Smelling Odors and Tasting Flavors: distinguishing orthonasal smell from retronasal olfaction[1]

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Abstract: It is arguably the case that olfactory system contains two senses that share the same type of stimuli, sensory transduction mechanism, and processing centers. Yet, orthonasal and retronasal olfaction differ in their types of perceptible objects as individuated by their sensory qualities. What will be explored in this paper is how the account of orthonasal smell developed in the Molecular Structure Theory of smell can be expanded for retronasal olfaction (Young, 2016, 2019a-b, 2020). By considering the object of olfactory perception to be the molecular structure of chemical compounds composing odor plumes, Molecular Structure Theory provides a means for determining an odor's olfactory quality, how odors can be identified and individuated, and how we perceive smellscapes. Surveying the differences between orthonasal and retronasal olfaction provides the basis for the central argument of the paper that the perceptible objects we refer to as smells and individuated on the basis of their olfactory qualities are only relative to orthonasal olfaction. Retronasal olfaction it is speculatively concluded might play an essential role in our perception of flavorful objects.

Keywords: Smell, Odors, Flavor, Orthonasal Olfaction, Retronasal Olfaction, Perceptual Modalities, Individuating the Senses.

1. Introduction

The olfactory system contains two separate senses (Smith, 2015): orthonasal and retronasal olfaction. The simplest example of a primary differences between these senses is by noting the anatomical pathways by which stimuli reach the olfactory receptors. Orthonasal olfactory perception occurs when we smell chemical stimuli (odorants) that are inhaled from the front of the nose. Retronasal olfaction occurs when odorants within the mouth are exhaled through the back of the throat and out the front of our nostrils. The difference in anatomical routes of stimulus delivery make it natural to think that despite each systems transducing the same type of distal stimulus (i.e. an odorant plume) nonetheless they differ in their kinds of perceptible objects[2], such that we exteroceptively smell odors within a smellscape via

[1] Portions of this paper have been presented at the *Olfactus* 2019 meeting held at *Stockholm University Brain Imaging Centre*, the *RUHR-UNIVERSITÄT Bochum*, *Philosophy Colloquium*, and the work in progress seminar at the Centre for Philosophical Psychology at Antwerp University. I would like to thank all of the members of the audience on these occasions for their helpful questions and feedback. In particular I would like to thank Asifa Majid, Barry Smith, Bence Nanay, Jonas Olofsson, Solveig Aasen, Tobias Schlict, and Keith Wilson for their comments on different aspects of this research project.

[2] Throughout this chapter the term perceptible object should be understood as being the same as O'Callaghan's (2008, 2016) locution of "object for perception" where this is to be understood as a wider, neutral, and more inclusive conception of perceptual objecthood that requires a suite of capacities that form the basis of object perception relative to a modality. O'Callaghan's framework allows for a broader notion for demarcating the objects of perception relative to a modality than intentional object conceptions, as well as being neutral enough to encompass relationionalist theories of perception. However, Young (2020) argued contrary to O'Callaghan (2016) that temporal structure must also be considered when conceiving of the object of olfactory distal perception in the same way that temporal mereological structure is responsible for determining the objective nature of auditory perceptual objects. Additionally, the conclusion of this chapter speculatively argues against his claim that flavor perception does not have an object for perception.

orthonasal transduction (Young, 2020) and retronasal olfaction plays an essential part in the multi-sensory perception of flavorful objects contained within our headspace (Auvray and Spence, 2008; Small, 2012; Prescott, 2015). It is this pretheoretic intuition that the paper seeks to explore - orthonasal olfaction counts as the perceptual system responsible for our perception of smells within our environment, while retronasal olfaction is one of the many sensory systems that combine to yield our perception of flavor.

What is fascinating about the olfactory system is that it contains two separate pathways of stimulus presentation that share the same type of distal stimuli, the same sensory transduction mechanism, the same sensory processing centers, and some of the same cortical processing areas, yet they differ in terms of what types of perceptible objects they transduce and the kinds of sensory qualities they generate. Elsewhere it has been argued that accounting for the question of "what are smells?" requires handling three nested issues. What are the perceptible distal objects transduced by the system, what is it about these stimuli that generate the olfactory quality of smells, and what is the intentional object of our experience of smells (Young, 2016)? A comprehensive account of our perception of smell requires accounting for the olfactory quality of the object of perception, its distal nature as an odor plume, and how we intentionally represent smell experiences. It has been argued that the Molecular Structure Theory (MST) of smells can viably provide an answer to each of the aforementioned nested issues based on its determination of smells as the molecular structure of chemical compounds within odor plumes composing a smellscape (Young, 2019a, 2020). The molecular structure of the chemical compound and the odor plume account for the smell's olfactory quality and distal nature (Young, 2016, 2019a), which can then explain the perceptible[3] object of olfactory experiences as odors within an overlapping gaseous sea conceived of as a smellscape (Young, 2019b, 2020).

By considering the perceptible object of olfactory perception to be the molecular structure of chemical compounds composing odor plumes, MST provides the means for explaining what determines a smell's olfactory quality, how smells are identified and individuated, and how we can perceive smell as odors plumