presented with a stimulus cue in a laboratory paradigm. It has been demonstrated that, in a choice response time task, participants can select the correct motor response (one of two button presses) when confronted with subliminal stimuli (see review in Hallett, 2007). Such unconscious efference binding also takes place in the case of reflexive responses to the natural environment, as in the *pain withdrawal reflex*. [Regarding neuroanatomy, in animals such as the dog, sophisticated and intentional forms of sophisticated behavior remain when much of the cortex is removed through surgery or deactivated (e.g., chemically inactivated; Bures et al., 1974), leaving intact only the ventral forebrain, including the paleocortex (the oldest part of the forebrain), the amygdala, and the neurohumoral brain stem stimuli (Goltz, 1892; Bures et al., 1974; Panksepp, 1998). See extensive treatments in Freeman (2004) and in Merker (2007).]

In summary, the actions resulting from such unconscious bindings can seem not adaptive, as if they are not influenced by the kinds of information by which they should be influenced. Hence, these actions have been described as *un-integrated actions* (Morsella and Bargh, 2011).

As discussed in Morsella (2005), in contrast to these forms of unconscious integration, there are forms of integration that always appear to involve conscious mediation. Such is the case for *integrated actions* (Morsella and Bargh, 2011), in which *two (or more) action plans that could normally influence behavior on their own (when existing at that level of activation) are simultaneously co-activated and trying to influence the same skeletal muscle effector* (Morsella and Bargh, 2011). Thus, integrated action occurs when one suppresses the urge to scratch an itch, holds one's breath, refrains from dropping a hot dish, suppresses a pre-potent response in a laboratory paradigm, or makes oneself breathe faster (Morsella, 2005; Morsella et al., 2009a). Integrated action involves the activation of more neural processes than does un-integrated action (DeSoto et al., 2001; Ortinski and Meador, 2004). Based on these observations, it has been proposed that consciousness is required, not for just any form of integration, but for integrations involving the skeletal muscle effector system. Specifically, it has been proposed that it is required for integrating two conflicting streams of efference binding (see quantitative review of evidence in Morsella et al., 2011). Such *efference–efference binding* results in integrated actions such as holding one's breath. Through consciousness, multiple response systems can influence behavior collectively (Morsella, 2005). Absent consciousness, only one stream can influence action control. This approach is unique in its ability to explain subjective data from (a) intersensory conflicts, which are largely unconscious, (b) smooth muscle conflicts, which, too, are largely unconscious, and (c) conflicts from action conflicts (e.g., holding one's breath and Stroop-like interference), which tend to involve consciousness.

CONSCIOUSNESS IS FOR VOLUNTARY ACTION

Delineating the intimate liaison between consciousness and skeletal muscle is outside the purview of the present treatise (see discussion in Morsella, 2005). For present purposes, it is important to note that this theorizing leads one to the conclusion that the integration achieved through conscious processing is intimately related – not to perceptual processing, semantic processing, smooth muscle control, or motor control – but to voluntary action. Simply put, *consciousness is for voluntary action.* In light of this, one realizes that it is no accident that, historically, skeletal muscle has been the only effector referred to as "voluntary" muscle. The appellation stems from the fact that this effector system is controlled through conscious mediation and that, without such mediation, adaptive integration fails to occur in this system, as in the case of un-integrated actions, such as reflexively dropping a hot (but expensive) dish of china or failing to hold one's breath underwater. These are the kinds of un-integrated actions that transpire when consciousness abates. (Consistent with this approach, it has been proposed that consciousness serves to prevent premature action that does not take into account important, alternative courses of possible action, as when one avoids temptation, holds off fear and anger, or takes time to reflect on the long-term consequences of an action; Freeman, 2004.) Specifically, skeletal muscle is "voluntary" muscle because it is directed by multiple, encapsulated systems that, when in conflict, require consciousness to yield adaptive, integrated action (Morsella, 2005). For this reason, for every voluntary action emitted by the organism, the organism can self-report a conscious content that was responsible for that action (Poehlman et al., 2012), regardless of whether such an introspection is accurate or based on an illusion (Wegner, 2003). (See Freeman, 2004, for a treatment of how the notion of "circular causality" can inform theories about the function of consciousness in the nervous system.)

From this theoretical standpoint, one can hypothesize that, in olfaction, perceptual information may become conscious only once it participates in a large-scale, inter-system integration that is in the service of voluntary action, which is, stated more precisely, adaptive and integrated skeletal muscle output (see related evidence in Mainland and Sobel, 2006). By extension, one could propose (a) that, for every voluntary action based on olfactory contents, the organism can self-report about a conscious olfactory content, and (b) that, if an olfactory content is unconscious, then neither voluntary action nor integrated action can result intentionally from that content.

THE "LOWEST HANGING FRUIT" IN THE STUDY OF THE NEURAL CORRELATES OF OLFACTORY CONSCIOUSNESS

We now conclude by reviewing what, in our review, appear to be the "lowest hanging fruit" regarding the isolation of the neural correlates of olfactory consciousness. First, regarding neuroanatomy, by synthesizing the data from various sources (including lesion studies, animal experiments, and phenomena such as blind smell and sensory habituation), investigators can determine whether peripheral structures (e.g., the olfactory epithelium and olfactory bulb) and thalamic structures (e.g., MDNT) are necessary for there to be a conscious olfactory experience of any kind, including an olfactory hallucination triggered by direct brain stimulation (e.g., in the OFC). At this stage of understanding, it seems that making such a determination would be more difficult in the case of the piriform cortex. It is important to reiterate that, if conscious olfactory experience can arise at the level of the piriform cortex, then this would be the only case in which a sensory system engenders conscious perception with little or no involvement of neocortical or thalamocortical circuits.

Second, investigators can compare the brain networks associated with (A) subliminal perception, which includes no conscious contents, (B) conscious detection of an odorant, which includes conscious contents and is indexed by self-report on the part of the subject, and (C) habituation, which contains no conscious contents. As discussed above, it remains challenging to identify the regions whose activations correspond to the phenomenal state of conscious detection versus the phenomenological nothingness of habituation. When making these contrasts, one should not be identifying the changes in neural activity associated with modulations of incentive/emotional states (e.g., hunger versus satiation). This is because, even though these states are part of the olfactory experience as a whole, they are more than just the subjective dimension of simple conscious olfactory experience. Simple conscious detection can occur (in some form) independent of these state variables. Third, if olfactory contents become conscious only when they become part of a large-scale integrative system, then what are similar kinds of integrations that can transpire *without* consciousness? Such a comparison may reveal that which is special about this form of integration. Again, it has been proposed (Morsella, 2005) that these conscious integrations differ from other forms of integration in terms of their relationship to the voluntary action system. Fourth, if olfactory consciousness cannot arise as a "microconsciousness" (Zeki and Bartels, 1999), but only when taking part in a larger-scale network, then researchers can attempt to isolate the brain rhythms associated with participation in such a network and contrast these rhythms with those occurring locally (rhythms which might not be constitutive of the conscious field).

It is our hope that, in the spirit of this special topic on *Olfactory Consciousness across Disciplines*, investigators will continue to investigate the olfactory system, the most ancient of sensory modalities, to answer these and other questions about the nature of consciousness, the most enigmatic phenomenon in nature.

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Human olfactory consciousness and cognition: its unusual features may not result from unusual functions but from limited neocortical processing resources

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Human and animal olfactory perception is shaped both by functional demands and by various environmental constraints seemingly peculiar to chemical stimuli. These demands and constraints may have generated a sensory system that is cognitively distinct from the major senses. In this article we identify these various functional demands and constraints, and examine whether they can be used to account for olfaction's unique cognitive features on a case-by-case basis. We then use this as grounds to argue that specific conscious processes do have functional value, a finding that naturally emerges when a comparative approach to consciousness across the senses is adopted. More generally, we conclude that certain peculiar features of olfactory cognition may owe more to limited neocortical processing resources, than they do to the challenges faced by perceiving chemical stimuli.

Keywords: olfaction, function, consciousness, comparative, cross-modal

INTRODUCTION

The aim of this manuscript is to explore two ideas. The first, and the one that occupies the most space, is that in human olfaction there are function-related reasons why consciousness and cognition are instantiated in an unusual way relative to the major senses (e.g., Herz and Engen, 1996; Zucco, 2003). To address this, we start by reviewing the main parameters that govern olfactory perception to identify and evaluate potential functional causes of olfaction's unusual features. This is followed by a case-by-case examination of the major differences in olfactory consciousness-related processing that have been identified in the literature. Included within this section are three broad types of finding: (1) differences in the content of consciousness (single vs. multiple representations; primacy of affect; universal synesthesia); (2) differences in attentional control and access (smell is a dual sense but without dual awareness; failure to reinstate the representation of a dishabituated smell); and (3) differences in conscious correlates of post-perceptual processing ("imagery" and "rehearsal" without conscious correlates). In each case we review the evidence for the claim of "specialness" and follow this with an examination of how it might relate to olfactory function. The final part of the manuscript examines the second idea, namely the value associated with taking a comparative, cross-modal approach to consciousness and cognition.

THE HUMAN OLFACTORY SYSTEM

The purpose of this section is to evaluate whether there are any unusual or unique aspects of human olfaction, with respect to stimulus and function that might explain its atypical psychological features. The olfactory system's principal function is to recognize the airborne (i.e., typically volatile) chemical correlates of biologically significant events (e.g., Wilson and Stevenson, 2006). In humans, these biologically significant events primarily relate to ingestion (e.g., detection of food), avoidance of environmental hazards (e.g., gas leaks) and social communication (e.g., kin recognition; Stevenson, 2010). The avoidance of environmental hazards, and social communication, all rely on recognizing the volatile chemical cues that are associated with these things—be it a predator or a potential mate. Section Chemicals as Stimuli (Chemicals as stimuli) considers whether the nature of the chemical stimulus places any particularly unusual burdens upon the brain.

While environmental hazards and social communication mainly rely upon the recognition of volatile chemicals in the external environment, ingestion-related olfaction brings with it a more unique problem. This is because the olfactory system has to associate events in the external world, namely the smell of food, with events in the body, such as the taste of food in the mouth and its delayed consequences—fullness, nausea etc. Section The Special Demands Imposed by Eating (The special demands imposed by eating) examines this particular problem.

CHEMICALS AS STIMULI

An important consideration when examining olfaction is to understand the physical stimulus that the system has evolved to detect (Hudson, 1999). Most chemical correlates of biological events are complex mixtures composed of tens or hundreds of different chemical components (e.g., Maarse, 1991). These mixtures contain varying amounts of each chemical, with the higher concentration components probably dominating perception (Weiss et al., 2012). Nonetheless, multiple low concentration components, even when each is below its own detection threshold, can act together to generate a smell (Laska and Hudson, 1991). The brain then has to recognize such multi-component mixtures, and in addition it also has to deal with stimulus fidelity. Chemical mixtures degrade in the environment through the effects of sun, rain and wind. In addition, there are many variations in the chemical mixtures coming from any given class of emitter (e.g., prey odor may change with diet, age, gender, health status etc.). In all of these cases the brain still needs to be able to recognize a weakened or variant signal.

A further problem concerns the continued presence of the same chemicals in one particular area. These may continue to stimulate olfactory receptors potentially masking the detection of new chemical events. Finally, and perhaps most importantly of all, chemical stimuli are poorly placed to support a flexible communication system. A flexible communication system is one in which novel information (e.g., via combining existing signals) can be transmitted and received in contrast to a fixed system where particular signals communicate just one or a limited range of meanings. While use of fixed chemical signals is a widespread feature of many animal communication systems, including in mammals (e.g., Broad and Keverne, 2008), chemicals cannot be readily used to transmit information flexibly, in the way that light and vibration can. A failure to support flexible communication is perhaps one reason why olfaction has remained a relatively minor sense in humans and in other higher mammals. And it is a minor sense, even though it is a highly sensitive and discriminating one (Yeshurun and Sobel, 2010). One reason for making such a claim is that it is easier to live without smell (anosmia), than it is to live without audition or vision. This can be seen in compensation provisions made by the AMA's (1993) *Guide to the Evaluation of Permanent Impairment*, which regards loss of smell as a 3% impairment, relative to deafness at 35% and blindness at 85%. While these figures cannot accurately reflect the full loss associated with anosmia (e.g., Hummel and Nordin, 2005), they do reflect the general distinction in utility between the major senses and smell.

The biological system that has evolved to detect and recognize volatile chemicals shares many features in common with the systems used to detect visual and auditory stimuli (Wilson and Stevenson, 2006). Thus, excepting the flexible communication issue, the problems outlined in the preceding paragraphs for chemical stimuli are *conceptually* similar to those for electromagnetic or vibratory stimuli. Chemicals are detected in humans by around 40 million olfactory receptor neurons located on the olfactory epithelium (Cunningham et al., 1999). Each side of the nose has its own discrete olfactory epithelium, which is positioned inside the upper part of the nasal cavity lying mainly on the cribiform plate (Doty, 2001). Each olfactory receptor neuron expresses one out of a large range of different G-protein coupled receptor types (hereafter, odorant receptors; Buck and Axel, 1991). In humans, there appear to be around 413 different odorant receptors (Glusman et al., 2001; Olender et al., 2012). It is the odorant receptor type that dictates the form of ligand that binds to each olfactory receptor neuron.

Animal research suggests that odorant receptor types are quite broadly tuned, so while maximally responsive to a group of related chemicals, they will still fire to more distantly related ones, especially at higher concentrations (Malnic et al., 1999). This is an important observation, because when combined with the finding that receptor neurons expressing the same odorant receptor types converge to form structures called glomeruli (Ressler et al., 1993), it suggests the basis for a pattern recognition system. That is the spatial activation across the glomeruli, as well as changes in activation over time, provide the input to a content addressable recognition memory system located within primary olfactory cortex (Haberly, 2001). Not only can a content addressable memory system recognize complex patterns and learn new ones, it can also recognize weakened and variant inputs. The primary olfactory cortex has another feature, in that it stops responding to the same receptor input very quickly, allowing it to filter out background stimulation. This occurs even though there is relatively little alteration in peripheral receptor input as measured in rodents (Wilson and Linster, 2008). A similar picture is supported in humans, with neuroimaging suggesting that primary olfactory cortex rapidly adapts to continuous odorant stimulation (Sobel et al., 2000).

While having 400 or so different odorant receptor types is clearly quite unlike vision or audition, the solution adopted to recognizing discrete events in the chemical world is similar to recognizing visual or auditory objects, namely a memory based pattern recognition system (see Stevenson, 2013a). Olfaction then is a system robustly capable of recognizing (and learning) complex stimulus inputs (and weakened or varietal inputs), with constant adjustment via habituation to maintain sensitivity to change.

THE SPECIAL DEMANDS IMPOSED BY EATING

One of the most important functions of the olfactory system concerns food selection (Hoover, 2010). This is especially so for omnivores, who need to remember the nutritional value of many different foods, and to avoid eating those that have made them sick (Rozin, 1976). This requires the olfactory system to perform an unusual feat. *De novo*, information about the nutritional value of a potential food can only be obtained via oral sampling (i.e., taste and somatosensation) and digestion (i.e., from nutrient signals arising in the gut). If smell is to signal the nutritional value of a food, then the body needs some way of detecting the smell of food in the mouth (so that the correct odor is targeted), so that this olfactory signal can then become associated with the food's nutritional value. A food's smell alone can then come to signal its potential nutrient value without the need for oral sampling (e.g., Hiramatsu et al., 2009). For this reason the olfactory system is able to perceive volatile chemical signals arising externally *and* internally, in the latter case via a set of nostrils (nares) located at the back of the throat (Mozell et al., 1969).

Smelling via the posterior nares (nostrils) in the throat is termed retronasal olfaction, in contrast to sniffing through the nose or anterior nares, which is termed orthonasal olfaction. While retronasal chemical stimulation is detected and processed in largely the same manner as orthonasal stimulation, it is not normally accompanied by any conscious awareness that it is an "olfactory" input. Instead, lay people refer to the sensory experience of eating and drinking as "taste" or "flavor" (Rozin, 1982; noting that flavor is the preferred technical term). The olfactory signals arising from food in the mouth can come to be associated with both the food's immediate (is it sweet, bitter, burning etc in the mouth?) and delayed consequences (is it nutritious or poisonous?; see Brunstrom, 2004). This enables the olfactory system to provide, encapsulated within the smell percept, information about the nutritional correlates of a potential food (e.g., is it energy dense?) when it is later encountered in the external world and is being evaluated for consumption. This olfactory information is then used to make decisions about ingestion in both people and animals (e.g., Hiramatsu et al., 2009). No other sense has this dual system architecture.

CONCLUSIONS ABOUT THE HUMAN OLFACTORY SYSTEM

The argument advanced in this section is that while physiologically olfaction has some unique solutions to perceiving odors (e.g., 350 different receptor types), the fundamental conceptual basis of this process is similar to that of the major senses (see Wilson and Stevenson, 2006; Stevenson, 2013a). Nonetheless, two function-related differences emerge as potentially important. One, which is highly distal, concerns the inflexibility of chemical stimuli as a communication medium. This may have contributed to olfaction remaining a minor sense in humans and other higher mammals. The other, which is more proximal, concerns food. Food choice requires the linking of external and internal events and this may have introduced information processing approaches unique to olfaction.

DIFFERENCES BETWEEN PROCESSING IN OLFACTION AND OTHER MODALITIES

In this section three types of processing differences are examined. The first concerns the content of olfactory consciousness, which is used here to refer to both the nature of that content and also its quantity (i.e., one or many percepts). This includes the unitary and serial nature of odor percepts, the dominance of affective processing and the presence of universal odor-induced taste synesthesia. The second concerns attention, and examines the dissociation between awareness of the content of consciousness and the sense modality generating that content, and the apparent absence of voluntary dishabituation. The third looks at the role of conscious post-perceptual processing in olfactory cognition (i.e., imagery and rehearsal). In each of these cases we start by outlining the evidence and then examine how the difference may relate to functional aspects of olfactory processing.

CONTENT OF CONSCIOUSNESS

Perceiving one smell at a time

In vision and audition, it has been argued that what can be experienced at any given moment exceeds what can be processed in greater detail. This is best captured experimentally in a series of studies reported by Sperling (1960). In a prototypical experiment, participants were briefly presented with a grid of letters, all of which they reported seeing. After the stimuli had vanished participants could only accurately recall a subset of the viewed set. Similar distinctions between the apparent phenomenal wealth of visual experience, contrasted with the more limited amount that can be accurately reported have now been observed in many studies (e.g., Simons and Chabris, 1999; Simons and Rensink, 2005). Block (2005, 2007) has described this succinctly as "phenomenal content overflowing accessibility" with somewhat similar distinctions being drawn by other authors (Dehaene and Naccache, 2001; Edelman, 2003). In olfaction, this does not seem to be the case. Olfaction might be better characterized as either "phenomenal content equals accessibility" or perhaps "there is only accessible content."

Many researchers have described olfactory experience as unitary (e.g., Yeshurun and Sobel, 2010; but not all, see Auffarth, 2013). By this it seems they mean: (1) that an olfactory percept cannot be readily broken into a set of parts; and (2) that the whole has some sense of coherence. There is some support for this type of definition. That odors cannot be readily decomposed into their component parts is suggested by an extensive series of experiments reported by Laing and colleagues (e.g., Laing and Glemarec, 1987; Livermore and Laing, 1996). In these studies participants were trained to identify particular odors. These odors were then combined into mixtures of increasing complexity and participants' task was to identify which odor or odors were present. A consistent finding has been that participants and even industry experts (e.g., perfumists) cannot reliably detect more than three odors in a mixture. This would seem to set one possible upper limit on the content of olfactory consciousness.

This upper limit of around three may be unduly optimistic. First, in these studies all of the participants were pre-trained to identify the odors alone, suggesting that the default mode of processing may be to treat "a smell" as precisely that—a singular "one smell." Second, the usual procedure adopted in these experiments is to ask participants to determine if a particular component is present in a mixture (i.e., a selective attention approach). What this procedure cannot tell us is whether it is possible to serially scan an odor mixture (or indeed to experience all three at once), and experience successively different percepts as each component is recognized in turn. We investigated this possibility, albeit indirectly, in a recent series of experiments using binary odor mixtures (Stevenson and Mahmut, 2013a). When participants experience a blend of two odors, there is evidence that across the course of successive presentations, perception can shift from that of a blend to perceiving mainly one component or the other. What is striking about these results is that participants cannot seemingly detect these transitions, even though evidence that they have occurred can be found in their ratings. Even alerting participants to the nature of the task does not improve awareness. These results suggest that when a stimulus is smelled it is perceived by default as *a* smell, and that even if it contains two or more detectable components, these may be hard to notice over successive exposures.

While detecting individual smells within an odor mixture may represent one type of multidimensionality, it may not be the only type. Odors can be characterized by their capacity to remind people of other smells, a phenomenon termed redolence (e.g., Dravnieks, 1982). How many they remind someone of is partly a function of familiarity, with more familiar odors being redolent of fewer smells than unfamiliar odors (Mingo and Stevenson, 2007). How many odors a smell reminds one of is not related to the chemical complexity of that odorant, as redolence appears to be a psychological construct and a reliable one at that even for odors that remind someone of many smells (Dravnieks, 1982). Redolence judgments normally occur when we are asked to describe an odor, and so perhaps they normally follow perception rather than accompany it (e.g., sniff then rate/describe). If the content of consciousness is generally unitary (or perhaps, at a maximum, ternary), and if this is followed by redolence judgments where the odor may remind us of many other odors (i.e., more than three), then for olfaction what is accessible (*perhaps* redolence judgments) at least equals and probably exceeds conscious content.

Is it possible then to explain this seemingly unusual "content of consciousness" with reference to the functional issues raised in Section The Human Olfactory System? There does not seem to be any obvious proximal function served by this form of "content of consciousness." Distal functional explanations may be more promising, as limited content could be a product of the relatively restricted neocortical processing resources devoted to olfaction (Kaas, 2013). One way of instantiating this at the psychological level of explanation would be to make odor selection (i.e., the content of consciousness) an automatic procedure. A potential implication of this would be that there is no phenomenal/access distinction for olfaction, instead all we have is automatically mandated access consciousness. In vision and audition a combination of exogenous and endogenous attentional processes dictate what object or objects are selected for further processing, and certain aspects of this are under volitional control (Sperling, 1960; Van Rullen and Koch, 2003). Some limited volitional control may also be evident in olfaction, notably during the search for a particular odor (Zelano et al., 2011). However, this may differ substantially from the major senses because for olfaction "searching" may only work effectively if it happens to coincide with the olfactory systems built-in tendency to focus on chemicals that are *new* to the search environment. Searching for a habituated odor may be ineffective, making the use of a conscious strategy more limited in this sense.

The advantage of thinking about the content of olfactory consciousness as being the result of an access only system, is that it readily accounts for why its information content (in terms of the number of objects which can become the focus of attention) is relatively low when contrasted with the apparent phenomenal richness of the major senses. It certainly does not have to be this way as the brain undoubtedly processes a considerable amount of information about the individual chemical components of an odor, and this could go to make a rich phenomenal experience, perhaps as it does in the major senses. However, for olfaction this information does not seem to be consciously accessible (e.g., Gottfried et al., 2006).

The primacy of affect

Engen noted that "Functionally, smell may be to emotion what sight or hearing are to cognition" (Engen, 1982, p. 3). It should not be surprising then given Engen's quote that an important aspect of olfactory experience is the hedonic tone that accompanies smelling. Some researchers have even argued that the affective response to a smell actually reflects the primary response, being more important than perceptually based means of recognition (Yeshurun and Sobel, 2010). While this strong claim may be unlikely, partly because recent experimental work indicates that recognition-related processes occur before hedonic judgments (Olofsson et al., 2012), there is good support for the idea that affect is a more central part of the olfactory experience than it is for vision or audition. One important line of evidence has come from multidimensional scaling experiments, which can be used to determine the underlying dimensions that mediate similarity judgments. A consistent finding in this literature has been that the primary dimension is typically hedonic (e.g., Schiffman, 1974). Another line of evidence comes from examining olfactory memories, which have been found to be more emotionally evocative than memories retrieved by comparable visual or auditory cues (e.g., Herz, 2004). Finally, an analysis of olfactory related words reveals them to be on average more affect laden, with unpleasant terms outnumbering pleasant terms, relative to words associated with vision or audition (Ehrlichman and Bastone, 1992).

While affect seems to be a central part of the olfactory experience, it has been noted that if people are asked to provide a list of their most affect-laden experiences, smells will not generally figure high on this list (Ehrlichman and Bastone, 1992). Rather visual and auditory experiences will tend to dominate in seeming contradiction to the arguments presented above. What seems to be special about olfaction is that the object that causes the smell seems to actively *contact* the body, that is it seems to be phenomenologically more proximal than vision or audition (e.g., Rouby and Bensafi, 2002). So the hedonics for smell feels more direct and visceral than the hedonics associated with vision and audition. This is best illustrated by the emotion of disgust. This emotion is frequently triggered by smell, probably because volatile chemicals are often a good cue for disease-related objects and events (Oaten et al., 2009). A characteristic feature of disgust is that contact with an elicitor of this emotion *feels* contaminating (e.g., Sherman et al., 2012), thereby compelling movement away from the object (Rozin and Fallon, 1987). While we might dislike looking at fake dog feces or plastic vomit, synthetic fecal or vomit odors still compel avoidance even if we know they are not real. Such smells just *feel* bad.

Functionally, it has been presumed that the primacy of affect reflects the need for rapid withdrawal or approach, without the need for (presumably) longer cognitive appraisal (Yeshurun and Sobel, 2010). Perhaps there is some merit in this idea when it is applied in the context of ingestive behavior, where detection of microbial contaminants or natural poisons, may require rapid rejection of a food from the mouth before it is swallowed. However, this particular set of circumstances would be rare, because if an off-smell were detectable in the mouth, it would almost certainly be detectable by the nose prior to ingestion. More generally, we seem well able to avoid dangerous situations when they are revealed to us by vision or audition (e.g., a looming object, avoiding road traffic, fire alarms etc.), suggesting that negative affect is not a necessary prerequisite for rapid withdrawal. That people can effectively avoid dangerous situations using non-affective means implies that affect-based processing is not uniquely effective in this regard. It could then be that the affect that routinely accompanies olfactory experience is actually just the product of economical cognition resulting from limited neocortical resources (i.e., no or limited relative to the other senses, dedicated unimodal neocortical tissue). Thus, this position contrasts with the idea that affect generation confers some special advantage over cognition in terms of promoting faster or more effective avoidance (although the bad contamination "feel" of olfactory disgust elicitors may be something special).

Universal synesthesia

While it has been known for many years that people routinely describe certain food odors as *smelling* of particular tastes (e.g., Harper et al., 1968), the unusual nature of these observations only started to attract attention relatively recently (e.g., Frank and Byram, 1988). Importantly, *pure* tastants do not trigger smell sensations (noting that tastants are often contaminated by volatile chemicals; Mojet et al., 2005), it is only smell sensations that can seem to trigger *both* smell and taste sensations even if they have no contact with taste receptors (e.g., Sakai et al., 2001). A further issue is that taste is a discrete sensory system from smell. Taste receptors are located mainly on the tongue and they send information to the brain via a different route to that of smell (Schiffman, 2002). Smell and taste information first converge in the brain, in secondary neocortical structures (Rolls, 1999). To say then that something smells "sweet, sour, bitter, salty or meaty" is directly akin to saying that visual objects routinely trigger sound sensations and vice versa (e.g., a telephone looks ringing).

While synesthesia has typically been explored in the context of the relatively rare individuals with grapheme-color synesthesia (e.g., Mroczko et al., 2009) or some other variant (e.g., lexical-gustatory synesthesia; Ward et al., 2005), a notable aspect of odor-induced tastes is that they seem to be experienced by everyone (Stevenson and Tomiczek, 2007). Although there are similarities between these rare synesthesias and odor-induced tastes, especially in the stability of these experiences over time, their automaticity and involuntariness, there are also differences. The most important seems to be the largely idiosyncratic nature of many synesthetic inducer-concurrent mappings (i.e., why *should* the letter A induce red color?; Deroy and Spence, 2013).

There are several possible mechanisms that could account for odor-induced tastes. One obvious one is that the use of taste-based terms to describe food odors could be metaphorical (e.g., people are sometimes described using taste-based terms). This appears unlikely. The most obvious metaphor is for affect as with saying someone is sweet. Several studies have now shown that odor-induced taste experiences are dissociable from odor hedonics (e.g., Yeomans and Mobini, 2006). A further and related alternative is that people simply employ taste terms for odors that they know explicitly are associated with particular tastes—in other words it is a purely verbal/semantic association (smell-knowledge). Several pieces of evidence speak against it being a verbal/semantic phenomenon: (1) odor-taste associations can be acquired implicitly, in the absence of explicit verbalisable knowledge of the odor-taste pairings (e.g., Stevenson et al., 1998; Brunstrom, 2004); (2) odor induced taste characteristics are reliably present even when participants are unable to identify the odor in question (e.g., Stevenson et al., 2012); (3) odors that induce particular taste sensations have physiological effects that parallel those observed when experiencing an actual gustatory experience (Prescott and Wilkie, 2007); and (4) a growing body of evidence indicates that odors can induce taste experiences in animals, and that these are acquired in the same way as in humans (e.g., Harris and Thein, 2005; Gautam and Verhagen, 2010). While metaphorical or verbal-semantic mediation accounts cannot be wholly excluded as explanations of odor-induced tastes, they seem unlikely.

A further explanation is that certain odors can activate brain regions also active during tasting, resulting in a taste-like experience that is highly perceptually similar to the experience induced by tastants on the tongue (e.g., the sweetness of sucrose on the tongue). That is odor-induced tastes arise from odor-taste associations that are based upon a link between these two percepts, such that the odor percept comes to activate the taste percept. This conclusion has emerged from nearly 20 years of research. Key findings include the observation that: (1) odors that smell of a particular taste can enhance the intensity of that tastant when they are added to it (e.g., Frank and Byram, 1988); (2) odors acquire taste-like properties via associative learning during flavor perception (e.g., Stevenson et al., 1998); (3) odors that smell of a particular taste facilitate identification of that taste (White and Prescott, 2007); (4) tastants that taste the same as an odor smells, facilitate the detection of that smell (e.g., Dalton et al., 2000); and (5) patients with centrally based taste impairments also have selective impairments in perceiving odor-induced tastes (e.g., Stevenson et al., 2008). Together with many other supportive findings not summarized here (see, Stevenson, 2012), these findings suggest that odors can induce taste-like sensations.

It has been suggested that the function of odor-induced taste is to assist in identifying prospective foods, so as to aid prediction of their likely taste in the mouth (Stevenson and Tomiczek, 2007). Currently, and as in our evolutionary past, human food selection is heavily dependent upon color vision, as it is in our fruit-eating primate ancestors where it evolved (Regan et al., 2001). Detecting a food's likely taste via smell is an adaptation that may have had much greater functional significance for animals less reliant on vision (although as in humans it may well augment visual decision making; Hiramatsu et al., 2009), especially rodents. Indeed, rodents can perceive "tasty-smells" just as we can (e.g., Gautam and Verhagen, 2010) and so our ability in this regard may represent the conservation of a function, which no longer confers a major benefit (beyond, perhaps, providing an insight into what it might be like to experience smell like a rat; Nagel, 1974).

Conclusion to content of consciousness

Olfactory conscious experience appears to be mainly singular with one odor event perceived at a time. The large array of objects potentially available to visual attention during perception contrasts with the more limited range available to smell. An odor will be redolent of other odors, it will be affectively toned, and if perceived before in a food, it will probably have taste-like qualities. The olfactory percept seems to directly encapsulate its meaning (especially taste, affect), and it does so with minimal effort, notwithstanding the making of redolence ratings. While visual and auditory percepts also contain considerable inherent information (e.g., depth, location, color, etc) they do not normally contain sense experience drawn from another modality (a quantitative difference). In addition, visual and auditory percepts are not usually accompanied by the visceral feel of affective contact (a more qualitative difference).

It might in theory be possible to explain these differences by reference to the demands and constraints of the olfactory system. However, there does not seem any compelling connection between the demands and constraints identified in Section

The human olfactory system, and the unusual characteristics of human olfactory conscious content. Instead, we suggest that most of the differences in conscious content may be explained by reference to olfaction's limited neocortical processing resources, the exception being odor-induced tastes, which may be a vestige (but still useful) of a once more adaptive food selection system. In the main, the processing differences examined in this section may reflect particularly economical forms of perception, cognition, and consciousness.

ATTENTIONAL PROCESSING

Mouth and nose

Odorants access the olfactory receptors either orthonasally via the nostrils on the face, or retronasally via the internal nostrils at the back of the throat during eating and drinking. One important distinction that has emerged here is that between content and modality awareness (Rozin, 1982; Stevenson, 2013b). When an odor is smelled at the nose, a person knows both that an odorant is present and that the sensory system involved is smell. When an odor is sensed in the mouth as part of a food (retronasally), alongside the anatomically discrete senses of taste and somatosensation (mouth feel), the person is capable of perceiving retronasal odor quality, intensity and hedonic properties. However, this is not routinely accompanied by an awareness of the sense modality (olfaction) involved in its perception (Stevenson, 2009a). While this may apply to naïve participants (as for most of the discussion below), it is likely that experts do have an awareness of olfaction's role in flavor, but this topic has not been well explored. For naïve participants then, sense experience in the mouth is routinely described as flavor or more colloquially as "taste," but not as smell (note that "taste" in single quotes refers here to the colloquial term for flavor, while taste refers to gustation).

The evidence for a dissociation of content and modality awareness in the mouth is quite strong, although it has not received a lot of contemporary research attention. Rozin (1982) asked participants which term they would use to describe a range of different foodstuffs, including several that had significant olfactory components. He found that the terms "taste" and flavor were used interchangeably, although flavor tended to be used more when the item had a greater olfactory component. Rozin (1982) also observed that of all of the major language groups that he had searched, none, including English, had a word that meant "smell in the mouth" (note, however, that experts clearly do have a term for this distinction—retronasal olfaction—although its meaning would probably be unknown to most naïve participants). Another manifestation of the content modality dissociation is seen in people who have lost their sense of smell. When people first present with this problem, they frequently complain of experiencing both a loss smell *and* "*taste*" (Deems et al., 1991). Upon examination it is evident that taste is intact, rather food now "*tastes*" bland as a consequence of the loss of smell.

While participants may attribute the portion of their sensory experience of food that rightly belongs to olfaction, to "taste," the olfactory content of that experience is clearly perceived (Small et al., 2005). The olfactory component of food is a major factor in our enjoyment of eating and drinking, as is made evident when one has a cold and retronasal olfaction becomes impaired. More formal psychophysical tests of peoples ability to identify particular odors in the mouth reveal a capacity to do so that is similar but somewhat poorer than the capacity at the nose (e.g., Marshall et al., 2006). The food industry clearly believes that people can experience smells in their mouth. They spend large sums of money on sensory evaluation panels that reliably judge many purely olfactory attributes of food, which result from the release of volatiles during eating and drinking (Moskowitz and Hartmann, 2008).

One way to consider these findings is to regard taste and smell in the mouth as one perceptual system—taste (but one could equally use the term flavor)—as originally suggested by James Gibson (1966). Gibson's idea can be operationalized by considering taste and smell as having a shared attentional channel in the mouth (Stevenson, 2013b). Although this dual-channel account has not been well investigated, it is consistent with two important findings. First, it does not seem possible to attend to a smell in the mouth without also attending to a co-present taste and vice versa, suggesting that both these senses are entwined (e.g., Ashkenazi and Marks, 2004). Second, if an odor is sniffed at the nose and a taste is placed in the mouth, the presence of the taste can generate an illusory transfer of the location of the odor from nose to mouth (Stevenson et al., 2011). That is the orthonasal smell now appears to be part of a flavor in the mouth. This phenomenon does not occur if an odor is sniffed at the nose and a tasteless somatosensory stimulus is placed in the mouth instead (e.g., a viscous fluid). Together, these findings suggest a special connection between taste and smell that is not shared between smell and oral somatosensation.

Functionally, a case can be made for the idea that the brain needs to connect olfactory information arising in the mouth with olfactory events in the environment so as to aid smell-based food selection (now or at least in the past). Irrespective of whether this view is correct, it still leaves the problem as to the benefit, if any, served by not knowing that smells in the mouth are smells. We suggest two possibilities. One is that it may be more efficient to learn the relationship between a food and its immediate and delayed consequences, if this information is automatically associated (i.e., within an attentional channel, rather than associations between channels). One consequence of this may be evidence of learning even in the face of contradictory explicit knowledge (e.g., falsely associating the nausea from cancer chemotherapy with a food, but knowing the food was not responsible; Bernstein, 1985). A second possibility is that there may have been no evolutionary pressure for awareness of smells in the mouth, and so we just retain an information processing system that predates a conscious reflective component, which is usually deemed necessary for human associative learning (e.g., Shanks, 2010).

Re-attending to smell

In many respects, olfaction shares with vision and audition basic aspects of attentional processing (Keller, 2011). Strong, unpleasant or novel odors may involuntarily attract our attention, and we can selectively attend to the olfactory modality, enhancing our reaction time to events in this channel (e.g., Spence et al., 2001). One reason to suspect that attentional processing differences do exist comes from the unusual neural architecture of olfaction

(Smythies, 1997). Unlike the major senses, which route all incoming information via the thalamus, the olfactory system is unique in having two routes to neocortex, a thalamic relay and a direct link (Tham et al., 2009). Thus, the olfactory system may be able to transmit information to the neocortex independently of the thalamus. This is important because the thalamus has been presumed to play a key role in attentional processing in the major senses (e.g., Portas et al., 1998).

Recent work has suggested that at least one particular aspect of attentional processing may be different for smell. As described earlier, the olfactory primary cortex undergoes a rapid reduction in neural response to continued chemical stimulation (e.g., Sobel et al., 2000). The presumed reason for this is so that the system is ready and able to detect new odorants as they arise. Importantly, this process of adjustment is principally a cortical change (or more properly a paleocortical one), and not a loss of sensitivity at the receptor level. In fact animal work shows convincingly that olfactory receptors retain sensitivity to an odorant that no longer generates any neural response in primary olfactory cortex (Wilson and Linster, 2008). The cortical locus of this reduced responsivity, combined with retained receptor sensitivity, suggests that it may be termed habituation (i.e., a brain-based phenomenon) rather than sensory adaptation (i.e., a receptor-based phenomenon), a division long recognized in the literature (Thompson and Spencer, 1966). In the major senses it is relatively easy to voluntarily attend to stimuli that are habituated. In the classic example of the ticking clock, one can voluntarily attend to the sound, but as attention is drawn to other stimuli the ticking again appears to pass out of consciousness (James, 1890).

This does not seem to be the case for the olfactory system as an experiment recently conducted in our laboratory suggests (Mahmut and Stevenson, submitted). Participants were placed in an odorized room and asked to describe its smell using redolence and certainty ratings. One group was then continuously exposed to the smell, but only in one nostril (this being counterbalanced across participants), the other nostril being blocked (recall that each side of the nose has its own discrete olfactory epithelium). Performance, in this group of subjects of their open nostril reflects the effects of peripheral adaptation *and* central habituation, while performance in their blocked nostril just reflects central habituation, which is bilateral (Cain, 1977). The other group of participants had both nostrils blocked, so as to equate exposure created when participants removed the nose plugs to make ratings of the room's odor. After a period of around 20 min exposure, we asked both groups to again describe the room's smell using redolence and certainty ratings. The key result is in the group that had just one nostril blocked, with the other open throughout exposure. When we tested the nostril that had been blocked throughout exposure, they were unable to describe the room's smell when their attention was directed toward it, relative to the way they had at the start of the experiment. This reflects the effect of centrally based habituation, as this nostril (and its associated receptors) had minimal prior exposure to the odor, and so no sensory adaptation should have occurred. Participants in the other group, who previously had both nostrils blocked, were still able to describe the odor in the same way as they had at the start of the experiment (i.e., no receptor adaptation or habituation). In sum, participants asked to attend to a centrally habituated odor seemed unable to voluntarily recover its conscious representation.

As we noted earlier, the olfactory system has to detect new odorants against the background of currently present odorants, and habituation may play a significant role in this process (noting that the persistence of one odorant will not necessarily block perception of another). While it would be tempting to describe failure to re-attend to a habituated odor as a consequence of keeping the olfactory system optimized to detect the advent of new odorants, this explanation seems inadequate. This is because all of the major senses face a similar problem of constant stimulation against which new events have to be detected, and all of them also show habituation (Thompson and Spencer, 1966). However, re-attending to habituated stimuli is still possible in the major senses (James, 1890). Perhaps then it is the nature of the chemical stimulus, which somehow precludes our ability to re-attend to a habituated odor, but it is not obvious why this would be so either. An alternative perspective based again on limited neocortical processing resources (see Section Mouth and Nose) may be needed. It is, we suggest, the absence of dedicated neocortical processing that prevents us from re-experiencing a habituated smell.

Conclusion to attentional processing

The division of olfaction into a sense of smell at the nose, where we are aware of both the modality and content, and a sense of "taste or flavor," where we are aware of content, but not modality, is probably an attentional phenomenon (Stevenson, 2013b). We suggested this might arise because either it is a more efficient means of learning or because it may be that this form of information processing has simply remained conserved over evolutionary history. The second attentional processes examined in this section concerned attending to a habituated odor. This can be conceptualized, as with our discussion of perceiving one smell at a time (Section Mouth and Nose), as being a further consequence of automatic stimulus selection, which in turn may result from limited neocortical processing resources.

POST-PERCEPTUAL PROCESSING

In the visual and auditory domains it is generally accepted that: (1) people can rehearse sounds or images in domain-specific working memory modules (respectively the visuo-spatial scratch pad and the articulatory loop); and (2) that these short-term memory processes are intimately connected with the capacity for conscious visual and auditory imagery (Baddeley and Andrade, 2000; Postma and Barsalou, 2009). The olfactory literature on these topics presents a far more complex and seemingly confusing picture. First, after decades of disagreement, it now appears that *trying* to imagine an odor does have several detectable consequences: (1) it activates brain regions, including primary processing areas, which are also active during real smelling (e.g., Djordjevic et al., 2005); (2) it improves various psychological capacities, such as enhancing the detection of threshold level odors (Djordjevic et al., 2004) and priming (Tomiczek and Stevenson, 2009); (3) it mimics various psychophysical parameters, relating to olfactory interactions, intensity and quality (e.g., Carrasco and Ridout, 1993); and (4) it generates olfactomotor responses (sniffing behavior) that closely approximate what is observed during actual smelling (e.g., Bensafi et al., 2003). While, a number of studies have failed to find improved psychological capacities (e.g., Crowder and Schab, 1995) or mimicking of psychological effects observed with real odors (e.g., Herz, 2000), the weight of evidence suggests that trying to imagine a smell can influence a variety of psychological, physiological and neural variables, in much the same way as actual smelling can. However, what is at issue here is whether these various effects, which result from trying to imagine an odor, are mediated or accompanied by a conscious representation of the imagined smell. We suggest they are not.

There are several reasons for thinking that trying to form a conscious odor image, or for that matter attempting to rehearse an odor representation in some form of "mind's nose," may not normally occur. The most obvious reason for doubting that it does comes from simply asking people what they experience when they try to form mental images in different modalities. In all of the studies that we are aware of olfaction is either reported as the modality in which it is most difficult to imagine a perceptual event (e.g., Betts, 1909; Ashton and White, 1980) or it is the modality where participants most frequently report being unable to form any sort of conscious image (e.g., Brower, 1947; Lawless, 1997). These findings do not seem to reflect a broader failure to be *able* to notice olfactory experiences in the absence of appropriate stimulation. Indeed, there is a large literature documenting reports of olfactory hallucinations in people who are not psychotic, but who experience epilepsy, brain tumors and migraine for example (see Stevenson and Case, 2005; Stevenson and Langdon, 2012). So when people say they cannot experience an odor image or that it is vague or indistinct, there seems no obvious reason to doubt the validity of their reports.

A further line of evidence concerns the relationship between psychological and psychophysical performance measures obtained during odor imagery experiments, and self-reports of imagery ability. For visual imagery there are well-established links between these two types of variable (e.g., McDermott and Roediger, 1994; Baddeley and Andrade, 2000). In olfaction, the links between the two appear to be weak at best. Djordjevic et al. (2004) failed to find a correlation between self-report ability and performance on their detection task, although this relationship did emerge when tested just in females. In fact Lyman and McDaniel (1990) are the only group to report a significant correlation between imagery and task performance, but this study has been criticized, as it is unclear whether the reported imagery performance was mediated by verbal codes (see Stevenson and Case, 2005). Other studies have failed to find any link with performance, including Lyman (1988), and Tomiczek and Stevenson (2009). The latter study explored in some detail the predictors of enhanced imagery performance. Participants reported ability to consciously experience an odor image was not found to be a predictor in any of their three experiments. We suggest based on these findings that while there may be good evidence that attempting to imagine an odor can generate a number of effects that broadly parallel real smelling, the evidence that these are accompanied by a conscious image is weak at best. This does not seem to be the case in the major senses, and it is possible that it may not be the case in olfactory experts either, although the evidence basis for this assertion is currently too small to be definitive (see Royet et al., 2013).

A similar picture also emerges in the olfactory short-term memory literature. Yet again, there is good evidence that there is a capacity for short-term memory in olfaction (e.g., White, 1998; Andrade and Donaldson, 2007). What is not clearly established is the representational code that underpins this, and whether it is instantiated discretely (i.e., a short-term olfactory module) or as a component of long-term memory (e.g., Yeshurun et al., 2008; Johnson and Miles, 2009). Evidence that one can hold a conscious representation of an odor in short-term memory once the stimulus had been removed, and perhaps even rehearse this image, is scarce. One potential line of evidence is the presence of primacy effects in the serial position curve, but these have not generally been found for olfactory stimuli (e.g., Miles and Hodder, 2005). Another concerns the two-back task (i.e., is the current stimulus the same as the one smelt before the last one?), which may require some form of active rehearsal to maintain and update working memory. Although olfactory performance on this task seems to depend heavily on participants naming the odor, there is evidence to suggest that the two-back task can be performed even when the odor is unfamiliar and thus likely to be difficult to name (Jonsson et al., 2011). There is then as yet little evidence that odors can be consciously rehearsed in some form of olfactory short-term store.

Based upon current evidence, it looks as if there might be a dissociation between an operational capacity for short-term storage, imagery and rehearsal, and an associated conscious state. That is, these cognitive operations do not seem to be routinely accompanied by a conscious representation. One possible functional benefit of such a conscious-*less* cognition is that it precludes troublesome interference between detection of odors new to that environment and any on-going cognitive operation. However, this appears a weak argument. First, in general, people do not seem to try and remember odorants, imagine them or whatever. While of course this may be because they cannot do so, there would not appear to be much day-to-day call for most of us to try and do so. Second, the major senses seem able to manage imagery-reality confusions, except where these are deliberately engineered to confuse participants by making the real stimulus weak (e.g., Segal and Fusella, 1971; Mathews et al., 2013). Of course it could be that because olfactory percepts are somewhat less vivid than the other senses (e.g., Cain and Algom, 1997), this has prevented the development of imagery-related processing (i.e., because if an imagery capacity evolved it led to fatal confusions between imagination and reality). If this were correct, then this in turn would raise the question as to why olfactory percepts are less vivid or weak. Answering this question would probably lead to the same conclusion as the one that prompted this discussion (i.e., absent conscious processing of imagery and rehearsal). That is olfaction seems to have this feature not because it faces a unique set of challenges, but because it has access to only limited neocortical resources. These limited resources produce tangible effects, one of which may be cognition with minimal conscious representation.

DISCUSSION

The main idea explored in this manuscript is that there are function-related reasons for the way in which consciousness and cognition are configured in human olfaction. In an earlier examination of olfaction's unusual psychological features, Stevenson (2009b) implied that proximal functional factors might be responsible, but he did not explore this issue in any depth. In the current article, which addresses this more directly, it would seem that many of the problems that the olfactory system has to solve to meet its basic function (e.g., recognizing biologically significant chemical mixtures) are in fact *common* to all of the senses. Even a relatively unique problem, such as the persistence of chemical stimuli in the environment, should not unduly constrain cognition. For example, the somatosensory system faces a similar problem of stimulus persistence (e.g., clothes), but this does not seem to preclude turning attention back to the way, for example, of how ones clothes feel. This does not seem to be the case for olfaction. Before turning to the more general explanation advanced here, it is important to note that at least one class of proximal function, unique to olfaction, does seem to have explanatory power. This is the need to link the immediate and delayed consequences of ingestion with the smell of food. This may have contributed to three unusual aspects of olfactory cognition, namely the primacy of affect, odor-induced tastes, and the lack of modality awareness for odors in the mouth. Notwithstanding, even these function-related features may be of lesser current value since the advent of color vision and the allocation of neocortical resources to this sense in our primate ancestors.

The main argument to emerge from this review is that many of olfaction's unusual features may be attributed to its limited allocation of neocortical resources. The capacities olfaction does have result then from its primary processing by many limbic system structures, with its paleocortical and subcortical centers. We have further suggested that the failure of olfaction to take space in the burgeoning neocortex of primates and early hominoids may have come about because chemicals represent a poor medium for flexible communication. The rapid expansion of neocortical tissue in our human ancestors left olfaction languishing as a minor sense (Kaas, 2013), without the need for the neocortical resources necessary to support the manipulation of units of sensory meaning, and their formation into ideas to communicate within the brain and between people. Importantly, this is not to say that olfaction is incapable of transmitting information. Olfaction represents information affectively, and can trigger powerful emotional states (e.g., disgust), and this can be communicated within the brain and to others (e.g., via facial expression). Nonetheless, this communicative capacity is considerably less flexible than one where perception, semantic memory and verbal thought are highly interconnected, as they are for all of the major senses (Revonsuo, 1999). One place this can be seen clearly is in the very well documented problem that most people have in naming even common odorants in the absence of visual or auditory cues (e.g., Cain et al., 1998). Another is the limited access they have to semantic memory systems in the absence of a name (e.g., Stevenson and Mahmut, 2013b). There is no doubt that olfaction is an effective sensory system, but it is a highly limited one relative to all of the other neocortical dependent perceptual systems that we possess.

The claim of limited neocortical resources is not as un-testable as it may at first seem. In a novel line of work, Plailly et al. (2012) have been exploring how olfactory perceptual expertise induces various types of functional reorganization of the brain. It may be that extensive practice can produce increases in neocortical processing power for smell, sufficient to propel what may be unconscious processes in naïve participants into conscious ones for experts. This is certainly what the experts' claim (e.g., Gilbert et al., 1998) and interestingly this seems to be accompanied by the creative use of these cognitive operations to imagine new perfumes or flavors and communicate these ideas to other professionals.

This leads to the second idea we wanted to explore in this manuscript, namely how cross-modal comparisons can be valuable in pointing to the functional benefits that accrue from conscious processing. First, we suggest that the fact that many successful olfactory operations can seemingly occur without conscious awareness, while being potentially conscious in the major senses, seems to imply that consciousness has a function (i.e., if it has not, why not stick with an olfaction-like conscious*less* information processing system?). Second, we suggest that one benefit of conscious processing is the availability of this information for further manipulation, typically for creative and communicative ends. Not surprisingly, it is with this end in mind that the long training period that accompanies olfactory expertise is aimed, and the ability to *control* what information is combined or contrasted with other information seems to be a hallmark of conscious processing in vision and audition, and one that is typically lacking in olfaction—except perhaps in experts.

To us, the most striking differences between olfaction and the major senses is in the content of consciousness itself. Here olfaction has far more limited content than the major senses. One argument we make is to suggest that the content of olfactory consciousness may be limited because all we can experience is the access component. On this basis we do not have phenomenal olfactory consciousness, which is perhaps a consequence of information processing in paleocortical tissue. Perhaps then paleocortical tissue cannot support conscious representations, and while there is evidence that could be mustered favoring this possibility [e.g., notably the temporal aspects of conscious content when smelling seem more correlated with secondary olfactory cortex (orbitofrontal neocortex) than they do with primary olfactory paleocortex (the piriform cortex)], it again points to the interesting possibilities that can emerge when contrasting the senses. Finally, there are now many theories that claim to explain different aspects of conscious processing. While it is beyond the scope of this manuscript to evaluate them all with respect to olfaction, we want to end by pointing out how valuable this might be. Here, we have focused on the phenomenal/access distinction. However one chooses to interpret the data mustered in this article, they do suggest that the phenomenal/access distinction is not the same for olfaction as it is for the major senses. Examining other theories may be equally revealing.

AUTHOR CONTRIBUTIONS

Richard J. Stevenson and Tuki Attuquayefio jointly prepared and wrote the manuscript.

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Same same but different: the case of olfactory imagery

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In the present work we present an overview of experimental findings corroborating olfactory imagery observations with the visual and auditory modalities. Overall, the results indicate that imagery of olfactory information share many features with those observed in the primary senses although some major differences are evident. One such difference pertains to the considerable individual differences observed, with the majority being unable to reproduce olfactory information in their mind. Here, we highlight factors that are positively related to an olfactory imagery capacity, such as semantic knowledge, perceptual experience, and olfactory interest that may serve as potential moderators of the large individual variation.

Keywords: imagery, olfaction, consciousness, comparative, expertise

INTRODUCTION

"We lay no great weight upon these results, though they are evidently in accord with those obtained with vision and audition" (Perky, 1910, p. 441). This statement summarized the opinion stated about the nature of olfactory imagery in one of the first studies targeting mental imagery. However, more than a century later the scientific evidence pertaining to our ability to form olfactory images is yet scarce although the topic has received an upsurge of interest during the past years. The aim of this work is to summarize the current findings from three angles; similarity, difference, and plasticity. First, we show that olfactory imagery shares many of the features known for visual and auditory imagery. Second, we propose that olfactory imagery is radically different in one important aspect; the large individual variation in the capacity to form olfactory images. Finally, we discuss factors that moderate the individual differences, such as semantic knowledge, perceptual experience, and olfactory interest.

SIMILARITIES AMONG VISUAL, AUDITORY, AND OLFACTORY IMAGERY

Although some researchers have declared that we are unable to form olfactory images (Engen, 1982, 1991; Crowder and Schab, 1995; Herz, 2000), support for an olfactory imagery capacity is currently pervasive. The bulk of this work suggests that many features of the olfactory image are shared by visual and auditory imagery. **Table 1** provides an overview of some of these features based on experimental observations across the olfactory, visual, and auditory modalities. For example, multidimensional scaling studies have demonstrated a correspondence between visual perception and imagery in judgments of shapes (e.g., Shepard and Chipman, 1970) and within audition, a strong association between perceived and imagined musical timbre has been documented (e.g., Intons-Peterson et al., 1992). In the olfactory domain, correspondences for pleasantness, intensity, and familiarity ratings have been established between olfactory perception and imagery (e.g., Carrasco and Ridout, 1993; Sugiyama et al., 2006). Moreover, studies have demonstrated that both visual (e.g., Craver-Lemley and Reeves, 1992) and auditory (e.g., Segal and Fusella, 1970) imagery can interfere with perceptual thresholds for the same imagery modality. Likewise, Djordjevic et al. (2004) observed that participants that were asked to imagine an odor and later presented with either the same or different odor were less able to detect the latter. A finding that proved modality-specific. In patient studies, clinical manifestations of visual, auditory, and olfactory hallucinations have been observed for a range of conditions, such as epilepsy (visual: Panayiotopoulos, 1999; auditory: Korsnes et al., 2010; olfactory: West and Doty, 1995), and as a result of cocaine abuse (Siegel, 1978). Dream studies have demonstrated sensory specific components included in visual (e.g., MacCarely and Hoffman, 1981), auditory (e.g., Zadra et al., 1998), and olfactory dream reports (e.g., Stevenson and Case, 2005a). Ocular motor activity in visual imagery (e.g., Laeng and Teodorescu, 2002), and subvocalization in auditory imagery (Aleman and Wout, 2004) have been demonstrated as important factors during imagery. Similarly, the peripheral motor act of sniffing have been shown to influence mental imagery in a modality specific manner, as a blocking of the nostrils decrease olfactory (Bensafi et al., 2003) but not visual imagery (Arshamian et al., 2008). Observations promoting the olfactory image as one of our imagery modalities can also be derived from brain research. For example, research indicates that stimulation of sensory specific brain areas can induce modality specific imagery in vision (Diederich and Goetz, 2000), audition (Moriarity et al., 2001) and in olfaction by electrical stimulation of the olfactory bulb and tract (Kumar et al., 2012).

INDIVIDUAL DIFFERENCES IN OLFACTORY IMAGERY

Although similar in many respects, the capacity to form olfactory images differs from that observed in visual and auditory imagery. For instance, only a minimal portion of the population is unable to create visual images (Kosslyn et al., 2006), whereas the olfactory

Table 1 | Experimental observations corroborating olfactory imagery observations with the visual and auditory modalities.

Observations	Visual imagery	Auditory imagery	Olfactory imagery
(I) Preserved properties between perception and imagery			
Correspondence in multidimensional scaling between perception and imagery.	Similar ratings of presented and imagined states of the US Shepard and Chipman (1970).	Similar ratings of perceived and imagined musical timbre Halpern et al. (2004).	Similar ratings between perceived and imagined odors Carrasco and Ridout (1993), Sugiyama et al. (2006).
Psychophysical correspondence between perception and imagery.	Preserved time properties following mental rotation of three-dimensional objects Shepard and Metzler (1971).	Preserved pitch distance in auditory imagery Intons-Peterson et al. (1992).	Preserved intensity for perceived and imagined odors Algom and Cain (1991).
(II) Interference in perceptual thresholds as a function of imagery	Visual imagery interference in vision Craver-Lemley and Reeves (1992).	Interference of imaged sounds on detection of auditory signals Segal and Fusella (1970).	Interference effects of odor imagery on odor detection Djordjevic et al. (2004).
(III) Sensory specific hallucinations			
Hallucinations in schizophrenia.	Bracha et al. (1989).	George and Neufeld (1985).	Stedman and Clair (1998).
Hallucinations in patients with epilepsy.	Visual hallucinations Panayiotopoulos (1999).	Auditory hallucinations Korsnes et al. (2010).	Olfactory hallucinations West and Doty (1995).
Hallucinations associated with migraine.	Visual hallucinations Schott (2007).	Auditory hallucinations Rubin et al. (2002).	Olfactory hallucinations Fuller and Guiloff (1987).
Hallucinations associated with drug abuse.	Cocaine induced visual hallucinations Siegel (1978).	Cocaine induced auditory hallucinations Siegel (1978).	Cocaine induced olfactory hallucinations Siegel (1978).
	Visual hallucinations during alcohol withdrawal Bayard et al. (2004).	Auditory hallucinations during alcohol withdrawal Saravay and Pardes (1967).	Olfactory hallucinations during alcohol withdrawal Stevenson and Langdon (2012).
(IV) Dream reports containing a sensory component	Visual dreams MacCarely and Hoffman (1981).	Auditory dreams Zadra et al. (1998).	Olfactory dreams Stevenson and Case (2005a).
(V) Volitional mental imagery			
Reports of volitional imagery involving a sensory component.	Involving vividness ratings of imagined pictures Marks (1973).	Involving vividness ratings of imagined sounds Willander and Baraldi (2010).	Involving vividness ratings of imagined smells Gilbert et al. (1998).
Correlations between different modalities in vividness for volitional imagery.	Correlation between visual and auditory imagery Hubbard (2010).	Correlation between visual and auditory imagery Hubbard (2010).	Correlation between olfactory and visual imagery Stevenson and Case (2005a).
Female advantage in reported volitional imagery vividness.	More vivid visual images White et al. (1977).	More vivid auditory White et al. (1977).	More vivid olfactory images White et al. (1977).
(VI) Peripheral motor activity			
Correspondence between sensory specific peripheral motor activity and imagery.	Similarity between scanpaths made when viewing objects and when later imagining the same object Brandt and Stark (1997).	Subvocalization during auditory imagery for verbal materials and familiar melodies Hubbard (2010).	Similarity between olfacto-motor activity during imagery and perception of the same odor Bensafi et al. (2003).
Diminished mental imagery following interference of peripheral motor activity.	Decrease in visual imagery when interfering with the ocular motor activity Laeng and Teodorescu (2002).	Decrease in auditory imagery when subvocalization is blocked Aleman and Wout (2004).	Decrease in olfactory imagery when sniffing is blocked, e.g., Bensafi et al. (2003), Arshamian et al. (2008).

(Continued)

Table 1 | Continued

Observations	Visual imagery	Auditory imagery	Olfactory imagery
(VII) Activation of sensory specific brain areas during imagery	Activation of primary and secondary visual cortices, Ganis et al. (2004).	Activation of primary and secondary auditory cortices, Halpern et al. (2004).	Activation of primary and secondary olfactory cortices, e.g., Djordjevic et al. (2005), Bensafi et al. (2007).
(VIII) Reports of mental sensation following electrical stimulation of the brain	Visual imagery following stimulation of the nucleus subthalamicus Diederich and Goetz (2000).	Auditory imagery following stimulation of the lateral temporal cortex Moriarity et al. (2001).	Olfactory imagery following stimulation of olfactory bulb and tract Kumar et al. (2012).
(IX) The effect of expertise on mental imagery			
The effect of domain specific expertise knowledge on mental imagery.	Enhanced recall of rapidly and randomly presented chess positions in professional chess players Gobet and Simon (1996).	Increased pith and temporal acuity in auditory imagery as a function of musical training Janata and Paroo (2006).	Olfactory experts reportingmore vivid olfactory images than nonexperts, e.g., Gilbert et al. (1998).
(X) The effect of expertise on modality specific brain plasticity			
Functional reorganization during mental imagery.	Functional reorganization for expert mnemonists for visual objects Maguire et al. (2002).	Functional reorganization as a function of musical expertise Groussard et al. (2010).	Experience induced functional reorganization in perfumers Plailly et al. (2012).
Structural reorganization	Structural reorganization among expert GO players Lee et al. (2010).	Effects of musical expertise on structural plasticity Groussard et al. (2010).	Experience induced structural reorganization in perfumers Delon-Martin et al. (2013).

modality is documented as the sense with the fewest instances of volitional imagery and with the highest frequency of individuals reporting that mental imagery never has occurred (Stevenson and Case, 2005b). Also, if an odor image is successfully produced it is typically experienced as less vivid than images generated from other modalities (Betts, 1909; Sheehan, 1967; White et al., 1978; Ashton and White, 1980). Also, Olivetti Belardinelli et al. (2009) demonstrated that self-rated reports of olfactory imagery vividness, unlike for example vividness ratings in visual or tactile imagery, did not correlate with modality specific brain activation. In an evolutionary context it is highly likely that the selection pressure for an imagery capacity was stronger for the visual and auditory systems among the early hominoids than for most other mammals. However, this circumstance does not entail that the capacity to form olfactory images reached extinction. A weaker selection pressure more likely resulted in a larger individual variation in the capacity to evoke olfactory images. Hence, the less vibrant olfactory image may be a direct result from an environment favoring proficient imagery abilities in the visual and auditory modalities. In this vein, it is of interest to note that Lawless (1997) reported that the frequencies of olfactory imagery (ranging from never to often) and the image vividness (ranging from 0 to 100%) were more normally distributed than visual and auditory imagery. For example, whereas all study participants had experienced a visual image a significant proportion reported never experiencing olfactory images. Also, the experienced vividness for visual and auditory images were heavily shifted towards vividness ratings over 75%, while more than half of the reported olfactory images had a vividness rating of 25% or less. Hence, an olfactory imagery capacity was probably of little survival value for the anatomically modern human. However, in animals, such as rats, where the olfactory sense is a main percept for survival, the capacity to form olfactory images appears exceptional. For example, April et al. (2013) demonstrated that rodent working memory capacity, as measured by odor span task, was in the magnitude of 72 stimuli, and that its structure more resembled an episodic-like memory. It has been hypothesized that the evolution of working memory, and thus imagery capacity, was partially evolved in the context of planning, recalling, and reasoning appropriately about food caching (see Carruthers, 2013 for a review). Thus, in contrast to rats the ability to evoke olfactory images probable had little, if any use for the modern humans with an evolved visual and auditory imagery capacity. However, as noted below, olfactory imagery may still play an important role in the everyday life.

FACTORS MODERATING OLFACTORY IMAGERY CAPACITY

Most of the arguments raised for the inability to experience smells without external stimuli gain support from studies targeting differences found between olfaction and other sensory modalities. One example speaking to this view is that evidence is yet inconclusive regarding the nature of olfactory working memory in humans (Engen, 1991; Wilson and Stevenson, 2006; Zelano et al., 2009). Other concerns pertain to the well-documented difficulty to name odors, while the corresponding objects to these odors are easy to name when seen (Cain, 1979; Larsson et al., 1999; Olofsson et al., 2013). As a functional working memory capacity and semantic knowledge are considered as prerequisites for an imagery capacity in general, these two factors appear as fundamental for the integrity of olfactory imagery. Hence, activities that may promote the development of these factors, such as perceptual practice and odor-name learning, may contribute positively to the individual variation.

Stevenson et al. (2007) examined the relationship between odor identification and the ability to form odor images. The results showed that odors that were difficult to name also were difficult to imagine and that prior learning of the odor names exerted a positive effect on imagery capacity. Moreover, Tomiczek and Stevenson (2009) reported that odor imagery priming was prevalent only among good odor namers and appeared to be the result of a generic activation of olfactory neural networks when the participants tried to form an odor image. Importantly, Tomiczek and Stevenson (2009) suggested that this could occur in dependently of any consciously reported olfactory image. Thus, the act of trying to imagine an odor could result in a behavioral change that is not accompanied by a consciousness experience of that odor (Stevenson, 2009).

Other factors that have been linked to olfactory imagery are olfactory dreams and interest. For example, Stevenson and Case (2005a) explored factors such as odor interest, prevalence of odor dreams, and self-rated olfactory imagery in relation to olfactory performance. The results revealed that individuals who experienced olfactory dream content identified more odors correctly than non-olfactory dreamers. Concomitantly, prevalence of olfactory dreams was positively related to olfactory imagery capacity and a higher interest of odors in general. Moreover, Arshamian et al. (2011) selected individuals with either high or low olfactory awareness as indexed by rated imagery ability, prevalence of olfactory dreams, and odor interest. The results replicated and extended Stevenson and Case (2005a) by showing that high olfactory awareness not only was related to a more proficient spontaneous odor identification but also to a better retention of olfactory information as compared to the group with low awareness. Notably, the better episodic memory performance was not driven by a higher proficiency to verbalize information (Larsson, 1997; Larsson and Bäckman, 1997). Hence it is possible that persons experiencing olfactory dreams and have high olfactory interest may be less dependent on semantic processes when remembering odors. Moreover, the individual variation in interest may partially be attributed to differences in attraction and attention towards odors. For example, Bensafi and Rouby (2007) showed that individuals who scored high in olfactory imagery also had a higher ability to experience pleasure, and perceived pleasant odors as more pleasant and familiar than poor olfactory imagers.

PLASTICITY IN OLFACTORY IMAGERY CAPACITY AMONG NOVICES AND EXPERTS

Studies indicate that indirect and moderate opportunities to stimulate olfactory imagery through perceptual exposure are effective. Recently, Bensafi et al. (2013) compared olfactory and auditory imagery in individuals that cooked on a daily basis with a group that played music and was musically trained with a group of control participants who neither cooked nor played any instruments. The results showed that individuals that cooked had shorter response times than musical and controls in judgments associated with olfactory imagery, but not auditory imagery, whereas response times in auditory imagery were shorter for the musical group. Hence, this observation suggests that indirect and moderate perceptual practice may exert positive effects on modality specific behavior.

Research focusing on training the sense of smell has mainly focused on wine experts and perfumers (e.g., Lawless, 1984; Melcher and Schooler, 1996; Parr et al., 2002; Plailly et al., 2012). One observation is that olfactory experts, such as perfumers, exhibit a higher volitional olfactory imagery capacity than novices (Gilbert et al., 1998) and that the skills primarily result from a higher conceptual knowledge, rather than an inherent higher chemosensory sensitivity (De Beni et al., 2007). For example, Melcher and Schooler (1996) reported that wine experts compared to novices performed better in a "triangle test" where one target wine had to be picked out from a group of three. Experts and novices had to verbally describe the target wine before picking it out after a 4-min retention interval. Whereas verbalization did not affect wine experts in recognition, the novices showed impaired wine recognition. Similarly, it has been shown that wine experts are less susceptible to verbal overshadowing than novices (Parr et al., 2002). Several studies report that the superior performance of wine experts is largely determined by their ability to form appropriate verbal descriptors that focuses on the sensory quality (Lawless, 1984). In this vein, Engen and Ross (1973) reported that odor memory decreased if participants gave loosely related verbal labels to the odors compared to odors that were not labeled. In line with this idea, Fiore et al. (2012) tested if short-term memory for flavors could be influenced by olfactory imagery and the usage of appropriate verbal labels in amateurs. The results showed that imagination of a wine flavor with descriptive oenological adjectives, enhanced memory for the specific wine. In contrast, Parr et al. (2002) observed that wine experts performed better in odor recognition memory, although there were no group differences in odor identification and verbal memory. Hence, verbal codes were not necessary for a better recognition among experts suggesting the use of other strategies (cf. Arshamian et al., 2011).

However, not only conceptual odor knowledge shows positive benefits from training. Plailly et al. (2012) used functional magnetic resonance imaging (fMRI) to study changes in functional activity as a function of extensive olfactory training. Student and professional perfumers were presented with odor names and were asked to create an olfactory image for each odor name. In general, the anterior part of the piriform cortex appeared as a crucial area for olfactory imagery, although students showed more activation in the posterior part of the piriform cortex. This indicated that that the two groups used different strategies when generating odor images. Interestingly, the duration of work experience in perfumers also modified the neural activity. A longer work experience was related to less brain activity in areas associated with olfactory imagery and perception (i.e., piriform cortex, orbitofrontal cortex, and the hippocampus). This type of experience-induced decrease in functional brain activity has been reported for other modalities, such as vision (Maguire et al., 2002) and audition (Ohnishi et al., 2001). However, caution should be made when drawing conclusions from olfactory cortex activity alone as several other factors, such as sniffing (Sobel et al., 1998), semantic labels denoting odors (González et al., 2006), cross-modal reactivation (Gottfried et al., 2002, 2004), and attention towards odors (Zelano et al., 2005, 2011) may activate olfactory cortex. Hence, activity in olfactory cortex may be conceived as a necessary, but not a sufficient condition for the integrity of olfactory imagery (see Royet et al., 2013, for a review). Plailly et al. (2012) also reported that the inferior temporal gyrus, an area involved in semantic memory processing (Irish et al., 2012), decreased its activity with increasing expertise. This observation may reflect that generation of an olfactory image is subserved by semantic memory, but that with more extensive olfactory knowledge the retrieval gets less dependent on semantic feedback. A follow-up study also demonstrated that the structural brain images were modified with olfactory expertise"(Delon-Martin et al., 2013). Specifically, perfumers had larger gray-matter volumes in areas associated with olfactory processing, which included the bilateral gyrus rectus/medial orbital gyrus and the anterior cingulate. Further, the gray-matter volume increased with experience in the primary olfactory cortex and in the left rectus/medial orbital gyrus. No differences in areas involved in semantic processing were reported suggesting that structural changes following extensive perceptual experience, and to some extent olfactory imagery training, were restricted to modality-specific areas, such as primary and secondary olfactory cortices.

ODOR IMAGERY IN PERSONS WITH SMELL LOSS

Flohr et al. (Submitted) investigated the relationship between olfactory loss and the capacity to form olfactory images. Patients with olfactory loss and a control group with a normal sense of smell performed odor imagery tasks in the fMRI whilst also factors that could potentially activate olfactory cortex (e.g., sniffing) were controlled for. The study took advantage of results from studies indicating that odor imagery mimics that of olfactory perception. Specifically, both unpleasant odors and their mental images induce stronger activity in the piriform cortex and insula as compared to activity related to pleasant odors and their respective images (Bensafi et al., 2007). The results from Flohr et al. (submitted) showed that although patients with olfactory loss showed activity in areas associated with olfactory imagery, it was, unlike the control group, not related to the hedonic quality to-be-imagined. Also, the longer the duration of the smell loss the more activity in regions associated with olfactory imagery was observed. Thus, olfactory loss shows a reverse activation pattern than that observed among perfumers, which showed less activity with increasing experience (Plailly et al., 2012). The conclusion was that patients with olfactory loss were unable to evoke olfactory images similar to controls and that a regular exposure to olfactory information is crucial for successful imagery and that there may be a gradual memory loss of olfactory representations over time.

CONCLUDING REMARKS

The capacity to form olfactory images in the normal population should be regarded as a continuous factor. At the opposite ends, individuals with anosmia and olfactory experts are located. Severe olfactory impairment and anosmia are associated with reductions in accessing conscious odor information whereas olfactory expertise is linked to a fluent and conscious retrieval of olfactory information (Flohr et al., submitted; Plailly et al., 2012). The majority of the population is, however, located at an intermediate position, where difficulties in experiencing and recreating an odor into a conscious image are typical. However, a continuous perceptual stimulation and exposure to olfactory information may eventually increase the likelihood to be able to recreate conscious olfactory percepts in the mind.

In conclusion, this overview suggests that the olfactory image shares many features with visual and auditory imagery although some major differences are evident. The most prominent discrepancy concerns the large individual differences reported for our capacity to reproduce a smell with our inner nose. Here, factors such as the identity of the odor, odor interest, and perceptual experience were discussed as potential moderators of the individual variation.

AUTHOR CONTRIBUTIONS

Artin Arshamian and Maria Larsson jointly wrote the manuscript.

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Smelling phenomenal

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Qualitative-consciousness arises at the sensory level of olfactory processing and pervades our experience of smells to the extent that qualitative character is maintained whenever we are aware of undergoing an olfactory experience. Building upon the distinction between Access and Phenomenal Consciousness the paper offers a nuanced distinction between Awareness and Qualitative-consciousness that is applicable to olfaction in a manner that is conceptual precise and empirically viable. Mounting empirical research is offered substantiating the applicability of the distinction to olfaction and showing that olfactory qualitative-consciousness can occur without awareness, but any olfactory state that we are aware of being in is always qualitative. Evidence that olfactory sensory states have a qualitatively character in the absence of awareness derives from research on mate selection, the selection of social preference for social interaction and acquaintances, as well as the role of olfactory deficits in causing affective disorders. Furthermore, the conservation of secondary processing measures of olfactory valence during olfactory imagery experiments provides verification that olfactory awareness is always qualitatively conscious—all olfactory consciousness smells phenomenal.

Keywords: consciousness, olfaction, awareness, qualitative-consciousness, access-consciousness, phenomenal-consciousness, olfactory imagery, anosmia

INTRODUCTION

Smells have a profound impact upon our daily behavior and overall quality of life even in the absence of our subjectively attending to them. There is mounting evidence that qualitative olfactory consciousness occurs in the absence of conscious awareness, however, what is even more fascinating is whenever we are aware of a smell it is qualitatively-conscious as well. Thus, it will be argued that all olfactory consciousness smells phenomenal.

The paper offers a nuanced distinction between Awareness and Qualitative-consciousness that is applicable to olfaction in a manner that is conceptual precise and empirically viable. Applying this distinct to empirical literature on olfaction shows that these kinds of consciousness do not fully dissociate for the entire modality of olfaction. Olfactory qualitative-consciousness can occur in the absence of awareness, but any olfactory state that we are aware of being in is always qualitatively conscious.

Debates regarding the nature of consciousness and its taxonomic kinds, often become conceptually murky, so it is best to initially clarify the terminological usages before entering into a discussion of the empirical evidence in support of each kind of consciousness. Pre-theoretically being aware, signifies that we can subjectively report undergoing the experience, being in the relevant state, and the content of the state. For my purposes I shall use awareness, to pick out that state in which the subject can report being in a state S with content p (or if you prefer, they are conscious of undergoing experience E that is of, or about, object x). Awareness, I shall stipulate, can be understood separately from qualitative-consciousness, such that an organism is in a qualitatively conscious state when there is something that it is like for it to undergo experience E which is distinguishable from undergoing experience E^*, and moreover the subject need neither be aware of being in state S (i.e., undergoing E) nor of state S's content p.

REFINING PHENOMENALITY

Of the many treatments of consciousness, few have been as influential in consciousness studies as access and phenomenal consciousness. Block (1995) is responsible for the claim that the concept of consciousness is not a cluster concept containing different kinds of relevantly similar concepts but a mongrel containing different kinds. The two kinds that Block is keen to distinguish are Access-consciousness and Phenomenal-consciousness (1993, 1995, 2001, 2007, 2008, 2009). However, the difference between these kinds of consciousness is defintionally opaque. Semantic and definitional clarity aside, a major difficulty with the distinction between *A-consciousness* and *P-consciousness* is that sometimes these states are differentiated and identified according to their representational content as an information processing issue (Block, 1996, 2007, 2008), while at other times *P-conscious* states are ostensitvely defines in light of their qualitative properties (Block, 1993, 1995).

Furthermore, the difference between these kinds of consciousness has been challenged as conceptually ambiguous (Rosenthal, 2002, 2007, 2009, 2010) and incapable of scientific investigation (Kouider et al., 2012). Moreover, a review of the literature on olfaction suggests the distinction between these kinds of conscious states might not be applicable to olfaction, because the experiential nature of *A-consciousness* and *P-consciousness* differs from the other modalities based on olfaction's unique neural architecture (Stevenson, 2009).

While the distinction on offer could be encompassed within Block's framework of *A-consciousness and P-consciousness*, further modulations and refinements of his usage of phenomenal-consciousness would be required, and as currently stated qualitative-consciousness and awareness provide greater precision and clarity in demarcation the relationship between these kinds of consciousness that is substantiated by experimental evidence from olfaction contrary to Stevenson's (2009) claim. Though it might be worried that further distinctions needlessly generate greater terminological ambiguity in an already murky subject, distinguishing between awareness and qualitative-consciousness provides clarity and nuanced evidence for the dissociation and relation between the two kinds of consciousness that Block's distinction is meant to track. As such what is offered is not meant to supplant Block's theory, but supplement it in a manner that can encompass the nature of olfactory consciousness.

Block's definition of phenomenal consciousness might be interpreted in one of two ways: as referring to states that have a qualitative character for the subject and which are conscious though not reportable or not fully accessible; or to states that have a qualitative character though the subject is in no way aware of being in the state (Rosenthal, 2002, 2007, 2009). The first interpretation corresponds to Nagel's (1974) what-it-is-likeness (WiiL) when the subject is aware of being in state *S* and *S* has a qualitative character though its content is not reportable or fully accessible. Nagel's precise usage of the phrase requires that there is a WiiL for the creature undergoing the experience. The notion of a phenomenal character of experience from a subjective point of view is inherent to the concept of WiiL. The latter interpretation of *P-consciousness* corresponds to qualitative-consciousness, since the subject is unaware of being in state *S*, yet *S* has a qualitative character of experience. This later kind arguably corresponds to that supported by Block's evidence for phenomenal consciousness from subliminal vision and extinction studies (Block, 2001, 2007, 2008, 2011).

Disambiguating these two kinds of phenomenality clarifies how the distinction of qualitative-consciousness and awareness offers greater theoretical nuance in demonstrating that qualitative olfactory states can occur in the absence of subjective awareness. The fuller conception of phenomenality as a WiiL cannot be employed in providing empirical evidence for the dissociation of these kinds of consciousness as it smuggles in awareness. Assuming WiiL would muddy the first half of my thesis that olfactory qualitative-consciousness occurs in the absence of awareness, since some manner of subjective awareness is inherent to these states, and begs the question in the second half of the thesis that olfactory awareness is always qualitative. Olfactory consciousness using the distinction between awareness and qualitative-consciousness demonstrates what the original distinction was intended to capture. Qualitative-consciousness does not smuggle in any aspect of awareness and secondary processing measures can establish the phenomenality of these states in the absence of any manner of awareness.

Methodologically employing a robust notion of awareness and contrastively the thinnest conception of phenomenal (qualitative) consciousness allows for greater conceptual clarity. Qualitative-consciousness provides the starkest way of showing that phenomenality can occur without subjective awareness. Furthermore, by stripping the subjective aspect from qualitatively consciousness states there should be no worry that some residue of subjective consciousness is smuggled in when it is shown that olfactory states that we are aware of being in are always qualitatively conscious.

QUALITATIVE CHARACTER AND SECONDARY PROCESSING MEASURES

It is no longer controversial that unconscious states and their content can mediate behavior and be employed in sequences of information processing, thus establishing that we can undergo cognitive states in the absence of awareness is difficult but not an insurmountable feat. The real challenge is establishing that states we are subjectively unaware of being in can have a qualitative character i.e., that there is something that it is like for the subject to undergo the experience in accordance with the aforementioned discussion of qualitative-consciousness [for further discussions of qualitative character including alternative conception see Young et al. (2014) in this research topic]. Attempts at demonstrating the qualitative character of unconscious states by inference from their similarity to conscious states often encounter the worry that the qualitative aspect present in the conscious experience is simply missing in the absence of awareness. If we cannot report the qualitative character of these states what evidence do we have of their qualitative character? One strategy for ascertaining the qualitative nature of subjectively unreportable states is Quality-Space Theory, which identifies the mental qualities in terms of their perceptual roles, such that we can ascertain the qualitative nature of these states independent of conscious awareness (Rosenthal, 1991, 1999, 2005, 2010; Clark, 1993). While this approach is applicable to olfaction (Young et al., 2014), the perceptual quality of olfactory valence permits a stronger line of evidence using secondary processing measures, which establish that the qualitative property is maintained even in the absence of awareness. Odor valence together with secondary processing measures provide an objective method of ascertaining the existence of qualitative character in the absence of awareness, thereby providing the means for demonstrating that qualitative-consciousness can occur in the absence of awareness.

The difficulty is assessing whether experiential qualities are preserved from veridical odor perception through olfactory states that we are unaware of undergoing. Since the veracity of subjective self-reports is difficult to measure and question begging in this situation, secondary-processing measures might be employed to verify that the qualitative character is conserved. Secondary processes are correlated properties or incidental effects (Cummins et al., 2001), such as speed, error rate, types of errors, or fatigue etc., of the system when it performs a task. In addition to a state's performance of a role, other secondary properties can be used to evaluate whether the role was performed utilizing the same physical realization.

Secondary processing measures are traditionally employed in debates regarding computational implementations of cognitive abilities, however, analogous measures are available in measuring perceptual states. In olfactory research the property of valence (the perceive pleasant or unpleasant property of an odor) provides just such needed measures for assessing a states qualitative properties independent of awareness. Behavioral measures such as sniff rate and volume, response time, and heart rate can all be used as independent measures of perceived valence that indicate the olfactory system is treating these stimuli in the same fashion regardless of whether we can subjectively report our perception of the qualitative character. Sniff rates relative to odor concentration and valence substantiate the inference that subjectively unaware olfactory states have a qualitative character.

There is a long history of considering the primary qualities of odors to be their pleasantness or unpleasantness. Plato is the most well-known instance of the claim that smells are primarily individuated in terms of their olfactory valence (*Timaeus* 66d–67b; Plato, 1997), which is echoed within Indian Philosophy (McHugh, 2012, Ch. 2). More recently it has been argued that valence is the primitive property that determinates odor identity (Yeshurun and Sobel, 2010). Unlike the identification and categorization of odor quality that is similar but varies across cultures there is greater agreement on the categorization and identification of odors using the properties of pleasant or unpleasantness (Haddad et al., 2010). However, recent evidence suggests that though valence might be a primitive property of odor's, the object of olfactory experience is more likely identified by humans in terms of its olfactory quality and not valence (Olofsson et al., 2012). Whether olfactory quality or valence is the property that determines odor identity, valence is considered to be one of the most basic perceptible qualities possessed by odors.

Sniff rates relative to odor concentration and valence provide confirmation of an olfactory state's qualitative character. Humans modulate their sniff rate and volume 150 ms after the onset of a stimulus relative to its concentration and valence (Johnson et al., 2003). The stimulus dependent response of human sniffing is such that intense and unpleasant odorants are sniffed less vigorously and with a decreased volume. Measurement of olfactory motor responses to odorants is reliable enough to be used as a non-verbal measure of human's detection and categorization of the odor (Frank et al., 2003). Additionally, anosmics show no such response indicating that the sniff response only occurs in accordance with the subject's experiencing the valence of the presented stimulus (Harland and Frank, 1997). Sniff rate and volume are not the only secondary measures for assessing odor valence. Response time is faster in detection and discrimination tasks for unpleasant odors (Bensafi et al., 2003a) and heart rate measurements show that we involuntarily categorize unpleasant odors (Bensafi et al., 2002).

In what follows it will be noted whenever secondary processing measures of odor valence can be used to establish that the state has a qualitative character. Furthermore, it will be argued that this aspect of olfactory processing together with the distinction of qualitative-consciousness and awareness allows a nuanced treatment of consciousness that can empirically support the claim that we can undergo qualitative experiences in the absence of awareness.

OLFACTORY SENSORY STATES ARE PHENOMENALLY CONSCIOUS

Olfactory sensory states have a qualitative character even in the absence of awareness. Evidence that olfactory sensory states have a qualitatively character in the absence of awareness, derives from research on mate selection, the selection of social preference for social interaction and acquaintances, as well as the role of olfactory deficits in causing affective disorders[1]. While none of these phenomena are decisive on their own and further research is certainly required, when taken together they provide a host of initial evidence indicating that qualitative-consciousness can arise independently of awareness.

MATE SELECTION

Evidence for the qualitative character of olfactory sensory states can be gleaned from research on mate selection. Further research on human olfactory mate selection is required, but the initial data indicates that mate selection in humans is influenced by smell (reviewed in Havlicek and Roberts, 2009)[2]. We might not be aware of it, but our reason for choosing sexual partners might be that their immune system smells pleasant to us.

Using olfactory cues we select mates based on the synergy of our combined immune systems for producing stronger offspring. If we mate with a partner whose major histocompatibility complex (MHC, alternatively termed human leukocyte antigen, HLA, in humans) is the converse of our own, this generates offspring with a more robust hybrid immune system. Thus, it is adaptive to be able to detect the structure of a possible mate's MHC.

However, the difficulty of studying human mate selection is readily apparent given our inability to control for intervening variables. Most studies examining HLA mate choice have proven inconclusive, which could be attributed to these studies

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[1] Blind smell is an olfactory phenomenon reminiscent of aspects of Blind Sight that is not nearly as well studied, but preliminary studies (Schwartz et al., 1994; Schwartz, 2000; Sobel et al., 1999) suggest that some healthy human subjects can detect the presence of an odor in the absence of subjective awareness. A subgroup of subjects in Schwartz et al.'s experiment provides suggestive evidence that olfactory qualitative states can occur in the absence of awareness. However, further research needs to be conducted to see the prevalence of sensitive subjects in the overall population using more robust measures for determining odor detection threshold than those employed by Schwartz et al. to ascertain that the subject was unaware of the odor stimulus. Additionally, Sobel et al.'s results are suggestive of there being dose dependent unconscious olfactory processing, but the qualitative status of these states is dubious, since their detection task employed a subliminal odor without any further measure of subjective feedback. Without further measures of the subject's experience of these stimuli the claim that these unconscious experience contained properties that are qualitative is unwarranted. This is not to discount the findings of both sets of experiments, but only to point out that further research is require before the phenomenon can provide support for the claim that olfactory qualitative-consciousness can occur in the absence of awareness.

[2] The nature and debate regarding human pheromones is irrelevant to all claims regarding the olfactory mediation of human mate selection within this paper, since all the evidence derives from olfactory perception utilizing the olfactory epithelium through higher levels of olfactory processing. The phenomena under discussion in this section does not conform to the definitional nature of pheromones and is not mediate by the veromenasal system as is the case in other mammals (for a more in depth treatment of pheromones consult Doty, 2010).

being conducted in heterogeneous populations in which the confounding effects of ethnic or racial self-preference could not be controlled. Nonetheless the importance of smell in mate selection cannot be discounted. Based on questionares rating the factors of mate selection, female subjects rated body odor as one of the most important factors in selecting sexual partners (Herz and Cahill, 1997; Herz and Inzlicht, 2002).

The qualitative character of a prospective mate's body odor plays a role in determining our choice of sexual partners, but to establish that this is related to odors derived by our HLA compounds, as detected by the olfactory system, and these mediate actual mate selection requires three steps. First, it will be shown that humans can detect and discriminate the same MHC compounds that determine olfactory mate selection in rodents. Second, it will be shown that we have the ability to detect the olfactory signature of HLA compounds and that these are treated as having a qualitative property. Lastly, the literature of actual human mate selection in relation to HLA compatibility will be selectively reviewed.

The causal mechanism for HLA detection is arguably the same as the mechanism responsible for MHC detection and recognition in animal models. Odors derived from MHC compounds play a role in determining mate selection in rodents. In mice and rats it has been demonstrated that MHC recognition is accomplished by the olfactory system (Yamazaki et al., 1979, 1980; Ehman and Scott, 2001). Further research has also shown that mice, rats, and humans can smell the difference between the urinary scents of rodents derived from different MHC strains of mice (Beauchamp et al., 1985). Taken together, these studies show that mammals certainly employ MHC-based mate selection and that the human olfactory system is sensitive to these same chemicals. When these findings regarding our olfactory sensitivity are combined with the research on human mate selection, strong evidence emerges that we engage in HLA-based mate selection as mediated by olfactory cues, in the same manner as other mammals.

Odors derived from our HLA not only mediate mate selection, but it can be shown that these odors have a qualitative character. Using two-day-old sweaty t-shirts of men, experimenters determined that females judge a t-shirt's odor most pleasant when it was derived from a man whose HLA system differed from their own (Wedekind et al., 1995; Jacob et al., 2002). In both these studies no single male body odor was universally agreed to be pleasant smelling; hedonic judgments differed across females relative to the dissimilarity of the donor's HLA. The major difference between these studies is that in Wedekind et al.'s study the more dissimilar the HLA, the stronger the hedonic rating; while Jacob's results displayed a degree of HLA overlap in paternal lineage implicated in the hedonic rating of the sweaty odor. Nevertheless, both studies clearly implicate the olfactory system as a possible means for selecting mates based on the qualitative character of body odor as determined by HLA.

However, these positive results at best establish a correlation effect between the MHC of the donor and judged pleasantness. Recently the work of Aksenov et al. (2012) demonstrated that MHC yields volatile odor compounds (VOC) at the cellular level. Their study was the first to demonstrate that MHC compounds give off unique detectable odor signatures, such that a change in a single allele produces unique odor fingerprint at the cellular level. The implication of these results is that each person unique genetic makeup and in particular HLA complex will generate VOCs with a unique odor signature, thus allowing the connection between the judged hedonic profile of complimentary HLA mates and the possibility that this is directly determined by the VOC generate by a person's MHC compounds.

Further evidence that humans can detect the odor profile generated by the HLA complex can be found in studies of perfume selection. Pre-theoretic intuitions suggest that humans perfume themselves to mask their body odor, since body odor on its own is commonly perceived as unpleasant. However, Milinski and Wedekind (2001) disproved the masking hypothesis by showing that we select perfumes that enhance our natural body odor. Not only is this effect only found for the self-selection of fragrances, which is explained by the fact that people usually purchase fragrances for themselves (Jellinek, 1951; Le Norcy, 1991), but also that the judged pleasantness of an odor as correlated with body odor was consistent over a 2 year period and not a matter of changing fashion.

In addition to a perfumes enhancement of the pleasantness of perceived body odor, Lenochova et al. (2012) discovered that a self-selected perfume boosted the judged pleasantness of body odor relative to each person, as shown by their control that presented a mixture of body odor and equally pleasant perfume that had not been selected by the subject did not generate the same judged odor enhancement. However, it should be noted that their study was only conducted with male subjects. Since, female body odor is generally less intense making it more likely prone to a masking effect, further research was required.

Recently Milinski et al. (2013) used female subjects to address this concern and replicated their previous findings that we can select perfumes based on the MHC profile of oneself but not others. Fragrances similar to the VOC given off by ones own MHC have a boosting effect on body odor. Moreover, using fMRI imaging Milinsky et al.'s study revealed specific activation to peptides consistent with humans' ability to detect MHC associated olfactory cues. Thus, HLA compounds generate VOC with a qualitative character that we can detect and behaviorally respond to.

The strongest evidence that human mate selection preferences are driven by avoidance of those with HLA haplotypes identical to ours is derived from Ober et al.'s (1997) study of Hutterite mate choice. Previous studies did not show an effect of HLA on mate selection, but were conducted in heterogeneous populations where olfactory factors of mate selection might have been overridden by socio-economic and ethnic factors. The Hutterite population served as a control, because it is a small homogenous population with easily traceable genetic lineages. By looking at the HLA haplotype matches between spouses, they concluded that less of an overlap existed than would otherwise be expected if the selection processes were random. Ober et al. concluded that MHC based mate choice is operant even in humans. Furthermore, they suggest that the mechanism for HLA detection and structural comparison might be mediated by the olfactory system. The olfactory system is quite capable of such chemical structural analysis and comparison, as demonstrated by the aforementioned results that humans can detect and discriminate the relevant MHC odorants in rodents, are sensitive to MHC compounds of their own body odor, and judge body odors of complimentary HLAs as more pleasant.

The Ober et al study is by far the most significant source of data on the role of MHC in actual mate choice in humans, because of its methodological soundness using a large sample within a closed homogenous population thereby controlling for social and ethnic confounds. Of the studies on the role of MHC in mate choice only four have shown that MHC is significant in determining actual mate choice (Giphart and D'Amaro, 1983; Rosenberg et al., 1983; Ober et al., 1997; Chaix et al., 2008), while seven have shown no significance (Pollack et al., 1982; Nordlander et al., 1983; Sans et al., 1994; Jin et al., 1995; Ihara et al., 2000; Garver-Apgar et al., 2006). However, it should be noted that aside from the most recent study (Chaix et al., 2008) which showed a limited effect in only their European American grouping, the previous studies with positive results all used large sample sizes, thus controlling for the variegated properties of genetic variation as well as additional societal and normative practices in selecting mates. The null results of previous studies might simply be attributed to lack of power due to small sample sizes in attempting to determine a complex human behavior with multiple intervening variables.

Most recently Chaix et al. (2008) showed that MHC mate selection is apparent in European and American populations, but not in African Yoruba populations. However, the statistical methods of testing their hypothesis was criticized, because the significance could be attribute to extreme mate pairs within the groups, as well as for not correctly adjusting their statistical thresholds for multiple hypothesis testing (Derti et al., 2010). After adjusting their previous results for multiple hypotheses (Laurent and Chaix, 2012), the critics agreed (Derti and Roth, 2013) that MHC based mate selection was an apparent, but not a robust result, which might simply be attributed to the small sample size. Further research is certainly called for on the role of VOC given off by MHC compounds in humans in the selection of mates across cultures. Currently the evidence indicates that odorant detection of MHC compounds influences sexual mates selection, but the extent and mechanism require further study using more stringent and universal methodologies with large samples (Havlicek and Roberts, 2009).

The argument put forward in this section is that VOCs derived from HLA have properties with qualitative character that are perceived using the olfactory system and modulate our mate selection behavior. Yet, we are not commonly aware of smells in general (Sela and Sobel, 2010) nor their specifically modulation our selection of mates. Further research is required using the secondary measures of odor valence (i.e., sniff rate and volume, response time, and heart rate) relative to the subliminal presentation of olfactory stimuli derived from the VOC of similar and dissimilar sets of HLA subjects to fully establish that HLA mate selection occurs in the absence of awareness based on genuinely qualitative states. However, at this initial stage the evidence strongly suggests that we select mates based upon the qualitative character of our olfactory states even in the absence of awareness.

SOCIAL ACQUAINTANCE SELECTION

Further evidence that olfactory sensory states have a qualitative character in the absence of awareness, can be derived from research on olfaction's effect in guiding social preferences. While it is uncontroversial that our awareness of perceived smells modulate our mood and affective responses toward people (Herz and Schooler, 2002; Jacob et al., 2002), subliminally pleasant and noxious odors can modulate our ratings of the likeability of social acquaintances (Li et al., 2007). Li et al.'s study showed that the valence of an odorant subliminally modulates social preference. Using a simple odor detection task (pleasant, unpleasant, neutral, and control) combined with a subjective rating of the likeability of pictures of faces, they demonstrated that pleasant and unpleasant odors presented subliminally, both had a physiological effect and modulated the subject's affective response toward pictures of human faces.

Independent of subjective awareness there was a significant change in the heart rate of each subject relative to the valence of the subliminal odors, thereby confirming the qualitative character of these states employing secondary processing measures. Furthermore, unpleasant odorants caused the subject to rate the face as being less likable, while pleasant odorants had the opposite effect. The modulation of likability relative to odorant valence only occurred with subliminal odorants and quickly disappeared if the subject was aware of the smell. Even in the absence of subjective awareness the odorant has a qualitative property of valence, which has a causal effect upon our predication of qualitative properties to others. Arguably this shows that qualitative-consciousness is independent of our subjective awareness of the pleasant or unpleasant character of the odor. Even if one is unaware of undergoing an olfactory experience, the valence of subliminal odorants are implicated in social acquaintance selection. I might like you, because you smell nice.

ANOSMIA—ARGUMENT FROM ABSENCE

A severely unethical, but clearly conclusive, experiment could be performed to test whether qualitative-consciousness arises at the sensory level of olfactory processing in the absence of awareness. The experiment would be to sever the olfactory tract in healthy humans to see if they could undergo qualitatively-conscious olfactory states. Though this experiment is ethically unfeasible some olfactory pathologies provide subjects with similar deficits that suggest it is not possible to have olfactory qualitative-consciousness without olfactory sensory states.

Anosmia is the most common disorder of olfactory pathology in which individuals lose their sense of smell. In some cases anosmia is due to the presence of a psychological disorder, but the vast majority of cases result from damage to the olfactory bulb either due to infection or head trauma. Individuals with fully functional olfactory systems modulate their sniffing in accordance with the pleasant or unpleasant character of an odor, yet anosmics show no such response (Harland and Frank, 1997) demonstrating that the sniff response only occurs when the subject perceives the valence of the presented stimulus. Thus, using secondary processing measures it is arguably the case that anosmic individuals lack the ability to perceptually experience the qualitative character of olfactory valence.

In addition to their inability to perceive olfactory stimuli, anosmic individuals also experience a decrease in their hedonic quality of life (Miwa et al., 2001) and motivational anhedonia (Keller and Malaspina, 2013) that is often causally implicated in the further development of depression (Deems et al., 1991)[3]. We are not aware of our olfactory experiences most of the time, but they imbue our lives with a qualitative character of experience, which is most striking in their absence.

To summarize, the Argument from Absence is that the absence of olfactory sensory states and anosmics inability to experience the qualitative valence of odors are causally implicated in lower quality of life scores and depression. Hence, these states are responsible for generating qualitative-consciousness even in the absence of awareness. The argument might not prove that all olfactory sensory states have a qualitative character, but the evidence certainly is significant and nicely fits with the mounting evidence thus far.

NO OLFACTORY AWARENESS WITHOUT QUALITATIVE-CONSCIOUSNESS

Evidence for the claim that olfactory awareness is always qualitatively-conscious might be derived from first-person reports and the reader's own awareness of olfactory experiences. Introspecting, remembering, or imagining an odor, tokens some manner of qualitative olfactory experience. Just thinking about the smell of the fresh cut grass elicits an olfactory experience for me. However, using first-person reports of phenomenology might be methodologically questionable. Aside from biasing us to only consider experiences that we are aware of as having a qualitative character, the veracity of olfactory first-person reports might be doubted given our limited attention to olfactory experience and subsequent lack of awareness of our experience of odors (Sela and Sobel, 2010).

Veridical odor perception could establish that anytime we are aware of an olfactory experience it has a qualitative character, but it is not a good test case. Situations of perceiving olfactory stimuli will activate a sensory state, which the previous section argued are qualitatively conscious, thereby making one aware of an olfactory quality. Consequently, anytime we are aware of perceiving an odor, the conscious state has a qualitative character, because qualitative sensory states are elicited as part of creating the perceptual state. Because first-person phenomenological reports are methodologically questionable and perceptual states might always have a qualitative character, olfactory imagery will serve as the test case for the conditional claim that if we are aware of an olfactory state then it must be qualitatively-conscious as well.

Methodologically one could exhaustively search for a case in which we are perceptually aware of an odor and yet the experience does not have any qualitative character. However, a stronger and more fatal test of my claim would be to find a state, such as olfactory imagery that is not perceptual, that we commonly do not think would be qualitative, and that people find difficult eliciting in the first place (Herz, 2000) and check if these cases of olfactory awareness are qualitatively conscious. High-level cognitive states concerning olfactory experience are paradigmatic test cases of conscious awareness where we would not expect some level of qualitative character. What will be shown is that just thinking about odors, even those that we have not previously experienced, will elicit a qualitative character of experience.

While the phenomenon of olfactory imagery is primarily conceived as an issue regarding the representational format of cognitive states in an analogous manner to visual imagery (Kosslyn, 2003; Kosslyn et al., 2003; Pylyshyn, 2003), it demonstrates that we can elicit a qualitative experience of a smell in the absence of an olfactory stimulus (reviewed in Rinck et al., 2009). Olfactory imagery demonstrates that all states of olfactory awareness are also qualitatively-conscious. Experimentally it has been shown that subjects can elicit the qualitative experience of smelling something in the absence of olfactory stimuli. Merely introspecting, imagining, or thinking about a smell elicits a qualitative experience of smelling an odor.

Even more fascinating is that olfactory imagery states mimic those of ordinary olfactory experiences such as odor mixing (Algom and Cain, 1991). Odor mixing experiments yield the interesting results that, when two similar odorants are combined to yield a configural compound, the resulting complex's odor is different from those of its constituents parts, while odorants that are dissimilar yield elemental compounds in which the odors of the constituents are clearly discernable. However, by simply changing the concentrations of the constituents, one can shift an elemental compound to a configural compound. What is of interest in olfactory imagery is that if one is asked to imagine the mixture of two odors and report the olfactory quality of the compound, the reports will mimic those given when smelling the actual odor.

However, for olfactory imagery to fully demonstrate that states of olfactory awareness are qualitative-consciousness it must be shown that these state's content and experiential properties are the same as the perceptual state. The most obvious way to test for such an overlap of content and qualities would be based on self-reports as employed in Algom and Cain's (1991) study, yet these must be marginalized for the same reasons as introspective reports of past olfactory experiences—we simply cannot methodically test the veracity of subjective self-reports regarding olfactory imagery (Djordjevic et al., 2004).

Self-reports are doubtless invaluable tools, but they must be corroborated with other measures of the content and qualitative character. If olfactory imagery is to demonstrate that whenever we are aware of an olfactory experience there is a qualitative character of experience what needs to be shown is that these imaginary creations of an olfactory state have the same experiential properties as if the subject where perceiving the imagined stimulus. A review of the literature on olfactory imagery suggests that this can be demonstrated using the similarity of sniff patterns between veridical perception and olfactory imagination. The sniffing patterns are similar between both types of experiences suggesting that to elicit an olfactory qualitative experience

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[3] These studies of anosmia do not specify the nature of the anatomical damage, since their focus is upon the resultant olfactory deficit. Thus, to fully test the claim that qualitative-consciousness occurs at the sensory level in olfaction in the absence of awareness further research needs to be conducted on anosmia resulting from a severed olfactory tract.

one must manipulate the olfactory epithelium and bulb (the sensory states), which then recreates the experience by activating the olfactory cortex (Djordjevic et al., 2005; Bensafi et al., 2007; Rinck et al., 2009). To think about a smell, one must token the initial sensory and perceptual states, which are arguably qualitatively conscious.

However, a more recent set of experiments (Tomiczek and Stevenson, 2009) calls this into question and argues that the same perceptual state is not elicited, rather similar structures that are utilized for olfactory perception in general are activated. Tomiczek and Stevenson (2009) assert that we do not imagine a specific odor, rather there is a general overall increase in activation across areas in the olfactory system that are responsive to odorants similar to the imagined odor. While their results indicate that the imagine state does not have the same exact content it does focus us in the right direction. Though these states might not be fully identical, secondary processing measures can be utilized to establish that the best explanation of their content must involve qualitative character.

The methodology of verifying the qualitative character of an imaginary mental experience as being the same as veridical perception using measures of sniffing is currently employed in olfactory imagery studies. Using olfactory motor activity during imagery as a criterion to test the veracity of participants claimed imagined olfactory percept, Bensafi et al. (2003a,b) confirmed that the same sniff parameters including sniff volume occur in imagery as in conscious veridical perception. They not only showed that sniffing is sensory dependent, but also sniffing in a similar fashion to veridical perception produce qualitatively more robust olfactory imagery (Bensafi et al., 2005; Bensafi and Rouby, 2007). Employing the same secondary processes increased the capacity for generating olfactory images and the strength of the olfactory quality indicating that these subjects had olfactory experiences with qualitative character.

Kleemann et al. (2009) lend further support to the conservation of sniff rates as indicating the preservation of the same olfactory quality of experience and extended them to breathing patterns. The overall sniff volume and breathing amplitudes are the same between imaginary and perceptual olfactory states. Subjects not only reported an ability to imagine an odor in these experiments, they also breathe and sniff in the same fashion as if they actually perceived the odor. Moreover preventing subjects from sniffing while imagining smells decreases the vividness of the imagined smell (Arshamian et al., 2008). These results further solidify the claim that olfactory imagery states are contentful cognitive states with qualitative character.

Additional secondary measures of response time and heart rate lend further confirmation of the qualitative nature of these imagined states. Response time is faster in detection and discrimination tasks for unpleasant odors (Bensafi et al., 2003a) and heart rate measurements show that we involuntarily categorize unpleasant odors (Bensafi et al., 2002). Given the role of sniffing in modulating olfactory imagery it is unsurprising that olfactory imagery increases our detection rate of the target odor in a manner that is modality and content specific (Djordjevic et al., 2004, 2005). The subject's experience of odor valence during olfactory imagery can be verified using behavioral non-verbal measure such as sniff patterns and response time. These secondary measures establish the occurrence of the qualitative experience of valence in olfactory imagery.

The preservation of secondary measures of sniff-rates (as well as other behavioral measures) enables the further inference that the experiential quality is being conserved in olfactory imagery. However, even with the corroborations of secondary measures it might still be objected that the subjects are merely employing their tacit knowledge of olfactory perception in generating their reports and behavior during these experiments.

Similar criticisms have been used against visual imagery, however critiques of this variety gain no traction in the case of olfactory imagery. The sniff responses in these cases make it absurd to claim that these states might be merely modulate by our propositional knowledge of olfactory perception, but contain no actual qualitative character. It seems fanciful that we could modulate our breathing and sniffing patterns in such a precise and automatic manner when we barely pay attention to these facets of our olfactory experience in normal cases of perceptions. Furthermore, our olfactory experiences are arguably not formatted in the same fashion as our descriptive linguistic resources (Young et al., 2014). If olfactory perceptual experiences and memories that we are conscious of are not formatted in the objections prescribed descriptive format it would be rather surprising if the same format was not preserved in olfactory imagery. Moreover, it has been shown that an increase in overall Anhendonia decreases our ability for olfactory imagery (Bensafi and Rouby, 2007; Rouby et al., 2009) thereby implicating some level of qualitative character in mediating olfactory imagery.

We can cognitively generate an olfactory experience that has an olfactory quality mimicking veridical perception in terms of its subjective report, behavioral measures, physiological responses, and cortical activation (Bensafi et al., 2007; Rinck et al., 2009). The fact that these states conserve and preserve all of these properties from veridical perception indicates that olfactory imagery states have a robust olfactory qualitative character. Thereby supporting the claim that any time there is olfactory conscious awareness these states are also qualitatively conscious.

CONCLUSION

Even while we are unaware of it, a world of odors continually envelops us exerting a profound influence on our behavior and the qualitative character of our everyday experiences. These smells contribute to the quality of our life and have a qualitative character such that it is possible for one to be in a qualitative olfactory state, but not be aware that one is undergoing the experience. What is even more controversial is that it is not possible for one to be aware of an olfactory experience without it having a qualitative character.

Olfactory qualitative-consciousness occurs in the absence of awareness, as demonstrated by research on social acquaintance selection, mate selection, and the Argument from Absence derived from the anosmic's decreased quality of life measures. Thus, the occurrence of olfactory qualitative-consciousness in the absence of awareness is compatible with Block's treatment of phenomenal consciousness and shows his distinction to be applicable to olfaction. The second line of evidence that all states of olfactory awareness are qualitatively-conscious suggests that the dissociation between these kinds of consciousness differs from expectations derived from vision studies. Further research is certainly called for, but at this initial stage of inquiry it seems plausible that qualitative-consciousness plays a constitutive role in the formation of olfactory awareness as these states arise at the sensory level and are elicited whenever we either have an awareness of an occurent odor experience or attempt to recollect, imagine, or think about olfactory experiences.

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The intentionality of smell

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If any sense modality represents, vision does, but argument is needed to show that smell does. This paper rebuts two reasons for doubting that smell represents, and offers several arguments that it does. The paper then considers several recent proposals as to exactly what a smell represents, and defends a version of the author's original proposal—that a smell represents a miasma in the air—against its competitors.

Keywords: smell, intentionality, representation, olfaction, objects

If any sense modality represents the world, vision does. But argument is needed to show that smell does; it has never been obvious that smell represents. This paper rebuts two reasons for doubting that smell represents, and offers several arguments that it does. The paper then considers several recent proposals as to exactly what a smell represents, and defends a version of my older proposal—that a smell represents a miasma in the air—against its competitors, though offering a concession or two.

In the next section I shall expound the main reasons for which people have denied representational status to smell. But first, I must say more precisely which of several possible things I mean by "smell." The word could mean, (i) olfactory *experience* as some writers put the question, (ii) *smelling*, whether "experienced" (i.e., consciously) or not[1], or (iii) the olfactory *system* as investigated by cognitive and neuroscientists. I shall try to mean (ii). (iii) Would be an entirely empirical matter, though obviously scientific results regarding the olfactory system bear fairly directly on our own issue. Moreover, it is possible that the olfactory system subpersonally represents properties that are not smelled by the whole person whose olfactory system it is. (i) seems needlessly restrictive, since (according to me) the difference between a type of mental state occurring non-consciously and that same type of state occurring consciously is superficial, a matter of whether the state is itself represented by a higher-order state (Lycan, 1996, 1998, 2004); it would not normally affect the state's own representational content.

So my opening question more precisely is, are worldly properties or things represented in and/or by person-level smelling? And as noted, I begin with the negative view.

THE CASE AGAINST

(1) There are two main reasons for doubting that smell (in particular) represents. First, if we focus introspectively on the specifically sensory character of an olfactory experience, we detect only that modification of our consciousness, the qualitative condition or event in us. Even if we infer the presence of horses from their characteristic smell, the smell does not itself present horses as its own representatum. We infer horses only because we already know from experience that that smell is typically produced by horses. (The overall phenomenology perhaps suggests otherwise: we just smell horses and notice no inference. But again, the smell has to have been associated empirically with horses; if you experienced it having never made that association, it would say nothing to you[2].)

Second, were you to experience a smell that represents X when no X is present, you would be misrepresenting, smelling falsely or incorrectly. But this does not seem to happen. There used to be a distinctive way in which a new American car smelled from the inside. Then someone manufactured an aerosol that replicated the new-car smell. You could buy it in auto parts stores; I think it was actually called "new-car smell." Suppose a friend had used the fake and given you a ride. The car smelled new to you even though it was several years old. This is misrepresenting of some sort, but it is not incorrect smelling. The nose itself was *not fooled*, for the new-car odor was really there and causing the smell experience in the normal way; the car's inside did have the new-car smell even though it is not a new car.

We characterize smells by reference to their normal environmental causes: horses, new cars; the smells of roses, natural gas[3],

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[1] Some writers use "experience" liberally, to include all cases of perceiving whether conscious or not. I prefer to reserve the term for sensing consciously, i.e., for sensings of which their subjects are aware.

[2] "Think, when we talk of horses, that you see them, printing their proud hoofs i' the receiving earth." Despite the point about empirical association, a more immediate way to imagine them is through their smell.

An anonymous reviewer has pointed out that vision too requires empirical association. If I am acquainted with horses only through the sounds they make, but then for the first time I come upon a field containing horses, cows, and ostriches, vision will not tell me which of the animals are horses. It is controversial whether vision ever represents natural kinds. Siegel (2010) argues that it does; for discussion, see Lycan (2014). It is not very controversial that vision does represent, but there are a few opponents, e.g., Campbell (2002).

[3] Such characterizations can be tricky in particular cases. Natural gas itself consists largely of methane (CH_4), and is odorless. What we commonly call the smell "of gas" is actually that of a pungent odorant added by the gas company

boiled spinach, locker rooms. But it does not follow that those causes are represented by the smells, because they can be counterfeited by other substances. Again, the point is not that we can misrepresent them; that would hardly show that they are not representata. Rather, in a counterfeit case the nose is not fooled, and the smell itself is not misrepresenting, even though we may form a false belief; and nothing yet has shown that we smell correctly either. (Conversely, of course, if you experience the locker room smell when you are not in a locker room, you are not smelling correctly, but it does not follow that you are smelling incorrectly[4].)

Nor do phenomenal smells represent, as some Gibsonians would have it, broader ecologically significant properties of things, for the same reason and for others[5]. Thus, it is tempting to conclude that smells merely accompany external objects with a fair degree of type–type reliability, but do not represent them.

REBUTTAL

(2) That is the case against smell's representing. It is not a very strong case. Vs. the first argument: Though introspection does seem to reveal that vision represents, its failure to do that for smell hardly shows that smell does not represent. Introspection is a blunt instrument, and cannot in general be relied on to determine whether a mental state has representational content. Witness the fact that philosophers disagree on such questions, despite being roughly equal in introspective competence. Further, though some mental states traditionally have not been thought to represent, there has been increasing consensus that those states do have some representational structure even though that is not functionally the most important thing about them and, more to the point, even though their representational structure does not leap out in introspection: pain; some of the emotions[6].

The second argument fails because there is no reason to assume that if smells represent at all, they represent the environmental causes by which we casually characterize them. As we shall see, there are several other candidates for representata. (I say no reason to *assume*; this is not to deny that a theory of representation[7] for smell might invoke such causes, though the second argument would itself count against such a theory[8].) And now I shall argue positively that smell does represent.

THE THESIS

(3) Consider that a main function of any sense modality is feature detection, the registering of environmental properties. It does not follow that the relevant sensory states represent those properties—at least not without addition of the dubious premise "If a state has the function of detecting feature F, the state represents F"—but I and others have argued positively that smell does represent. I claim that a smell actually has semantical properties: reference, a truth- and/or satisfaction-condition. A smell can be treated formally, *ála* Hintikka, as a function from possible worlds to truth-values, and any such function corresponds to a proposition expressed[9]. A smell can be incorrect, a *mis*representation. If these perhaps surprising things are true, then surely smells are indeed representations.

And I believe they are true. It may *seem* that, phenomenally speaking, a smell is just a modification of our consciousness, a qualitative condition in us, lingering uselessly in the mind without representing anything. And as noted, disinclination to think of smells as representations increases when we ask what they might be representations of. If the "smell of roses" represented roses, then it would be true or satisfied or correctly tokened only in response to roses, false or incorrect otherwise; and it would determine a function that, given a world, spit out exactly the set of roses at that world. The rose smell does neither of those things. Yet, as I have observed, there are other candidates for external representatum.

For one, consider what an *odor* is, in one public sense of the term. It is a miasma in the air, a vaporous emanation, a diffusing collection of molecules typically given off from a definite physical source. It is itself a determinate physical thing, distinct from its source object, that makes physical contact with the smell receptors in one's olfactory epithelium and sets them to firing. We are publicly, commonsensically and often mutually aware of such odors; they are public physical entities available for sensing by anyone who happens by. Now, an odor is a candidate for representatum, and the idea of an odor as an intentional object of smell resists the objection I have made to the more colloquial candidates. For things other than roses can give off the odor "of roses," and roses can fail to give off that odor. (Again, I am talking only about the match in the physical world between types of object and types of odor.) Perhaps, then, smells represent odors[10].

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in order that an otherwise fatal gas leak will be readily apparent; the connection between the adulterant and the gas itself is entirely conventional. So the smell "of gas" is not that of gas, but of the chemically unrelated odorant.

[4] The point holds even of smells that purport to identify individual things, such as the competent dog's master-indicating smell. Although for a dog the smell of an individual human being may be unique in fact, it is still true that were another human being to duplicate the dog's master's particular smell, and the dog were to smell that smell and expect master, the dog would not be mistaken in smelling it, on something else that did smell the same way, even though the dog's ensuing expectation would be false.

Here too (cf. fn 2, and thanks to the same reviewer) there is a visual analog. The interior of an old car may have been freshly painted and detailed, causing you to believe that the car is new, but the eyes themselves are not fooled. It seems to me very unlikely that vision represents so sophisticated a category as "new car" (on this, see again Lycan, 2014). But here too, it is not widely doubted that vision does represent.

[5] See Ch. 3 of Perkins (1983).

[6] Pain: Armstrong (1968), Pitcher (1970), Tye (1995, 2005), Crane (2003), Hill (2005). Emotions: Prinz (2004). Lycan (1996) argues that even the vaguest moods, such as "free-floating" anxiety, depression, and general optimism, have definite though comparatively uninteresting representational content. Vivat Brentano.

[7] A "psychosemantics," to the philosophers.

[8] In sec. 10 below I shall allow that the normal environmental causes may be represented by smell experiences, albeit in an indirect way.

[9] This is a standard account of the propositional meanings of natural-language sentences. E.g., "There is a moose in Caldwell Hall" is false in our actual world, but is true in some other possible worlds; the function from worlds to truth-values represents the range of circumstances under which that sentence would be true.

[10] If smells represent odors (or any other external phenomenon), it is open to one who holds the Representational theory of sensory qualities—"qualia" in one of that mutilated term's many senses—to identify those qualities inhering in smell experiences with the relevant representata. (According to the

But why think that, even so? Perhaps, to the contrary, all there is to the relation is that smells are highly but imperfectly correlated with odors, and that is not enough to make for a case of representing.

THE CASE FOR

(4) Actually there are several positive arguments for awarding representational status to smell, now that the main objections have been circumvented. A first is that once smells are correlated with odors rather than with types of object, a kind of incorrectness does manifest itself, hence a correctness- or truth-condition. If I hallucinate a rose smell in the absence of any rose *or anything else* that is giving off the rose odor, I am misperceiving. The point is not just that my belief that a rose is present is erroneous. I may not even have that belief, knowing full well that my olfactory experience is hallucinatory. Something is perceptually wrong; my olfactory bulb is saying "Rose odor" when there is no rose *odor* physically present, and that report is a lie. Where there is falsehood there is representation.

[Of course this can be resisted. One can grant that a detector or indicator is registering a false positive without being forced to admit full-bore representation, if one wishes to place further conditions on what it takes for something to be a genuine representation (cf. Ramsey, 2007)]. My claim for this first argument is only that smell has a possibly unreal, non-actual representatum in at least the rudimentary sense that detectors and indicators have representata. However, I would add that smell's strong and multifarious functional connections to memory and other cognitive agencies suggest a stronger representational connection as well.]

(5) Richardson (2013) persuasively attacks the phenomenological view on which our first anti-representationalist argument was based (section 1 above), that "considered only phenomenologically, a smell seems a modification of our own consciousness rather than a property of a perceptual object that would exist unperceived" (p. 406, quoted from Lycan, 2000, p. 277). She argues to the contrary that smell, like vision, is "exteroceptive," i.e., that even phenomenologically, the sensible qualities inhering in a smell sensation "seem . . . to be qualities of objects distinct from our bodies" (p. 405), the "objects" for the case of smell being odors, and the seeming is not just a matter of cognitive association[11]. Exteroceptivity is also connected to *finding out*: "In exteroceptive experience we find out about the [relevant] qualities of objects . . . by their seeming to have the qualities in question" (p. 406). Richardson carefully makes the case that olfactory experience is exteroceptive *despite* its lack of vision-like spatial features. I am persuaded that she is right.

N.b., exteroceptivity does not entail representation; it is phenomenological only. (Nor does Richardson claim that smell represents.) But this gap can be bridged using a type of argument deployed by Byrne (2001) on behalf of the Representational theory of sensory qualities (see again note 9; cf. also Thau, 2002). He appeals precisely to the notion of seeming: "if the way the world seems to [a subject] hasn't changed, then it can't be that the phenomenal character of his experience *has* changed" (p. 207). Suppose a subject has two consecutive experiences that differ in phenomenal character, i.e., in how they subjectively feel to her. If she notices the change in phenomenal character, Byrne argues, the way things seem to her when she has the second experience must differ from the way they seemed to her while she was having the first. For suppose that consecutive experiences are the same in content. Then the world seems exactly the same to the subject during both. She "has no basis for" noticing a change in phenomenal character either, and by the previous premise it follows that there was no change in phenomenal character (p. 211). Byrne concludes that experiences cannot differ in phenomenal character without differing in representational content[12].

Thus, if a subject's phenomenology changes merely by the addition of an olfactory component, there must have been a change in representational content, and the obvious candidate is the addition of an olfactory representatum.

(6) A further argument can be adapted to the purpose from one of Moreland Perkins' (1983, p. 63ff). Perkins points out that when we sniff an object and for the first time perceive its odor, we find out something about the object. What we find out is, seemingly, its odor. Now according to the view I have expounded earlier, odor is just a physical diffusion of relevantly shaped particles in the air. But, Perkins argues, what I find out when I "find out the object's odor" is not (*per se*) anything about a physical diffusion of relevantly shaped particles in the air. Rather, to find out the odor in the relevant sense is to find out what the odor is like to smell.

"Like" in that last formula, as in the phrase "smells like," does not mean resemblance. In Perkins' Farrell-Nagelian sense, one can find out and know what a new odor smells like without there being anything in one's previous experience that it resembles. Perhaps we would do better to speak of finding out how the odor smells; "It smells like this" and "It smells this way" do not seem to differ in meaning. How the odor smells is something that one can know only if one has either actually smelled it or has smelled something sufficiently

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Representational theory more generally, any sensory quality such as a color, pitch, taste, or texture is, veridically or not, being represented as a feature of something in the environment. For example, if I have a yellow patch in my visual field occasioned by seeing a lemon, the mental yellowness is just that of the external lemon, represented by the visual system in the experience. If I hallucinate a similar lemon, the mental yellowness is still just that of the now non-actual external lemon, non-veridically represented in the experience.)

I myself do hold the Representational theory and do so identify subjective smell qualities with properties of external odors (Lycan, 1987, 1996), but I also insist that the overall phenomenal character of a smell experience outruns the experience's representational content, because the specifically sensory quality in question is only a proper component of the overall phenomenology (Lycan, 1998). The main dialectical connection between the present paper and the Representational theory, then, is this: If I am wrong here and smell experiences do not represent, then either the Representational theory is false or, surprisingly, smell experiences do not feature sensory qualities at all.

[11] "This castle hath a pleasant seat. The air nimbly and sweetly recommends itself unto our gentle senses."

[12] For the record, I reject that blanket conclusion; see footnote 10. But we can understand Byrne as using the term fairly narrowly, excluding, e.g., conative and affective features of the experience.

similar that one can be told by comparison how the first odor smells.

I shall break off at this point in Perkins' line of reasoning (which is actually a long defense of a version of a none too clear doctrine he calls "Indirect Realism"), for it is all I need as a foundation for my own argument. Much to the alarm of all, however, I shall start off in my own direction by noting that one could know all the objective scientific facts there are—about a physical odor, its effect on the olfactory epithelium, the ensuing excitations in the bulbs, and all further results in the thalamus, the neocortex, the limbic system and so on at any length—without knowing what the odor smelled like (how it smelled).—Please, stay calm. I am not about to invoke Leibniz' Law and infer that there is a fact left out which eludes all of science and which philosophical materialists feloniously ignore. Not even Leibniz' God would have the power to make that follow, for it simply does not follow[13]. However, we do have to make sense of the admittedly odd fact that I can know that P and fail to know that Q even when the fact that P just is the fact that Q on a suitably coarse-grained individuation policy for "facts."[14]

I can know that I have salted a tomato without knowing that I have put NaCl on it, even though the fact of my salting it is one and the same as the fact of my putting NaCl on it. That is because what is the very same substance, salt or NaCl, can be represented by me in each of two psychologically inequivalent ways. Knowing is hyperintensional; if you like, its object is not just a fact but a fact under a particular representation.

As is painfully well-known, this hyperintensionality is similarly manifested by mind-brain identities. Suppose for rude simplicity that pain is simply the firing of X-fibers. Even if that were so, I could know that I was in pain without knowing anything about X-fibers, and I could know physiologically all about X-fiber firings without knowing what it is like to feel pain, if I have never felt it myself (had my own X-fibers firing). This is possible, again, so long as the same fact is represented in two psychologically inequivalent ways. The fact, of the pain or (indifferently) the firings, can be represented in a public way, in physiological terms, as well as by the use of the English word "pain." But much more commonly it is represented introspectively by its owner—for short, it is felt. One can know all the publicly accessible facts about pain without knowing what pain feels like so long as one has not introspected any pain oneself. One comes to learn what it feels like when one first does introspect it, when one thus begins to represent it in a first-person way.

So with smell. I can know all the chemistry of a rose, the physical properties of the rose odor, the neurophysiology etc. of olfaction and all the other scientific facts about smell without knowing how the rose odor smells. But how the rose odor smells, or what it smells like, just is the complex of fact I have just mentioned, which by hypothesis I do know. The appearance of contradiction can be resolved just as in the case of pain, and (more to the point for my argument) I do not see any other way of resolving it: I can know the complex of osphresiological fact without knowing how the rose smells because knowing is knowing-under-a-representation, and the same fact can be known under one representation but not under another. Here, I know the facts under their textbook descriptions; what I fail to do until I have smelt a rose is to know them under their introspective descriptions, their first-person representations supplied by my introspector. I will come to know what the rose odor smells like only when I do represent it introspectively, that is, when I smell it. That is how the Farrell-Nagel puzzle is resolved. And that solution entails that olfactory experience involves representation.

However, a gap remains: I have so far ignored a complication needed to make the smell story truly parallel to the case of pain. There are really two tiers of representation. The rose odor causes an olfactory sensation, a smell, which represents it, and that sensation is in turn represented by my introspector—an attention mechanism—when I concentrate on the sensation's phenomenal character. (If I never do attend to the smell-sensation, if my introspector happens never to be directed upon it, then I will never be consciously aware of the sensation; cf. unfelt pain. This picture is defended at length in Lycan, 1996). Now, someone might ask, though the present Nagelian argument does require that the introspector's output be a representation, why should we believe that its representatum, the first-order smell sensation, itself represents the physical odor? Perhaps it is merely caused by the odor before being represented by the introspector. I reply, again following Perkins, that according to common sense and parlance, what we come to know when we attend to the smell of our first rose is what the rose odor smells like (and derivatively what the rose itself smells like), not just what it feels like to have the smell sensation that happens to have resulted from contact with the odor; as Perkins said, we find out something about the odor, viz. how it smells. I see no reason not to take common parlance at face value here, and accept that the smell sensation ascribes a sensory quality to the odor itself[15].

(7) The picture I have presented yields an explanation of a further phenomenon: the ineffability of smell, the fact that smells (and odors) can be described in words only by comparison to other smells (and odors) or by reference to their external causes. For my internal representation of an odor is a lexeme of a private language, the medium of representation in which my introspector makes its reports. That lexeme has any number of co-referring descriptions framed in public natural languages, but (for reasons emphasized in Lycan, 1996) no such description that shares its

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[13] That and why it does not follow has been explained at length by so many writers in philosophy of mind that it would be tedious even to begin naming them.

[14] One can of course hold out for a finer-grained individuation policy, as recommended by Chisholm (1976). But that policy proliferates "leftover facts" everywhere, not just in the philosophy of mind. On this issue in particular, see Lycan (2003).

[15] There is a perennial problem, much discussed in the "self-knowledge" literature, of how an introspective representation of a first-order mental state represents the latter state's own representatum in particular. But that problem is everyone's, or at least afflicts any view that posits higher-order representation of a state that is itself representational. It is not a special objection to the present argument.

To pursue the analogy with pain: When I first felt the pain I now have in my left shoulder socket, did I find out anything about my shoulder? I believe so. I found out that there is damage or some other physical disorder in it—which belief was then confirmed by X-rays.

meaning. Nothing equivalent can be said in English (though of course we could introduce a public word—"samantha"—and try contra Wittgenstein to stipulate that it is to be synonymous with my introspective term)[16].

Recently it has been suggested that the ineffability thesis has been exaggerated and that cross-cultural data refute or at least impugn it. Majid and Burenhult (2014)[17] investigated a claim they express variously: that "the experience of a smell is impossible to put into words" (abstract, p. 266); that "people find it difficult, if not impossible, to name odors" (p. 266); that "people universally struggle to describe odors" (p. 269). These things may be true of Anglo-Americans and others from "Western Educated Industrialized Rich Democratic communities" (p. 267), but they are not true of some less urban and industrialized peoples. In particular, Majid and Burenhult studied the Jahai, a nomadic hunter-gatherer tribe on the Malaysian peninsula, and found that they have a very rich lexicon of odor terms, comparable to their color vocabulary.

But those results do not bear on my own still pretty traditional ineffability thesis. The claim is not that we cannot name or identify or classify odors—though we Anglo-Americans cannot as well as the Jahai do. Majid and Burenhult's first formulation comes closest to it ("the experience of a smell is impossible to put into words"), the operative term being "experience": The claim is that once we do have a subjective smell all named and identified and classified, *then* if we are asked "But what is it like *in itself* to experience that smell [so named, identified and classified]," we go tongue-tied.

Doubtless the foregoing case for smell's representational status could be resisted by a sufficiently determined anti-representationalist, and we know they are out there. But I believe it is a strong case, and, importantly, it militates against *selective* anti-representationalism. That is, it makes it hard for a theorist to admit that vision and perhaps hearing represent but deny that smell does.

I return to the question of *what* smell represents. My position to date has been that it represents odors in the sense of particulate miasmas in the air, but in recent years differing proposals have been offered.

WHAT DOES IT REPRESENT?

(8) Vision *ostensibly* represents things or objects and ascribes properties to those things. Batty (2010) asks whether an olfactory experience does the same. Introspection cannot settle that question. Instead, Batty first appeals to the fact that there are no known olfactory illusions (as opposed to hallucinations), i.e., cases in which a real object is perceived as having a property that it does not have[18]. Second, she observes that there is no obvious Many-Property Problem (Jackson, 1977) for smell[19]. Third, she argues that smell *per se* is not spatial, and so cannot (alone) identify a worldly object spatially; nor is there any other means of doing so[20].

On their face, these points would suggest that smell does not represent in the first place. It may once again now seem that "olfactory experiences are mere smudges on our consciousness" (p. 518). But Batty does not accept the points as showing that, for as she rightly says, having representational content does not entail representing particulars and ascribing properties to them[21]. Rather, she suggests that smell represents properties "abstractly," as merely existentially quantified: *There is F-ness here* (where "here" means only something like, present to me[22].) What in fact makes such a quantificational content true is something in the air—something we know on other grounds to be an odor—but that is itself no part of the bare representational content.

I am not sure how much disagreement there is between Batty's "abstract" theory and my (1996) view. The latter certainly did not entail that smell represents odor particulars in the way that vision (allegedly) can. It does entail that smell represents odor universals. Disagreement depends on detail. As her leading example (p. 530), Batty offers "$\exists x$(x is smoky, lavendery & at L_0," where L_0 is the default ambient location for all smells and "smoky" and "lavendery" are counterparts of the color and shape predicates that would figure in a parallel "abstract" visual representation.

If "smoky" and "lavendery" are being used as adjectives, then as Batty seems to intend, the semantics is blind to x; x is an I-know-not-what that nonetheless smokyizes and lavenderizes. But if the "is" is that of instancehood, "smoky" and "lavendery" can be taken as kind terms, and the representation can be read as, "There is some smoky and some lavendery at L_0." (We know,

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[16] For much more detail and defense of all this, see again Lycan (1996).

Austen Clark (1993) speaks of a transparent/opaque ambiguity in phrases like "lilacs odor." Taken transparently or de re, the latter phrase must refer to what some lilacs are up to, regardless of the smell sensation produced. On its opaque use, it describes the qualitative character of an olfactory experience regardless of what is going on in the environment.

[17] Thanks to a reviewer and to Bence Nanay for bringing this literature to my attention.

[18] Most philosophers have accepted this, but the psychologist R. J. Stevenson (2011) does not. He cites a number of empirical studies (cf. Wilson and Stevenson, 2006) in which are shown mismatches between olfactory percepts and the stimuli that caused them. Batty (2014) does not dispute the data, but argues that such mismatches do not rise to the level of illusion intended by the philosophers.

[19] That problem was an objection raised by Frank Jackson against "adverbial" theories and others that tried to avoid commitment to individual phenomenal things' figuring in a subject's phenomenal field. A visual field, for example, cannot be described simply by means of a list of color properties and shape properties such as {blue, red, circle, triangle}, because that list alone would not distinguish a field containing a blue circle and a red triangle from one containing a blue triangle and a red circle. Even phenomenally, colors and shapes group into individual objects.

Batty's point goes back to Clark (2000) and Smith (2002).

[20] In such arguments she follows Smith (2002) and Matthen (2005).

[21] Later in her paper (pp. 513–514) she does offer two quick arguments for the claim that smell represents, without supposing they are decisive: Each is an instance of what she calls the Unification Thesis: that "certain philosophical issues about perception should be settled in the same way for each of the sense modalities." (1) All senses function as informational systems. "As guides of behavior and grounds of belief, the experiences of the sense modalities form a common kind." (2) In particular, since some animals' olfactory experiences "are for them as vision is for us," in that they are clearly "world-directed" and help the animals map the world, then if our visual experiences are representational, so are their olfactory experiences; and if their olfactory experiences represent, then so do ours however less richly.

[22] Richardson rightly urges that the location is more specific: present to my nose. This distinguishes odor from, e.g., ambient temperature, where temperature is perceived as being "around me" more generally.

as the natural-kind semantics does not, that smoky and lavendery are really odors, i.e., miasmas in the air.) It is this second interpretation that is hard to distinguish from my view.

The adjectival interpretation invites the question of what properties smokiness and lavenderiness are, given that they are properties of odors rather than odors themselves. Perhaps they are response-dependent relations between odors and perceivers. But this would raise problems of the sort that bedevil dispositional theories of color, and Batty has not (at least not here) supplied motivation for doing so.

The natural-kind interpretation forces a question for Batty about entailment: Does "There is some smoky and some lavendery at L_0" entail both "There is some smoky at L_0" and "There is some lavendery at L_0"? If it does, I see little difference between her view and mine. If it does not, we need to hear more about how to parse her formula, "$\exists x$(x is smoky, lavendery & at L_0." What *would* be the relation between "smoky, lavendery," "smoky," and "lavendery?"

(9) Young (2013) challenges the odor theory, at least a strong and distinctive form of it. His main complaint is that existing odor theories have either implied identity and individuation conditions for smells, which conditions are untenable, or they have been sullenly silent on identity and individuation and therefore need filling out by tenable conditions. On the first horn of that dilemma, his paradigm seems to be the Platonic idea that an odor is an emanation of "detached proper parts of ordinary objects" (p. 3). That idea explains some of the phenomena noted in section 1 above, such as the veridicality of a smell even though the source object is itself long gone. But, Young argues persuasively, smells do not always track their source objects or even (at the level of types) their usual or typical source objects.

Of course, odor-theory phrases like "a miasma in the air" do not commit us odor theorists to the Platonic source-object thesis, but that is because they are vague. Young demands that we be able to tell him *what types* of miasmata, exactly, produce which smells. Why, for example, does a particular synthetic chemical compound have the same olfactory quality as a rose (p. 7)? He offers a proposal that he defends by appeal to a good deal of empirical literature. (He is willing to call the proposal a "modulation of" the odor theory.) The proposal is to identify olfactory objects, not with molecular compounds, but with "the three-dimensional chemical structures of molecules" (p. 21), "actual three-dimensional structures formed by their constituent functional groups and their placement in space and time."

If I understand Young correctly, the main contrast between this Molecular Structure theory and "the Odor theory" (now capitalized) is that it appeals to "micro-objects derived from the structure of matter" rather than to merely small bits of a source object (p. 27). If "the Odor theory" is thus characterized, I believe Young wins and anyone who holds it should stop doing so. But I know of no one who does hold it as such; I and the other odor theorists whom I have read fall on the other horn of his dilemma, simply not having said enough about the relevant "miasma" to be tested against the science.

Nor am I nearly knowledgeable enough to contest his assessment of the empirical findings. If the operative elements of what hangs in the air are situated three-dimensional molecular structures, so be it, and I provisionally accept the friendly precisification. But I have one comparatively a priori worry about it.

Young grants (section 4.2) that a synthetic odorant that mimics the smell of a natural object may differ from that object in molecular structure. Does this not create a problem of metamers? For predictive purposes, he need furnish only bottom-up sufficiencies, and his theory will succeed by his lights if he is able to predict that structure A will trigger a rose smell, and so will structure B and so will structure C. But our own question was, exactly what does the "rose smell" represent? In the face of metamers, is it now ambiguous as between three different representata, A, B, and C (and however many more synthetics the future might reveal), so that it will differ contextually in accuracy condition?

It is tempting to look for a more abstract, higher-level property that is being implemented by A, B, and C; but Young explicitly rejects that move (p. 27). Yet the ambiguity view is an extreme form of externalism, and though generally an externalist myself, I do not think perceptual representation in particular should be so fraught. As a friendly retreat from Young's friendly precisification, I offer the analog of my own view of color metamers (Lycan (1996); not that I think Young would welcome it)[23].

The view construes color representata as physical properties of objects, but only as very modest ones. They are roughly the properties that constitute the objects' dispositions to produce the corresponding sensations in normal sentient observers under normal viewing conditions; and as we all know, those properties are an unruly, rough, and ragged lot. Certainly they form no natural kind at the level of physics or chemistry. A physical color, then, is taken to be a pathetically disjunctive microstructural property of objects. It is of interest only because of its relation to the human visual system.

The latter fact seems damning: "(1) You pick out the 'property' in question only by reference to the human visual system. And in fact, (2) all 'its' instances have in common is that they do produce the relevant sensations in people. Moreover (3) you have admitted that it constitutes its subject's disposition to produce such sensations. For these reasons, the property you're talking about is just that of *being disposed to cause people to sense* in the corresponding way." We had been trying to explicate phenomenal color as a matter of representing worldly color, but now we are tacitly understanding "worldly color" in terms of the phenomenal; circular and viciously so.

But the foregoing argument is a bad one. As admitted, the kind of property I am talking about is ontologically and scientifically ugly; but not even the conjunction of the premises (1)–(3) justifies the argument's conclusion. Despite its ugliness, my sort of property inheres in an object on its own; regardless of how it is picked out or identified by me or anyone else, regardless of its ever producing sensations in anyone (or being detected by any being at all), and, surprisingly, regardless of its actually constituting a disposition to produce sensations in anything. For in principle it can be specified or defined independently of its doing any of those things. It is as it is, whether or not anyone identifies it or refers to it, whether or not it ever produces sensations of any sort, whether

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[23] It is inspired by if not just swiped from Armstrong (1984, pp. 170–182; also 1987).

or not it constitutes any disposition, and even if none of those things were true.

If this view, unsatisfying as may be, is nonetheless correct, it can be extrapolated to the problem of smell metamers. What a smell represents is then a (probably open-ended) disjunctive property—the property that serves as the categorical basis of an odor's being disposed to cause the corresponding smell sensations in humans, but not (metaphysically) because it so serves. This removes the threat of multiply ambiguous reference, at the cost of positing a single referent that is in its own metaphysical right ugly and misshapen.

LAYERING?

(10) One may tentatively suppose, then, that phenomenal smells represent odors in the sense I have tried to specify. But (in conversation) Ruth Millikan has contended against me that my arguments and others' against the idea that smells represent environmental objects must be flawed. If we are to agree with anything like her pleasantly Panglossian evolutionary-historical account of representational content (Millikan, 1989, 1995), we must suppose that if smells do represent anything, they do after all represent environmental objects of potential adaptive significance. Surely that is what olfaction is *for*, to signal food, predators, shelter, mates, and other objects of interest ultimately derivative from those; and signaling is at least a crude form of representing.

I am inclined to think Millikan is right about that (bar "if smells do represent anything"). And there is further pressure to expand the field of representata and make it still more distal: Phenomenologically, it seems that we do smell roses, horses, and even individual things or people.

But these two considerations do not force me to abandon my claim that smells represent odors. Even if I accept them both, I suggest that smells represent adaptively significant environmental entities, and worldly things and people, and they *also* represent odors. In fact, they represent the environmental entities *by* representing odors. By smelling a certain familiar odor I also smell—veridically or not—an actual rose or roasting lamb or my least favorite aunt.

Let me back up. The present sort of issue has long since been encountered in the philosophy of vision[24]. In that literature, there are conservative positions (vision itself represents only colors and shapes), very liberal positions in the tradition of Hansen and Kuhn (suitably trained and informed vision can represent practically anything), intermediate positions (vision can represent natural kinds and causal relations, but not expensiveness or uninhabitedness or uninhibitedness or global warming or an economic downturn)—and layering positions, according to which visual states have multiple intentional objects and we see more abstract and worldly things in and by seeing simpler and more primitive ones.

Here are some of the layering views. Peacocke (1992): We represent indexical "scenario" content; low-level properties (non-conceptual); and high-level properties; it is, I think Peacocke meant, the same vehicle that does both representings. Lycan (1996): We represent high-level properties by representing scenario content and low-level properties of external objects. The model here is that of deferred ostension: Pointing at a chalk mark on a blackboard, we refer to a numeral; thereby we refer to a number; thereby we refer to an office in Emerson Hall; and thereby we refer to its occupant, a person. Noë (2004): We perceive high-level properties, though only as "present as absent," by actually-perceiving "perspectival properties" (="appearance properties") of external objects. Schellenberg (2008): We perceive "situation-dependent" properties of external objects, and thereby the high-level properties of the same objects, the perception of the latter depending epistemically on that of the former. (It is important to grasp that the situation-dependent features are perfectly real and mind-independent.)

Returning to my original argument against the idea that the rose smell represents roses: It was essentially that if I experience the rose smell when the rose odor is present but no actual rose is, I am smelling correctly, and if I experience the smell when an odorless rose is present, I am not smelling correctly. But in the face of my own layering view for the case of vision, this argument is too simple. For that view introduces the possibility that a mental representation can have more than one truth value at once. And indeed, I think it is fairly plausible to say that in the first case—that of experiencing the rose smell in the absence of any rose—I am representing *both correctly and incorrectly*, the odor correctly and roses incorrectly.

My suggestion, then, is that a given sensory state typically has, not just a single intentional object, but two or more arranged hierarchically by the "by" relation. As before, a good model here is that of deferred linguistic reference.

But there are problems. The first is the above-noted objection that my rose representation is only the result of unconscious inference from the lower-layered olfactory representation rather than being olfactory itself, especially since the "rose" response seems to depend on acquired empirical association. That objection is not decisive, but it is serious[25].

My (1996) layering view depended on a visual ontology of "shapes," some of which items are real physical objects but most are non-actual. Whether or not one can abide that ontology, it has no obvious analog for smell, because the notion of a "shape" was motivated by visuocentric considerations of size, direction, distance, and surface. I have given up my (1996) position in favor of Schellenberg's superior layering view. But (second problem) it is far from obvious that her "situation-dependent" properties have olfactory analogs, either. Situation-dependent properties are, she says, "(nonconstant) functions of the intrinsic properties

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[24] For summaries, see Siegel (2010) and Lycan (2014).

[25] Philosophy has not entirely resolved the general question of whether the incredibly busy pre-processing that goes on in our perceptual modules should be counted as un- (because pre-)conscious inference—or how modular the modules are to begin with, given what is now called "cognitive penetrability" (Macpherson, 2012); on these matters, see Lycan (2014). For now: Even if my rose representation is the result of unconscious inference in one sense, that does not disprove the claim that it is also itself olfactory. A reviewer has further suggested that the mechanism connecting the rose odor to the rose is, rather, cross-modal binding.

of the object and the situational features" (p. 60). The cup on the table has

> one side closer [to me] than the other; one part faces away from me. Its shape is presented in an egocentric frame of reference, which in turn means that the object and its parts are presented as standing in specific spatial relations to me. The way the cup is presented to a location is on the suggested view an external and mind-independent, albeit situation-dependent property of the world. Any perceiver occupying the same location would, ceteris paribus, be presented with the cup in the very same way. (p. 61)

Schellenberg says similar things about color: The relational properties of an external object that make it appear colored to us as it does in this setting and lighting conditions are, tautologously, properties of the object.

Do objects have mind-independent, situation-dependent odor properties? Obviously roses have relational properties which cause them to smell as they do to us. But I do not offhand see that simply by detecting those properties we detect roses without benefit of background knowledge. Perhaps I am wrong.

(11) I believe that I together with others have made it very plausible that smell represents, and I have defended roughly my original view of what it represents first and foremost. I would still like to accommodate Millikan and common parlance in the matter of ecodistality, through layering. But I of all people cannot assume that a view that is plausible for vision will extrapolate to any other sense modality.

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The illusion confusion

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In Batty (2010b), I argue that there are no olfactory illusions. Central to the traditional notions of illusion and hallucination is a notion of object-failure—the failure of an experience to represent particular objects. Because there are no presented objects in the case of olfactory experience, I argue that the traditional ways of categorizing non-veridical experience do not apply to the olfactory case. In their place, I propose a novel notion of non-veridical experience for the olfactory case. In his (2011), Stevenson responds to my claim that there are no olfactory illusions. Although he agrees that it is natural—or at least commonplace—to think there are no olfactory illusions, he argues that there are and provides examples of them, many of which he suggests have analogs in the visual and auditory domains. In this paper, I examine the nature of the disagreement between us. I argue that Stevenson fails to argue against my conclusion that there are no olfactory illusions.

Keywords: illusion, olfaction, olfactory misperception, olfactory illusion, object perception, olfactory objects, olfactory object perception

INTRODUCTION

AGAINST OLFACTORY ILLUSIONS

Let me begin with an overview of my previous arguments[1].

In Batty (2010a), I argue for a view according to which olfactory experience has representational content—that is, there is a way that the world appears to a subject when she has an olfactory experience. I set this discussion against suggestions previously in the literature (albeit brief) that olfactory experience may have no representational content—that is, that there is *no* way that the world appears to a subject when she has an olfactory experience[2]. These are views according to which olfactory experiences are "mere sensations," or "raw feels." I argue that driving these suggestions are differences between visual and olfactory phenomenology—that is, differences in what these two kinds of experiences are like for the subject. Visual experience is incredibly rich, seemingly offering up an array of three-dimensional objects. For this reason, the view that visual experience is world-directed—indeed directed at the objects in our environment—comes naturally to us, with the most common version of such a view the representational, or content, view. The case of olfactory experience is different. Although we might think that it presents a wealth of apparent properties, it does so with much less structure than its visual counterpart. As I have put it elsewhere, compared to visual experience, olfactory experience is "just plain smudgy."

Despite this, I argue that there is a representational view of olfactory experience available and, as it turns out, we are able to draw that view from a certain debate about visual content. In the visual domain, there is significant disagreement about how visual experience represents that objects are thus and so. One view is that visual content is *abstract* and that your visual experience of a ripe tomato, for example, represents that there is "*something or other*" at a given location that it is red, round, and so on. This view is contrasted with the view that visual content is *object-involving*. On this view, the tomato itself (that *very thing*, there, before you) is a constituent of the content of your experience. That is, your experience represents that the *particular* tomato is at a given location and it is red, round, and so on. Unlike what the abstract view claims, your experience does not represent merely that "something or other" has those properties.

Drawing on several examples, I argue that olfactory experience does not represent particular objects in the way that some have argued vision does and, as a result, an object-involving view of olfactory experience is not available[3]. These examples all draw on what we might call day-to-day, or typical, olfactory experiences—namely, those that we have out in the world and not those that

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[1] It must be noted that all of my previous arguments concern human olfaction. I will have something to say about the olfaction of other creatures at the end of the paper.

[2] For example, both Peacocke (1983) and Lycan (1996, 2000) suggest that the phenomenology of olfactory experience does not uphold a representational view. In the opening chapter of his Sense and Content (1983), Peacocke suggests that "a sensation of [smell] may have no representational content of any sort, though of course the sensation will be of a distinctive kind" (3). This is all he has to say, however. Still, his remarks suggest a sensational view of olfactory experience. Echoing Peacocke, Lycan claims that "phenomenologically speaking, a smell is just a modification of our consciousness, a qualitative condition or event in us" (2000, 281), "lingering uselessly in the mind without representing anything" (1996, 245). Lycan does go on to argue that olfactory experience is representational; but it is clear from these remarks that he thinks that we cannot uphold such a view on the basis of the phenomenology of olfactory experience. He, in turn, proposes that the appropriate notion of content for olfactory experience is a teleological one (1996).

[3] These examples all show that olfaction cannot solve the Many Properties Problem—that is, the problem of distinguishing between scenes in which the same properties are instantiated, but in different arrangements. Vision can solve this problem, and it does so by grouping perceptual features together in space. This grouping amounts to the presentation of sensory individuals. Olfaction, I argue, does not achieve this kind of perceptual grouping. For these examples, see Batty (2010a, 2011).

we might have in a controlled laboratory environment[4]. As most of us will never find ourselves in the laboratory environment, there remains an interesting question regarding the content of our typical olfactory experiences. Examining these typical cases olfactory experiences, I demonstrate that everyday olfactory experiences do not possess the robust spatial representation present in the visual case and, as a result, does not allow us to single out particular objects in our environment[5]. That is to say, unlike visual experience, olfactory experience does not reveal the particular objects that, in the case of veridical experience at least, bear the olfactory properties that it presents. This claim, I argue, is just the claim that olfactory experience does not achieve figure-ground segregation. Still, as I argue, an abstract view is a remarkably good fit for the olfactory case and suggestions that olfactory experience is merely sensational incorrectly cast an object-involving view as the only option for olfactory experience. The right view about the representational content of olfactory experience, I conclude, is one according to which it has a weak form of abstract content. In any circumstance, a given olfactory experience represents that there is something or other "here," or "at" the perceiver, that has certain olfactory properties. I call this the *abstract view* of olfactory content.

In Batty (2010b), I turn to issues of misrepresentation with respect to the typical olfactory experience. In particular, I argue that the abstract view of olfactory content explains some of our intuitions about how olfactory experience can misrepresent the world. I point out that the notion of an olfactory hallucination is something that comes naturally to us while the notion of an olfactory illusion does not. This is reflected in the scientific literature on olfaction, in which reference to hallucination is common, but illusion rare. It has also been reflected in the philosophical domain—albeit in personal conversation and not in print—with a hesitancy in answering the question "*Are there olfactory illusions?*" As we know, the answer to the visual analog is quick and easy: yes there are visual illusions, and there are many examples at the ready. In my experience, the olfactory question is met with a sense of cautiousness, even confusion, over just what the question itself is asking. Whether there are olfactory hallucinations, however, is met with immediate assurances that there are.

Taking this discrepancy as a datum, I argue that the abstract view of olfactory content can explain the discomfort we have with the notion of an olfactory illusion as well as the apparent comfort we have with its counterpart—the olfactory hallucination. What the abstract view shows us is that, in the case of olfactory experience, the traditional distinction between illusory and hallucinatory experience does not apply. In turn, it directs our attention to a novel notion of non-veridicality—one that has been absent from philosophical discussions of illusion and hallucination.

Traditionally, philosophers have thought that a perceptual experience can misrepresent, or be non-veridical, in one of two ways: the experience can be illusory or it can be hallucinatory. To take a common example, a navy blue sock can look back to you. What you suffer in this case is an illusion with respect to the sock's color. The sock is there, but your visual experience "gets its color wrong"; the experience attributes a property to the sock that the sock does not have. In the case of a hallucination, there is no object there and your experience is not accurate even in that sense. Macbeth famously suffers in just this way; there is no dagger before him and when it appears as though there is, he undergoes a hallucination. Central to the traditional notions of illusion and hallucination, then, is a notion of object-failure; in each, an experience fails in representing a particular object. This much illusion and hallucination have in common. But the nature of that object-failure falls into two kinds. In the case of illusion, a visual experience misattributes a property to an existent object. In the case of hallucination, experience reports that there is an object there, when there is no such object. This difference in the kind of object-failure committed marks what I call the "traditional distinction" between illusion and hallucination.

In order to see why the traditional distinction does not apply to the olfactory case, consider for a moment the visual case. In the case of the typical visual experience, we can ask two separate questions of the object of experience, *o*:

For any property F that o appears to have, does *o* really have F? (*V-Attribution*)

Is *o* there at all? (*V-Existence*)

If the answer to either is "no," then visual experience fails to present an object accurately. As I put it above, it commits object-failure. But, as we know, they commit object-failure in different ways. If the answer to *V-Attribution* is "no," my experience misattributes a property to an existent object. And if the answer to *V-Existence* is "no" my experience reports that an object is present when it is not. This difference in the kind of object-failure committed—the difference between visual illusion and visual hallucination—is marked by the different content of *V-Attribution* and *V-Existence*, in what we ask of a given object of experience.

Now consider the olfactory case. If there were olfactory analogs of *V-Attribution* and *V-Existence*, we could ask of an object of olfactory experience, *x*:

For any olfactory property *F* that *x* appears to have, does *x* really have *F*? (*O-Attribution)*

Is *x* there at all? (*O-Existence*)

But, as I have argued previously, olfactory experience only ever reports that there is something or other at a perceiver that is F. This is unlike the visual case where a perceiver's experience typically represents particular objects in one's environment. That is to say, unlike visual experience, olfactory experience is disengaged from any particular object. This is why an object-involving account of its content is unsuitable. In what follows, I will refer to this point as the claim that there are no "presented objects" in olfactory experience[6].

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[4] As I cite in my previous paper (Batty, 2010b), studies suggest that that humans are able to achieve some measure of spatial discrimination in highly controlled laboratory settings. See, for example, Porter et al. (2005) and von Békésy (1964).

[5] Unless it is important to otherwise note, in what follows, my use of "olfactory experience" or "olfactory experiences" will denote those typical, day-to-day, olfactory experiences.

[6] Although we might say that, on the abstract view, olfactory experience presents objects, I intend "presented objects" and its counterpart "presents

This explains why we are uncomfortable with the notion of an olfactory illusion. The idea that a smell is misattributed to an object does not grip us and this is because the content of olfactory experience does not support this kind of claim. That is, in olfactory experience, there is no particular thing of which we can ask, as in *V-Attribution*, "it *appears* to be F, but is it really as it appears?" For this reason, I conclude that there are no olfactory illusions[7].

But, now we are faced with a puzzle. This is because, for the same reasons, there are also no olfactory hallucinations. There is no particular thing of which we can ask, as in *V-Existence*, "yes, it *appears* to be there, but is it?" But, as I have argued, the notion of an olfactory hallucination *is* a notion that we are comfortable with. If what I say about the illusion case is right, however, it ought not to be.

The abstract view of olfactory content can solve the puzzle. As we have seen, the abstract view draws attention to the kinds of questions that we are unable to ask of olfactory experience—namely, questions that refer to particular objects. But, as any account of content will, it also draws attention to the kinds of questions that we are *able* to ask in evaluating an olfactory experience. And, considering *these* questions, I argue, is the key to solving the puzzle.

What questions are we able to ask, then? Given the content of olfactory experience, we can ask of a given olfactory experience and an apparent property F: is there something or other at the perceiver that is (or has) F? In asking this question, we do not pick out any particular object (as olfactory experience does not allow for this). Rather, we ask whether there is *anything at all* around that is F. And, due to its content, a question of this type is the only one we can ask of when evaluating an olfactory experience for veridicality. Notice, however, that this question bears similarities in form to *O-Existence*—the question that is meant to capture a traditional notion of hallucination for olfactory experience. *O-Existence* asks whether a particular object that appears to be F is around; the present question asks whether there is anything around that is F. We do not ask whether F has been misattributed to an object—as we would in *O-Attribution*—but whether F-ness is instantiated at all. The only difference between the present question and *O-Existence* is that it is not a particular object after which we ask. Instead, we ask after a certain property. In each case, however, we ask whether it exists or, better yet, *is there*.

Because of these similarities, I argue that it is understandable that the notion of an olfactory hallucination resonates with us. To be sure, as it turns out it is not the traditional notion of hallucination that does. But it is a notion of hallucination nonetheless—and a novel one at that. As we have seen, when olfactory experience is non-veridical, it incorrectly reports that something or other at the perceiver has a certain property. But this is just to say that when olfactory experience is non-veridical, it incorrectly reports that a certain property is present in the perceiver's environment. As a result, I conclude that the notion of non-veridicality that is suited to olfaction is one of *property hallucination*. It is a notion of misrepresentation, or non-veridicality; but it is one that is disengaged from any particular object. This novel notion of non-veridicality explains two features of the olfactory case. First, it provides the key to understanding why we are comfortable with the notion of an olfactory hallucination, but not comfortable with that of an olfactory illusion. Secondly, in providing a new way of thinking of non-veridicality for the olfactory domain, it also solves the puzzle brought about by the conclusion that there are no olfactory illusions. In particular, it draws attention to reasons for thinking that there are olfactory hallucinations other than those provided by the traditional distinction between illusion and hallucination[8].

IN SUPPORT OF OLFACTORY ILLUSIONS: STEVENSON'S VIEW

In what follows, I will take the premises of my argument for granted—in particular, the claim that, in the typical olfactory case, olfactory experience does not achieve figure-ground segregation and, in turn, object-involving status. Recently, Richard Stevenson has responded to my argument that, based on these considerations, there are no olfactory illusions[9]. As we will see, although his embody conclusions of empirical study, Stevenson's

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objects" to denote circumstances in which olfactory experience presents particular objects, as an object-involving view of its content would have it.

[7] Note that it will not help here to argue that sometimes physical objects ("source objects," as we might call them) seem to have properties that they do not in fact have. My claim is that, given the nature of the phenomenology of olfactory experience, we are never in a position to know what particular object has, or is the source, of the properties that we perceive. That is to say, while olfactory experience predicates properties of "something or other," it is otherwise silent on the nature of that object—whether it be, in fact, an odorous effluvium or a "source object." Interrogating olfactory experience further will not tell us what olfactory objects are. So, although we do attribute—and at times incorrectly—properties to source objects, we do not do this on the basis of olfactory experience alone. Arguably, when we do, we do so on the basis of a network of background beliefs about source objects gained from past experience and/or the exercise of other modalities in discovering those sources. Again, those source objects are not revealed to us in olfactory experience itself and, as a result, any mistaken attribution to them we make does not provide a counterexample to my conclusion.

[8] One might worry that my claim that non-veridical olfactory experiences are best characterized as property hallucinations blurs certain intuitive distinctions that we make. For example, consider the two following cases: (1) a case in which there is no odorant at all in the room, and yet you smell coffee, and (2) a case in which there are only dry flowers in the room but in which you misrepresent their smell as coffee. On my view, the experiences of each would both count as property hallucinations. They are each cases in which, on the abstract view, the content of their respective experiences will be the same. And, in turn, in evaluating the veridicality of each, all we can ask is "is the coffee smell instantiated?" Still, just because the content of olfactory experience does not distinguish between a case in which we have an odorant, or odorant source, and one in which we do not, this is not to say that we cannot maintain the intuitive difference between these two cases. It remains open to explain that difference as a result of inference from past experience, background beliefs as well as the contribution of other sense modalities—the latter, in particular, for the case of (2). See also fn. 7 for a related point.

[9] Stevenson does not directly address my notion of property hallucination. Given that my arguments for property hallucination in the olfactory case turn on my arguments against the existence of olfactory illusions, we can interpret his failure to do so as resulting from his denial of my conclusion regarding olfactory illusion. If there are olfactory illusions as tradition would have them, then there is no need to posit a novel notion of non-veridicality for the olfactory case. I will, however, return to the benefits of this novel notion later in the paper.

own examples of illusion comprise contextual and constancy effects that could, or do, occur in day-to-day olfactory interactions with the world. The empirical studies he cites simply make it clearer that there are such effects. As the point of the present paper is to examine whether Stevenson's cases succeed in overturning my arguments against olfactory illusions in these typical olfactory cases, my and Stevenson's question is the same: are standard cases of non-veridicality for olfactory experience rightly characterized as olfactory illusions?

Stevenson's argument proceeds in two, roughly consecutive stages. First, Stevenson argues that there are olfactory illusions by drawing attention to those cases in which we find them. Secondly, Stevenson examines why the notion of an olfactory illusion has not resonated with us. In this way, his approach is like mine. It is true, according to Stevenson, that we are (or have been) uncomfortable with the notion of an olfactory illusion. Like me, he believes that this is in need of explanation.

Stevenson begins by spending some time discussing the term "illusion" and the kinds of phenomena that it denotes. He tells us that the term "illusion" derives from the Latin "illusio" which, as he cites, has the following meaning: "deceit, to mock or make sport with, the saying of the opposite of what is meant" (1888)[10]. Stevenson takes this definition to involve both an objective and a subjective component. On the objective side, a subject is presented with what is not the case—the "opposite" of what is the case, as the definition states. In this way, the subject is deceived, mocked, or made sport with. But, given that the subject is deceived, she does not notice that there is a disparity between the way the world is and what is being presented to her as the case. Still, she is capable of noticing, Stevenson suggests, given the right kind of circumstances or instruction. This is what Stevenson means by the subjective component of the definition. I take it that it is the term "deception" which "suggests a potential for subjective awareness of [the] disparity" (1888); "illusion," defined in terms of "deception," also carries with it that suggestion.

As Stevenson notes, these two aspects of the meaning of "illusion" are not always apparent in the empirical literature on olfaction. Rather, it is the objective component of the term that has currency of use. Although there are subtle differences in the use of "illusion" in the empirical literature, he tells us that, in general, it is used to refer to "a disparity between some objective state of the world and ones [sic] perception of it" (1888). This forms what I will call his *working definition of "illusion."* This definition, he claims, captures those phenomena that psychologists accept as cases of visual, auditory and somatosensory illusions. Although Stevenson claims that this definition proves enough to pinpoint cases of olfactory illusion, he recognizes that it leaves out any reference to an awareness of the misrepresentation. As he claims, this omission is of little consequence for the cases of visual, auditory and somatosensory illusions. But, as he argues, it has invited the view that there are no olfactory illusions. As evidence of our resistance to the notion of an olfactory illusion, he observes, like me, that the indices of many popular perception textbooks, as well as those of recent specialist books on olfaction, lack any mention of olfactory illusion.

As a way drawing out to the difference between us, then, Stevenson argues that we could take this evidence as indicating one of two things: either (1) that there are no olfactory illusions or (2) that those illusions escape notice. As I outlined above, I argue for (1) and this itself explains our discomfort. As we know, my arguments turn on the traditional distinction between illusion and hallucination together with observations about the phenomenology of olfactory experience. Because olfactory experience is not object-involving, the notion of an olfactory illusion not only has no resonance with us, but also has no application to the olfactory case. Unlike me, Stevenson opts for (2). After arguing that there are cases in which olfactory illusions occur, Stevenson claims that we are typically unaware of having experienced an olfactory illusion, and this accounts for why we might think that there are none. He states this point in terms of verification. We are not only typically unaware that we are undergoing (or have undergone) an olfactory illusion; even if we suspected that we were, we are unable in most cases to verify whether we are (or were) in fact suffering one. Still, as he claims, we would be mistaken to move from this epistemological point to the conclusion that there are no olfactory illusions. Instead, we ought to see our tendency to make this move as the result of a failure to appropriately consider the subjective aspect of the meaning of "illusion" and realize that, unlike their visual, auditory and somatosensory counterparts, olfactory illusions are not the kinds of things of which we are typically aware.

In arguing for (2), however, Stevenson first provides evidence against (1). It is his argument against (1) that I am primarily concerned with in this paper. I will, however, turn to his argument for (2) in my conclusion. At present, I turn to (1).

AGAINST (1): EMPIRICAL EVIDENCE OF OLFACTORY ILLUSIONS

My discussion of (1) proceeds in two stages, in line with what I take to be the two arguments that Stevenson gives for the existence of olfactory illusions. His first argument forms the bulk of his discussion and involves setting out examples of olfactory misrepresentation that fit his working definition of "illusion." The second of his arguments occurs in the discussion section of his paper and requires substantial reconstruction. In doing so, we see that Stevenson employs a further notion of illusion—one that, I argue, is the same as the traditional notion that I adopt. Given this, we see that there are two notions of illusion at work in his paper. I will argue that Stevenson is not successful in showing that, in accordance with either of these two notions, there are olfactory illusions.

Let us turn, then, to the first stage of Stevenson's argument. According to Stevenson, what are the cases that we can rightly describe as those of olfactory illusions? Given his working definition of "illusion," each involves a "disparity" (1888), as he puts it, between the way the world is and one's experience of it. In turn, his arguments assume that there is indeed an objective way that the world is with respect to olfactory phenomena (e.g., quality, intensity, hedonic value), and one that could in principle be accurately represented in olfactory experience. As he puts it: "[a] misperception assumes that there is a veridical state, in which the mind accurately reflects some objective state of the environment" (1893).

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[10] All references to Stevenson will be to Stevenson (2011).

According to Stevenson, cases meeting his working definition fall into two categories, each defined by the type of disparity that exists between the external stimulus and a subject's experience[11]. There are the cases in which the same stimulus is experienced differently by a given subject at different times. And there are the cases in which different stimuli are experienced by a subject as the same. According to Stevenson, both of these types of disparity parallel accepted cases of illusion in other modalities[12].

Let us consider cases of same stimulus-different percept first. According to Stevenson, this category contains a set of cases in which context is thought to affect olfactory experience—in particular, contextual effects of perceived quality, intensity, and hedonic value. In what follows, I will set out several examples of these contextual effects. Stevenson does provide more cases for each category. He also provides examples of variation in the perceived location of a chemical stimulus, as well as an example of an olfactory analog of binocular rivalry. I will set aside these latter two cases. For my purposes, it is enough to consider the perceptual phenomena that fall under the category of "contextual effects[13]."

In the qualitative category, Stevenson tells us that experiments have shown that the compound dihydromyrcenal is perceived to be more "woody" when smelled in the context of citrus smelling odors, and more "citrusy" when smelled in the context of "woody" smelling odors. In each case, the stimulus remains the same; how a subject perceives that stimulus to be—i.e., the odorant's apparent properties—changes given what other odors it is perceived alongside. If we recall that Stevenson's working definition of an illusion is "a disparity between some objective state of the world and ones [sic] perception of it" (1888), then it would seem that such a case meets this definition. Given that, in each case, the target odorant appears to be "more F," for some apparent property F, the implication is that there is some way that the target odorant is, irrespective of context[14]. On Stevenson's definition, then, both the "more citrusy" and "more woody" contextual effects constitute illusions with respect to perceived quality.

Stevenson claims that similar effects are reported for perceived intensity and hedonic value. For example, in the case of intensity ratings, experiments have shown that intensity ratings of a range of odor concentrations are affected by intermediate exposure to the same stimulus at weaker, or stronger, concentrations. So, for example, if after having initially rated the intensity levels of a range of odor concentrations subjects are then exposed to a stronger concentration of the same odorant as a biasing task, those subjects later judge the initial concentration range to be less intense. And, as Stevenson tells us, the opposite effect results from intermediate exposure to a weaker concentration. According to Stevenson, this is a case in which there is a disparity between the objective state of the stimulus, as he would put it, and a subject's perception of it. As in the case of perceived quality above, the stimulus remains unchanged throughout the experiment; however, how that stimulus appears to be—that is, its perceived intensity—changes given the context of perception, in this case one created by the biasing task. The suggestion is that, prior to the biasing task, there is no disparity between the intensity properties of the stimulus and the subject's perception of them. It is only after the biasing task that the subject suffers an illusion with respect to the intensity of that stimulus.

Finally, in the category of hedonic judgment, Stevenson cites a series of experiments in which labels reflecting positive and negative contexts have been shown to affect judgment of the pleasantness of an odorant stimulus. As he tells us, in a particular experiment, previous exposure with the label "toilet cleaner" (i.e., a negative context) affects the judgment of a pine odor's pleasantness in later contexts labeled "Christmas tree" (i.e., a positive context). Similarly, initial exposure to the same odorant with the label "Christmas tree" affects judgment of its pleasantness in later context labeled "toilet cleaner." In the first case, perceivers judged the shift in pleasantness to be less than they did in the second case, when the labels were reversed. This is despite the odorant stimulus remaining constant throughout. Verbal labels, then, can affect judgments of pleasantness.

Although Stevenson does not state this explicitly, these are, for him, cases of illusion because of the relation that experience bears to our hedonic judgments. In particular, the case suggests that those judgments are made on the basis of experience such that a difference in judgment indicates a difference in the associated olfactory experience. It is only if this is true that differences in

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[11] In discussing Stevenson's examples, I adopt his use of "disparity" to refer to that difference between the way things appear and the way that they are. It is a term that is rarely used in the philosophical literature, with philosophers often adopting characterizations in terms of the inaccuracy of a representation.

[12] I will avoid going into the details of these illusions in other modalities. For present purposes, it enough to note that he thinks that there is this parallel.

[13] I set aside cases of perceived location and binaral rivalry for reasons other than brevity. To give Stevenson's discussion of olfactory localization full treatment would involve dealing with difficult questions regarding the status of the retronasal as truly olfactory. Given that my claims regarding olfactory illusion center on orthonasal olfaction, I consider only the orthonasal. I set aside his consideration of binaral rivalry because it isn't clear that it constitutes an illusion, even in his working sense. In the case of binaral presentation, one's olfactory experience switches back and forth from the presentation of an odor located discretely at one nostril to an odor located discretely at the other. In each case, the odorant is indeed at the nostril at which one's experience represents it as being. What one's experience does not represent is that there is another odorant present at the other nostril. (Assume that experience gets the quality and intensity "right." He does not claim that there is any other disparity that that of localization.) But surely in each case (switching from one nostril to the other) one's experience "accurately reflects some objective state of the world" (1888)—namely, that a certain odorant is located at a certain nostril. What it does not report is that there is an additional odorant located at the other. But this is just a failure to perceive something in one's environment. By Stevenson's own lights, the experience hasn't conveyed any information that is false; it has simply failed to convey all of the information about the perceiver's environment. Accurately representing some objective state of the environment does not involve representing every feature of that environment. That is too strict a constraint on veridicality—arguably one that we would never meet. What matters for determining whether an experience is veridical is whether what experience does represent is represented correctly—i.e., veridically.

[14] In line with Stevenson's characterization of illusion, I take it that this is a feature of the odorant that could in principle be represented veridically in olfactory experience. In what follows, I will leave out reference to these counterfactual circumstances. But it should remain understood that, according to Stevenson, they could obtain.

hedonic judgment could tell us anything about the existence of illusions in the olfactory case. For illusions are cases of perceptual misrepresentation, as Stevenson claims earlier; they cannot only be matters of inaccuracy of judgment—although, if we take our illusory experiences at face value, our judgments will be inaccurate as well. With this in mind, it is clear that, for Stevenson, cases of variation in hedonic judgment involve a disparity between some objective state of the stimulus and a subject's perception of it. The stimulus remains the same, after all. To be sure, in the experiment he cites, this disparity might underlie each of the subject's initial judgments, given that in both cases the odorant is perceived with verbal labels. It might be that "the veridical state, in which the mind accurately reflects some objective state of the environment" (1893) is one had in the absence of any verbal label. (And, prima facie, this seems plausible). Despite this, even double disparity in this case shows that, on Stevenson's working definition, there are cases of olfactory illusion. That is, if both labeling cases are ones of disparity, then so much the better for his argument that there are olfactory illusions[15].

Now to cases of different stimulus-same percept. In this category, Stevenson cites two instances of perceptual stability, or constancy phenomena. The first example involves intensity. According to Stevenson, research has found that variations in the flow and, in turn, concentration of an odorant over the olfactory epithelium is registered by neural responses of the olfactory nerve. Despite this, such variation does not arise at the level of experience. Rather, despite variation in the concentration of an odorant passing over the olfactory epithelium, subjects perceive odor stimuli as relatively stable with respect to intensity. Stevenson suggests that these results show that the epithelium is not only sensitive to the stimulus itself, but to the rate of airflow over it. Due to this added sensitivity, the olfactory system adjusts for variations in concentration relative to changes in airflow. The result is constancy with respect to the perceived intensity of the stimulus. Given Stevenson's working definition of "illusion," we have a case where there is disparity between the objective state of the stimulus and the nature of the experience resulting from it. In this case, we have a difference in odorant concentration that fails to show up at the level of experience. This subdued sensitivity to differences in an odorant stimulus amounts to an illusion, Stevenson suggests, because a veridical experience of it would represent its actual concentration (presumably in the form of what we call intensity of olfactory quality). Because that actual concentration is not represented at the level experience, Stevenson indicates that atleast some of our representation of concentration is illusory[16].

Stevenson's second example involves constancy in perceived quality despite differences in, or changes to, the chemical constitution of an odorant stimulus. Drawing on work he presents in Wilson and Stevenson (2006, 2007), Stevenson tells us that degraded input, or varying formulations of a stimulus at the receptor site, can be completed at the level of experience. Because of the complexity of the olfactory environment, one might not receive information about all of the components of a certain odor stimulus, for example coffee, and yet still be able to smell that that coffee is present. What accounts for this ability are prior encodings of odorant stimuli in the form of stored templates of patterns of receptor excitation in the olfactory cortex. As Stevenson claims, a "perfect fit" (1892) between input and template is not required; rather the olfactory system is able to recognize certain sub-patterns of receptor activation against existing templates of activation. The result is, however, not a "partial" experience of coffee; it is an experience of coffee. Without these templates, Wilson and Stevenson (2006, 2007) claim, it is unclear how such constancy might be achieved. Like constancy of intensity, then, it would seem we have a case where there is disparity between the objective state of the stimulus and the nature of the experience resulting from it. In this case, we have a difference in chemical constitution that fails to show up at the level of experience.

In sum, Stevenson alleges that all of the cases of same stimulus-different experience and different stimulus-same experience involve misrepresentation and, in particular, illusion. He argues that each case involves a circumstance in which there is a disparity between some objective state of the world and a subject's experience of that state. In accordance with his working definition of "illusion," then, these are all cases of illusion.

OLFACTORY ILLUSIONS?

In what follows, I will take for granted that each of these cases is one that we can assess for veridicality. I will also take for granted that there is some objective state of the world that our olfactory experience is capable of misrepresenting and does so in each of these cases. Given these assumptions, I want to now consider whether, or how, Stevenson's arguments affect my own.

As a way of making headway on these questions, it is important to first note that my notion of non-veridicality could handle these cases of alleged illusion[17]. Recall that my notion of non-veridicality involves the consideration of whether, for a certain olfactory feature F, there is anything at all at the perceiver that is F. So, to take the case of dihydromyrcenal as an example, evaluating the "more woody" case for veridicality involves asking whether there is anything at all at the perceiver that has, objectively, that degree of woodiness. Or, as I have also put it, it involves simply

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[15] Stevenson cites similar experiments in which a target stimulus is judged to be more pleasant if presented with odorants that are typically judged to be less pleasant, and less pleasant if presented with odorants that are typically judged to be more pleasant. Again, it must be that, for Stevenson, underlying cases of variation in hedonic judgment is a disparity between some objective state of the stimulus and a subject's experience of it. If this is true, these cases also constitute illusions on his working definition of "illusion."

[16] Given that Stevenson presents these as relatively common instances of perceptual constancy, it might turn out that much of our representation of concentration is illusory. It is unclear whether this is something that Stevenson would be happy to accept. One way to avoid that result would be to claim that olfactory experience represents concentration relative to air flow over the epithelium. In this case, our judgments of intensity would be more eligible for accuracy at the level of experience. I leave this proposal, however, for another time. The important point is that it is not a proposal that Stevenson wishes to entertain, opting instead for claims of illusion in these cases.

[17] In what follows, I will simply refer to my notion of non-veridicality for the olfactory case, as opposed to my notion of property hallucination for it. Given that I argue that the latter is the only way that (human) olfactory experience can be non-veridical, there is no room for confusion here.

asking whether, in those perceptual circumstances, that degree of woodiness is instantiated. If the answer is "no," then the experience is non-veridical. As I am assuming with Stevenson, that degree of woodiness is not instantiated at the perceiver—there is nothing at all that is "more woody" at the perceiver. In this case, then, the answer to my question is "no," and one's experience in this circumstance counts as non-veridical.

Notice, however, that my notion of non-veridicality for olfactory experience is no different than Stevenson's notion of illusion. Remember that, according to Stevenson, an illusory experience involves "a disparity between some objective state of the world and ones [sic] perception of it" (1888). But this is just what, on my notion of non-veridicality for olfactory experience, a non-veridical experience involves. To consider whether F-ness is instantiated at a perceiver is to consider whether the perceiver's experience "accurately reflects some state of [her] environment" (1893). If it does not, then there is a disparity between that state of the environment and a perceiver's experience of it. To return to the case of one's experience of the woodiness of dihydromyrcenal, Stevenson's notion of illusion requires that we ask whether that degree of woodiness is instantiated by some state of the environment, where "environment" presumably denotes the space around the perceiver eligible for inhalation[18]. But my notion of non-veridicality asks the same—that s, whether that degree of woodiness is instantiated at the perceiver. Given what Stevenson has told us, then, "Does S's experience of F-ness accurately reflect some state of the environment?" amounts to asking "Given that S has an experience of F-ness, is F-ness instantiated at the perceiver?" Just like Stevenson's notion of illusion, my notion of non-veridicality does not ask after any particular thing that appears to be F. Rather, in asking whether anything at all instantiates F-ness, it asks whether, to use Stevenson's terms, there is a state of the environment in which F-ness is instantiated.

As it stands, then, Stevenson's working notion of illusion fails to address my arguments against olfactory illusions. Both of us provide the same analysis of his cases. But if we truly disagree, then we ought to provide different analyses of them. At this point, then, any purported disagreement between us amounts to a mere difference in terminology. He calls his cases of disparity illusions, while I do not. But, other than that label, our characterizations of them amount to the same. Because of this, if Stevenson is to refute my arguments, he must do more to address them directly.

I hinted at what else is required above when I claimed that, because my notion of non-veridicality does not ask after any *particular thing* that appears to be F, it amounts to the question of whether there is a state of the environment in which F-ness is instantiated. My conclusion that there are no olfactory illusions hinges on the observation that olfactory experience is not object-involving, that there are no presented objects in olfactory experience. Recall that, on that traditional way of categorizing non-veridical experience, both illusion and hallucination involve what I call object-failure—that is, a failure to represent a particular object accurately. If there are no presented objects, then that categorization fails. And, as I argue, there are no such objects. This is because the very nature of olfactory experience—its "smudginess," as I have put it—doesn't allow for a distinction between figure and ground. These considerations of phenomenology constitute my reasons for denying that there are olfactory illusions. What is required for Stevenson to address my arguments, then, is an argument for the conclusion that, in the cases of alleged illusion he cites, there *is* a presented object that appears to be other than it is.

Stevenson appears to argue for just this in his later discussion section—although he does not turn back directly to his example cases. Before moving on to these arguments, it is important to note some potentially misleading claims that Stevenson makes when introducing this discussion. After presenting his alleged cases of olfactory illusion, Stevenson claims that "the apparent actuality of olfactory illusions would seem to call into question Batty's (2010b) claim that olfactory experience lacks object status" (1895). As it stands, this claim is far too quick. It carries with it the implication that Stevenson has discussed his cases of olfactory illusion in terms of presented objects. But he does not make any claim of the sort, focusing instead on states of the environment. But, as we have seen, casting these alleged cases of illusion in terms of mere states of the environment is not enough to address my arguments. As it stands, then, "the apparent actuality of olfactory illusions" does not "call into question Batty's (2010b) claim that olfactory experience lacks object status" (1895)[19]. As I claimed above, more needs to be said to establish this claim.

Stevenson then seems to recognize this when he goes on to claim that olfactory experiences do in fact achieve "object status" (1895). Although he cites other authors who have claimed that olfactory experience achieves object status, it is most helpful to consider what Stevenson himself has argued with respect to this claim. Wilson and Stevenson (2006, 2007) argue for an object-based model of theorizing about olfaction, a model they call the Object Recognition Model (from hereon ORM). In particular, they argue that olfactory experiences represent "olfactory objects." Given that they also refer to these objects as "odor objects," it is safe to assume that, on the ORM, the objects represented in olfactory experience correspond to odors—or, collections of volatile molecules in a perceiver's environment. One of their common examples is the "coffee object."

Returning to a type of view about content that I discussed in section one, we will see that the ORM suggests that olfactory experience is object-involving—that is, that it represents that a particular object is present in your environment as opposed to some object or other, as my abstract view maintains. In turn, this suggests that Stevenson's notion of illusion at this point of his paper is in fact the more robust, traditional notion rather than the "working definition" that he relies on previously. If

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[18] If "environment" denoted anything greater, then we would have to count as veridical cases in which there is nothing at a perceiver that is F, although there appears to be, but in which there is something "farther out" in the perceiver's surroundings that is F—although the perceiver does not take any of that odor in. Presumably we want to still count these cases as non-veridical.

[19] Strictly speaking, I do not deny that olfactory experiences lack object status. I argue that olfactory experiences represent objects, just not particular objects, and not in a way that allows for olfactory illusion. That is, I argue that olfactory experience is not object-involving. Given this, I will assume that by "lacks object status" Stevenson means "is not object-involving."

olfactory experience is object-involving, then it is eligible for misrepresentation in both of the traditional ways. In particular, to return to a previous question, we *can* ask of an object of olfactory experience, *o*:

For any property *F* that *o* appears to have, does *o* really have *F*? (*O-Attribution)*

That is, there is some particular thing of which we can ask, as in *O-Attribution*, "it appears to be F, but is it really as it appears?" But *O-Attribution* is the question that captures the traditional notion of illusion. If the ORM is true, then, my claim there are no olfactory illusions is shown false.

What are we to make of the ORM? If the ORM is to encompass a successful response to my argument against olfactory illusions, then olfactory experience must single out objects in the requisite way—that is, it must be object-involving. As a way of understanding why Wilson and Stevenson think it does, it is important to look briefly at the traditional model of theorizing about olfaction that their ORM aims to replace—and why it does so. They call this model the Stimulus Response Model (from hereon, SRM). Given the history of scientific theorizing about olfaction, we can extract two core claims of the SRM. First, the SRM assumes that olfactory experience is *analytic*—that is, those features of a chemical stimulus that trigger receptor excitation will map onto features of the resulting experience. In other words, the SRM claims that, in some important sense, olfactory experience can be "broken down" into those initial features of the stimulus and/or receptor types sensitive to those features. Secondly, and relatedly, the SRM assumes that a characterization of olfactory experiences is exhausted by an account of how the particular features of the stimulus and/or receptor site are presented in experience. On the SRM, no appeal to objects is necessary to provide that characterization.

According to Wilson and Stevenson, the SRM proves unsatisfactory because olfactory experience doesn't live up to the standards that the SRM sets for it. This is because olfactory experience is, as they tell us, largely synthetic. That is to say, rather than producing an experience of an array of discriminable properties, the various properties of the stimulus produce a largely irreducible experience—a "wholistic unitary percept" (2007, 1821), as they put it. One particularly telling way that they deliver this point is by asking us to consider the complexity of the average odorant stimulus. Much of what we encounter with our noses are chemical mixtures. The coffee odor, for instance, consists of over 600 volatile compounds that together give rise to what we might call the "coffee experience." It is a distinctive experience—one that gets us up in the morning. But it is not an experience in which we are able to discriminate anything close to the number of causally efficacious components of the stimulus responsible for it. As it's been noted in the empirical literature, it is now commonly accepted that even the experts are only ever able to distinguish two or three of the major components that constitute a given odor. So, while the coffee stimulus has a remarkable complexity, it does not have a *perceived* complexity[20]. Compared to the complexity of the stimulus itself, the coffee experience is simple. It's just *of coffee*. But this is not the way that our experience of the coffee odor should be if the SRM is true. Although, as Wilson and Stevenson concede, olfactory experience can fail to be wholly synthetic, if it were analytic, our experience of the coffee odor would be different than it in fact is. We might think that, if the SRM were true, there would be no such thing as *the* coffee smell *per se*—just an array of apparent properties. But there is. Given this, the SRM fails to capture the phenomenological facts of our experience. Wilson and Stevenson therefore conclude that it is a misguided model and must be rejected.

In place of the SRM, Wilson and Stevenson propose the ORM. We already know that such a view is object-based, that olfactory experience represents "olfactory objects," or "odor objects." We also know that it is safe to assume, given to their name, that these objects correspond to odors in our environment. But, what are these perceptual objects? Or, to put it another way, in what sense do odors in the environment show up at the level of experience? Their criticism of the SRM provides the answer to this question. According to Wilson and Stevenson, odors show up as those "wholistic unitary percepts" (2007, 1821), as the synthetic percepts that the SRM fails to predict. The "coffee object," then, is that largely synthetic percept that results from sniffing the coffee odor.

Now, it is not simply because olfactory experience is largely synthetic that Wilson and Stevenson claim it is object-involving. It is rather what it can achieve as a result of its being synthetic that they claim secures the view. According to Wilson and Stevenson, the "defining feature for [perceptual] objecthood" (2007, 1823) is figure-ground segregation, and they argue that olfactory experience can achieve just that[21]. Their reasons for thinking so draw on similar considerations as those of Stevenson's case of constancy of perceived quality[22]. In order to draw attention to how olfactory experience achieves figure-ground segregation, Wilson and Stevenson ask us to consider the complexity of our olfactory environment. At any given moment, we are barraged with volatile molecules given off by the various things in our environment. Insofar as almost everything in our environment gives off these molecules, we can say that *everything smells*. And a remarkable number of those molecules make their way to the olfactory epithelia with every intake of breath. Despite this, our olfactory system is able to achieve the most impressive of discriminatory feats. In the midst of the "confusion" of our olfactory environment, as they put it, we are able to smell *coffee*. The "wholistic unitary percept" (2007, 1821) *coffee* is an apparent figure, one that stands out in the midst of a complex, and noisy, background. This "experiential prominence" in the midst of that noisy background is what Wilson and Stevenson refer to as figure-ground segregation.

It must be noted, however, that, unlike the visual case, Wilson and Stevenson claim that figure-ground segregation is achieved aspatially. According to Wilson and Stevenson, olfactory experience is, in and of itself, aspatial. To return to our previous example, the coffee object is an apparent object—just not one that

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[20] This would explain why we are surprised to hear of the complexity of the coffee odor.

[21] According to Wilson and Stevenson (2007), they adopt this definition from Kubovy and Van Valkenburg (2001).

[22] See page 6 of this paper.

is presented in space. Still, according to Wilson and Stevenson, given experiential prominence and, in turn, the achievement of figure-ground segregation, it is an apparent object nonetheless. After all, figure-ground segregation is, for them, the defining feature of perceptual objecthood and, if correctly characterized as such and achieved, constitutes the presentation of an object. Wilson and Stevenson agree with me, then, in an important respect—namely, that spatial figure-ground segregation is not something that applies to olfactory experience. Other than myself and Stevenson's common focus on standard olfactory experiences, then, there is an additional point of agreement between us. But is this enough to show that, in such cases, olfactory experience presents objects and, in turn, is eligible to be illusory?

As a way of answering this question and in order to compare our respective views, we need to say something more about the ORM. According to Wilson and Stevenson, underlying experiential prominence is the template mechanism that I referred to earlier, in my discussion of Stevenson's case of constancy of perceived quality[23]. Wilson and Stevenson argue that, over time, the olfactory system builds up a store of templates in the olfactory cortex of patterns of receptor input. Once stored, these templates allow the system to recognize those patterns against variable arrays of receptor input. In turn, this kind of processing endows us with important discriminatory abilities such as the ability to smell coffee although there are other smelly things about. Contributing to these achievements, then, are learning and memory. In short, the growing store of templates constitutes learning; drawing on those templates in processing olfactory information amounts to the execution of memory[24].

If experiential prominence is rightly characterized as figure-ground segregation, then Wilson and Stevenson's view is one according to which olfactory experience is object-involving. This is because the very nature of figure-ground segregation is such that it allows a perceiver to single out a particular object in her environment. We must now consider whether experiential prominence demonstrates that olfactory experience is object-involving and, in turn, secures the claim that it achieves figure-ground segregation.

It is not clear that experiential prominence establishes this. The problem lies in the fact that my view is consistent with all of the phenomenological data that Wilson and Stevenson cite. In order to see that this is so, let's return to the coffee example and look at what my view of olfactory representation is able to say about this case. On my view, when we smell the coffee, there is a distinctive property, or set of properties, presented to us in olfactory experience. I will also grant that, in certain circumstances, that property, or set of properties, stands out from other properties instantiated in a perceiver's environment—namely in those circumstances in which we smell coffee. Given the complexity of the olfactory environment, and the way that olfactory experience is given those facts, it would be foolish to deny this experiential prominence. Moreover, I can also grant Wilson and Stevenson's claim that, in olfactory experience, such prominence is achieved in virtue of a relative match between stored templates in the olfactory cortex and patterns of receptor excitation. Where my view will differ from Wilson and Stevenson's is in what the result of that template matching is—that is, in what that experiential prominence amounts to. On my view, it amounts to the presentation of a property, or a small set of properties presented together as a result of that template matching[25]. This much is in keeping with Wilson and Stevenson. But, unlike what Wilson and Stevenson claim, that those properties "show up" at the level of experience indicates the presence of some object—just not any object in particular.

Notice that, at this point, I have granted all of the perceptual data that Wilson and Stevenson cite in favor of figure-ground segregation. In doing so, I stop short of positing that the presentation of those properties, as distinct in a complex environment, amounts to the presentation of a particular object. But, again, it does not stop short at the expense of any of the perceptual data that Wilson and Stevenson cite in favor their view. In particular, and most importantly, that data that they take to be indicative of figure-ground segregation is accounted for without taking that step.

What this shows is that it isn't clear that experiential prominence is best characterized as figure-ground segregation. This is because, as a comparison with my view has demonstrated, Wilson and Stevenson haven't shown that it is an apparent *figure* that shows up at the level of experience. But demonstrating that there is such a figure—or object—is exactly what is required in order to establish that the more robust notion of illusion is one that can occur in olfactory experience. To return to our previous question, Stevenson must establish that *O-Attribution* is a question that we can ask of olfactory experience. But his own "object-based" view of olfactory experience does not. Given this, he fails to demonstrate that my claim there are no olfactory illusions is false.

It is important to note that responding to present worries about ruling out my abstract view requires more that simply drawing attention to the fact that there exist patterns of excitation at the receptoral level, nor to the fact that that such patterns are stored in long-term memory to expedite later olfactory discrimination. What is at issue is whether these patterns and combinations show up, at the level of experience, as perceptual objects. The question is whether the experiential output of template matching—Wilson and Stevenson's "wholistic unitary percepts" or "synthetic odor objects"—ought to be characterized in object-involving terms. And it isn't clear that there are the materials with which to adjudicate between that kind of view and

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[23] Again, see page 6 of this paper.

[24] Wilson and Stevenson say much more about the physical mechanisms underlying what I have referred to as "template mechanisms." For my purposes, it is enough to provide a model of their view.

[25] Here I am not claiming that olfactory experience achieves the perceptual grouping required to solve the Many Properties Problem. I am simply, for the sake of comparison, adopting Wilson and Stevenson's claim that, in some cases, we are able to distinguish two or three components of an odorant stimulus. While they claim that, even in these cases, we are presented with olfactory objects, I here claim that a view that denies that there are such objects can accommodate the data they cite. It is important to note that amongst the data they cite is not the claim that olfactory experience can report on different arrangements of those properties along some dimension—e.g., the spatial dimension. But it is this kind of achievement that underlies the ability of a sensory system to solve the Many Properties Problem.

mine—at least if we are relying on observations of experiential prominence to decide it.

Are we now left at an impasse, with each of us able to account for the relevant data and nothing left to adjudicate the issue? I think that we are not. I grant that figure-ground segregation allows us to single out a particular object in our environment. That is, I grant that figure-ground segregation forms the basis of object-involving content. Wilson and Stevenson agree. But they also assume something stronger than I do: that if the distinction is to apply in the realm of olfaction, it must apply non-spatially. But not only has this revision of the concept proven problematic, it also deprives us of the ordinary spatial notion of figure ground, a notion which we *do* need—just not for humans. To see that this is so, compare our olfactory experiences to those of other animals. The hammerhead shark, for example, enjoys a sense of smell that is directional. Given its extremely wide head, a stimulus coming from the extreme left of the hammerhead's head will arrive at the left nasal cavity before it does the right. If the stimulus is blood, the hammerhead's response is instantaneous— it turns in the direction of its source. I take it that we are quite happy to admit that the hammerhead represents the location of a food source, much in the same way that we are able to represent, via audition, the location of a "bang" outside. In the latter case, we are happy to admit that auditory experience achieves figure-ground segregation—and does so spatially. Given this, it is plausible to conclude that the hammerhead also achieves the same in its olfactory experience. That is to say, the hammerhead shark is a creature that enjoys spatial figure ground representation and thus object-involving olfactory content. Clearly we are not like the hammerhead, as Wilson and Stevenson admit. But it would be strange to conclude that the hammerhead's olfactory experiences are to be evaluated according to one notion of figure-ground segregation, while ours are not. If we are to account for the difference between us and the hammerhead, then, we require the spatial notion of figure-ground segregation.

What this shows is that the spatial notion of figure-ground segregation remains useful in the olfactory case. We can make distinctions with it that we need to make—for example, we can explain the difference between us and the hammerheads. What's more, it allows for a unified notion of figure-ground segregation across the sense modalities. In those types of experience in which we think of figure-ground segregation as achieved—vision, audition and touch, for example—we do so on the basis of the richness of its spatial representation. In those types of experiences in which we worry whether, or wonder if, figure-ground segregation is achieved—arguably olfaction and taste—I take it that we so on the basis of the observation that those types of experiences are not as spatially rich as those where we grant happily that there is figure-ground segregation. What this suggests is that figure-ground segregation forms a kind, one defined by the type of spatial representation achieved by an experience.

If, as I have argued above, we ought to evaluate olfactory experience in accordance with this notion of figure-ground segregation, then we ought to accept my abstract view. And, if we accept that view, then we are committed to accepting three further things. First, we are committed to accepting my analysis of experiential prominence over Wilson and Stevenson's, driven as mine is by the abstract view of olfactory content. Second, and relatedly, we ought to accept my conclusion that there are no olfactory illusions. Finally, given the accuracy conditions set forth by the content of olfactory experience, we ought to accept that the appropriate notion of non-veridicality for the olfactory case is one of property hallucination.

Now Stevenson says little about the notion of property hallucination *per se*, focusing instead on the negative stage of my 2010b argument that there are no olfactory illusions. Still, let me say something further about the benefits of adopting a notion of property hallucination and of a non-object based notion of non-veridicality. Scientists and philosophers alike have long been interested in non-veridicality, or perceptual misrepresentation. But it has also been assumed that non-veridicality falls into one of two categories—illusion and hallucination. As I noted in section 1, these ordinary notions each involve the misrepresentation of objects, or "object-failure," as I have called it. It is true that, with property hallucination, I am also talking about non-veridicality. But what is interesting about property hallucination is that it is a form of non-veridicality that current accounts of non-veridicality do not allow for, focused as they are on the representation of particular objects. Drawing attention to property hallucination, then, identifies a new category of non-veridicality. Given that both scientists and philosophers have been interested in the information putatively conveyed in olfactory experience, and the nature of the ways in which experience may misinform a subject, the introduction of property hallucination presents a novel way of thinking about, and categorizing, olfactory misrepresentation.

But the interest of property hallucination for olfaction is not only restricted to the olfactory case. It is also helpful in driving further thinking about perceptual experience in general. That is, its introduction forces us to re-think the nature of veridicality and non-veridicality more generally across all of perceptual experience. For example, the notion of property hallucination opens up the possibility that there are cases in other modalities that are best characterized as those in which we do not perceive particular objects but only certain properties, and that this novel notion of non-veridicality best accounts for those cases. One case that I have discussed previously is the visual experience of looking at a uniformly colored expanse[26]. To be sure, this is not a typical visual experience, as I argue the analog case for olfaction is; but it is one that, if in fact a misrepresentation of color, is plausibly categorized as a case of property hallucination. A third category of non-veridicality, then, is incredibly interesting because it allows us to look deeper at the experiences of other modalities, comparing and contrasting the ways in which experiences in those can mislead.

Finally, adopting my third category of non-veridicality directs our attention to the possibility that there might be even further categories of non-veridicality—whether these other, previously unconsidered notions turn out to be categories in their own right, or sub-species of those we already adopt. Not only, then, does my notion of property hallucination introduce a new category that we previously lacked in describing perceptual misrepresentation; it also directs attention to the possibility that our account

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[26] See for example, Batty (2011).

of non-veridicality might be lacking in further, equally interesting, ways. And this further result, I take it, would be interesting for philosophers and scientists alike.

CONCLUSION

Earlier I promised to say something further about what I labeled Stevenson's (2), namely his claim that olfactory illusions typically escape notice. Obviously I disagree that they do. I argue that there are no olfactory illusions and so there is nothing in this case to escape our notice. Still, my abstract view of content can explain why we might think, like Stevenson claims, that the difference between olfaction and other modalities, "relates to issues of verification (i.e., ones [sic] capacity to independently confirm what one is smelling" (1888). To take the case of vision as an example, it is easy to see how we are able to verify what we seem to see. In the case of visual experience, because we are able to discriminate individual objects, we are able to ask, and in principle capable of verifying, whether *that object* is in fact in the scene before our eyes. Given that it is presented as such, we are also in principle capable of verifying whether the properties it appears to have are those that the object in fact has. In each case, we go out and explore the environment; we go to that object that we appear to see and "interrogate" further. These two capacities for verification are implied by our previous two questions about misperception, *V-Existence* and *V-Attribution*.

But, as I have argued, the olfactory analogs of each—*O-Existence* and *O-Attribution*—do not in fact apply to olfactory experience. This is because there are no presented objects in olfactory experience; olfactory experience is not object-involving. It is unclear, then, how we are able to verify what we smell. Like the visual case, we may very well explore our environment further; but it is not the case that we are able to pinpoint that object we appear to smell and "interrogate" it further. The most we are able to do is locate those properties we appear to smell, to determine if it is in fact what we thought it was, or if it appears to be elsewhere around us. But notice that this is just to ask after whether a property, or set of properties, is instantiated in the environment. It is not to ask after any particular object.

It is no wonder, then, we feel suspicious about our abilities to verify our olfactory experiences. We simply are unable to do so in the same way as we are in the visual case. But, unlike what Stevenson claims, this difference is a result of the fact that there are no presented objects. In fact, if we take Wilson and Stevenson at their word, then it would seem that we *would* be able to verify what we smell in the much stronger sense of "verification" present in the visual case. That is, we ought to be able to pinpoint a particular object in our environment and ask after it. But we cannot. Not only, then, is abstract view vindicated with respect to its claims about olfactory illusions; it is also able to explain those considerations about verification that, as it turns out, Stevenson himself is unable to accommodate.

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Olfaction, valuation, and action: reorienting perception

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In the philosophy of perception, olfaction is the perennial problem child, presenting a range of difficulties to those seeking to define its proper referents, and its phenomenological content. Here, we argue that many of these difficulties can be resolved by recognizing the object-like representation of odors in the brain, and by postulating that the basic objects of olfaction are best defined by their biological value to the organism, rather than physicochemical dimensions of stimuli. Building on this organism-centered account, we speculate that the phenomenological space of olfaction is organized into a number of coarse affective dimensions that apply categorically. This organization may be especially useful for coupling sensation to decision making and instrumental action in a sensory modality where the stimulus space is especially complex and high dimensional.

Keywords: piriform cortex, value encoding, olfactory bulb model, affective neuroscience, hedonic valence, categorical perception, object perception

Describing the phenomenology of smells is notoriously difficult. Why is this? One idea is that odor percepts are "impoverished," as they are initially processed by phylogenetically older parts of the brain via a shallow processing stream, with no obligatory relay in the thalamus. By this logic, olfaction is presumed to be something like visual sensation in cortically blind individuals: there is some basic stimulus awareness, but stimuli simply are not perceived in a feature-rich way that provides grist for analysis and description. One might, alternatively, interpret the putative computational shortcomings of olfaction as artifacts of the representational problem to which the olfactory system is addressed. Visual and auditory processing transform topographically encoded physical quantities into representations of stable object properties that facilitate physically interactive behavior like object recognition, reaching, grasping, orienting, or avoiding. Olfactory processing, on the other hand, begins with a diverse, high dimensional, and niche-specific set of physicochemical stimuli (Bargmann, 2006), and yields affective responses that facilitate the evaluation of the biological significance of stimuli. These object features and phenomenological responses don't sort easily into a clear metric for organizing and understanding either the physicochemical space of odorants or the phenomenal space of olfactory experience. The conjunction of these facts about the disorderly stimulus space and phenomenology of olfaction has led some philosophers to question whether olfactory percepts have any representational content at all (see Batty, forthcoming):

> "Smell has little in the way of apparent structure and often floats free of any apparent object, remaining a primitive presence in our sensory manifold"
>
> (Chalmers, 1996)

> "Phenomenologically speaking, a smell is just a modification of our consciousness, a qualitative condition or event in us"
>
> (Lycan, 2000)

> "a sensation of [smell]. . .may have no representational content of any sort, though of course the sensation will be of a distinctive kind"
>
> (Peacocke, 1983)

Recent research suggests that philosophical skepticism about the representational capacities of olfactory perception is a straw man, and more importantly, perhaps beside the point. Stimulus representation isn't the primary business of olfaction. Rather, its job is solving a problem of valuation, rapidly encoding the biological salience of a stimulus and priming our multisensory representation of it to contextually appropriate action.

We develop our perspective in two parts. We first review physiological and functional imaging studies showing that it is quite appropriate to regard odors as objects – that is, as perceptual phenomena bearing most of the hallmarks of object-based processing. In doing this, we underscore the critical idea that the "feature-poor" nature of odor objects is not a bug, but rather an important computational feature of the system tagged to the function of olfactory representations in the broader cognitive economy of human perceptual systems. In fact, the olfactory system is amply equipped to represent information about discrete molecular features, yet actively discards or reformats these representations in favor of more economical or parsimonious representations. In the second part of our perspective, we speculate on what these representations might be. In brief, we suggest that the objects of olfaction consist of coarsely specified and categorical affective dimensions that each serve as an invitation to a prescribed kind of action or consummatory behavior. By "affective," we mean to designate bodily states that carry information about the biological value of a stimulus, and that serve as the foundation for approach and withdrawal behaviors. We propose that a given odor percept is a coordinate point along one of these dimensions, and furthermore that these dimensions are best defined from the perspective of the organism in an ecological context.

This "reorienting" of perception may help develop a satisfying philosophical stance on olfaction that also provides impetus for physiological study.

ODORS AS OBJECTS

Philosophical skepticism about the representational capacities of olfaction arises as a question about the nature of olfactory percepts: do smells represent discrete, publically shareable perceptible objects as visual percepts do or are they more akin to subjective feelings, affective states that carry interoceptive information about bodily state? We think that this distinction is ill-formed. For instance, a range of recent studies demonstrate that many of the hallmarks of object-based visual processing readily apply to olfaction. We can, for example, segregate an odor from its surround, recognize discrete, non-overlapping "views" as representations of the same odor object, categorize different odors as exemplars of the same type, and discriminate individual stimuli within categories of odor objects (Stevenson and Wilson, 2007; Gottfried, 2010; and references therein). Critically, however, the chemosensory features that support this kind of object-based processing are unavailable to conscious awareness. The olfactory system therefore extracts information about the ensemble of structural features in a molecule and uses it to discriminate and identify smells in the local environment, as this information is readily encoded in bulbar and early cortical representations of the anterior piriform cortex (APC) (Gottfried et al., 2006; Kadohisa and Wilson, 2006). However, and this is the real rub, the olfactory system ultimately reformats this stimulus information into a range of affective dimensions efficiently tuned to the behavioral needs of the perceiver.

In this regard, it is interesting to consider the different neural codes employed to encode stimulus information by the APC vs. the posterior piriform cortex (PPC). To broadly summarize a number of studies (see Gottfried, 2010), the distributed patterns of odor-evoked activity in APC encode a snapshot of the composite sum of an odor's constituent features as a configural cue. Over time, the connectivity that defines these distributed activation patterns is reinforced and comes to serve as a template, or a cue-dependent, content addressable memory of the constituent image of that odor. In this context a novel view or degraded stimulus might contain sufficient information to activate a memory representation of the target odorant, accounting for perceptual constancy across sniffs and natural ecological variance.

Neural codes in the PPC, in contrast, may encode qualitative perceptual similarities and differences among individual odorants, facilitating the construction of common odor categories that are called upon in categorization and discrimination tasks. Although the distributions of activity for odors differing in perceptual quality are spatially diffuse and overlapping like their APC cousins, multi-voxel pattern analysis (which is sensitive to the particular distribution of activity) in PPC demonstrates that qualitatively distinct odorants elicit unique patterns of activation. Notably, the degree of overlap among qualitatively similar odorants is higher than for dissimilar odorants, and voxel-wise patterns can be used to accurately predict category membership for a given stimulus (Howard et al., 2009). The quality space of conscious olfactory perception thus seems well-modeled as a value space defined by the relative pleasantness of odorants, and shaped in part by associative learning. In this regard, the object information carried in conscious olfactory events is information about the significance of odor sources to our apical and instrumental goals.

ODOR ECOLOGY

As many have noted (Yeshurun and Sobel, 2010), and intuition will confirm, it is trivially easy to report whether one likes a given smell. Notably, this "readiness" to like or dislike doesn't extend to visual stimuli, suggesting there may be range of tacit value judgments that are intrinsic to olfactory objects. Thinking about these phenomenological differences in light of the distinct ecological contexts in which vision versus olfaction predominate can be instructive. Visual objects are sensorimotor representations of stimulus structure that articulate the shape, identity and affordances of objects and events so that we can recognize them, orient our bodies to them and interact with them. Simply stated, fine grained shape information is what we need to accomplish these tasks. An olfactory object, we would argue, is a qualitative judgment of the biological significance of the odor source, its utility to our metabolic needs and the apical goal of survival – an implicit decision about whether something is worth approaching, or is best avoided.

To early single-celled denizens of the pre-Cambrian, counting double-bonds and tallying functional groups on a molecule were probably not useful in themselves. Rather, they were likely only useful to the extent that they led to good decisions about whether toxins, nutrients, and discrete signals from conspecifics were fled, pursued, ingested, or prompted consummatory behavior. An upshot of this view is that it readily explains those well-known cases in which chemicals with quite different structures elicit highly similar percepts (their physical differences aside, they happen to point to the same biological need/want), and vice versa – chemicals that are close "neighbors" in physicochemical space may elicit very different percepts (their physical similarities aside, one is a toxin, say, whereas the other is a nutrient). By carving the phenomenal space of olfaction into a number of prescribed affective categories (which can be plied substantially by experience), evolution may have ensured that olfactory perception is intimately coupled to stimulus-prompted decision making.

THE PRIMACY OF AFFECT, AND ITS MANIFESTATION IN OLFACTORY BRAIN AREAS

The primacy of affect in olfactory experience has long been appreciated, and recent work applying dimensionality reduction techniques to odor profiling databases underscores this basic idea. Khan et al. (2007) and Zarzo (2011) used principal components analysis to identify hedonic valence as a factor accounting for about 40% of the variance in olfactory percepts when a wide range of odors is assessed. Intriguingly, when similar dimensionality reduction techniques were applied independently to the physicochemical space of odors, the major axis of this space – something like "molecular compactness" – was mapped onto hedonic valence. In a sense then, pleasantness is "written into" a monomolecular odorant. In studies extending these sorts of analyses above, a second (though much more speculative) candidate dimension –

"edibility" – has been postulated (Zarzo, 2008). We note that many other candidate dimensions have been proposed by others as well, however, the existence and commonality of these is contested.

Consistent with this claim on the primacy of affect, affect has interesting correlates even in the most peripheral stages of olfactory processing. Whereas the receptor epithelia for vision, audition, and somatosensation are topographically organized to encode information about spatial proximity and/or basic physical variables pertaining to stimuli, the (human) olfactory epithelium appears to represent relative stimulus pleasantness topographically (Lapid et al., 2011). Similar principles of organization by hedonic valence also seem to extend to early central brain representations in both mammals and invertebrates (Haddad et al., 2010).

Building off of this work, we speculate that the affective (hedonic) dimension of olfactory experience is fundamental, and that olfactory categories, as a result, carry information about the behavioral salience of their sources as opposed to the specific identities of either the odorant perceived or its source (see also Mamlouk et al., 2003). We are not claiming that the olfactory system fails to map those features of the sensory periphery that facilitate object discrimination, recognition, etc., Indeed, certain elemental features of monomolecular odor stimuli, including information about constituent functional groups, are readily encoded and available to the olfactory system, as seen above. However, we propose that they are encoded in conscious olfactory experience as a fixed (if potentially quite large) number of coarsely specified affective dimensions. Put more plainly: the olfactory system is not a casual art viewer, who slowly scans the individual brushstrokes on a painting and dithers on whether these add up to something he likes or doesn't. The olfactory system is instead a curmudgeonly and narrow-minded critic who knows he loves Picasso, despises Monet, is indifferent to Kandinsky, and rapidly judges the value of a work by its resemblance to one of these categories.

While pleasantness is undisputably a key organizing dimension of olfaction, and the one that currently has the deepest experimental support, it needn't be the *only* dimension. Organisms may have multiple ways of evaluating odors as good, and multiple ways of evaluating them as bad. For example, floral odors may have one set of affordances (approach, but do not necessarily consume), whereas odors comparable in pleasantness – say citrus odors – may have another set of affordances (approach and consume). In short, olfactory percepts may be defined by multiple categorical affective dimensions, rather than a single smoothly varying dimension.

In our own studies, we recently revisited the issue of perceptual organization in odor profiling data, using non-negative matrix factorization (NMF) instead of principal components analysis, and observed that odor profiles are well described by ~10 perceptual dimensions (Castro et al., 2013). Notably, these dimensions were near-orthogonal, despite the fact that orthogonality is not guaranteed by NMF, and appeared to apply categorically: that is, a given odor tended to belong to one perceptual dimension to the *exclusion* of others. Interestingly, the basic dimensions identified all seemed to have clear ecological value. Future work will be needed to extend these findings to larger panels of odorants, and to test whether there are neural substrates of the coarse affective categorization we propose.

Nevertheless, these sorts of either-or representations may have some observable analogs in olfactory physiology. The possible categorical nature of odor representations is supported by studies performing slow "morphs" between two different odors, in which the concentration of one odor is gradually decreased, while the other is slowly ramped up. In these studies, one observes rapid changes in ensemble activity in the olfactory bulb (Niessing and Friedrich, 2010), implying that at least for some considerations of odor pairs, the bulb has a fixed number of preferred discrete states, rather than smoothly spanning the potential state space. More centrally, at the level of piriform cortex, Yoshida and Mori (2007) have observed categorical representations for food odors in the APC, whereas Howard et al. (2009) have used multi-voxel analysis in human fMRI studies to show clustered hotspots of activity in PPC that correspond to specific odor qualities (minty, woody, citrus, etc).

SUMMARY AND CONCLUSION

By summarizing recent work on object-based processing in olfaction, as well as odor ecology, we have argued that the basic phenomenological objects of olfaction are not things "out there" but rather prescribed affective categories – likely niche and organism specific – to which stimuli are rapidly assigned, and which are richly pliable through learning and with context. We are quick to note, of course, that we are *not* arguing that odor stimuli are irrelevant to this categorization process. Our account is necessarily speculative, but aligns in several compelling ways with existing results, and makes predictions about the types of representations one expects to find in the olfactory system. Contrary to some of the modern philosophical thinking on olfaction, we speculate that a careful and exhaustive cataloging of behaviors supported by olfaction may be a key to understanding the phenomenology of odors.

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Time to smell: a cascade model of human olfactory perception based on response-time (RT) measurement

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The timing of olfactory behavioral decisions may provide an important source of information about how the human olfactory-perceptual system is organized. This review integrates results from olfactory response-time (RT) measurements from a perspective of mental chronometry. Based on these findings, a new cascade model of human olfaction is presented. Results show that main perceptual decisions are executed with high accuracy within about 1 s of sniff onset. The cascade model proposes the existence of distinct processing stages within this brief time-window. According to the cascade model, different perceptual features become accessible to the perceiver at different time-points, and the output of earlier processing stages provides the input for later processing stages. The olfactory cascade starts with detecting the odor, which is followed by establishing an odor object. The odor object, in turn, triggers systems for determining odor valence and edibility. Evidence for the cascade model comes from studies showing that RTs for odor valence and edibility assessment are predicted by the shorter RTs needed to establish the odor object. Challenges for future research include innovative task designs for olfactory RT experiments and the integration of the behavioral processing sequence into the underlying cortical processes using complementary RT measures and neuroimaging methods.

Keywords: olfaction, response-time, affect, emotion, valence, object

INTRODUCTION

A philosophical thought experiment was recently proposed in which two distinct scents were to be imagined in rapid alteration – an "olfactory trill" (Cooke and Myin, 2011). While it is easy to imagine an auditory trill, as in Chopin's *Nocturne, Op 62, No 1*, an olfactory percept that rapidly alternates between, say, a woody note and a floral note, is likely unimaginable to even the most sophisticated nose. A starting point for this review is the observation that the temporal resolution of odor perception is limited, at least compared to that of some other senses. The thought experiment described above suggests that the time-scale of the human olfactory system is a defining feature of olfactory experience (Cooke and Myin, 2011).

The current review focuses on evidence from response-time (RT) measures that suggests how important perceptual attributes unfold in time. Little attention has been devoted to integrating findings from olfactory RTs, despite the fact that the first empirical reports were published nearly a century ago (Zwaardemaker, 1925; Wells, 1929). Although several methods may be used to study olfactory processing speed, this review focuses on RTs generated by button-press responses in olfactory tasks that may be completed in one single sniff. The review discusses findings from detection-RT tasks, which typically require a single button-press response, as well as choice-RT tasks, which involve more than one response option and are thus used to study sensory discrimination and cognitive processing. Experiments that are based on subtle odor differences or complex odor mixtures often require evidence accumulation over several sniffs, and are thus outside the scope of the present article (e.g., Bowman et al., 2012).

A key assumption in studies of human information processing is that performance is mediated by a sequence of time-consuming processes, which include perceptually encoding a stimulus, accessing stored information in memory, decision-making, and preparing and executing an appropriate response (Meyer et al., 1988). Attempts to outline mental processes underlying visual cognition have yielded a vast body of literature. It is beyond the scope of this review to give justice to this literature, but it has been reviewed elsewhere (Luce, 1986; Meyer et al., 1988). Despite the challenges of establishing information processing stages in human olfaction, the field has matured enough to begin to integrate findings within a chronometric framework. Below, I provide a brief overview of the role of time in the neurophysiological and perceptual encoding of odors, followed by an overview of studies on human olfactory RTs. I then introduce the cascade model of olfactory perception based on recent evidence. Finally, I discuss theoretical and methodological issues that may be critical for advancing this line of research. A general theme is that methods of studying olfactory RTs are complementary to neuroimaging methods with high spatial resolution but low temporal resolution.

TEMPORAL ENCODING IN THE OLFACTORY SYSTEM

The issue of time in the neuronal encoding of odors was highlighted in the pioneering works of Maxwell M. Mozell, who discovered that different molecules migrated through the olfactory mucosa with different time-scales. Mozell suggested that "this chronographic differentiation may be one of the mechanisms underlying olfactory discrimination" (Mozell, 1964; Mozell and Jagdowicz, 1973). The time for the transduction of the olfactory stimulus to the nervous system can be approximated to 150 ms (Firestein et al., 1990). These observations have since informed a vast literature on the role of temporal coding in the olfactory system.

Timing is critical for the encoding of odors in the olfactory epithelium and bulb (Schaefer and Margrie, 2007). Studies on several species have shown that olfactory receptor neurons are activated in an odor- and concentration-dependent manner, leading to a temporal pattern of activation that corresponds to distinct stimulus features. Principal neurons in the olfactory bulbs of vertebrates, and the homologous antennal lobes of insects, respond to odor input by changing the timing and frequency of neuronal spikes; these temporal changes enable the behavioral discrimination of distinct odors through a variety of mechanisms (Laurent, 2002). Neurons in the immediate downstream projection sites of the principle neurons (e.g., the piriform cortex in vertebrates; mushroom bodies in insects) read out a converging afferent input that evolves over the time-scale of a sniff. Recent findings from optogenetic imaging in mice suggest that in the mammalian olfactory system, the temporally defined output from the olfactory bulb is translated into a spatial ensemble code at the level of the piriform cortex. The piriform cortex may thus act as a "sequence detector" of output from the olfactory bulb (Haddad et al., 2013). Neurons in the piriform cortex further propagate sparse signals that are highly specific to particular odors. The rapid evolution of an olfactory percept within the sniff cycle is critical for adaptive behavior. Schaefer and Margrie (2007) illustrated the importance of time in odor discrimination by evoking the metaphor of two jigsaw puzzles. When the jigsaw puzzles depict two very similar pictures, many pieces have to fall in place before it may be determined that the pictures are different. When the jigsaw puzzle pictures are very different, only one or a few pieces are needed to make this decision. Analogously, two very similar odors gradually activate glomeruli in the olfactory bulb over the course of a sniff, and a reliable behavioral discrimination may only be established when most or all of these glomeruli have become activated. In contrast, two very different odors may be discriminated early in the evolution of glomeruli activation. It has been suggested that latency patterns of output from the olfactory bulb may contain the most critical piece of information needed for higher brain centers to identify odors (Junek et al., 2010).

OLFACTORY OBJECT PERCEPTION

It is widely agreed that the underlying molecular features of an odor are not directly accessible to conscious experience (e.g., Wilson and Stevenson, 2003). The neural mechanisms reviewed above suggest instead that the "qualia" of human olfactory sensations likely evolve with the time-scale needed for the olfactory cortex to determine the unique spatiotemporal firing properties elicited by a particular odor stimulus. But bottom-up mechanisms are not enough to explain perceptual representations of odors – instead, the neural response to the multiple molecular features of a smell is thought to be synthesized into a unified percept, which is commonly referred to as an olfactory object (Wilson and Stevenson, 2006). These objects are not only the products of molecular features, but also of perceptual memory; odor inputs are matched to perceptual object templates ("engrams") that have been established at prior exposure, and a good match produces a subjective feeling that the odor is familiar (Stevenson and Boakes, 2003). When a chemical component is added to or subtracted from a complex but familiar odor mixture, neurons in the piriform cortex retain a uniform response (Barnes et al., 2008). Such neuronal mechanisms of pattern completion and pattern differentiation help to maintain stable representations of odor qualities and enable odor recognition despite stimulus variability. Olfactory object perception thus resembles visual object perception, but unlike the visual system, olfaction has a limited capacity to process multiple objects in parallel. Instead, molecular odor features interact to produce a unique perceptual quality (Snitz et al., 2013). Although the ability to dissociate odor features may be enhanced somewhat through training, most individuals are not capable of distinguishing three or more familiar odors when they are presented in a mixture (Livermore and Laing, 1996). In humans, this synthetic processing that translates odor features to objects likely takes place in areas such as the piriform cortex (Gottfried, 2010) and the orbitofrontal cortex (Li et al., 2006). The olfactory object-system might modify perceptual odor objects even after only a few minutes of exposure (Li et al., 2006). However, highly familiar odors correspond to well-established odor templates, and using such odors may bring out the full benefits of object-based perception. The overlap between an odor quality and a corresponding template may be empirically established by having participants rate an odor's "perceptual quality," that is, how well a given odor (e.g., rose essential oil) represents an olfactory template (indicated by the label "rose").

BEHAVIORAL RESPONSE-TIMES TO ODORS

OLFACTION AND MENTAL CHRONOMETRY

The use of response latencies as a measure of physiological events in the nervous system was the invention of Helmholtz, who already in the 1850s designed the simple-response time design in which a participant presses a button upon sensing a stimulus (Helmholtz, 1883). Helmholtz showed convincingly that mental processes and their neural underpinnings involve time-consuming events, and paved the way for further chronometric investigation of mental phenomena. Not long thereafter, Donders (1868/1969) invented the binary choice-response time paradigm for rapid stimulus evaluations, which allowed the researcher to address more elaborate psychological questions. Donders also introduced the subtraction method to establish the time-scale of underlying component processes; for example, the speed difference between the time needed to classify a stimulus compared to the time needed to simply detect its presence defines the temporal extent of the "classification" processing stage. Pioneers such as Moldenhauer (1883) and Zwaardemaker (1895) invented olfactory stimulation techniques that paved the way for applying the basic chronometric paradigm to human olfaction.

An early use of olfactory RTs in psychology is a study by Wells (1929), where participants rapidly classified odors as being either pleasant or unpleasant. The results showed that these evaluations of odor valences could be accurately produced with button-press RTs within about 0.9 s of the sniff onset. This result provided evidence that such emotional responses could not be the result of the brains interpretation of a peripheral bodily response, as had been suggested by William James and Carl Lange. Instead, olfactory valences were rapidly and directly produced by the brain.

TEMPORAL INTEGRATION IS PRESENT IN HUMAN OLFACTION

Early research on human olfactory perception established that faint odors were detected more reliably when participants sampled the odor with vigorous sniffs rather than with longer sniffs (Le Magnen, 1945). This finding suggested that odor-evoked activity is integrated over a time-window to generate a signal average, and that the amplitude of this signal determines whether the odor reaches consciousness. This temporal averaging in human olfaction appears to plateau within 500 ms of odor sampling at "natural" sniff velocities. Further increased sampling does not influence odor thresholds or perceived odor intensities. The plateau is thus well-established within a normal sniff, which lasts for about 1.6 s (Laing, 1983, 1985).

ODOR VALENCE AND OVERALL PROCESSING SPEED

A long-standing issue in human olfactory perception is whether certain classes of odors enjoy the privilege of "early access" to the perceptual system due to their great adaptive relevance (see e.g., Doty, 2010). As humans readily evaluate odors based on their valence, and unpleasant odors may be harmful to the organism, it may be hypothesized that unpleasant odors are detected faster than pleasant odors. This hypothesis is congruent with the notion that valence might be rapidly decoded by the brain at the earliest processing levels, and that the neural response to odor valence provides input to all further sensory analysis (Yeshurun and Sobel, 2010). The early study by Wells (1929) found that detection-RTs were the same for pleasant and unpleasant odors. Since that early negative finding, a few studies have directly compared the latencies of detection-RTs and choice-RTs for unpleasant and pleasant odors. In a study using unirhinal odor stimulation, Bensafi et al. (2001) found that unpleasant odors yielded shorter RTs than pleasant odors. However, this effect was only present during valence assessment, and not during detection, familiarity, or intensity assessments. Moreover, the effect was only seen for right-nostril stimulation, and not for left-nostril stimulation. Similar results followed from an experiment with odorants lacking trigeminal effects (vanillin and indole; Bensafi et al., 2002). Since the olfactory nerve projects ipsilaterally to downstream sites, the authors interpreted their findings within a framework of emotional lateralization, and concluded that emotional processing of unpleasant odors was emphasized in the right hemisphere. A further experiment found that unpleasant odors were processed faster than pleasant odors, but again, this effect was only present in valence evaluations and not in detection, intensity, or familiarity assessments (Bensafi et al., 2003). While the results from these studies show that odor valence is lateralized, they do not show that unpleasant odors have "early access" to the olfactory-perceptual system, as this would have resulted in faster RTs independent of task and nostril. Instead, the results are compatible with the notion that odor valence was determined downstream, as the lateralized effects of valence did not carry over to other tasks, as would have been the case if odor valence evaluation was an early and mandatory stage in a causal processing chain.

More recent studies have focused on odor detection-RTs but have provided mixed results. One study reported shorter RTs for an unpleasant odor compared to a pleasant odor over a range of concentrations (valeric acid and isoamyl acetate; Jacob and Wang, 2006). Another study investigated RTs in a detection task for four different odors that represented variation in both perceived valence (high/low) and edibility (edible/inedible; Boesveldt et al., 2010). The results showed that an unpleasant odor from an edible source (resembling fish) was the most rapidly detected within the odor set. Among odors from inedible sources, there were no differences according to valence. While the authors expressed caution because data were only obtained for one odor per category, it was proposed that humans might have evolved a mechanism for the rapid detection of ecologically relevant food odors that warn of potential danger (i.e., unpleasant odors emanating from edible sources). However, a recent study did not find such RT differences between a pleasant and an unpleasant food-related odor in a detection task (La Buissonniere-Ariza et al., 2013). In our studies on RTs for a wider range of odors, odor valence is not correlated with RTs in detection, identification, valence, or edibility decision tasks, whether the odor is from edible or inedible sources (unpublished observations).

The results reviewed above have not provided ubiquitous support for the notion that odors are encoded differently depending on their valence. In future studies, certain methodological aspects should be considered. It is unclear whether task-related differences (e.g., simple detection-RT versus binary choice-RT) have contributed to the inconsistent pattern of results. Most previous studies did not include assessments of how familiar the odors were to the participants or how well the odors matched familiar object templates, but such variables may influence olfactory RTs. For future investigation, it might be hypothesized that if the human brain had evolved a particular system for rapidly encoding intrinsically unpleasant odors (assuming such odors exist), this processing advantage is likely to be stronger for complex natural odors that are often encountered in the environment rather than unfamiliar monomolecular odors, and to manifest in detection-RT tasks as well as in downstream processes assessed with choice-RTs, such as classifications of valence and edibility and matching odors to labels or pictures. These criteria have not yet been met. In fact, while particular odors may be more rapidly detected than others based on a variety of stimulus factors, available evidence from olfactory RTs suggests that odors may not be encoded differently depending on their valence.

A CASCADE MODEL OF HUMAN OLFACTORY PERCEPTION BASED ON CHOICE-RTS

The idea at the center of this review is that the speed of olfactory decision-making, assessed with choice-RTs, may be theoretically informative as to the fundamental psychological processing of odors. The flow of information within the olfactory system upon sensory input may be described as a cascade; a causal chain of rapidly unfolding perceptual features. RT measurements may be particularly useful to map this olfactory cascade. Of particular relevance to this discussion are theories that assume radically different activation sequences of olfactory-perceptual features (Wilson and Stevenson, 2003, 2006; Yeshurun and Sobel, 2010). According to the object-centered account, odor objects are constructed early in the processing sequence. The result of the object processing feeds into other systems to determine valence, edibility, and other important attributes, based on previous experiences with the odor object. In contrast, the valence-centered approach assumes that odor valence is determined by molecular stimulus features (Khan et al., 2007). Through evolution, mammals developed mechanisms by which the intrinsic odor valence is rapidly and effectively decoded (Yeshurun and Sobel, 2010). The stimulus-driven, intrinsic valence of odors might also be decoded from cortical processing patterns (Haddad et al., 2011). According to this view, semantic analysis of odors is impaired relative to the visual system because odor names and identities have to be reconstructed from their unique valences, which is a very difficult task (Yeshurun and Sobel, 2010).

Below, I present a cascade model that offers a chronometric approach to understand human olfactory perception. It emphasizes the succession of processing stages that unfold when we encounter a recognizable odor. This model is based on recent RT evidence from odor detection, object categorization, label matching, valence, and edibility evaluation tasks that reveal how different features of the olfactory percept unfold in time. These studies involve binary choice-response tasks in which the odor set, sniffing behavior, and button-press response format were the same for all odor tasks. The RT differences between tasks are therefore assumed to roughly reflect the time required for the task-specific olfactory-perceptual computations. The principal features of the cascade model are reviewed below.

EARLY ACTIVATION OF ODOR OBJECTS

A key assumption of the cascade model is that differences in RTs across tasks are indicative of processing stages within the olfactory cascade. Tasks that are faster to carry out for a given set of odors engage in earlier processing stages than tasks that require longer processing times. The first stage of odor processing is detecting odors, regardless of their quality. We have found that in a sequence including 50% blank trials and 50% odor trials of varying odors, detection takes about 800 ms from the onset of the sniff-cue to an accurate button-press response that confirms an odor is present (Olofsson et al., 2013a). Previous studies have yielded similar RTs (Wells, 1929; Laing, 1986; Laing and MacLeod, 1992).

The task of odor matching to labels is a method of probing access to odor objects, and objects may be established early in the processing sequence (Stevenson and Boakes, 2003; Wilson and Stevenson, 2006). In the matching task, a label is presented prior to the odor; when the odor is released, participants indicate whether it is congruent or incongruent with the label. As predicted from the object-based account, odor matching to labels was executed with near-ceiling level accuracy at about 1000 ms after sniff onset (Olofsson et al., 2013a). This result suggests that an odor object is established at about 200 ms following detection. Evaluations of valence (rapidly choosing whether the odor was pleasant or unpleasant) and edibility (rapidly choosing whether the odor came from an edible or inedible source) were carried out at a slower speed of around 1100–1200 ms. Binary evaluations of odor valence and edibility were significantly slower than the evaluations of odor objects. Follow-up analyses confirmed that odor valence and edibility RTs were not affected by odors that were ambiguous in their valence or edibility, which could have prolonged RTs. The RT advantage of odor object processing before valence processing was also found in a recent study that used a different task design (Olofsson et al., 2012). In that study, two categorization tasks were constructed – one requiring access to objects and one requiring access to valences – in which two odors were delivered on two consecutive sniffs. The object-task was to classify the second odor as belonging to either the same object category or a different category as the first (odors belonged to one of four categories: floral, fuel, mint, and fish). The valence task was to determine whether the second odor was more or less pleasant than the first. Results showed slower RTs and plenty of internal inconsistencies in the valence task compared to the object category task, consistent with the object-based approach to olfactory perception. Even when omitting "difficult" trials in the valence task (i.e., those that included two similar odors) from analysis in order to achieve similar accuracy rates across tasks, responses were slower in the valence task (Olofsson et al., 2012). The results suggest that odor objects are processed before valence and edibility evaluations in the olfactory system.

OBJECT-LEVEL SEMANTIC PRIMING

Semantic priming is a facilitation of stimulus processing that is based on extracting the meaning of a prior stimulus. By using verbal cues to prime odor-based decisions, information may be gained about the olfactory system. When the trial structure includes a verbal cue (e.g., "orange") that is followed by an odor that is either matching or non-matching to the cue, choice-RTs to the odor are decreased when odors are matching (orange odor) compared to non-matching (other odors) (Olofsson et al., 2012). Odor processing is thus facilitated by the information provided by the cue. In contrast, cues that provide categorical information about the odor valence (e.g., "pleasant") do not facilitate processing speed for congruent odors (e.g., orange odor is regarded as pleasant). This supports the notion that specific object templates may be preactivated by a verbal cue at an early-stage of processing (Stevenson and Boakes, 2003). Similarly, functional magnetic resonance imaging (fMRI) results suggest that a cue that instructs the participant to focus on an odor in a binary mixture leads to a "pre-activation" of a neural pattern of activity in the piriform cortex prior to the odor delivery; this pattern resembles the pattern of activity that is activated by the odor itself (Zelano et al., 2011). This result and other findings from pattern-analyses of fMRI data (Howard et al., 2009) suggest that templates for odor objects and categories are encoded as distributed patterns of activity in the human piriform cortex.

As it was proposed that odor valence is encoded at the earliest perceptual stages (Yeshurun and Sobel, 2010), we investigated whether valence similarity between the label and the odor would cause semantic interference in the priming task. It was predicted from the valence-based approach that when the label of a pleasant odor (e.g., the word "lemon") was followed by a similarly pleasant odor (e.g., the odor of rose), participants would need more time to decide that the trial was incongruent because these odors have similar valence, but when the label "fish" was followed by the odor of rose the RTs would be shorter. However, there was no such interference from valence on the odor object processing speed (Olofsson et al., 2012). In sum, semantic priming was only effective at the level of odor objects. These results indicate that valence does not affect semantic analysis at the early object stage, but support the notion that odor valences are computed after odor objects.

CAUSAL RELATIONSHIPS AMONG PROCESSING STEPS

A key aspect of the cascade model is that different processing stages are causally related (i.e., at least partly "serial" rather than completely "parallel" processing), and that these relationships manifest as temporal contingencies that can be measured with RTs. As causal relationships cannot be directly observed, they must be inferred from temporal covariation. **Figure 1** illustrates hypothetical RT outcomes in a case where there is a causal relationship between these constructs, and a case where there is no such relationship. We used regression-based analyses to model the assumed causal relationship between odor detection, odor object identity, odor valence, and edibility (Olofsson et al., 2012, 2013a). The hypothesis, derived from the object-based approach, was that the time needed to conduct a perceptual decision about the valence or edibility of a given odor would be systematically delayed by the time it took to establish its perceptual object. Although object-based RTs for a given odor may differ across individuals, the cascade model assumes a systematic prolongation of valence and edibility decision times for the individual. In our first experiment (Olofsson et al., 2012), we were able to successfully predict valence-based categorization RTs from the more rapid object-based categorization RTs using a regression approach. The effect occurred after controlling for differences related to participants, as well as stimulus factors. This result suggested not only that objects were established before valences, but objects also appeared to trigger valences in a causal way. In a subsequent experiment (Olofsson et al., 2013a), we further supported this notion of causality using mediation analysis (Preacher and Hayes, 2004). We modeled the pathway from odor detection to valence and edibility via odor object identification as a mediating variable. We constructed a mediation model of the RT data that included a "direct" processing route from detection (the predictor) to valence (the outcome), and an "indirect" route linking detection and valence by way of identification (the mediator). By determining the significance of the direct and indirect routes, the model tested whether the relationships between our key variables would conform to either parallel routes (no mediation), a serial (mediated) route, or dual-processing routes (both mediated and unmediated). Results indicated dual-processing routes to odor valence; object-mediation played a significant role in processing odor valence, but there was also information that bypassed objects. When replacing valence RTs with edibility RTs as outcomes, the result suggested a complete mediation of edibility by odor objects (serial route). However, when adding valence as a second mediator to determine olfactory edibility RTs, the explained variance of edibility RTs increased further. That result suggested that the valence RT for an odor helps to determine its edibility RT. Thus, in two experiments we showed that not only were object decisions faster than valence and edibility decisions, but that there also appeared to be a causal connection such that objects trigger valence and edibility evaluations. The results from RTs in the different olfactory tasks, combined with the results from mediation analysis, are summarized in an illustration of the cascade model (**Figure 2**). The figure shows how different processing steps are activated at different time-points upon the receipt of an odor and which processing routes are activated to complete a given task. When a decision is made, the corresponding motor response is executed. As shown in **Figure 2**, the processes unfold at different time-points and are causal in that earlier processes mediate later processes. The pathways in the figure are inter-connected, which is supported by the result that the relatively long RTs of odor edibility are better predicted from a combination of the shorter RTs of several upstream processes.

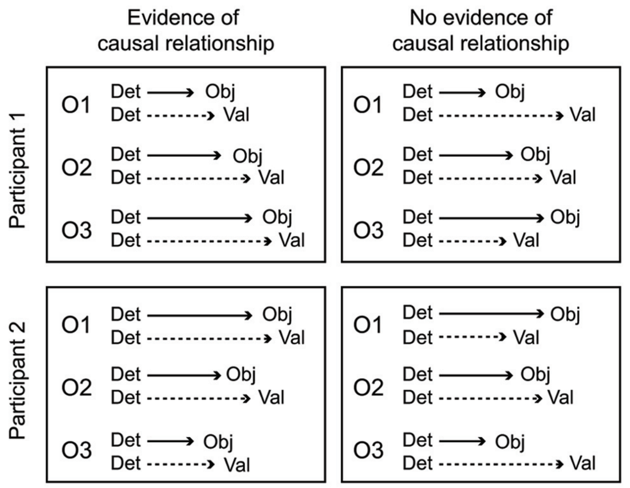

FIGURE 1 | Hypothetical RT outcomes in one case of causal mediation of odor valences by objects (left panel), and one case of no causal relationship between object processing and valence processing (right panel). In both cases, data from three odors (O1, O2, O3) have been aligned to the time of odor detection, a starting point for further conscious processing. A causal relationship between odor objects and valences is inferred in the left panel because odor valence decisions are executed at a predictable lag following object decisions. However, in the right panel these decisions are uncorrelated, and completely independent processing pathways cannot be refuted. The causal relationship in the left panel holds for both hypothetical participants, even though the olfactory processing speed is fastest for O1 in participant 1, but fastest for O3 in participant 2.

FUTURE DIRECTIONS

Although human olfaction may be regarded as a slow and imprecise sensory system, studies of olfactory RTs show that untrained participants are able to carry out rapid olfactory-based decision-making. In fact, after subtracting the time needed for sniff onset (about 200 ms; Olofsson et al., 2012), chemical interactions with the olfactory receptor neurons (about 150 ms; Firestein et al.,

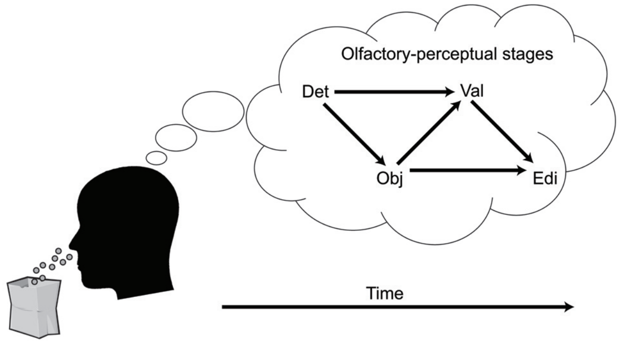

FIGURE 2 | A cascade model of olfactory perception. The figure proposes four stages of perception that unfold upon an olfactory input: Detection (DET), Object processing (OBJ), Valence (VAL), and Edibility (EDI). Decisions that require processing at later processing stages are mediated by processing at earlier levels.

1990), and the time required to execute a behavioral response on a visual cue without olfactory involvement (about 300 ms; Brown and Heathcote, 2008), major olfactory decisions may be confined to a rapidly unfolding cascade of inter-connected processing steps within a 500 ms interval. Within this interval, recent results suggest that odor detection is followed by the establishment of an odor object, which in turn is used to activate valence and edibility evaluation systems (Olofsson et al., 2012, 2013a), an outcome that aligns with the object-based approach to olfactory perception (Wilson and Stevenson, 2006). Challenges for future research are discussed below.

CONCEPTUAL ISSUES

A key challenge for future research is to develop new experimental designs by which to assess the sequence of processing stages in the human olfactory cascade. It should be noted that there is not yet a consensus on what the major olfactory processing features are, or how they should be measured in an unbiased way. Although the available evidence suggests that odor objects exist, that they are established early in the processing stream, and that they causally mediate responses in other perceptual tasks, the sequence proposed in the cascade model needs to be further validated across different task designs. Insights into how different operationalizations affect olfactory processing speed will minimize the risk of bias. For example, it may be assumed that valence is a continuous construct whereas the odor objects (or functional categories) are binary constructs. Thus, a binary assessment of odor valence in previous studies might have put the valence dimension at an operational disadvantage. However, this operationalization was motivated by theoretical concerns. According to the valence-based approach, continuous valence encoding is the starting point for olfactory processing (Yeshurun and Sobel, 2010), including any binary categorization into floral, fuel, mint, or fish odor groups, or deciding whether an odor matches the label "lemon." Such object evaluations are effortfully achieved only after the exact valence of an odor is decoded. Therefore, under the assumption of the valence-based approach, it should be impossible for participants to complete an object-categorization task faster than a valence-categorization task. However, as reviewed above, such results emerged consistently (Olofsson et al., 2012, 2013a). If, on the other hand, this assumption is abandoned for a view that odor objects and object categories are binary constructs, but valences are continuous constructs, there is still a possibility that odor valences may in fact be processed early, even though this early processing did not manifest in short RTs in previous studies. However, available data do not support the notion that valence processing speeds were at a disadvantage because of the binary tasks used in previous studies (Olofsson et al., 2012, 2013a); for example, odors of ambiguous valence (e.g., garlic odor was often evaluated by participants as mildly unpleasant) did not generate slower RTs than more extremely valenced odors such as fish (Olofsson et al., 2013a). However, binary valence decisions (e.g., indicating that an unpleasant fish odor was unpleasant) were slower and less accurate than object decisions for the same odor. This finding appears difficult to reconcile with any model in which valence is processed faster than objects. Instead, the available evidence from detection-RTs and choice-RTs indicates that odor valence is not encoded at the earliest stage of odor perception, but is instead slower and more inconsistent than evaluations related to odor objects. While previous studies were designed to assess predictions from the object-based and valence-based approaches to olfaction, future studies should not be constrained by these specific theories and instead focus on constructing novel task designs that might provide further converging evidence as to how the olfactory cascade unfolds over time.

INTEGRATION OF RESULTS FROM RTS AND CORTICAL METHODS

The cascade model of human olfaction suggests that RT measures of olfaction may provide a new source of information into the hierarchical nature of the olfactory system. The idea that olfactory processes are organized in a hierarchical fashion is not new, but it has until now been supported mainly by lesion data (e.g., Zatorre and Jones-Gotman, 1991; Olofsson et al., 2013b) and functional neuroimaging data (e.g., Savic et al., 2000). As the olfactory system is characterized by extensive feedback loops between higher and lower centers, functional neuroimaging methods may not easily dissociate "early-stage" activation from recurrent activation through feedback from downstream centers. Structural neuroimaging techniques may be used successfully in groups with focal neurological damage to reveal hierarchical functions within the olfactory system. However, compensation and reorganization effects following a lesion preclude definitive conclusions (Rorden and Karnath, 2004). The olfactory cascade model assumes that tasks that produce shorter RTs are computed upstream from tasks that produce longer RTs, and that a temporal contingency between these RTs required to carry out two different tasks (e.g., establishing objects and valences) on an odor-by-odor basis is evidence of a causal link between the mental operations required to carry out the tasks. The logic underlying the olfactory cascade model makes it complementary to functional and structural neuroimaging methods.

Event-related potentials (ERPs) might provide a means to monitor the rapid unfolding of olfactory-cognitive processing stages in real-time. So far, there has been little theoretical integration of results from olfactory ERPs and results from RTs. Perhaps this is partly due to the fact that effects of stimulus intensity and individual differences on ERPs are profound and may overshadow more subtle cognitive processing signatures (e.g., Hummel et al., 1998; Olofsson and Nordin, 2004; Nordin et al., 2005; Olofsson et al., 2005). From the perspective of the olfactory cascade model, semantic priming paradigms may be particularly suitable to investigate ERP responses in olfactory decision-making. In semantic priming paradigms, the ERP differentiates between semantically incongruent and congruent targets in a negative deflection known as the N400 effect (Kutas and Hillyard, 1980; Kutas and Federmeier, 2011). Only a few studies have used odor targets to elicit an N400 component (e.g., Grigor et al., 1999; Safarzi et al., 1999; Kowalewski and Murphy, 2012). Little is yet known about the exact timing and neural generators of the olfactory N400. But future investigations might integrate ERPs with behavioral RT paradigms to probe the neural correlates of the olfactory cascade as it unfolds in real-time.

CONCLUSION

Time is a critical feature of the neural processing of odors in the olfactory epithelium and bulb. This review shows that time might also be essential for understanding the psychological processing of odors. The temporal resolution of olfactory perception appears to be confined within the time limits of a sniff. As our system for conscious odor perception likely co-evolved with the respiratory system by which we sample odors, our failure to imagine high-frequency "olfactory trills" might be expected. Despite these constraints, recent studies that measure RTs for odors reveal that several perceptual processing stages unfold in a cascade-like manner already within the first second following sniff onset. These findings provide the basis for a cascade model of human olfactory perception. According to the cascade model, odors are encoded through distinct processing steps that are causally related: detection, object, valence, and edibility. For a given odor and individual, the time needed to establish the odor object will influence the time needed to establish valence and edibility decisions downstream. Challenges for future studies include the invention of novel task designs to assess key olfactory processing features, and the integration of behavioral results with assessments of cortical processing. Such developments will further elucidate how odor evaluations rapidly unfold as a causal sequence of mental operations within the time-course of a sniff.

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Multiple sources of conscious odor integration and propagation in olfactory cortex

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INTRODUCTION

How do airborne plumes of molecules docking on olfactory receptors emerge as conscious odors in the brain? How are they interpreted in space, time, and biological meaning? And how do they lead to fast and adaptive decisions and actions?

In general, conscious (reportable) perception supports neural adaptation to novelty, judgments of self-relevance, and voluntary decision-making. Conscious processes have a number of established properties that are markedly different from unconscious ones (Seth et al., 2005). A growing experimental literature has explored conscious perception with a wide array of recording techniques. Similarly, conscious olfaction "as such" can be studied by comparing novel vs. habituated odors, attended vs. unattended ones, and rivaling olfactory percepts, comparable to visual rivalry (Stevenson and Mahmut, 2013). State comparisons of odor processing during waking vs. sleep, general anesthesia, and impaired consciousness are also important.

Neural activity underlying conscious percepts should follow the known psychophysical features of the stimulus. A specific conscious odor should correspond to a specific trajectory in the olfactory perceptual space derived from psychophysical stimulus matching and discrimination (e.g., Berglund et al., 1973; Koulakov et al., 2011).

Global workspace theory (GWT) has been used as a framework for experimental studies of conscious brain processes for more than two decades, leading to a family of related models and experimental predictions. GWT begins by analyzing a reliable set of properties of conscious events (Baars, 1988, 2002). For example, while conscious perception shows limited momentary capacity, it also supports access to non-conscious functions, like memory, executive control, and automatic skills (Baars and Franklin, 2003). By comparison, unconscious stimuli do not afford such very widespread access to unconscious brain capacities.

In general terms, a global workspace (GW) is a functional hub of binding and propagation in a population of loosely coupled signaling elements, such as neurons (Izhikevich, 1999). A GW is commonly compared to the stage of a theater, or a playing field in a large football arena, allowing many specialized knowledge sources to compete and cooperate to resolve focal problems. GW architectures are useful to resolve ambiguous and novel stimuli, such as words in natural language. Conscious percepts often result from a process of ambiguity reduction, and GW architectures have therefore been proposed as models of conscious perception. They are also consistent with highly interactive information flow in the cortico-thalamic (C-T) system (Baars et al., 2013). Edelman et al. (2011) suggest that GW theory is consistent with Neural Darwinism and its many ramifications.

GWT predicted widespread "broadcasting" of conscious events, a prediction that is now widely accepted. In a recent study of visual rivalry in the macaque, content-specific "global broadcasting" from temporal to lateral prefrontal cortex was observed for both oscillatory population signaling and multi-unit recordings (Panagiotaropoulos et al., 2012). Similarly, long-distance cortical phase-linking is associated with the waking state but not slow-wave sleep (see Baars et al., 2013 for a review). In general, conscious sensory input has been repeatedly found to evoke more widespread, high amplitude, and phase-linked oscillations in cortex.

Baars et al. (2013) have proposed that neuronal source coalitions may emerge anywhere in cortex, becoming subjectively conscious and reportable when a convergent winner-take-all source coalition comes to a momentary equilibrium, able to drive many other regions. During the waking state the visual cortex shows reentrant signaling among more than 40 visuotopical maps (Steriade, 2006). In vision the occipito-temporal cortex identifies the perceptual features that emerge in consciousness, from high-resolution visual details to lower-resolution object and event representation (IT and MTL). For the sight of a visual coffee cup or a flower garden, input convergence is believed to occur at high levels of the visual hierarchy, including object perception in area IT and event perception in MTL. However, a simple stimulus, like the sight of a single star on a dark night, might equilibrate early in the visual hierarchy, since areas V1 and LGN have the highest spatial resolution. This highly flexible version of GWT in the C-T system has been called Dynamic GWT (dGWT).

Thus, visual cortex may integrate visual gestalts and broadcast them to frontoparietal, anterior temporal, and subcortical regions. In contrast, non-sensory "feelings of knowing" (FOKs), including expectations and intentions, may arise and propagate from frontal and anterior-temporal regions to caudal sites (Cole et al., 2010; Baars et al., 2013).

Direct brain recordings in human patients show widespread neocortical signaling by way of cross-frequency phase-linking among cortical arrays, especially theta-gamma and alpha-gamma signaling. Single neurons have been shown to phase-adapt to dominant theta oscillations, suggesting a mechanism by which individual neurons may be recruited by population oscillations. Such spatiotemporal coding allows for an extremely rich signaling vocabulary, but specific coding schemes are just beginning to be understood (see Baars et al., 2013 for a review).

CONCEPTUAL FRAMEWORK

Stimulus ambiguity is pervasive in the natural world. Even simple stimuli like a single point of light in a completely dark room are perceived to wander long subjective distances. Ambiguity resolution appears to be a basic feature of sensory systems. For animals the environment is full of unpredictable dangers and opportunities, so that there may be a general evolutionary pressure for brains to resolve focal ambiguities as quickly as possible. Odorant molecules can also be highly ambiguous—they may be sparse, fleeting, masked by other odorants or by attentional distraction, they are often physically degraded, or ambiguous in their biological implications. Conscious olfaction may therefore benefit from the capacity of a GW architecture to concentrate multiple knowledge sources on resolving focal uncertainties.

dGWT suggests that each functional cortical hub passes through two phases, a *convergence* phase combining many cortical sources into single gestalts, and a *broadcasting* phase, in which the gestalt ignites a broadcast of about 100–200 ms, driving widespread adaptation in existing networks. To account for the great range of conscious contents over time, the theory suggests an *open set* of source coalitions, which may broadcast via theta/gamma or alpha/gamma coupling, like AM radio channels competing for a limited band of carrying frequencies (Hoppensteadt and Izhikevich, 1998).

In mammals the C-T core is believed to underlie conscious aspects of perception, thinking, learning, FOKs, felt emotions, visual imagery, working memory, and executive control. The hippocampus and rhinal cortex show similar properties, evolving from pre-mammalian roots. It seems therefore that 3-6-layered cortex may generally support conscious perception (Butler, 2008)[1].

Because C-T neurons are linked bidirectionally, the system can act as a "unitary oscillatory machine" (Steriade, 2006). The question "which area comes first?" may therefore change dynamically, depending on the balance of expectation-driven vs. stimulus-driven information. Stimulus detection may also change with payoffs: predator odors may have a lower detection threshold than food odors, because the cost of being wrong about predators is higher than the cost of missing food. However, in drought conditions animals may risk greater nearness to predators in order to drink from shared water holes. dGWT allows such context-sensitive factors to shape emergent activity in cortex.

MULTIPLE NEURAL SOURCES CONVERGE TO DEFINE PERCEIVED ODORS

This paper is focused on conscious odor perception, odor interpretation and odor-guided action control. Since exploratory sniffing is crucial for odor identification, olfaction is directly tied to behavior, including breathing, touching, active tasting, vomeronasal "yawning," reaching, oral grasping, behavioral stimulus tracking, and the like.

Many olfactory stimuli are reportable "as conscious" with great accuracy by humans, and meet demanding match-to-sample criteria in other animals. Other odorants are processed unconsciously, without direct reportability. The brain differences between conscious and unconscious olfaction are not well understood.

Neuroanatomists traditionally emphasized the differences between six-layered neocortex and ancestral 3–5 layered cortex. Hippocampus is three-layered cortex, but it is often treated as a non-cortical tissue. The entire cortical sheet, including hippocampus and paleocortex, may flexibly support the integration and broadcasting of source coalitions (Baars et al., 2013). For example, olfactory regions project forward to the orbitofrontal cortex. Kay and Sherman (2007) propose that the olfactory bulb may act as an analog of the sensory thalamus. In spite of different gross anatomy, conscious olfaction be similar to conscious vision.

Freeman (2005) has proposed that the microanatomy of dendro-dendritic neuropil provides the basis for such widespread interactivity. Others have focused on the vertical axonal connections of the C-T system (Steriade, 2006). These views are not incompatible, so that cortical signaling may combine both horizontal and vertical signal propagation. Both old and new phylogenetic cortex supports this kind of signaling.

There is debate about the earliest olfactory region where odors are identified as conscious gestalts. Freeman and colleagues suggest that the olfactory bulb analyzes stimuli by destabilizing a pre-existing equilibrium, resulting in a distinctive, high-dimensional attractor landscape incorporating both old and new stimulus parameters. Once the olfactory bulb adapts to the new stimulus, a novel attractor equilibrium propagates as a rapid phase-change in each hemisphere (Kay et al., 1996).

Other approaches point to the posterior piriform and even orbitofrontal cortex for the identification of conscious odors (Gottfried, 2010). Nearby regions are reported to serve multimodal and spatial contextual integration of olfactory stimuli.

From a dGWT perspective, olfactory percepts may come to an equilibrium in different regions of cortex, depending on the precise "source coalition" of active cortical arrays. "Raw" olfactory sensations might arise in the posterior piriform region and spread forward to related regions of cortex. However, "feelings of knowing" about a predictable odor may arise frontally and spread caudally. The peak cortical locus of olfactory percepts may therefore change with expectations, receptor input, the distal spatial and temporal context, selective attention, biological and personal significance, and the current task. In rats, the rate of sniffing (1–12 Hz) also drives theta oscillations, while beta oscillations are

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[1] Crick and Koch (2005) have suggested that cortico-claustral circuits may be involved in consciousness, given the widespread input and output connections of the claustrum. However, the exact role of the claustrum is still unclear (Smythies et al., 2012).

reported to encode odor quality (Kay et al., 2009).

AFTER GESTALT FORMATION: CENTRIFUGAL BROADCASTING

Global workspace theory suggests both converging source integration and diverging gestalt broadcasting. The best-known example of global propagation in this region is the hippocampal-neocortical dialog, which supports accurate coding of conscious events in episodic memory (Ferkin et al., 2008). The hippocampal complex also seems to support conscious event organization (Baars et al., 2013; Lee and Park, 2013).

Olfactory stimuli have remarkably widespread effects in the brain, including the limbic system, hypothalamus, amygdala, reward pathway, orbitofrontal, and insular cortex (Savic, 2005). One example of long-distance brain signaling may be Kay and Freeman's (1998) reported widespread cortical gamma coherence in the rat. According to these authors, coherent oscillatory "wave packets" may broadcast odor gestalts to other regions, using theta-to-beta phase-linked oscillations. In mammals, prefrontal regions support voluntary decisions evoked by conscious stimuli. The ability to report a conscious stimulus, and to perform match-to-sample tasks, plausibly requires prefrontal cortex (Asplund et al., 2010).

Olfaction is sometimes thought to be "primitive," but it is actually highly sophisticated. In nature, odors must be identified, interpreted, and acted on, to determine how long ago a tree was scent-marked, and whether the marking animal was a predator or a potential mate. The ancestral smell brain has been proposed to be an autonomous olfactory-motor system, since odors trigger rapid, adaptive behavior, as in detecting and running from the smell of a predator. Many factors, like wind direction, ambient temperatures, mating readiness, health and immune status, inferred age of the stimulus, concentration gradients, and the nature of the scent-marked surface must be interpreted accurately. Intervening rain or snow changes the composition of odor mixtures, which must still be identified correctly. Accurate olfaction and taste are also vital for food sampling and toxin avoidance, digestion, elimination, reproduction and sexual behavior, immunity, biological cycles, the health/illness dimension and its emotions, and the vagus-insula interoceptive system.

CONCLUSION

Conscious perception emerges from a complex, highly interactive process of resolving ambiguous and context-dependent stimuli. Baars et al. (2013) propose that sensory cortex gives rise to neuronal source coalitions that emerge into reportable consciousness when they drive many other cortical regions. By contrast, non-sensory cortex may give rise to FOKs, such as the "tip of the tongue" experience. Animals following an odorant trail often show a kind of expectant "tip of the nose" pose, tasting the air, and the ground for more information about a suspected odor source.

Because odorants may be fleeting, sparse, intermittent, masked, physically degraded, or ambiguous, conscious odor perception may also benefit from the interactivity of a GW capacity. In mammals both the new and old cortex support such interactivity.

The GW framework has been used to study conscious vision and audition. It may also help to clarify a world of conscious odors.

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Olfactory consciousness and gamma oscillation couplings across the olfactory bulb, olfactory cortex, and orbitofrontal cortex

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The orbitofrontal cortex receives multi-modality sensory inputs, including olfactory input, and is thought to be involved in conscious perception of the olfactory image of objects. Generation of olfactory consciousness may require neuronal circuit mechanisms for the "binding" of distributed neuronal activities, with each constituent neuron representing a specific component of an olfactory percept. The shortest neuronal pathway for odor signals to reach the orbitofrontal cortex is olfactory sensory neuron—olfactory bulb—olfactory cortex—orbitofrontal cortex, but other pathways exist, including transthalamic pathways. Here, we review studies on the structural organization and functional properties of the shortest pathway, and propose a model of neuronal circuit mechanisms underlying the temporal bindings of distributed neuronal activities in the olfactory cortex. We describe a hypothesis that suggests functional roles of gamma oscillations in the bindings. This hypothesis proposes that two types of projection neurons in the olfactory bulb, tufted cells and mitral cells, play distinct functional roles in bindings at neuronal circuits in the olfactory cortex: tufted cells provide specificity-projecting circuits which send odor information with early-onset fast gamma synchronization, while mitral cells give rise to dispersedly-projecting feed-forward binding circuits which transmit the response synchronization timing with later-onset slow gamma synchronization. This hypothesis also suggests a sequence of bindings in the olfactory cortex: a small-scale binding by the early-phase fast gamma synchrony of tufted cell inputs followed by a larger-scale binding due to the later-onset slow gamma synchrony of mitral cell inputs. We discuss that behavioral state, including wakefulness and sleep, regulates gamma oscillation couplings across the olfactory bulb, olfactory cortex, and orbitofrontal cortex.

Keywords: olfactory cortex, orbitofrontal cortex, tufted and mitral cells, olfactory bulb, olfactory consciousness, gamma synchronization

INTRODUCTION

The human brain has the faculty of conscious olfactory perception. The orbitofrontal cortex (OFC) is thought to play a critical role in the generation of olfactory consciousness (Plailly et al., 2008; Li et al., 2010). In the olfactory pathway of primates, including humans, the OFC is the first neocortical stage that integrates multi-sensory modalities, including olfaction and taste, and computes reward value of the multi-sensory information to adaptively modify behavioral output (Rolls and Baylis, 1994; Rolls, 2006; Gottfried, 2007; Price, 2007; Wallis, 2007). Particularly, neuronal circuits in the human OFC are thought to be involved in the conscious perception of food flavor that requires integration of not only olfactory and taste signals but also virtually all sensory modalities (Rolls, 2006; Shepherd, 2006, 2007). A key feature of the conscious perception in general is that all of the multi-modality sensory components of objects are integrated as a unified whole (Tononi and Edelman, 1998; Crick and Koch, 2005).

Rodent OFC is also a key player in multi-modality integration and the reward valuation of sensory information for the flexibility of associative encoding (Schoenbaum et al., 2007). Although it is controversial whether rodents have the faculty of conscious olfactory perception and there is considerable anatomical variation in the organization of olfactory OFC across mammalian species (Gottfried, 2007; Price, 2007), we argue that understanding the neuronal circuit mechanisms that allow external odor information to become available to the rodent OFC during alert wakefulness will substantially contribute to understanding the neuronal circuit mechanisms which underlie human olfactory consciousness.

Here, we initially review recent advances in knowledge of the structural architecture and functional properties of the neuronal pathways that convey the odor information detected by sensory neurons in the nose to the OFC of rodents. We address the question of how and in which timing during a single inhalation-exhalation sniff cycle the external odor information is transmitted via the neuronal circuits of the olfactory bulb and piriform cortex to the OFC. We then propose the hypothesis that gamma oscillatory inputs from tufted cell and mitral cell axons play distinct functional roles in processing odor information in the piriform cortex and OFC.

As shown in **Figure 1**, odor molecules are received by olfactory sensory neurons in the olfactory epithelium. Olfactory sensory neurons send the odor information via their axons to the olfactory bulb, the first information processing center in the olfactory system (Mori et al., 1999; Shepherd et al., 2004). Principal neurons in the olfactory bulb, namely tufted cells and mitral cells, receive excitatory synaptic input from olfactory sensory neurons and send the signal directly or indirectly via olfactory peduncle areas to the pyramidal cells in the piriform cortex, a phylogenetically old cortex (paleocortex) with a relatively simple three-layered structure (Neville and Haberly, 2004). The odor signal is processed in the piriform cortex and then sent to higher olfactory association regions such as the amygdala, olfactory tubercle, and OFC. Pyramidal cells in the anterior piriform cortex (APC) project axons directly to the OFC, the first stage of the olfactory system in the neocortex. In the shortest pathway, therefore, the OFC is only three synapses distant from the olfactory sensory neurons. This characteristic short pathway from olfactory sensory neurons to the OFC is in a striking contrast with other sensory modalities, such as the visual and auditory systems, which involve many more relay stages before the sensory information reaches the prefrontal cortex. The short pathway of the olfactory system makes it an excellent and simple model system with which to analyze neuronal circuit mechanisms for the transfer of sensory information from the sensory neurons to the prefrontal cortex in the mammalian brain (Shepherd, 2007).

In the neocortex, thalamus, and hippocampus, synchronized spike discharges of large ensembles of neurons occur at gamma-range frequency (30–100 Hz) during alert wakefulness, and are thought to be associated with the spatial "binding" of distributed components of a sensory percept (Singer, 1999; Engel et al., 2001; Fries, 2009; Buzsaki and Wang, 2012). Behavioral state, including wakefulness and sleep, regulates the generation of gamma oscillations. In addition, gamma oscillation coupling is widely observed in the neuronal pathways of the mammalian brain and is an efficient way of transmitting information from one region to its target regions (Buzsaki and Wang, 2012). Gamma oscillations in thalamocortical networks during alert wakefulness are thought to be associated with the global "binding" of distributed aspects of a sensory percept (Gray et al., 1989; Singer and Gray, 1995; Singer, 1998).

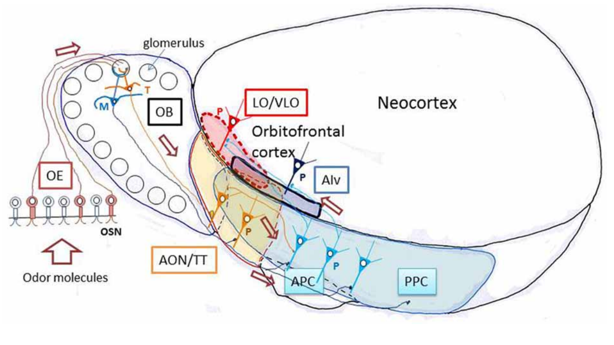

FIGURE 1 | Olfactory pathways to the orbitofrontal cortex in rodents. A schematic diagram of the lateral view of the rodent brain illustrating the neuronal pathways from olfactory sensory neurons through the olfactory bulb and olfactory cortex to the orbitofrontal cortex. AIv, ventral agranular insular cortex; AON, anterior olfactory nucleus; APC, anterior piriform cortex; LO, lateral orbital cortex; M, mitral cell; OB, olfactory bulb; OE, olfactory epithelium; OSN, olfactory sensory neuron; P, pyramidal cell; PPC, posterior piriform cortex; T, tufted cell; TT, tenia tecta; VLO, ventrolateral orbital cortex. The orbitofrontal cortex (LO/VLO) is surrounded by red broken line.

Gamma oscillations of local field potentials in the olfactory bulb and olfactory cortex have been studied extensively (Adrian, 1942; Freeman, 1975; Mori and Takagi, 1977; Bressler, 1984; Buonviso et al., 2003; Friedman and Strowbridge, 2003; Kay, 2003; Neville and Haberly, 2003, 2004; Cenier et al., 2008; Rosero and Aylwin, 2011). The rodent OFC also shows gamma oscillations during olfaction-dependent tasks (van Wingerden et al., 2010), suggesting that gamma oscillatory activity of the central olfactory system plays a functional role in conveying odor signals from the olfactory bulb to the OFC via the APC. In the present study, we focus on the functional roles of odor inhalation-induced gamma oscillations in the olfactory bulb, APC and OFC, and discuss the possibility that behavioral state regulates gamma oscillation coupling across these areas in such a way that the transfer of odor information to the OFC is greatly facilitated when rodents are awake and paying attention to the odor information, but is diminished during sleep. We also discuss the occurrence of gamma oscillation couplings across the OFC, olfactory cortex and olfactory bulb during the exhalation phase of a respiratory cycle, the phase in which the brain is isolated from external odor information but receives strong retronasal stimulation from internal odors that originate from foods within the mouth.

NEURONAL PATHWAYS FROM OLFACTORY SENSORY NEURONS TO THE ORBITOFRONTAL CORTEX

Before discussing the possible manner of odor information transmission along the olfactory pathways to the OFC, we will briefly review the characteristic structural organization of the central olfactory system, starting from the olfactory sensory neurons in the olfactory epithelium (**Figure 1**). Odor molecules are received by odorant receptors expressed on the cilial surface membrane of olfactory sensory neurons (Buck and Axel, 1991). Approximately 1000 different odorant receptor species occur in the mouse, and each olfactory sensory neuron expresses only one functional odorant receptor gene (one cell—one receptor rule). Each olfactory sensory neuron projects a single axon (olfactory axon) to a single glomerulus in the olfactory bulb, which has ~1800 glomeruli spatially arranged around its surface. Axons of numerous olfactory sensory neurons expressing the same type of odorant receptor converge onto two target glomeruli located at fixed positions in the olfactory bulb. Each glomerulus therefore represents a single type of odorant receptor (one glomerulus—one receptor rule) and detects specific "molecular features" of odorants (Mori et al., 1992, 1999). The spatial arrangement of glomeruli thus forms odorant receptor maps at the surface of the olfactory bulb (Mori et al., 2006; Mori and Sakano, 2011).

Within each glomerulus of the olfactory bulb, olfactory axons form excitatory synaptic connections on the terminal tuft of primary dendrites of two types of projection neurons, tufted cells, and mitral cells (**Figure 1**). Because of the one glomerulus—one receptor rule, all the olfactory axons and all the tufted and mitral cells that project to a single glomerulus form a functional module (glomerular module or glomerular unit) that represents a single type of odorant receptor (Shepherd et al., 2004; Mori and Sakano, 2011).

Individual mitral cells have their large cell bodies in the mitral cell layer and send dispersedly-projecting axons to virtually all areas of the olfactory cortex, including the piriform cortex (APC and posterior piriform cortex), areas in the olfactory peduncle [anterior olfactory nucleus (AON), tenia tecta, and dorsal peduncular cortex], olfactory tubercle, cortical amygdaloid nuclei, and lateral entorhinal cortex (Haberly and Price, 1977; Luskin and Price, 1983; Shipley and Ennis, 1996; Neville and Haberly, 2004; Igarashi et al., 2012). Tufted cells have smaller cell bodies that are distributed in the external plexiform layer (EPL). Each tufted cell projects axons selectively to focal targets in the olfactory peduncle areas (AON and tenia tecta) and the rostroventral part of the APC (Igarashi et al., 2012). Pyramidal cells in the AON give rise to associational axons that terminate in the piriform cortex.

Pyramidal cells in layer II of the APC project axons to the OFC and ventral agranular insular cortex (AIv) of the neocortex. The projection from the APC to the OFC/AIv is composed of two parallel pathways (**Figure 2**) (Ekstrand et al., 2001). Pyramidal cells in the ventral part of the APC (APCv) project axons to the ventrolateral orbital cortex (VLO), while those in the dorsal APC (APCd) send axons to the lateral orbital cortex (LO) and AIv.

In addition to direct projection from the APC to OFC/AIv, indirect transthalamic pathways are also present. The APCd projects axons to the endopiriform nucleus (En), which projects axons to the mediodorsal nucleus (MD) of the thalamus (**Figure 2**). Thalamocortical neurons in the MD project to the LO and AIv. The APCv connects with the pre-endopiriform nucleus (pEn), which projects axons to the submedius nucleus (SM) of the thalamus. Thalamocortical neurons in the SM send axons to the VLO.

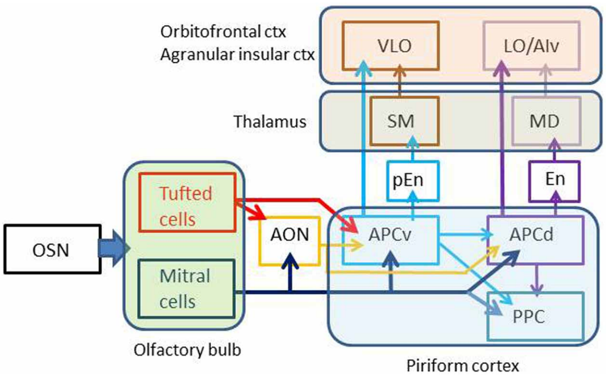

FIGURE 2 | Multiple parallel pathways from the olfactory sensory neurons to the orbitofrontal cortex. Arrows indicate axonal projection. AON, anterior olfactory nucleus; APCv, ventral part of the anterior piriform cortex; APCd, dorsal part of the anterior piriform cortex; PPC, posterior piriform cortex; pEn pre-endopiriform nucleus; En, endopiriform nucleus; SM, submedius nucleus of thalamus; MD, mediodorsal nucleus of thalamus; OSN, olfactory sensory neuron; VLO, ventrolateral orbital cortex; LO, lateral orbital cortex; AIv, ventral agranular insular cortex. Olfactory bulb gives rise to parallel tufted and mitral cell pathways to the olfactory cortex. APCv sends odor information directly to the VLO or indirectly via the pEn and SM, while APCd transfers odor information directly to the LO/AIv or indirectly via the En and MD.

FAST AND SLOW GAMMA OSCILLATIONS IN THE OLFACTORY BULB: RELATION TO TUFTED CELL AND MITRAL CELL CIRCUITS

As early as 1942; Adrian reported prominent gamma range oscillatory activity in the olfactory bulb (Adrian, 1942). Since then a number of studies have shown that odor inhalation induces gamma oscillations of local field potentials (LFPs) in the olfactory bulb (Freeman, 1975; Bressler, 1984; Buonviso et al., 2003; Neville and Haberly, 2003; Cenier et al., 2008; Rosero and Aylwin, 2011). The gamma oscillations reflect synchronized spike discharges of tufted cells and mitral cells (Kashiwadani et al., 1999). Dendrodendritic reciprocal synaptic interactions between the excitatory projection neurons (tufted and mitral cells) and inhibitory interneurons (granule cells) participate in the generation of gamma oscillations in the olfactory bulb (Rall and Shepherd, 1968; Mori and Takagi, 1977; Friedman and Strowbridge, 2003; Lagier et al., 2004; Shepherd et al., 2004).

As indicated in **Figure 3**, mitral cells (blue) project long lateral dendrites in the deeper sub-lamina of the external plexiform layer (EPL) and have dendrodendritic reciprocal synaptic interactions in the sub-lamina preferentially with mitral cell-targeting granule cells [Gr(M)], forming a mitral cell circuit (Mori et al., 1983; Orona et al., 1983; Greer, 1987). In contrast, tufted cells (red) extend relatively short lateral dendrites in the superficial sub-lamina of the EPL and have dendrodendritic synaptic interactions mainly with tufted cell-targeting granule cells [Gr(T)], forming a tufted cell circuit. These results raise the possibility that the odor inhalation-induced gamma oscillations encompass two distinct gamma oscillatory sources, a mitral cell circuit, and a tufted cell circuit.

From this notion, we studied the temporal structure of the gamma oscillations and spike activity of tufted cells and mitral cells during a single inhalation-exhalation sniff cycle. As exemplified in **Figure 4**, simultaneous recordings of respiratory rhythm and local field potentials in the olfactory bulb of freely behaving rats show that each sniff induces early-onset fast gamma oscillation (65–100 Hz) followed by later-onset slow gamma oscillation (40–65 Hz) (Manabe and Mori, 2013). A key point is the time lag between the fast and slow gamma oscillations: the onset of the fast gamma oscillation precedes that of the slow gamma oscillation by about 45 ms on average. Under anesthetized conditions also, odor inhalation induces a shift from fast gamma to slow gamma oscillations similar to that observed in freely behaving rats.

In agreement with the difference in the time window of the fast and slow gamma oscillations, tufted cells and mitral cells differ in their signal timing of odor-induced spike responses. We previously showed in anesthetized rats and mice that odor-inhalation induces early-onset high frequency (about 100 Hz) burst discharges of tufted cells at the middle of inhalation. In contrast, most mitral cells start to respond with low frequency burst

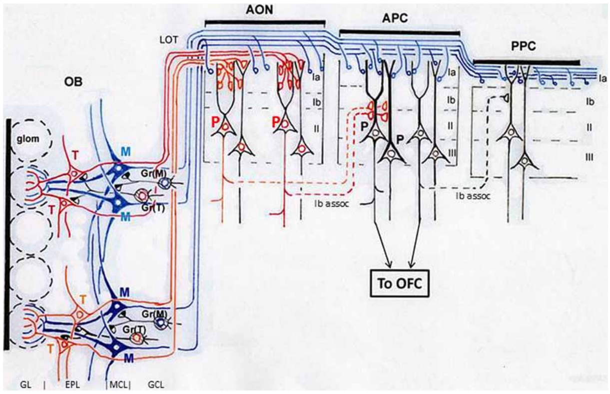

FIGURE 3 | Structural organization of tufted cell circuits and mitral cell circuits in the olfactory bulb and olfactory cortex. In the olfactory bulb (OB), tufted cells (red and orange T) extend relatively short lateral dendrites in the superficial sub-lamina of the EPL and make dendrodendritic reciprocal synaptic connections mainly with tufted cell-targeting granule cells [Gr(T)]. Mitral cells (blue M) extend long lateral dendrites in the deep sub-lamina of the EPL and form dendrodendritic synapses mainly with mitral cell-targeting granule cells [Gr(M)]. Tufted cells project axons (red and orange lines) to focal targets in the olfactory peduncle areas including AON. Mitral cells project axons (blue lines) dispersedly to nearly all areas of the olfactory cortex. Layers of the olfactory bulb: GL, glomerular layer; EPL, external plexiform layer; MCL, mitral cell layer; GCL, granule cell layer. Layers in the olfactory cortex: Ia, layer Ia; Ib, layer Ib; II, layer II; III, layer III. LOT, lateral olfactory tract; Ib assoc, Ib associational axon. Red P indicates pyramidal cells in the AON. Black P shows pyramidal cells in the APC. Glom, glomerulus; OFC, orbitofrontal cortex.

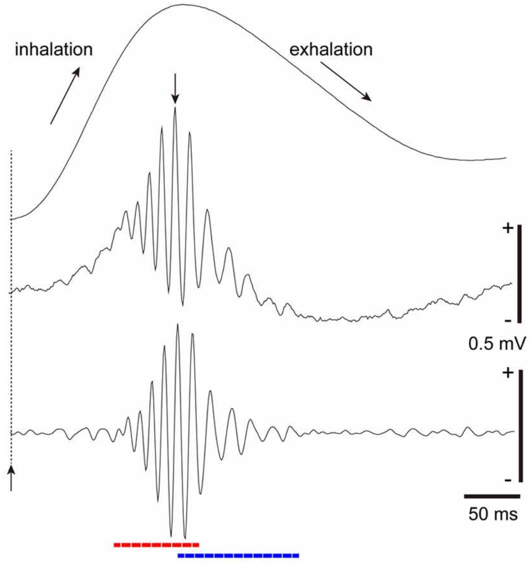

FIGURE 4 | Fast and slow gamma oscillations in the olfactory bulb. Middle trace: sniff rhythm-paced gamma oscillations recorded from the granule cell layer of the olfactory bulb of a freely behaving rat. The sniff-induced local field potentials (LFPs) were averaged ($n = 277$ sniffs) in reference to the peak (a downward arrow) of gamma oscillations that occur near the phase of transition from inhalation to exhalation. Bottom trace: the local field potential shown in the middle trace was band-path filtered between 30 and 140 Hz. The sniff-paced gamma oscillations consist of early-onset fast gamma oscillation (red dashed line) and later-onset slow gamma oscillation (blue dashed line). Uppermost trace: respiration monitor via a thermocouple implanted in the nasal cavity. Upward reflection indicates inhalation. Sniff-onset is indicated by a vertical broken line with an upward arrow.

discharges (about 45 Hz) at the later phase of the inhalation or at the phase of transition from inhalation to exhalation (Nagayama et al., 2004; Igarashi et al., 2012). The time window of early-onset fast gamma oscillations corresponds to the early-onset response of tufted cells while that of later-onset slow gamma oscillations corresponds to the later-onset response of mitral cells. Based on these observations, we suggest that the sniff-paced early-onset fast gamma oscillations are generated mainly by the tufted cell circuit, while the later-onset slow gamma oscillations are largely due to the mitral cell circuit (Manabe and Mori, 2013) (**Figure 3**).

How many sister mitral cells and sister tufted cells project their primary dendrites to a single glomerulus? The rabbit olfactory bulb has ∼1900 glomeruli, each with a relatively large diameter. Allison and Warwick (Allison and Warwick, 1949) estimated that a single glomerulus in the rabbit olfactory bulb receives primary dendrites from 68 sister tufted cells and 24 sister mitral cells on average. In the mouse olfactory bulb, the size of individual glomeruli is relatively small. A recent study using dye injection into a single glomerulus in the mouse (Kikuta et al., 2013) showed that a single glomerulus is innervated by at least 7 mitral cells, 3 middle tufted cells and 17 juxta-glomerular cells (which include external tufted cells and periglomerular inhibitory neurons). Because dye injection within a single glomerulus may not label all the mitral and tufted cells that innervate the glomerulus, we roughly estimate that a single glomerulus in the mouse olfactory bulb may receive primary dendrites from ∼10 sister mitral cells and 20 sister tufted cells.

Thus, the tufted cell circuit of a single glomerular module in mammalian olfactory bulb consists of ∼20–68 sister tufted cells and a much larger number of tufted cell-targeted granule cells with intense dendrodendritic synaptic interactions among them in the superficial sub-lamina of the EPL. Because tufted cells extend relatively short lateral dendrites, tufted cells belonging to an activated glomerulus may have small-scale interactions with those tufted cells belonging to nearby co-activated glomeruli and synchronize their activity at fast gamma frequency. We suggest that the tufted cell circuits are the substrate for the sniff-paced early-onset fast gamma oscillations. Tufted cells may send the early-onset signal to focal targets in specific areas of the olfactory peduncle and rostroventral part of the APC with fast gamma synchronization.

The mitral cell circuit of a glomerular module consists of ∼10–24 sister mitral cells and numerous mitral cell-targeting granule cells with intense dendrodendritic synaptic interactions in the deeper sub-lamina of the EPL. Because mitral cells project very long lateral dendrites, mitral cells may have large-scale interactions and synchronize at slow gamma frequency with those mitral cells that are distributed over a wide area of the olfactory bulb. The mitral cell circuits may be responsible for generating later-onset slow gamma oscillations. Mitral cells might thus convey later-onset signals dispersedly to nearly all parts of the olfactory cortex with slow gamma synchronization.

The tufted cell circuit and mitral cell circuit can communicate with each other via synaptic and extra-synaptic mechanisms within the glomerulus and also via dendrodendritic synapses of type I granule cells that arborize apical dendrites in both superficial and deep sub-laminas of the EPL (Mori et al., 1983; Orona et al., 1983; Greer, 1987).

Electrical couplings (via gap junctions) between inhibitory interneurons and those between principal cells are involved in the generation of gamma synchronization in the mammalian brain (Galarreta and Hestrin, 2001; Bennett and Zukin, 2004; Hameroff, 2010). Because tufted and mitral cells form gap junctions among themselves within glomeruli and with a subset of periglomerular cells and granule cells (Kosaka and Kosaka, 2005; Kosaka et al., 2005), these gap junctions might be involved in the generation of sniff-paced fast and slow gamma oscillations in the olfactory bulb (Christie et al., 2005; Migliore et al., 2005).

TUFTED CELLS MAY PROVIDE SPECIFICITY-PROJECTING CIRCUITS, CONVEYING ODOR INFORMATION WITH FAST GAMMA SYNCHRONIZATION

The piriform cortex is thought to use spatially distributed overlapping ensembles of active pyramidal cells to represent odors (Neville and Haberly, 2004; Wilson and Sullivan, 2011). Piriform cortex neurons that respond to a given odor are dispersedly distributed across the wide space of the piriform cortex without spatial preference (Litaudon et al., 1997; Illig and Haberly, 2003; Rennaker et al., 2007; Stettler and Axel, 2009; Mitsui et al., 2011). On the other hand, excitatory responses of individual neurons in the piriform cortex are tuned to specific combinations of stimulus odorants (Litaudon et al., 2003; Yoshida and Mori, 2007; Poo and Isaacson, 2011; Wilson and Sullivan, 2011). Therefore, while odor-induced activity is sparsely distributed, odor responses of individual neurons are tuned to specific odorant combinations in the piriform cortex.

An interesting question regarding these apparently opposite properties of the piriform cortex is which of the two afferent axon pathways from the olfactory bulb (tufted cell pathway or mitral cell pathway) mediates each of the properties: “sparse distribution of the odor-induced activity” and “odor tuning of individual neurons.” Pyramidal cells of the APC extend long apical dendrites superficially to layer I and receive afferent axon synaptic inputs from the olfactory bulb at the distal segment of the apical dendrites in layer Ia (APC in **Figure 3**). In the ventrorostral part of the APC, axons terminating in its layer Ia originate from both mitral cells and tufted cells. In the dorsal and caudal parts of the APC and whole parts of the posterior piriform cortex (PPC), in contrast, almost all afferent axons to layer Ia originate from mitral cells (Haberly and Price, 1977; Neville and Haberly, 2004). Pyramidal cells in the APC also receive inputs from associational axons originating from pyramidal cells of the olfactory peduncle (AON and tenia tecta) and APC itself and terminating on proximal segments of apical dendrites in layer Ib (Ib associational axons, **Figure 3**).

Poo and Isaacson (2011) have shown that odor tuning of individual neurons in the APC is mediated by Ib associational axon input, rather than direct afferent axon input from the olfactory bulb. Given that individual tufted cells in the olfactory bulb project axons densely to focal targets in areas within the olfactory peduncle (AON and tenia tecta) (Igarashi et al., 2012) (**Figure 3**), we hypothesize that specific odorant receptor information conveyed by tufted cell axons is synaptically relayed to pyramidal cells in the olfactory peduncle (red P in **Figure 3**) and then sent to the pyramidal cells of the APC (black P in **Figure 3**) via Ib associational axons of olfactory peduncle pyramidal cells. In this hypothesis, the odor tuning of individual neurons in the APC is mediated mostly via the tufted cell axon—olfactory peduncle Ib association axon pathways (red lines in **Figure 3**).

As shown in **Figure 6**, local field potentials in the APC show sniff rhythm-paced fast and slow gamma oscillations. The early-onset fast gamma oscillations in the APC correspond well in timing and frequency with the early-onset fast gamma oscillations in the olfactory bulb, which are mainly generated by tufted cell circuits. These observations lead us to hypothesize that (1) tufted cells provide specificity-projecting circuits which convey specific odorant receptor signals with early-onset fast gamma synchronization to specific target pyramidal cells in the olfactory peduncle: and that (2) the activated pyramidal cells in the olfactory peduncle then send the signals presumably with fast gamma synchronization to specific target pyramidal cells in the APC via their Ib associational axons (red, orange and pink lines in **Figure 5**).

Haberly (2001) proposed that the AON, a major area in the olfactory peduncle, detects and stores correlations between “molecular features,” creating representations of particular odorants and odorant mixtures. We speculate that tufted cell signals originating from different glomeruli converge in a specific way onto individual pyramidal cells in the AON, giving rise to the odor tuning of its pyramidal cells (Lei et al., 2006; Kikuta et al., 2008). However, it is not known how the tufted cell signals from different glomerular modules are combined or integrated in individual pyramidal cells in the olfactory peduncle (Brunjes et al., 2011).

We further speculate that Ib associational axon signals from different pyramidal cells in the olfactory peduncle converge under specific rules onto individual pyramidal cells of the piriform cortex, thereby providing the odor-tuning specificity of the pyramidal cells. In fact, pyramidal cells in the pars lateralis of the AON project Ib associational axons to the ventral division of APC (APCv), whereas those in the pars dorsalis of the AON send associational axons to the dorsal division of the APC (APCd) (Haberly and Price, 1978; Luskin and Price, 1983). Future study will detail the connectivity pattern of Ib associational axons of olfactory peduncle pyramidal cells to the pyramidal cells in the APC.

MITRAL CELLS MAY PROVIDE DISPERSEDLY-PROJECTING FEED-FORWARD BINDING CIRCUITS, SENDING THE RESPONSE SYNCHRONIZATION TIMING WITH SLOW GAMMA SYNCHRONIZATION

If the odor-tuning specificity of individual pyramidal cells of the APC is determined mainly by the tufted cell axon—olfactory peduncle Ib associational axon pathways, what is the functional role of the direct afferent axon inputs from mitral cells? It has been demonstrated that afferent inputs from a single glomerulus (presumably mitral cell axon inputs) to a pyramidal cell in the APC evoke only weak excitation (Davison and Ehlers, 2011), suggesting that the direct afferent axon inputs from sister mitral cells belonging to a glomerulus may contribute little to the odor-tuning specificity of individual pyramidal cells of the APC.

On the other hand, dye-labeling of physiologically identified mitral cells showed that individual mitral cells project axons dispersedly to nearly all areas of the olfactory cortex, including nearly all parts of the piriform cortex (**Figure 3**) (Igarashi et al., 2012). Furthermore, sister mitral cells belonging to a given glomerulus project their axons to the piriform cortex in a highly dispersed pattern, with their terminals distributed throughout the piriform cortex (Ghosh et al., 2011; Sosulski et al., 2011). The highly dispersed pattern of mitral cell axon projection to the piriform cortex is independent of the position of the labeled glomerulus in the olfactory bulb (Sosulski et al., 2011), suggesting that sister mitral cells belonging to any glomerulus may project axons to the piriform cortex in a highly dispersed pattern.

Given that mitral cell circuits generate later-onset slow gamma oscillatory activity, we speculate that sister mitral cells belonging to an activated glomerulus provide a mechanism for the dispersion of later-onset slow gamma oscillatory activity across whole parts of the piriform cortex and even across many different areas of the olfactory cortex (Manabe and Mori, 2013). It has been shown that individual target pyramidal cells receive converging inputs from many mitral cells distributed over wide regions of the olfactory bulb (Miyamichi et al., 2011). Because of the widespread projection of lateral dendrites of mitral cells and their intensive dendrodendritic interactions with numerous granule cells, mitral cells belonging to different glomerular modules can synchronize their discharges at the slow gamma range frequency when co-activated (Mori and Takagi, 1977; Kashiwadani et al., 1999). Therefore, mitral cells that are co-activated by odor inhalation would provide later-onset synchronized inputs at slow gamma frequency to pyramidal cells across whole parts of the piriform cortex (**Figure 5**).

Although input from a single mitral cell axon is weak, nearly simultaneous arrival of synchronized spike inputs from many mitral cell axons may effectively summate their EPSPs in pyramidal cells and thereby strongly modulate pyramidal cell activity in synchrony with the slow gamma oscillatory inputs. We hypothesize that the gamma-synchronized coincident inputs from many mitral cell axons coordinate response timing of pyramidal cells that are spatially distributed across whole parts of the piriform

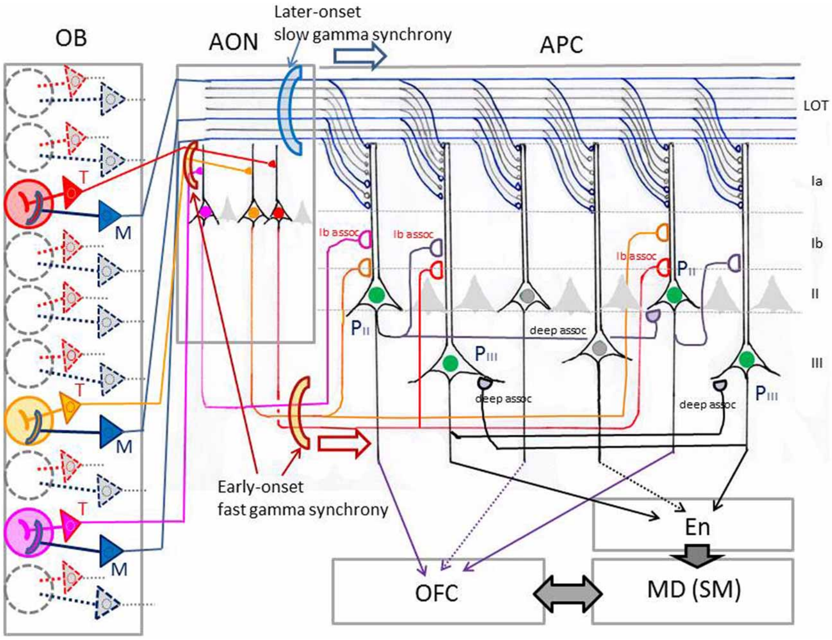

FIGURE 5 | Schematic diagram of possible functional differentiation between the tufted cell pathway and mitral cell pathway in odor information processing in the neuronal circuits of the piriform cortex. In this model, red, yellow, and pink glomeruli are assumed to be activated simultaneously by an odor inhalation. Activated tufted cells (T, shown by red, orange, or pink) send the odor information with early-onset fast gamma synchrony to specific target pyramidal cells in the AON, which in turn send the information presumably with fast gamma synchrony to specific-target pyramidal cells in the APC. Activated mitral cells (M, shown by blue) provide dispersedly-projecting feed-forward binding circuits transmitting the spike synchronization timing with later-onset slow gamma synchrony to whole pyramidal cells in the APC. Pyramidal cells in layer II (PII) of the APC project axons directly to the OFC. The layer II pyramidal cells and those in layer III (PIII) of the APC form recurrent association axon synaptic connections (deep assoc. and Ib assoc.) with other pyramidal cells, forming feed-back binding circuits. These pyramidal cells project axons also to the endopiriform nucleus (En), which sends axons to the mediodorsal nucleus (MD) or submedius nucleus (SM) of thalamus. MD and SM provide thalamocortical projections to the OFC, while OFC sends feed-back corticothalamic connections to the MD or SM. LOT, lateral olfactory tract; Ia, Ib, II, and III, layers in the APC. Pyramidal cells with green nucleus in the APC indicate neurons co-activated by an odor inhalation. Recurrent collateral excitatory synaptic connections (deep assoc) among these neurons form feed-back binding circuits.

cortex over a sustained time window, providing one of the key elements in "binding" together the spike activities of numerous co-activated pyramidal cells with different tuning specificity (**Figure 5**).

Recordings of local field potentials in the APC indicate that odor inhalation induces fast gamma oscillations followed by slow gamma oscillations with a time course which closely resembles those observed in the olfactory bulb (**Figure 6**). This raises the possibility that pyramidal cell activity during the early onset fast gamma oscillations may be due to the tufted axon—Ib associational axon inputs to the pyramidal cells, while that during the later-onset slow gamma oscillations are induced by the combination of preceding tufted cell axon—Ib associational axon inputs and later-onset synchronous inputs from many mitral cells. It is tempting to speculate that the later-onset synchronized inputs from mitral cell axons may cause profound spike synchronization of those pyramidal cells that had been depolarized by preceding early-onset inputs from tufted cell axon—Ib associational axon pathways, while the synchronized inputs may have little influence on those pyramidal cells that had not been depolarized by the tufted cell axon—Ib associational axon inputs. If this is the case, the later-onset diffuse mitral cell inputs might selectively bind the spike activities of only those pyramidal cells that were co-activated via specificity-projecting tufted cell axon—Ib associational axon inputs.

RECURRENT ASSOCIATION AXON SYNAPTIC CONNECTIONS AMONG PYRAMIDAL CELLS OF THE PIRIFORM CORTEX

Recurrent axon collaterals of pyramidal cells in the piriform cortex form excitatory synaptic connections on dendrites of other pyramidal cells that are distributed widely in the piriform cortex (**Figure 5**) (Haberly and Presto, 1986; Johnson et al., 2000; Chen et al., 2003; Yang et al., 2004). These recurrent axon collaterals are classified into those that terminate in layer Ib (Ib associational axons) and those that terminate in layers II and III. For example, recurrent axon collaterals of pyramidal cells in the PPC terminate mostly on basal dendrites of other pyramidal cells in layer III, and only a small percentage of them terminate on apical dendrites in layer Ib (Haberly, 2001). We refer to recurrent collaterals that terminate in layer Ib as Ib associational axons and to those that terminate in layers II and III as deep associational axons (**Figure 5**).

It has been proposed that the Ib and deep associational axon synaptic connections among pyramidal cells in the piriform cortex form networks with iterative recurrent re-excitatory pattern that can store input patterns from the olfactory bulb by plastically changing their synaptic connections (Marr, 1971; Barkai et al., 1994; Haberly, 2001; Neville and Haberly, 2004; Wilson and Sullivan, 2011). A simple model is that during the storage of input patterns the associational synaptic connections would be strengthened between pyramidal cells with different tuning specificity that are co-activated by odor inhalation, while the associational synaptic connections would be weakened between activated and non-activated pyramidal cells. After the learning of the input pattern, the strengthened associational synaptic connections could temporally synchronize the spike activity of those co-activated pyramidal cells with different tuning specificity when the same or similar input patterns arrive from the olfactory bulb (Neville and Haberly, 2004). Computer modeling studies showed that the recurrent associational networks can store and retrieve multiple input patterns that may include olfactory images of numerous different objects (Barkai et al., 1994). The recurrent associational connections among pyramidal cells can thus provide a mechanism for feed-back "binding" of co-activated pyramidal cells based on the memory traces of previously stored input patterns.

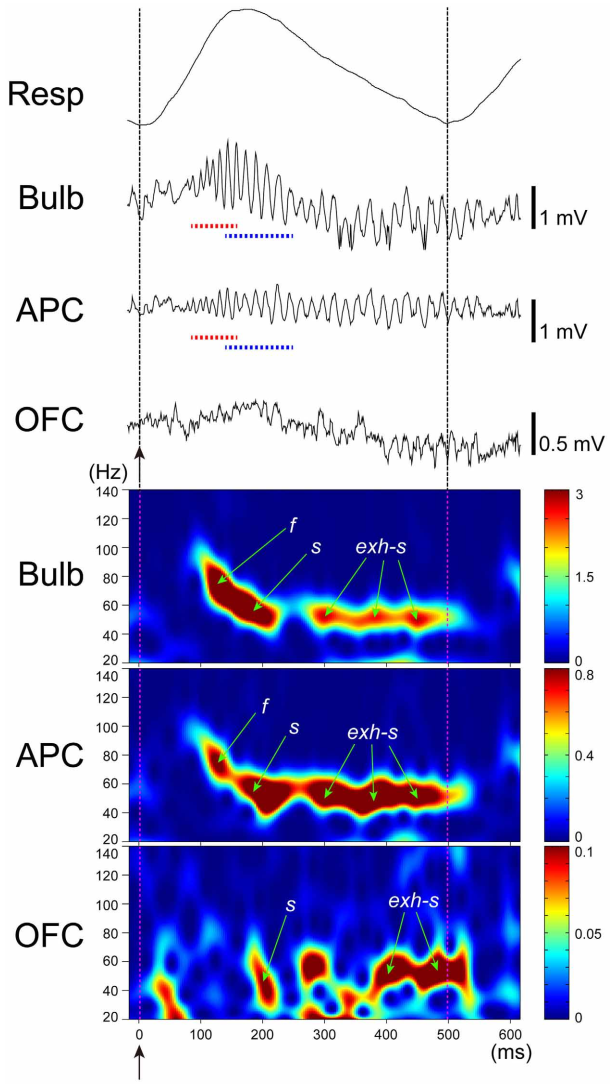

FIGURE 6 | Gamma oscillation couplings across the olfactory bulb, anterior piriform cortex, and orbitofrontal cortex. Simultaneous recordings of respiratory pattern (Resp, upward swing indicates inhalation), LFP in the granule cell layer of the olfactory bulb (Bulb), LFP in layer III of the APC (APC), and LFP in the deep layer of OFC (OFC), during micro-arousal. Wavelet analyses of the LFPs are shown in the lower three figures. Broken lines and upward arrows indicate sniff onset. Early-onset fast gamma oscillation is shown by f or red broken line, and later-onset slow gamma oscillation by s or blue broken line. Slow gamma oscillation during the exhalation period is shown by exh-s.

As described above, we hypothesize that the synchronous gamma oscillatory inputs from mitral cells cause temporal "binding" of the spike activities of numerous pyramidal cells with different tuning specificity that are co-activated via tufted cell axon—Ib associational axon pathways during odor inhalation. The mitral cell-induced spike synchronization of pyramidal cell activities would facilitate the strengthening of the associational synaptic connections among the co-activated pyramidal cells during the storage of input patterns that are provided by tufted cell—Ib association axon pathways. In summary, we propose a model in which mitral cell pathways provide feed-forward binding circuits, sending the spike synchronization timing to facilitate the storage of olfactory sensory input patterns by causing the spike synchronization of co-activated pyramidal cells at the slow gamma frequency, and thus strengthening association axon synapses among co-activated pyramidal cells with different tuning specificity.

GAMMA OSCILLATION COUPLINGS ACROSS THE OLFACTORY BULB, OLFACTORY CORTEX, AND ORBITOFRONTAL CORTEX

In addition to numerous pyramidal cells, the piriform cortex contains several types of inhibitory interneurons (Neville and Haberly, 2004; Bekkers, 2013). Large horizontal and layer Ia neurogliaform cells in layer I are GABAergic inhibitory neurons that terminate their axons on the distal part of apical dendrites (in layer Ia) of pyramidal cells. Because these Ia inhibitory neurons receive direct synaptic inputs from tufted cell axons or mitral cell axons, they provide feed forward inhibition of pyramidal cells. In the olfactory peduncle areas, fast gamma synchronization of tufted cell activity might be transmitted to pyramidal cells not only by monosynaptic excitatory input from tufted cells but also by di-synaptic inhibitory input via the Ia inhibitory neurons. Similarly, Ia inhibitory neurons in the APC might be used to effectively transmit the slow gamma synchronization of mitral cells via the di-synaptic inhibitory input to pyramidal cells.

Another characteristic type of inhibitory neuron in the olfactory cortex is fast-spiking large multipolar cells that are distributed in layers II and III. Many large multipolar cells are GABAergic basket cells which form basket-like inhibitory terminals around the cell bodies of pyramidal cells. Because the GABAergic basket cells receive deep associational axon inputs from pyramidal cells, they form local feedback inhibitory circuits. This raises the possibility that the local feedback inhibitory circuits form gamma oscillatory sources in the APC and that gamma oscillatory inputs either from tufted cell axon—Ib association axon pathways or mitral cell pathways entrain the gamma oscillations of the APC circuits.

Given that pyramidal cells in layer II of the APC project axons to the OFC, the sniff-paced gamma oscillatory activity of APC pyramidal cells may be transmitted to the OFC. To examine this possibility, we recorded local field potentials simultaneously from the olfactory bulb, APC and OFC (**Figure 6**). During awake exploratory behavior or awake resting, olfactory bulb and APC typically show sniff-paced early-onset fast gamma oscillation (*f* in **Figure 6**) followed by later-onset slow gamma oscillation (*s* in **Figure 6**). In many cases, the early-onset fast gamma oscillation in the APC shows phase-coupling with the early-onset fast gamma oscillation in the olfactory bulb, suggesting a strong functional coupling between the APC and olfactory bulb. Later-onset slow gamma oscillations in the APC also typically show phase-coupling with the later-onset slow gamma oscillations in the olfactory bulb, again suggesting a functional coupling between them.

During awake exploratory behavior and awake resting, the rat OFC occasionally shows sniff-paced fast and slow gamma oscillations with a time course closely resembling those in APC and olfactory bulb (**Figure 6**). In some sniffs, both fast and slow gamma oscillations occur in the OFC with a similar time course to fast and slow gamma oscillations in the APC, while in other sniffs, the OFC shows only the slow gamma oscillations (**Figure 6**). These slow gamma oscillations of the OFC sometimes phase-couple with those of APC and olfactory bulb, although the degree of gamma oscillation coupling is weaker than that of the gamma coupling between the APC and olfactory bulb. These results suggest that sniff-paced fast and slow gamma oscillations generated in the olfactory bulb are occasionally transferred to the OFC via the APC.

During awake resting in which rats show a slow respiration pattern with relatively long exhalation phase, the olfactory bulb and APC sometimes show strong coupling of slow gamma oscillation during the long exhalation phase (Manabe and Mori, 2013) (exh-s in **Figure 6**). This late slow oscillation at the exhalation phase sometimes last for an extended period up to the initial part of the next inhalation phase (**Figure 6**) and presumably corresponds to the late slow gamma and beta oscillations reported in anesthetized animals (Buonviso et al., 2003; Neville and Haberly, 2003; Cenier et al., 2008). Generation of these late slow oscillations is thought to require mutual interactions between the olfactory bulb and olfactory cortex. We observed that the OFC also shows gamma oscillations that are coupled with those of the APC and olfactory bulb during the long exhalation periods (exh-s in **Figure 6**), which suggests that gamma oscillation coupling among the olfactory bulb, APC and OFC can occur not only during the inhalation phase, in which the external odor information is transmitted via a bottom-up pathway from the olfactory bulb, but also during the long exhalation period in which the central olfactory system is temporally isolated from the external odor information. This observation raises the possibility that these gamma oscillations can be generated centrally either in the OFC or APC and travel via a top-down pathway to the olfactory bulb. In other words, gamma oscillatory couplings among the olfactory bulb, APC and OFC can be generated either by olfactory sensory inputs or centrally in the brain.

The functional role of this gamma oscillation coupling among the olfactory bulb, APC and OFC during the exhalation-phase remains to be elucidated. It should be noted that rats typically show slow sniffs with a long exhalation phase during eating and that prominent gamma oscillation couplings occur across the olfactory bulb, APC, and orbitofrontal cortex during the long exhalation phase. Because the brain receives retronasal odor stimulation from foods in the mouth during the exhalation phase (Gautam and Verhagen, 2012), these observations raise an interesting possibility that the gamma oscillation couplings are involved in the process of perception of food flavor in the mouth (Shepherd, 2006).

BEHAVIORAL STATE REGULATES THE GENERATION AND COUPLING OF GAMMA OSCILLATIONS ACROSS THE OLFACTORY BULB, PIRIFORM CORTEX, AND ORBITOFRONTAL CORTEX

In the neocortex, gamma oscillation and spike synchronization depend on behavioral state and increase with arousal, attention, and expectancy (Herculano-Houzel et al., 1999; Fries, 2009). They are absent or greatly diminished during sleep states. Similarly, conscious awareness of olfactory sensory information of the external world depends on behavioral state, occurring during alert wakefulness but absent during sleep states. Several studies have pointed out the relationship between gamma oscillations in the olfactory cortex and behavioral states (Freeman, 1975; Kay, 2003). We therefore addressed the question of whether behavioral state regulates the generation of sniff-paced fast and slow gamma oscillations in the olfactory bulb, and found that the sniff-paced gamma oscillations occur throughout the waking states, but disappear during slow-wave sleep and REM-sleep (Manabe and Mori, 2013). During the shallower stage of slow-wave sleep, rats sometimes show micro-arousals for a short period, and the sniff-paced fast and slow gamma oscillations occur only during these short periods of micro-arousal. At the end of micro-arousal, the neocortical EEG resumes the slow-wave sleep pattern, and the sniff-paced gamma oscillations disappear. These results indicate that gamma oscillation generation in the olfactory bulb is under the control of behavioral state, particularly the awake and sleep states. In other words, activated states of olfactory bulb are required, in addition to odor inhalation, to generate gamma-band synchrony of tufted cells and mitral cells. Furthermore, it has been shown that task demands enhance gamma oscillations in the olfactory bulb (Beshel et al., 2007).

Neuronal mechanisms for the behavioral state dependency of gamma oscillation generation are not well-understood. Because mitral/tufted cells and granule cells in the olfactory bulb are under the control of centrifugal neuromodulatory systems (cholinergic, noradrenergic, and serotonergic systems) which change their activity with behavioral state, these neuromodulatory systems are candidates for the mediation of behavioral state dependency. For example, a behavioral state-dependent global change in cholinergic tone modulates granule-to-mitral/tufted dendrodendritic synaptic inhibition and thus modulates gamma oscillation generation (Tsuno et al., 2008).

Behavioral state also regulates the generation of sniff-paced fast and slow gamma oscillations in the APC (Onisawa et al., unpublished). The fast and slow gamma oscillations are frequently observed in the APC during awake behaving periods, but are almost completely absent during slow-wave sleep and REM sleep. Recurrent inhibitory circuits between pyramidal cells and GABAergic basket cells are thought to be responsible for gamma oscillation generation in the APC, and are also under the control of the neuromodulatory system (Gellman and Aghajanian, 1993; Barkai and Hasselmo, 1994; Hasselmo and Barkai, 1995). In addition, state-dependent sensory gating in the olfactory cortex is regulated by strong neuromodulatory input from the brainstem reticular activation system, which includes areas surrounding the pedunculo-pontine tegmental nuclei (Murakami et al., 2005).

In the OFC also, sniff-paced gamma oscillations are regulated by behavioral state, being occasionally present during wakefulness but absent during sleep. Furthermore, the coupling of sniff-paced gamma oscillations among the olfactory bulb, APC and OFC occurs occasionally during awake periods, but is absent during sleep periods. This suggests that external odor information can be transmitted with gamma oscillation from the olfactory bulb through the APC to the OFC during wakefulness, but that transmission is completely shut down or greatly reduced during sleep. The neuronal circuit mechanism for the generation of gamma oscillatory activity in the OFC is unknown. Because optogenetic activation of fast-spiking inhibitory interneurons induces gamma oscillations in the neocortex (Cardin et al., 2009), we speculate that fast-spiking inhibitory interneurons may participate in the generation of sniff-paced gamma oscillatory activity in the OFC. However, virtually nothing is known about local neuronal circuits in the OFC.

An intriguing question for future research is whether the attention and expectancy that accompany cholinergic activation modulate gamma oscillation coupling across the olfactory bulb, APC and OFC in such a way that odor information transfer to the OFC is greatly facilitated when animals are paying attention to the odor information or expecting an odor-associated reward.

POSSIBLE FUNCTIONAL ROLES OF GAMMA OSCILLATION COUPLINGS IN CONSCIOUS OLFACTORY PERCEPTION

In summary, we propose a model of the neuronal circuit mechanism of odor information transfer via gamma oscillation couplings across the olfactory bulb, APC and OFC. In this model, the spatial arrangement of glomerular modules in the mouse olfactory bulb can be viewed as a map of the ~1000 types of odorant receptor-specific gamma oscillators. To perceive an odor, brain needs to know the input pattern from these gamma oscillators; i.e., the specific combination of gamma oscillators co-activated by the odor inhalation. Each glomerular module contains two types of gamma oscillatory source with different onset latencies, tufted cell circuit, and mitral cell circuit. We propose that the sniff-paced early-onset fast gamma oscillations are mainly generated by tufted cell circuits, whereas later-onset slow gamma oscillations are mainly due to mitral cell circuits. Sniff-paced fast and slow gamma oscillations also occur in the APC with similar onset time lag. The early-onset fast gamma oscillations in the APC often show phase-coupling with early-onset fast gamma oscillations in the olfactory bulb, suggesting functional coupling between tufted cell inputs and fast gamma oscillation in the APC. The later-onset slow gamma oscillations in the APC occur in synchrony with the later-onset slow gamma oscillations in the bulb, suggesting that afferent axon inputs from mitral cells are responsible for the later-onset slow gamma oscillations in the APC.

We propose the hypothesis that tufted cell circuits and mitral cell circuits play distinct functional roles in odor information processing and memory formation in neuronal circuits of the piriform cortex. Tufted cells may provide specificity-projecting circuits which send specific odor information to focal targets during the time window of early-onset fast gamma synchronization, while mitral cells give rise to dispersedly-projecting feed-forward binding circuits, transmitting the response synchronization timing with later-onset slow gamma synchronization to all parts of the piriform cortex. Our model suggests a sequence of bindings in the piriform cortex: a small-scale binding by early-phase fast gamma synchrony of tufted cell inputs followed by a larger-scale binding by later-onset slow gamma synchrony of mitral cell inputs. One possible scenario is that the later-onset slow-gamma synchrony of mitral cell inputs cause spike synchronization of the large ensemble of piriform cortex pyramidal cells that had been co-activated by the preceding early-onset fast-gamma synchrony of tufted cell axon—Ib associational fiber inputs. The larger-scale feed-forward binding by later-onset mitral cell inputs may induce selective "binding" of the spike activity of co-activated pyramidal cells with different odor-tuning specificity, causing plastic changes in the recurrent associational synaptic connections among them. The large-scale feed-forward binding by mitral cell inputs and the large-scale feed-back binding by the recurrent associational synaptic connections may work together both for the memorization and retrieval of odor images of objects. If the groupings of pyramidal cell activities are associated with reward or punishment, the temporal binding of activities of the large ensemble of pyramidal cells may lead to either appetitive behavior or aversive behavior (Choi et al., 2011).

Conscious perception of visual, auditory, somatosensory, and gustatory senses is thought to depend on thalamocortical circuits. A basic consensus in the studies of neuronal mechanism of consciousness is the need to rapidly integrate and bind information that is situated across distinct cortical and thalamic regions (Llinas et al., 1998; Baars, 2002; Crick and Koch, 2005). A large ensemble of widespread populations of neurons in the thalamus and neocortex shows synchronous oscillatory activities at the gamma frequency range during conscious cognitive processes (McCormick and Bal, 1997; Steriade, 2000). It has been proposed that large-scale gamma oscillation couplings of activities across many thalamo-cortical and cortico-thalamic networks generate the functional states that characterize conscious cognitive processes (**Figure 7**) (Llinas et al., 1998).

In exploring the function of these thalamo-cortical networks, Jones (2001, 2009) classified thalamo-cortical projection neurons into two types, core neurons and matrix neurons, and proposed that they provide a basis for the gamma oscillation couplings in the thalamus and neocortex. Core neurons project axons in a topographically ordered fashion to middle layers of the neocortex in an area-specific manner, forming a basis for the relay of place- and modality-specific information to the neocortex. In striking contrast, matrix neurons project axons diffusely to superficial layers of the neocortex over wide areas, unconstrained by boundaries between areas, forming a basis for the dispersion of activity into the thalamocortical network across large areas of neocortex (**Figure 7**).

It should be underscored that the possible functional differentiation between tufted and mitral cells in the olfactory bulb closely resembles that between core and matrix neurons in the

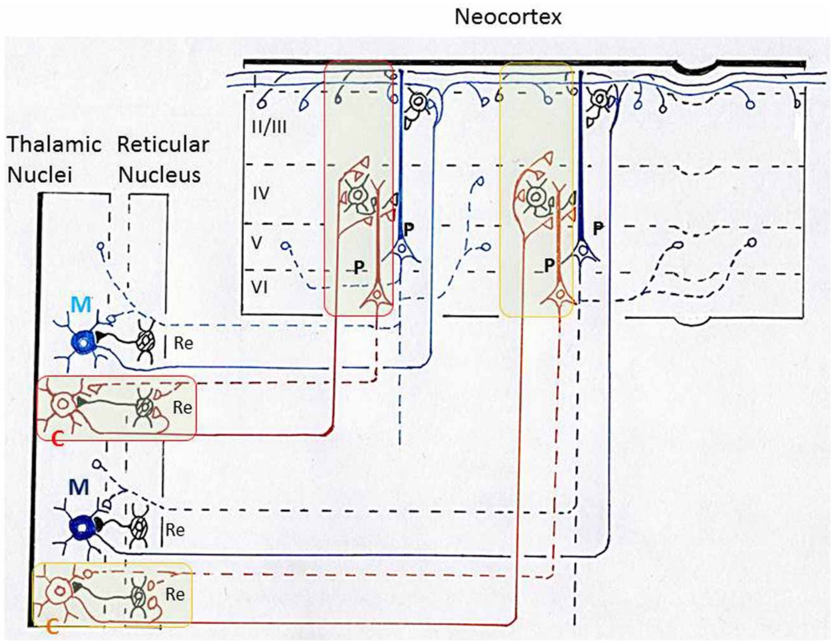

FIGURE 7 | Schematic diagram illustrating thalamo-cortico-thalamic networks and the "matrix and core theory" of Jones. This diagram is based on Llinas et al. (1998) and Jones (2001). Core neurons (C) in the thalamus form specificity-projecting circuits (shown by brown lines and surrounded by red or yellow lines) that involve specific cortico-thalamic connections from layer VI pyramidal cells. Matrix neurons (M) in the thalamus give rise to non-specific binding circuits (shown by blue lines) that involve diffuse projections from layer V pyramidal cells. Jones proposed that the above two types of thalamo-cortico-thalamic networks form a substrate for synchronization of widespread populations of neurons in the thalamus and cortex during high-frequency oscillations that underlie discrete conscious events (Jones, 2009). P, pyramidal cells in the neocortex; Re, inhibitory neurons in the reticular nucleus of thalamus; I, II/III, IV, V, VI, layers in the neocortex.

thalamus: tufted cells and core neurons may provide specificity-projecting circuits, whereas mitral cells and matrix neurons may provide dispersedly-projecting binding circuits. Both the thalamus and olfactory bulb have parallel pathways with a distinct axonal projection pattern. These results raise the possibility that the thalamus and olfactory bulb may use a similar neuronal circuit logic of parallel pathways for the transfer of sensory signals to the cortex and for the binding of widely distributed cortical neuron activity with small-scale and large-scale gamma synchronizations. Such neuronal circuit logic, together with the dispersed axonal projection, might provide a basis for generating large-scale synchronized activities of cortico-cortical or thalamocortical networks that underlie the conscious perception of objects.

We suggest that generation of olfactory consciousness requires neuronal circuit mechanisms for the binding of distributed neuronal activities in which each constituent neuron might represents a specific component of an olfactory percept. Besides the olfactory bulb, piriform cortex and OFC, sniff rhythm-paced gamma oscillations are observed in the olfactory tubercle, cortical amygdaloid nuclei, lateral entorhinal cortex, and medial prefrontal cortex. A major challenge in future studies of the neuronal circuit mechanism of olfactory consciousness is therefore to elucidate the basic logic of large-scale gamma oscillation couplings and the "binding" of activities of widespread populations of neurons over many different areas of the olfactory cortex, as well as across the olfactory cortex, prefrontal cortex, thalamus and basal ganglia. Couplings of odor-induced and centrally-generated synchronized oscillatory activities across large-scale networks in the central olfactory system might also be a basic strategy for the transfer of cognitive information of odor objects into neuronal circuits for the planning of behavioral responses.

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Quality-space theory in olfaction

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Quality-space theory (QST) explains the nature of the mental qualities distinctive of perceptual states by appeal to their role in perceiving. QST is typically described in terms of the mental qualities that pertain to color. Here we apply QST to the olfactory modalities. Olfaction is in various respects more complex than vision, and so provides a useful test case for QST. To determine whether QST can deal with the challenges olfaction presents, we show how a quality space (QS) could be constructed relying on olfactory perceptible properties and the olfactory mental qualities then defined by appeal to that QS of olfactory perceptible properties. We also consider how to delimit the olfactory QS from other modalities. We further apply QST to the role that experience plays in refining our olfactory discriminative abilities and the occurrence of olfactory mental qualities in non-conscious olfactory states. QST is shown to be fully applicable to and useful for understanding the complex domain of olfaction.

Keywords: quality-space theory, quality-space, olfaction, mental qualities, phenomenology, perceptual qualities, consciousness

QUALITY-SPACE THEORY

Conscious perceiving always subjectively involves conscious qualitative character. Conscious vision involves qualities of color and of visible shape, size, and location; conscious audition involves qualities of pitch, loudness, timbre, and audible location; and conscious olfaction involves mental qualities that correspond to the various odorants and, possibly, qualities that correspond to their locations.

Perceiving occurs not only consciously, but without being conscious as well, in masked priming and other forms of subliminal perceiving (e.g., Marcel, 1983; Sobel et al., 1999; Breitmeyer and Öğmen, 2006; Öğmen and Breitmeyer, 2006; Zucco et al., 2013). In the conscious cases, we know about the qualitative character of perceptual states subjectively, by how they appear to consciousness. So many are tempted to conclude that when perceptual states do occur without being conscious, there is no way to know about their qualitative character, and hence no qualitative character in that case to know about.

This line of thought has led many in philosophy to deny that non-conscious perceptual states exhibit any qualitative character, properly so called (e.g., Nagel, 1974). It has also led many in philosophy to see the qualitative character of perceptual states as deeply problematic. It has been argued that neural processes cannot constitute or give rise to conscious qualitative character (Chalmers, 1996), or that, if they can, we cannot in any case explain how that can be (Levine, 2001). And it has been urged that since we know about qualitative character only by way of consciousness, i.e., only by first-person access, the specific types of mental quality that figure in perceiving a particular physical property might differ from one individual to another in ways that are empirically undetectable (e.g., Shoemaker, 1975/1984). Carrying this to an extreme, it has been held that an individual that is physically indistinguishable from us and functions in ways perceptually indistinguishable from us might nonetheless lack conscious mental qualities (Chalmers, 1996). And many not in philosophy have found these conclusions tempting as well.

Concern with these apparent conundra has generated a large literature in philosophy, with many arguing that these problems cannot be sidestepped or resolved and others proposing solutions that seldom gain lasting wide adherence. But both sides in this debate typically operate on the assumption that since qualitative character occurs only in conscious perceiving, that we can know about qualitative character only by way of subjective, first-person access.

The demonstrable occurrence of perceiving that is not conscious forces reexamination of the assumption that subliminal and other non-conscious perceiving is actually devoid of qualitative character, and that non-conscious perceiving discharges its psychological and biological function without benefit of mental qualities. And any such reexamination shows that it is by no means obvious that non-conscious perceiving lacks qualitative character.

For one thing, we describe non-conscious perceptual states in the same qualitative terms we use to taxonomize conscious perceptual states. That is evident, for example, in experimental work on masked priming. Participants visually but non-consciously perceive stimuli in respect of their colors and shapes; we classify the non-conscious visual states in respect of those qualitative terms despite those states' not being conscious. More important, it is clear in conscious perceiving that differences in qualitative character are responsible for the discriminative ability characteristic of perceiving; in conscious perceiving it is plain that we would be unable to distinguish color, shapes, sounds, and odors without our conscious perceptual states' differing in qualitative character in ways that make such discriminations possible. But unconscious perceiving also enables the discrimination of various environmental properties, indeed largely the same discriminations we make in conscious perceiving. In addition, when experimental participants guess about degraded stimuli (Cheesman and Merikle, 1986; Merikle, 1992; Dienes and Seth, 2010), where guessing taken to be an indication that the perceiving is not conscious, they guess about colors and other qualitative character, indicating non-conscious qualitative states that reflect those qualitative properties. So it is natural to infer that differences in qualitative character in unconscious perceiving as well, enabling us to make those discriminations.

Consider the visual case. Consciously seeing something red is being in a visual state that is more like seeing orange than like seeing blue or green; similarly, subliminally seeing something red is being in just such a state, except the state is not conscious. Without some compelling independent reason, reserving the notion of mental qualitative character for conscious states is an arbitrary and unwarranted stipulation from a time when the occurrence of non-conscious perceiving was not recognized. And as with empirical and theoretical issues generally, we must rest with the strongest considerations available to us.

The assumption that non-conscious perceiving lacks qualitative character seems tempting only if one sees no way to learn about and describe mental qualities except by how they subjectively appear in consciousness. But it is worth stressing that appeal to that assumption begs the question at hand. If unconscious perceiving lacks qualitative character, then we will have access to qualitative character primarily, and perhaps exclusively, by way of consciousness. Some independent consideration is needed to settle the issue about whether qualitative character ever occurs without being conscious.

Quality-space theory (QST; Rosenthal, 1991, 1999, 2005, 2010, in press; Clark, 1993) offers just such an independent reason. It constructs an alternative to the exclusive reliance on subjective consciousness, by explaining the nature of mental qualities by appeal to their role in perceiving. Since perceiving can occur without being conscious, QST provides an explanation of qualitative character that applies to perceiving independent of whether it is conscious, and hence without in any way relying on conscious access to qualitative character.

The core idea of QST rests on the discriminative function of perception mentioned above. Perceiving always involves discrimination of properties accessible by a particular sensory modality. And to discriminate two properties, p_1 and p_2, a creature must be able to be in psychological state of two distinct types, each type corresponding in some suitably differential way to one of the two perceptible properties. The two types of perceptual state must differ in respect of some psychologically relevant properties.

The conscious perceptual states that enable discrimination of perceptible properties differ in respect of qualitative character. So it is natural to identify as mental qualities the differential psychological properties that enable discrimination of perceptible properties, whether that discrimination occurs consciously or not. Perceptual states enable discrimination of perceptible properties by differing in respect of mental quality. Mental qualities are the psychological properties in virtue of which a creature can distinguish among the various properties accessible to each perceptual modality.

One can measure discriminative ability by testing for just-noticeable differences (JNDs) between barely discriminable properties for a particular modality. Methodological issues arise because discriminability is not transitive; p_1 may be just noticeably different from $p_2$and p_2 from p_3 even though p_1 and p_3 are indistinguishable (e.g., Goodman, 1951). But despite that, one can use JNDs to construct a quality space (QS) that represents all the discriminations that a particular individual can make among the perceptible properties accessible by a particular modality. The dimensions of this space will emerge as needed; it may be that though p_1, p_2, and p_3 are just noticeably different in a linear fashion, several other perceptible properties are just noticeably different from each of p_1, p_2, and p_3, in ways that induce a new dimension for the QS of the perceptible properties accessible by that modality (Clark, 1993, pp. 84–89).

The QSs constructed in this way describe discriminability of the perceptible properties accessible by a particular modality. But because mental qualities are the differential psychological properties of states that enable such discriminations, the very same space will also capture the differences and similarities among those mental qualities. So that QS describes and explains what mental qualities are, and how we taxonomize them by type. And since the relevant discriminability among stimuli accessible by a particular modality occur in both conscious and non-conscious perceiving, a QST account of mental qualities is independent of how they present themselves subjectively to consciousness.

Indeed, one can establish non-conscious JNDs. As noted earlier, when stimuli are degraded, subjects' JND judgments remain accurate even when subjects take themselves to be merely guessing (Cheesman and Merikle, 1986; Merikle, 1992; Dienes and Seth, 2010). Since taking oneself to guess indicates that one is not consciously aware of JNDs, it reflects perceptual states that are not conscious.

The QS of perceptible properties matches that of the mental qualities that enable discrimination among those perceptible properties. One might conclude that such a match cannot be established without subjective awareness of the relevant mental qualities, and so QST cannot after all apply to non-conscious perceiving. This is a mistake. The match between QSs is established not by comparing the space of discriminable perceptible properties with the space of corresponding mental qualities. Rather, it is established by extrapolating from the space of perceptible properties to that of mental qualities. That extrapolation is an inference to the best explanation of what makes possible the discriminations used to construct the QS of perceptible properties.

Constructing QSs using discriminative abilities does not appeal to normal or typical conditions of perceiving. JNDs are used to construct the QS of perceptible properties; so optimal conditions for each individual tested are what matter. Moreover, the QS of perceptible properties will not in general reflect the physical properties of the stimuli, since the space is constructed not by appeal to the physical nature of the stimuli, but to how an individual discriminates among them.

A dramatic case of this occurs with color, where there are different wavelength distributions that are perceptually indistinguishable. So on QST, these different wavelength distributions result in the same mental qualities. If the space that determined mental qualities were constructed from the physical properties of stimuli, such stimuli would determine distinct mental qualities. On a space of perceptible properties constructed from discriminability, as determined by JNDs, these stimuli occupy identical positions, and so determine identical mental qualities. But it is important that this kind of phenomenon apart, perceptible properties are grouped for purposes of QST not by appeal to their physical characteristics, but by the ability of perceivers to discriminate among them.

Perceptual acuity can differ not only between individuals but also within an individual over time. Perceptual acuity can improve, e.g., by perceptual learning or maturation, which results in an enhanced or more fine-grained space of discriminable stimuli, and a correspondingly enlarged or more fine-grained space of mental qualities. And though one tests individuals, averaging over members of a species will capture average discriminability for that species. There are other refinements (Rosenthal, 2005, ch. 7, 2010, in press), but these will not bear on our purposes here.

Each stimulus type an individual can discriminate from its neighbors is physically distinct from other stimuli; so it is describable on its own, independent of any others. But because the QS of perceptible properties is constructed from the discriminability relations that JNDs deliver, the locations in the space of all the perceptible properties is determined relative to the location of other perceptible properties.

No perceptible property has a fixed position independent of its discriminability relations to the others. The space is not constructed by first having some fixed locations for some privileged perceptible properties and locating others relative to them; it is constructed by determining the relations of discriminability among all the properties accessible by a particular modality. So the theory represents each type of perceptible property comparatively, by appeal to which other properties it is discriminable from. And QST accordingly also represents each type of mental quality comparatively, by appeal to relative discriminability of stimuli.

By contrast, theories that explain the nature of mental qualities by appeal to the way they subjectively appear in consciousness result in a non-comparative, non-relational taxonomy of the types of mental quality, typing each independently of all others. Relying on first-person, subjective access to mental qualities tends to result in a non-comparative taxonomy, since consciousness by itself can access only the token mental qualities, independent of how they are typed. Having picked out token mental qualities, subjective awareness can then compare them; but subjective awareness must on such an account be able to individuate token mental qualities independent of any such comparisons.

It is this feature of the reliance on consciousness in explaining what mental qualities are that makes it appealing to imagine that one person's mental quality on seeing a red stimulus could undetectably be the same as another person's on seeing a green stimulus. If first-person access could trump everything else we know about mental qualities, there would be no way to exclude that strange apparent possibility.

QST, by contrast, precludes such undetectable inversion. The QS for every known perceptual modality is asymmetric (see, e.g., Kuehni, 1998, 2003, ch. 6, 2005, ch. 6; Ramanath et al., 2004). Even the one-dimensional space of grayscale shades is asymmetric, due to the anchoring effect in which the lightest shade in any local framework appears to be pure while (Gilchrist, 2006). And though sufficiently detailed work on the discriminability space of other perceptible properties has not been done, there is no reason to expect that the resulting QSs will turn out in any such case to be symmetrical.

The mental qualities that pertain to visible colors are a useful initial test case for QST, partly because the dimensions of the QS are few in number and well understood, and partly because color plays such a prominent role in our conscious experience. Individuals discriminate among colors along various dimensions, which turn out to correspond to the standard properties of hue, saturation, and brightness. When individuals are tested for discrimination of neighboring color stimuli, it turns out that these are dimensions that emerge, resulting in a three-dimensional QS of discriminable color properties (e.g., CIE, 1932; Clark, 1993).

QST builds from a QS of perceptible colors, and extrapolates to determine the various types of mental color quality in terms of their relative location in a QS isomorphic to that of the perceptible colors. But it may be tempting to suppose that there are after all perceptual primitives for color, fixed not comparatively as in QST, but in an absolute, non-comparative way.

Focusing on how we consciously perceive things makes it inviting to posit perceptual primitives that operate in a non-comparative way. Subjective awareness of mental color qualities makes it seem that each of the colors is what it is just on its own, and not as a function of relations with others. Consciousness can compare the various mental color qualities, but only by treating each as independently fixed. So subjective consciousness cannot represent the mental qualities as fixed in a comparative, relational way.

But since perceiving also occurs without being conscious, if there were perceptual primitives, they would be common to conscious and non-conscious perceiving. So the way consciousness represents mental qualities cannot by itself ground the positing of perceptual primitives. The JNDs used to construct QSs, by contrast, fix perceptible properties by relative discriminability and hence comparatively; the corresponding mental qualities follow suit.

One might argue that a comparative taxonomy of mental qualities cannot be correct if subjective awareness does not present them comparatively. But it is far from obvious that subjective awareness does present mental qualities non-comparatively. We have subjective access to each token mental color quality, for example, in respect of its comparative location in our field of vision, as fixed by the boundaries of that field, beyond which there are no more mental color qualities.

Consciousness aside, however, perhaps the relevant neural machinery fixes some perceptual primitives in an absolute, non-comparative way. In color vision, appeal to opponent-processing theory (Hurvich and Jameson, 1957) may seem to underwrite such perceptual primitives. On opponent-processing theory, channels in the optic nerve code retinal color information as relative strengths of opponent colors, red vs. green, blue vs. yellow, and black vs. white.

But even if the opponent-processing hypothesis is correct, it would not undermine QST, which seeks to explain not the mechanisms of perceiving, but the qualitative character of perceptual states that such perceptual machinery subserves. And the mental qualities distinctive of each modality are a matter of the discriminative ability that the perceptual apparatus, whatever it may be, enables; they are properties of perceptual states in virtue of which an individual can discriminate instances of a range of perceptible properties. Even if particular types of stimulus are especially salient for the perceptual apparatus of a particular modality, such perceptual primitives do not figure in fixing the types of mental quality for that modality.

There is a striking illustration of how mental qualities may depart from what underlying perceptual mechanisms seem to dictate. On opponent-processing theory, seeing red and seeing green each result from outweighing the opponent color in the red–green channel; similarly for blue and yellow. So the theory should preclude so-called forbidden colors, such as reddish green and as yellowish blue.

But image stabilization, in which a retinal image is made to hold constant despite saccading, can produce cortical filling in that leads subjects presented with adjacent red and green stripes to report seeing reddish green; similarly for yellow and blue (Crane and Piantanida, 1983; Billock et al., 2001). These findings do not undermine opponent-processing theory, since opponent processing would occur in optic-nerve channels prior to the cortical filling in that results in these subjective experiences. But they do show that individuation of mental-quality types is not settled by appeal to underlying perceptual mechanisms. The typing of mental qualities rests on discriminability of one perceptible property from another.

Colors are not the only perceptible properties accessible by vision; vision also represents spatial properties of size, shape, and location. It captures these spatial properties as boundaries of discriminable colors; without discriminable differences in color, including the achromatic colors (black, gray, white), vision could not access size, shape, or location. And as just noted, some retinal motion relative to visual stimuli is needed for the normal visual perception of spatial boundaries, i.e., visible sizes, shapes, and locations QST handles the spatial mental qualities as it does other mental qualities. One can test for JNDs of visible shapes, sizes, and locations, and collate the results in QSs of those visible properties. And since mental qualities are the properties of perceptual states that enable perceptual discrimination, the QSs of visible shapes, sizes, and locations also determine the mental visual qualities of shapes, sizes, and locations (Meehan, 2001; Rosenthal, 2001, in press).

Perceptible objects have sizes, shapes, and locations independent of being perceived, and hence independent of the modality by which those spatial properties are perceived. But the mental qualities that pertain to these spatial perceptible properties are tied to particular modalities. Vision accesses the physical location of things, e.g., by boundaries of discriminable colors, taction by discriminable resistance, pressure (Kappers and Bergmann Tiest, 2013), and texture, and audition by stereo effects of discriminable sounds. So distinct testing of JNDs is needed to establish QSs that capture the spatial perceptible properties discriminable by each modality, and those distinct QSs will in turn then fix the spatial mental qualities for each modality.

QST fixes the mental qualities of both conscious and non-conscious perception. So the theory cannot by itself explain how conscious perceiving differs from perceiving that is not conscious; an additional theory is needed to do that. If an individual is in a mental state of some type but is wholly unaware of being in that state, that shows that the state is not conscious; this test dominates work in experimental psychology and as well as our common sense views about conscious states. So a state is conscious only if the individual is aware of it in some suitable way. A successful explanation of what is distinctive of conscious perceiving differs will doubtless proceed along such lines (Rosenthal, 2004, 2005).

Since QST is not a theory of the difference between conscious and non-conscious states, the main theories of consciousness are not in direct competition with QST. Indeed, there are few if any theories that compete with QST in directly addressing the nature of mental qualities, as against mental representation more generally. The main alternative views are those that hold that our knowledge about qualitative character is limited to what subjective awareness reveals (e.g., Nagel, 1974; Kripke, 1980; Block, 1995; Chalmers, 1996; Levine, 2001). For further extended arguments against these views and their variants (see Rosenthal, 2010), which also advances compelling general considerations to think that QST is correct.

In this paper we do not attempt a comprehensive review of QST and the competing theories. Instead, we want to test if QST can deal with the challenges that olfaction presents. Each modality may raise its own issues about the dimensions of the relevant QSs, the possibility of perceptual primitives, the contrast between QST and an exclusively first-person, consciousness-based approach to mental qualities, the nature of mental qualities if any that occur in connection with spatial perception, and others. Here we use olfaction as an especially challenging test case for the theory.

THE OLFACTORY QUALITY SPACE

The color QS based on JNDs is well-established. However, in other modalities much less progress has been made. We are, for example, not aware of any attempt to construct an olfactory QS based on JNDs. Furthermore, so far all attempts to arrange olfactory qualities based on other aspects of perception have failed (Berglund and Höglund, 2012; Kaeppler and Mueller, 2013), casting some doubt on whether there is any olfactory QS analogous to the color QS. However, there are good reasons to believe that there is such an olfactory QS and that the reason why it has not been described yet is that it is much more complex than the three-dimensional color QS.

Most attempts to establish an odor QS have been attempts to arrange individual odorous molecules (benzaldehyde, hexanal, vanillin, and so on) in a perceptual space based on the similarities in their perceived smell (Wise et al., 2000). Such a space would only cover a very small fraction of all olfactory qualities because mixtures of odorous molecules frequently have qualities that are different from the qualities of its components. No two mixtures of different odorous molecules that are perceptually indistinguishable have so far been identified. Furthermore, the use of a small number of odorous stimuli may reflect the idea that there are some perceptual primitives, which runs counter to the methodology of QST.

Because of the unique perceptual properties of each mixture, there is no easy way to use the space of the perceived qualities of individual odorous molecules as a basis to construct an olfactory QS that includes all olfactory qualities, including those found only in mixtures. The space of the perceived olfactory qualities of molecules would have to have the feature that no line connecting the perceptual qualities of two molecules crosses another such line (as this would be a case of two mixtures that are perceptually indistinguishable).

To construct an olfactory QS that covers all olfactory perceptual qualities, one has therefore to include the olfactory qualities of mixtures, which are also the qualities we are familiar with because the smells encountered in nature are almost always mixtures. The characteristic scent of a rose, for example, is produced by a mixture of 275 different odorous molecules (Ohloff, 1994, pp. 154–158). An olfactory QS of odor mixtures can be constructed based on JNDs by gradually altering the ratios of the components of one mixture until it becomes an olfactory stimulus distinguishable from the original.

It is easy to see that the QS constructed in this way would have to accommodate a very large number of distinguishable olfactory sensory qualities. There are 166 billion molecules with 17 or less atoms (Ruddigkeit et al., 2012) and a large majority of those that have been studied have an odor. Almost all these odorous molecules have a smell that can be distinguished from the smell of all other odorous molecules (Laska and Teubner, 1999a,b). The only instances of two different odorous molecules that have indistinguishable smells are certain pairs of enantiomers (mirror-symmetric molecules; Laska and Teubner, 1999b; Laska, 2004) and some pairs of molecules that differ only in that the hydrogen atoms have been replaced by deuterium atoms (Keller and Vosshall, 2004). Other pairs of enantiomers and pairs of molecules that differ only in hydrogen isotopes can be distinguished (Laska and Teubner, 1999b; Laska, 2004; Gane et al., 2013).

Odorous molecules can also be mixed in different combinations and ratios, further increasing the large number of possible olfactory stimuli. Only a very small fraction of these mixtures has ever been studied, but the fact that among those mixtures that have been studied there are none that are indistinguishable from others shows that many mixtures have unique olfactory qualities, and so would occupy a distinct locution in an olfactory QS.

On the other hand, there is independent reason to believe that not all mixtures have a unique smell. In one of the most significant recent discoveries in olfactory psychophysics, Tali Weiss and colleagues showed that mixtures with many components converge perceptually. This means that mixtures of random odorous molecules with a large enough number of components smell similar and share an olfactory quality that has been called "olfactory white" (Weiss et al., 2012). The reason why the complex mixtures of odorous molecules that we encounter when we smell roses or coffee do not smell similar is because the components of these mixtures are not a random sampling of odorous molecules and because in these naturally occurring mixtures there are some components represented at much higher intensity than the majority of the components. How many components are necessary in mixtures to render them indistinguishable from one another is not yet known, but on average, mixtures of 30 or 60 components can still be discriminated (Weiss et al., 2012).

These considerations suggest that there are very many perceptible properties in the olfactory modality that can be distinguished by human subjects, and consequently very many olfactory mental qualities that we must posit as responsible for such fine-grained olfactory discriminability ability. One thousand different odorous molecules can be mixed into $3e^{+23}$ different mixtures of 10 components. Even if each of those mixtures had the same smell as, on average, one trillion other mixtures, there would be $3e^{+11}$ different olfactory qualities. In comparison, there are approximately 340,000 tones (Stevens and Davis, 1938) and between 2.3 and 7.5 million colors (Nickerson and Newhall, 1943; Pointer and Attridge, 1998) that humans can distinguish.

From a biological perspective it would not be surprising if there were many more distinguishable odors than distinguishable colors. Color perception is mediated by differential activation of three different types of receptor whereas olfactory perception is mediated by differential activation of around 400 different types of receptors (Olender et al., 2012) and the possible combinations of 400 far exceed the possible combinations of three.

However, it is an interesting question how such a large number of perceptual qualities might be arranged into a QS. The two mathematical solutions to this problem, which are not mutually exclusive, are that the resolution along the dimensions of the space is very high or that there is a large number of dimensions in the olfactory QS. QSs are mathematical constructs that have whatever number of dimensions is needed to capture the discriminability relations of the relevant stimuli and the corresponding mental qualities. The QS for thermosensation for example seems to be one-dimensionality, along a dimension from cold to hot. Interestingly, this is so despite the fact that several types of receptors contribute to temperature sensation (Dhaka et al., 2006). The fact that the activity of several receptor types can result in a one-dimensional QS illustrates dramatically that QSs are not based the sensitivity of receptor types, but on JNDs. The color QS, like physical space, has three dimensions (hue, saturation, and brightness; Hilbert and Kalderon, 2000). That there are also three types of color receptors is a coincidence and irrelevant for the construction of the color QS. It has been suggested that the olfactory QS has a much higher dimensionality than QSs in other modalities (Berglund and Höglund, 2012; Auffarth, 2013).

It simply is not possible to arrange all olfactory qualities in a low-dimensional space. Qualities of odor mixtures (at least in most cases) are intermediary between the odor qualities of their components; the perceptual qualities of mixtures occupy the space delimited by their components in the QS (Wise and Cain, 2000; Berglund and Höglund, 2012). Two odorous molecules and all their mixtures fill a one-dimensional QS. Four molecules and their mixtures fill a two-dimensional QS, eight molecules and their mixtures a three-dimensional QS with the eight components of the mixture in the corners of a cube. To accommodate 1,000 odorous molecules and all their mixtures, approximately 10 dimensions would be required. To accommodate 100,000 odorous molecules and their mixtures, one would need a 17-dimensional space.

These considerations show that despite the failure of all previous attempts to do so, there is no reason to suppose that there is not an olfactory QS that is based on JNDs and methodologically on a par with the color QS. The difference between the two QSs is that the olfactory QS is larger and more complex than the color QS. The color QS arranges a few million qualities in a three-dimensional space whereas the olfactory QS arranges vastly more qualities in a substantially higher-dimensional space. The numerous failures to describe an olfactory QS are merely due to the extremely large dataset required to do so.

THE OLFACTORY MODALITY

The odor QS represents olfactory qualities and the color QS represents color qualities, but how do we know which mental qualities are part of the color QS and which are part of the odor QS? Traditionally, sense modalities have been individuated by criteria, but there has been dispute over which criteria to use. The four main approaches current in the philosophical literature are to use a representational criterion, the phenomenal character criterion, the proximal stimulus criterion, or the sense-organ criterion (Grice, 1962; Macpherson, 2011). We will here discuss an alternative way of individuating modalities that does not depend on criteria, but instead individuates modalities based on the results of forced-choice discrimination tasks, the same methodology which is used to construct QSs.

The traditional criterion-based approaches largely agree in how they individuate vision and audition. However, with other modalities they often produce contradictory results. There is, for example, a type of molecular receptor (called TRPV1) that is sensitive both to hot temperature and to capsaicin, the pungent chemical found in chili peppers (Caterina et al., 1997). If the sensory-organ criterion is applied, capsaicin and heat are two stimuli in the same modality. If the stimulus criterion is applied, then the TRPV1 receptor mediates perception in two different modalities. Two stimuli that are sensed by the same molecular receptor will result in the same neuronal activity and therefore in the same phenomenal character; but the phenomenal-character criterion would judge heat and capsaicin to be two stimuli in the same modality. However, what is represented by the stimuli is a botanical compound in one case and temperature in the other. There are other examples of receptors that are sensitive to different types of stimuli for which the same analysis applies (Dhaka et al., 2006).

Since the four criterion-based approaches come to contradictory results outside of vision and audition, they cannot all be correct and philosophers have argued over which approach is the correct one. Instead of contributing to this debate, we will introduce here an alternative to criterion-based modality individuation. We propose to individuate modalities using the same type of behavioral tests used to construct QSs: forced-choice discrimination tasks. Suppose you have two stimuli. What you want is to see whether the two can be manipulated (altered gradually so as to be more similar) so that in the end they are JND, and then make them a bit more similar so that they come to be totally indistinguishable. If so, then the two original stimuli are accessible by the same modality. If they cannot be made JND and then made to match, then they were not the same modality to begin with. This appeals to discriminative responses to stimuli made problematic by, e.g., the TRPV1 receptor; it is not an appeal to the physical nature of the stimuli themselves. Since capsaicin cannot be gradually altered to turn into heat, TRPV1 mediates perception in two different modalities according to the JND-method.

The JND-method allows individuating senses sensitive to light, sound, temperature, pressure, magnetic field, and electric field. What all these stimuli have in common is that they can be gradually altered by arbitrarily small steps, thereby providing a basis for the JND-method. Most stimulus types represent a continuum like wavelength or temperature that is amenable to this treatment. Chemical stimuli may seem to be an exception because chemical stimuli consist of discrete molecules. Molecules cannot be altered by arbitrarily small steps, instead, the smallest gradual change to a molecule is to add or remove one atom or to replace one atom with a similar atom. In almost all cases, a molecule can be distinguished by smell from the chemically most similar molecule (Laska and Teubner, 1999a,b). However, as discussed in detail in the above section on constructing the olfactory QS, the olfactory stimulus space consists predominantly of mixtures of molecules and the ratios of the components of a mixture can be altered in arbitrarily small steps. Two odorous molecules A and B are connected by JND steps through mixtures of A and B with different ratios of the two components. The JND-method of modality individuation can therefore also be applied to the chemical senses much in the same way in which it can be applied to all other senses.

It has to be pointed out, however, that applying the JND-method of modality individuation requires a prior decision on what stimuli to include as components of mixtures. If one allows mixing of, for example vanillin (a tasteless odorant) and sugar (an odorless tastant), then odor and taste will be individuated as a single modality by the JND-method, if, as can be expected, orally administered mixtures of vanillin and sugar can be gradually altered from pure vanillin to pure sugar along a line of indistinguishable mixtures of different ratios. If one prevents mixing of tastants and odorants then odor and taste will be individuated as two modalities. If chemical stimuli are allowed to be mixed with touch and temperature stimuli inside the oral cavity, the JND-method will individuate the multisensory modality called "flavor" (Taylor and Roberts, 2004; Shepherd, 2011; Small and Green, 2012).

In summary, when the JND-method of modality individuation is applied, the same method that is used to constructing QSs can be used to individuate modalities. This approach, which individuates modalities through behavioral tests, provides an empirical alternative to the traditional criterion-based approaches. It can be readily applied to senses sensitive to continuous stimuli like light, sound, temperature, pressure, magnetic field, and electric field. To apply it to the chemical senses, it has to be supplemented by a limit on the stimuli that can be mixed. JNDs fix the mental qualities specifically and exclusively by appeal to the perceptual role that states with those mental qualities play, independent of whether the states are conscious states. So if we are to find a supplement to JNDs that puts limits on the mixing of stimuli for purposes of constructing the relevant QS, we would want to explore possibilities that appeal in one way or another to the perceptual role of states with the relevant mental qualities, independent of whether those states are conscious. Any such supplement to JNDs would conform the spirit of QST.

Because the JND method of modality individuation requires behavioral experiments, the outcome of applying this method is at this point speculative. It therefore remains to be seen how the outcome of this approach compares to the outcomes of the criterion-based approaches. However, regardless of the results, the JND method has two advantages over the traditional approaches. First, the same method that is used to individuate the senses is used to construct QSs of the perceptual qualities in the individual senses. This is an elegant way of arranging all sensory qualities in just a single step. Second, the JND method is based on an empirical procedure and it is therefore transferable to any situation. Unusual senses (echolocation, polarized light, tactile vision, etc.) or unusual subjects (aliens, synesthetes, etc.) that often require special treatment by the criterion-based approaches therefore pose no special problem for the JND-method of modality individuation.

How a modality is individuated has, of course, important consequences for the features attributed to it. For example, how olfaction is individuated determines whether it exhibits a spatial aspect, perhaps calling for an independent QS that specifically determines olfactory spatial mental qualities. It is commonly thought that smells seemingly just appear within our nostrils or as undifferentiated transparent odorous clouds within our surroundings. This has a led a large number of philosophers to argue that olfactory perception does not represent the location or direction of olfactory stimuli (Lycan, 2000; Smith, 2002; Matthen, 2007; Peacocke, 2008; Batty, 2010). Almost all odors activate at suitable concentrations both the first cranial nerve (the olfactory nerve) and the nerve endings of the fifth cranial nerve (trigeminal nerve) in the nasal cavity (Doty and Cometto-Muñiz, 2003). What types of spatial aspects olfaction exhibits depends on whether what is mediated by the trigeminal nerve is considered to belong to the olfactory modality.

Even if one considers olfaction to be only what is mediated by the olfactory nerve, these philosophers may be mistaken. Humans can locate a smell using differences in concentration. Locating the source of a smell requires active exploration; movement of the whole body or at least of the head (Richardson, 2011). In this respect, locating an odor source is similar to locating a heat source (Smith, 2002). Olfactory experience can, across time (diachronically), have spatial structure, although it can be debated if this structure is represented in perception or cognitive. At any particular time (synchronically), olfactory experience has no spatial structure.

If one individuates modalities in a way so that the trigeminal nerve contributes to the olfactory percept (as the JND method does), then olfaction also presents us synchronically with spatial properties, in a similar fashion to audition, in which comparisons between the inputs into the two ears supports locating sound sources. Although it has been shown that for stimuli that activate only the olfactory nerve subjects cannot tell if the odor is in the left or right nostril (Radil and Wysocki, 1998; Frasnelli et al., 2008), this is easily possible for stimuli that activate the olfactory and the trigeminal nerve (Kleemann et al., 2009). This enables us to determine the location of the odor source because there are small differences in timing and intensity of the stimulus between the two nostrils that enable us to locate odorants within 7–10 degree of their location (von Bekesy, 1964). Further evidence supporting the claim that each nostril creates a different olfactory percept is substantiated by Zucco and Chen (2009, p. 1564), who demonstrate that binaural rivalry exists between the nostrils, such that "alternating odor percepts [occur] when two different odorants are presented to the two nostrils." The difference between the perceptible properties presented to each nostril has also been shown to allow us to track an olfactory stimulus through an environment over time (Porter et al., 2007).

Thus, whatever the QS may be for olfactory qualities, the spatial perceptible properties of olfaction will require an additional QS dedicated specifically to reflect the JNDs of spatial location of olfactory perceptible properties. Olfaction does present spatial perceptible properties that can be ascertained in accordance with JND judgments. The percept mediated by the olfactory nerve does so diachronically and the percept mediate by the trigeminal nerve synchronically. Those who deny any spatial aspect to olfactory experience are simply mistaken. Olfactory perception does present objects with perceptible spatial properties, but they are diffused across the environment in a manner that is dissimilar to the way the spatial aspects of objects are presented to vision. Odors have spatiotemporal perceptible properties, yet locatedness might not be a perceptible olfactory property that makes it unlike vision. Whatever the case about spatial aspects of olfaction, however, there is no conflict with QST, since the theory allows for different types of QS for different modalities in general, and so also in respect of spatial properties.

EXPERIENCE-DEPENDENT OLFACTION

As noted in the introductory section on QST, the theory predicts that the space of mental qualities is enhanced or made more fine-grained by improvements in perceptual acuity. The acuity of our perceptual discriminations themselves, independent of conscious awareness, can improve either through maturation of the perceptual system itself or by way of perceptual learning. These processes lead to an enlargement or more fine-grained development of the QS, and enable us to make a greater number of perceptual discriminations. And QST posits that the ability to make more perceptual discriminations is due to the occurrence of a correspondingly greater number of mental qualities.

In this section we explore what is currently known about the processes by which olfactory acuity is improved through perceptual learning in application to QST. The evidence surveyed discounts the role of maturation, but supports the claim that the enhancement of perceptual acuity need not depend upon or even be accompanied by, consciousness or subjective awareness. Our subjective awareness of the contents of perception might well, sometimes at least, be modulated and even enhanced by our conceptual repertoire and descriptive resources, since we can often report on more nuanced aspects of our experiences as we acquire more fine-grained conceptual resources. But since QST defines the mental qualities independent of subjective awareness of them, the enhanced ability to report arguably reflects only subjective awareness of the qualities, and not the mental qualities themselves (e.g., Rosenthal, 2005, p. 187). In what follows we show that these claims are perfectly in keeping with what is known about experience-dependent olfaction based on the studies survey below that enhanced olfactory acuity need not depend upon subjective awareness or an increase in conceptual repertoire and descriptive resources.

There is some indication that enhanced perceptual acuity in olfaction supports the claim by QST that an enhancement of the QS independent of any subjective awareness can enhance our discriminative abilities. An increased presentation of an odorant even subliminally can generate further olfactory abilities for detecting and discriminating that stimulus from others. Wysocki et al. (1989) demonstrated that merely increasing the presentation of a stimulus enables a subject to gain the ability to detect and discriminate an odorant they were previously unable to smell at all. Thus, increased exposure to an odorant that one could not subjectively report smelling yielded a larger QS and thereby enhanced perceptual acuity in detecting and discriminating the odorant that is in keeping with the evidence, about to be surveyed below, from the enhanced perceptual acuity of perfume workers and the sensory training of wine experts.

Olfactory acuity is not always enhanced by the number of experiences one undergoes or by increased exposure to an odorant. Indeed, a subject's ability to discriminate between odorants can be adversely effected by increased exposure to the binary mixture of these odorants, such that familiarity with the mixture decreases the subject's ability to discriminate the components odorants (Case et al., 2004). These results might be attributed to so-called acquired equivalence, in which two odors that are judged similar and that frequently co-occur become increasingly difficult to discriminate (Stevenson and Boakes, 2003). Acquired equivalence is of relevance to QST, since it suggests a reduction in the number of distinct olfactory mental qualities resulting from decreased ability to discriminate odorant stimuli. This arguably shows that not only does improvement in perceptual acuity lead to an enhanced QS of mental qualities, but a decrease in discriminative perceptual abilities is reflected in a reduction in the fineness of grain of the QS of olfactory mental qualities.

Olfaction that is influenced by experience is especially fascinating with regards to QST claims regarding enhanced perceptual acuity, since linguistic tags and semantic resources are known to play only a limited role in improving olfactory acuity. Olfactory perception and discriminative ability are enhanced primarily through an increased number of stimulus presentations and olfactory experiences, and linguistic tags and linguistic resources for describing olfactory experiences play only a limited role in improving olfactory discriminative ability. This fits well with QST, which defines mental qualities independent of subjective awareness; linguistic tags and descriptive resources would presumably enhance only the subjective awareness of the olfactory mental qualities, and not the mental qualities themselves, which are fixed just by discriminative ability independent of subjective awareness.

However, it should be noted that in what follows none of the studies surveyed below employed forced-choice discrimination tasks using subliminal stimuli. Thus, their results do not directly bear on the claim by QST that mental qualities are determined according to judgments of JND that can occur independent of conscious awareness of stimuli. Rather, the literature below on consciously mediated enhanced olfactory perceptual acuity is surveyed below for the sake of completeness. Furthermore, these studies are instructive as it is arguable that if in adult testing conscious olfactory acuity is only slightly influenced by linguistic tags and semantic resources, then the same should hold for non-conscious olfactory acuity. Additional research needs to be conducted to confirm that conclusion, by examining whether these same results do occur in the discrimination of subliminally presented olfactory stimuli.

The process of maturation is unlikely to be a major influence in the increased fineness of grain of olfactory perceptual acuity, since the olfactory QS is relatively consistent from age three through old age. The olfactory system is fully developed and functional *in utero* and is responsible for an infant's ability to identify its mother (Russell, 1976; Porter and Winberg, 1999), as well as the ability to distinguish relatives from strangers (Porter et al., 1986). Children's olfactory capacities are fully developed by age three in terms of odorant detection threshold and hedonic judgments (Stein et al., 1958; Steiner, 1977; Schmidt and Beauchamp, 1988; Schmidt, 1992; Soussignan et al., 1997). There is some difference in detection thresholds, but this is most likely due to adaptation to ecologically important stimuli. Furthermore, while some studies have shown that children's ability for odor recognition and identification is inferior to that of adults, when linguistic competence and overall vocabulary are controlled for, these apparent differences disappear (Schmidt and Beauchamp, 1988; Lehrner et al., 1999). And though maturation does not enhance acuity, deterioration does play a role in the loss of olfactory perceptual acuity starting at about age 40 (Dulay et al., 2008).

Conscious perception is doubtlessly influenced by our conceptual abilities and linguistic practices that enable us to utilize vocabulary to describe perceptible properties. Conscious olfactory perceptual acuity is influenced by verbal mediation in terms of learned linguistic tags, but also to a large extent by the number of exposures to an odorant. In a classic set of experiments, Rabin (1988) demonstrated that increased exposure to an odorant improved the subject's ability to discriminate that odor from others. In the first experiment the exposure condition showed an increase discriminative ability as compared to the control, yet the subjects in a further condition in which they learned relevant linguistic tags showed an even greater increase in discriminative ability. The results from the second experiment partially address this by demonstrating that the familiarity of an odorant allowed an enhanced discriminative capacity for similar odorants. But all this could reflect the relevance of linguistic tags to subjective awareness of olfactory mental qualities, and not to the mental qualities themselves, which are on QST fixed independent of any such subjective awareness.

Since perceptual acuity increases even for identity and naming in accordance with familiarity of the odor (Homewood and

Stevenson, 2001) and practice (Cain, 1979), it is worth considering how olfactory acuity is mediated by memory. Our almost pathological inability to name odors (Olofsson et al., 2012) has led many to question the format of odor memory. The underlying mechanisms and processes are still being investigated, but a growing body of evidence suggests that olfactory memory is not mediated by linguistic tags or verbal coding. Odor memory is possible without verbal mediation (Møller et al., 2004). Olfactory coding and experiences are non-linguistically formatted and do not dependent on language processing (Goodglass et al., 1968; Herz, 2000). There has been no direct research concerning the format of non-conscious olfactory mental qualities. However, if olfactory memory, which is arguably independent of subjective awareness, does not depend on linguistic tags or verbal coding, then the QS of olfactory mental qualities, which is also independent of subjective awareness, is unlikely to depend on linguistic tags and verbal reports.

Perfume experts do have enhanced olfactory discriminative abilities. That enhanced ability might in part be due to increased descriptive resources or linguistic labels, though the number of experiences has a much greater influence (Gilbert et al., 1998). Perfume experts and novices mostly overlap in their odor categorization, as determined by their sorting of perfumes into groups based on consciously perceived similarities and differences. The perfume experts were more parsimonious in the number of groupings, but the difference was not statistically significant. Moreover, despite the expert's more exacting usage of linguistic descriptors for odor groups, their groupings themselves were mostly similar to those of the novice consumers. Not only did the perfumers' enhanced semantic repertoire and linguistic tags show no marked affect in their categorical groupings of odors, but where they did differ in similarity judgments, the differences are best explained by the larger number of times the experts had been previously exposed to the stimulus (Veramendi et al., 2012). Thus, even the slight increase of the experts' parsimony in the number of groupings, itself not statistically significant, is best attributed to the number of experiences, rather than linguistic sophistication.

Further support for the idea that stimulus exposure leads to and is primarily responsible for an increase in olfactory acuity comes from studies that show that our conscious olfactory discrimination abilities increase with training and exposure. More familiar odors are easier to discriminate than those that are unfamiliar to us (Jehl et al., 1995). Perfume shop workers have an increased ability to discriminate odors, yet their stimulus detection threshold and ability to identify odors from a list of descriptors is not enhanced (Hummel et al., 2004). These results suggest that peripheral sensory plasticity or increased descriptive resources are not the determining factor in this increased discriminative ability. Instead, this increase appears to be driven by some sort of perceptual sensory template. Olfactory memory enables our capacity for perceptual discrimination in a manner that is not linguistically driven, yet in perfect keeping with the claim of QST that perceptual acuity can be improved through a sheer increase in the number of conscious or unconscious experiences that the subject undergoes, thereby enhancing our perceptual ability for making judgments of JND, which results in an enlarged or more fine-grained QS.

That odor acuity improves with an increase in olfactory experiences and training independent of linguistic mediation has also been documented in studies of wine experts. Wine experts outperform novices at odor discrimination (Solomon, 1990; Melcher and Schooler, 1996; Bende and Nordin, 1997) and their increased ability results from greater perceptual skill and not verbal or descriptive resources (Parr et al., 2002). Parr et al. showed that the experts had an enhanced ability to recognize odors, but that they did not outperform novices either in terms of their sensitivity threshold for odorant detection or the verbal memory task. When this result is combined with their findings that odor naming and odor recognition were not positively correlated, it provides further reason to think that increased olfactory recognition and discriminative acuity do not depend on an increased availability of linguistic tags or semantic descriptors.

This does not preclude the possibility that novices are sometimes aided in coming to discriminate odors consciously in more fine-grained ways by learning new tags or descriptive resources for distinct mental qualities (Rosenthal, 2005, chapters 1 and 7). The tags or descriptive resources would be relevant to novices' subjective awareness of mental qualities, which might well already differ. Further testing based on subliminal presentation of olfactory stimulus using forced-choice methodology or the equivalent is needed.

More recently it was shown that wine experts can more accurately discriminated between two varieties of wines as indicated by their correctly sorting samples into their respective groups (Ballester et al., 2008). Moreover, these results showed an intersubjective convergence of the experts on their judged typicality of each variety of wine, which the authors interpret as indicating that the experts discriminated each kind of wine in respect of its perceptual characteristics. However, these results do not address the question whether the increased perceptual ability and judgments of typicality are caused by an enhanced perceptual strategy that is more analytic and focuses upon the perceptible qualities of the stimulus, as against being due instead to enhanced descriptive repertoire that allows greater conscious discriminative ability. At least one study suggests that it is the former. In this study, wine experts were trained to detect and discriminate between key sensory characteristics using sensory training (Tempere et al., 2012). By exposing experts to key odorous wine compounds Tempere et al. increased the experts' perceptual abilities by lowering their detection threshold through increased exposure to the key compounds in a fashion that only allowed them further discrimination within that group of qualitatively similar perceptible properties.

Taken together, the results from these studies provide evidence that olfactory acuity improves with the number of olfactory experiences in a manner that does not depend upon maturation of the olfactory system or the nature or richness of linguistic representation of the olfaction qualities. Human discriminative abilities increase in accordance with the overall perceptual QS of olfaction that is evidently not mediated by linguistic or verbal coding. In the wine-training research the overall effect was specific to the training stimulus, which indicates that an enhancement of the olfactory mental-QS is determined by the perceptible properties we can discriminate among.

A key test for the claim that olfactory discriminative acuity is mediated by experience and not linguistic coding or descriptive resources is cross-cultural comparisons of odor perception and categorization. Linguistic conventions and conceptual naming strategies differ between cultures, yet there is great overlap in overall odorant categorization as determined by odorant sorting experiments using consciously judged perceptual similarities (Chrea et al., 2005a,b). In these studies, American, French, and Vietnamese students were shown to sort odor samples into similar groupings that were not consistent with their groupings of the odor labels that would be associated with the olfactory samples presented in the odorant sorting task. Since the odorants were categorized differently from the labels, there is reason to believe that the verbal labels did not determine odorant grouping. Additionally, the differences between the different cultural groups in odor grouping displayed a familiarity effect. Individuals from cultures that were more familiar with an odor categorized it similarly, thereby showing that the number of exposures was the best indicator of olfactory discriminative ability for odor categorization in this type of odorant-sorting task.

Experience-dependent olfactory perceptual abilities pose no problem for QST. However, there is another result that might at first sight seem to do so. Research on olfactory sensitivity, using classical conditioning, has demonstrated that enantiomers can be discriminated by subjects despite their subjective reports that they possess identical olfactory qualities (Li et al., 2008). Li et al. demonstrated that supraliminally indistinguishable optical isomers are discriminable after classical conditioning. According to QST, discriminative ability determines mental quality. In this case there is an increase in discriminative acuity and thus an enhancement of the olfactory QS in respect of discriminative ability, yet no subjective report of any increase in perceived olfactory quality.

But despite initial appearances, this is readily explained by QST, since the mental qualities that discriminative ability determines on the theory are independent of any subjective awareness of those mental qualities. In this case we have increased refinement of mental qualities that is not reflected in a corresponding ability to distinguish those qualities. Thus in the next section we turn to non-conscious olfactory qualities and to whether we have good reason to think there are non-conscious mental qualities corresponding to each of the enantiomers post-conditioning that we cannot report on.

OLFACTORY QUALITIES IN NON-CONSCIOUS OLFACTORY STATES

Non-conscious olfactory states that are genuinely qualitative might be inferred from the phenomena of blind smell (Schwartz et al., 1994; Sobel et al., 1999; Schwartz, 2000), mate selection (reviewed in Wilson and Stevenson, 2006), social acquaintance selection (Li et al., 2007), and an argument from absence which would explain the deterioration in quality of life following the onset of anosmia. Anosmia is the most common disorder of olfactory pathology in which individuals lose their sense of smell. In some cases anosmia is due to the presence of a psychological disorder, but the vast majority of cases result from damage to the olfactory bulb due to either infection or head trauma. In addition to their inability to perceive olfactory stimuli, anosmic individuals also experience a decrease in their hedonic quality of life (Miwa et al., 2001; Keller and Malaspina, 2013), which in turn is often causally implicated in the further development of depression (Deems et al., 1991). We are not aware of our olfactory experiences most of the time, but they imbue our lives with a qualitative character of experience, which becomes most striking when it is absent (for a review of all these phenomena and their relation to other theories of non-conscious qualitative states, such as Block, 1993, 1995, 2001, 2007, 2008, 2009) distinction between access and phenomenal consciousness, see “smelling phenomenal” by Young (in press) in this special research topic.

But a concern regarding each of these phenomena as evidence for unconscious olfactory qualitative states is that humans are not commonly aware of their olfactory experience and generally discount their overall olfactory abilities (Sela and Sobel, 2010). So one might question whether we should conclude, in accordance with QST, that non-conscious olfactory perceptual states do have genuine mental qualities.

But it turns out that olfaction can provide independent evidence using secondary processing measures that non-conscious olfactory discriminative ability matches that of conscious discriminative ability, thereby corroborating the view of QST that olfactory mental qualities do indeed occur independent of consciousness. They occur not merely in the absence of attention, but in the absence of subjective awareness itself.

Secondary processing measures are traditionally employed in disputes regarding computational implementations of cognitive abilities; but similar measures are also available in the measuring of perceptual states. In addition to a state’s role in enabling discrimination of olfactory stimuli and in addition also to any of distinctive role it may have, there might be other secondary properties we can use to judge whether or not the same type of state occurred, utilizing a very similar if not always wholly identical physical realization. Secondary processes are correlated properties or incidental effects (Cummins et al., 2001), such as speed, error rate, types of errors, or fatigue, etc., of a perceptual system in the performance of particular tasks.

In olfactory research the perceptible property of valence (the perceived pleasant or unpleasant property of an odor) provides just such this type of measure for assessing the veridical nature of this perceived olfactory property, independent of subjective reports based on conscious awareness. Behavioral measures such as sniff rate and volume, response time, and heart rate can all be used as independent measures that indicate the olfactory system is treating pleasant or unpleasant olfactory stimuli in the same fashion, regardless of whether we consciously perceive the odors or can subjectively report upon their olfactory qualitative character or their valence. The perceptible property of olfactory pleasantness or unpleasantness can be employed using sniff rates as a secondary measure to verify the perceived pleasantness or unpleasantness of an odor even when the subjects are subjectively unaware of any relevant olfactory mental qualities.

Humans modulate their sniff rate and volume 150 ms after the onset of a stimulus depending on the odor’s concentration and valence (Johnson et al., 2003). The stimulus-dependent response of human sniffing is such that intense and unpleasant odorant are sniffed less vigorously and with a decreased volume. Measurement of olfactory motor responses to odorants is reliable enough to be used as a non-verbal measure of human's detection and categorization of the odor (Frank et al., 2003). Additionally, it has been shown that while individuals with fully functional olfactory systems modulate their sniffing in accordance with the valence of the odor, anosmics show no such response (Harland and Frank, 1997). This shows that the sniff response only occurs when the subject perceives the valence of the presented stimulus and can arguably be used to show that the variable of sniff rates can be used to demonstrate the occurrence of mental qualities independent of conscious subjective reports, and hence in the absence of subjective awareness.

Sniff rate and volume are not the only secondary measures for assessing odor valence. Response time is faster in detection and discrimination tasks for unpleasant odors (Bensafi et al., 2003), and heart rate measurements show that we involuntarily react in distinctive ways to unpleasant odors (Bensafi et al., 2002). The subject's non-conscious perception of odor valence can be verified using behavioral non-verbal measure such as sniff patterns, response time, and physiological response of heart rate. These measures, and in particular the invariance of sniff rate between conscious and non-conscious presentations of an odor, further support QSTs methodology of identifying mental qualities in light of a state's perceptual role in enabling perceptual discriminations, independent of whether the subject can report undergoing an experience with qualitative character and so independent of subjective awareness.

The sameness of perceptual role of olfactory states in conscious and non-conscious olfaction as assessed by the secondary measures of sniff-rates (as well as other behavioral measures) is what supports the methodology of inferring sameness of perceptual content and mental quality. Thus, these secondary measures can be employed as empirically sound tools for verifying the perceptible property of valence independently of subjective reports.

Secondary processing measures corroborate QSTs conclusion that occurrence of mental qualities can be established independently of subjective awareness. However, further research is required on the sniffing parameters of subjects during judgments of JNDs, since olfactory imagery generates consciously imagined percepts. In addition, of the aforementioned phenomena that provide evidence for non-conscious olfactory states that are genuinely qualitative, only the work of Schwartz et al. (1994) on blind smell employed a forced-choice discrimination task, but without measurements of sniffing patterns. Nonetheless these further measures provide a promising way to strengthen the extrapolation of the QS of perceptible JNDs to the QS of mental qualities, since they provide further motivation that the best explanation must involve the existence of non-conscious mental qualities. The alternative explanation that non-conscious olfactory states do not exhibit qualitative character is unmotivated, because behavioral and physiologically measures can indicate that at least for the perceptible property of valence the olfactory system is treating certain non-conscious olfactory states as equivalent to those that exhibit conscious qualitative character.

Even employing secondary measures, the aforementioned Li et al. (2008) study provides what appears superficially to be a problem for QST. Their findings indicate that even though the subjects can be trained to discriminate between enantiomers with identical olfactory qualities, the subjects' ratings of the valence, intensity, and familiarity of these structures were not affected. Training might have produced the ability to detect the differences in the enantiomer's structure, such that subjects could discriminate between the enantiomers, but it did not lead to a reportable change in the qualitative character of the olfactory quality of the conditioned enantiomer. Furthermore, secondary processing measures indicate that even after training the perceptible properties of each enantiomer remained the same. These results may seem to run contrary to what QST would predict, since the increased discriminability should yield further mental qualities.

However, QST defines mental qualities independent of conscious awareness of olfactory stimuli, in terms simply of discriminative ability, whether conscious or not. So Li et al.'s results do not after all threaten QST. It is perfectly possible that mental qualities occur non-consciously in a more fine-grained way than we are subjectively aware of, and hence in a more fine-grained way than we can report.

Indeed, as Rosenthal (2005, ch. 7, 2010) has argued, that is very likely the best explanation for the way novices can quickly learn to distinguish consciously previously indistinguishable stimuli, such as two wines or two musical instruments, when given terms to attach to the two stimuli. Having distinct terms for the two experiences, the experiences come to be consciously distinct. The best explanation is that distinct mental qualities already occur on tasting the two wines or hearing the two instruments, but only non-consciously. Learning the new terms facilitates those unconscious mental qualities' becoming conscious. Li et al.'s fascinating research on enantiomers would present a challenge to QST only if the theory implied that discriminative ability in the non-conscious case is always matched in the conscious case. But the theory does not imply that, and indeed implies that the opposite is likely.

CONCLUSION

QST fixes and describes the mental qualities for each perceptual modality by appeal to the discriminative ability that yields JNDs, independent of whether the relevant perceptual states are conscious. Such JNDs among perceptible properties allow the construction of a QS of those properties. Because the perceptual states that discriminate perceptible properties differ in mental quality, a QS of discriminable perceptible properties serves also to fix the mental qualities that are operative in such discrimination.

The construction of a QS for the visual mental qualities is relatively straightforward. The construction of a QS that would do justice to olfactory stimuli, however, poses special challenges. This is due in part to the vastly greater number of olfactory discriminations we can make compared to those we can make, for example, among visible stimuli. The challenge for constructing an olfactory QS becomes especially formidable in connection with mixtures of olfactory stimuli. Because of these and related factors, the olfactory QS will inevitably have a huge number of dimensions. Nonetheless, there is no reason to doubt that a QS can be constructed that would capture the ability to discriminate among olfactory stimuli, and thereby the olfactory mental qualities that underlie that ability.

A question arises also about what distinguishes olfactory stimuli from stimuli of other types and, more generally, about how to distinguish each perceptual modality from others. It turns out that QST helps here as well; the same appeal to discriminative ability that fixes the mental qualities can be harnessed to distinguish the various modalities. This way of distinguishing the modalities, moreover, is arguably superior to more traditional ways of doing so. And the QS methodology has the additional benefit of allowing a QS treatment of mental qualities that figure specifically in the sensing of location, as well as perceptible size and shape for those modalities that enable the discrimination of those spatial perceptible properties. Moreover, it provides the tools to confirm just which spatial properties each modality can discriminate.

QST accommodates the perceptual learning and maturation known to occur with olfaction and other modalities. Such processes result in the enhancement of the relevant QS, either by expanding it or by increasing its fineness of grain. This applies both to conscious changes in olfactory discriminative ability and to non-conscious development. But it is likely that an increased linguistic repertoire for olfactory experiences and the acquisition of new linguistic tags to refer to them enhances the way we are consciously aware of olfactory stimuli, but not the underlying ability to discriminate among olfactory stimuli. QST predicts this, since it fixes mental qualities independent of their being conscious and also independent of such linguistic tags and repertoire.

QST proceeds independently of whether the mental qualities are conscious because the theory fixes and describes mental qualities by their role in discriminating among barely discriminable stimuli, and such discriminations occur both consciously and not. Mental qualities are posited to explain the differences among perceptual states that enable such discriminations, whether or not those discriminations are conscious. In the conscious case, there is in addition first-person access to those mental qualities, but QST fixes the mental qualities solely by their role in discrimination, independent of such first-person access. So the theory readily accommodates mental qualities that are not conscious. And olfaction provides compelling independent corroboration of non-conscious olfactory mental qualities by appeal to the secondary processing measures of non-conscious olfactory perception.

In conclusion, QST provides a powerful theoretical tool for the understanding and the scientific study of olfactory mental qualities and olfactory perception. Olfaction in turn provides further evidence in support of QST, which has now been shown to be consistent with empirical findings in different modalities.

AUTHOR CONTRIBUTIONS

All authors wrote the paper together.

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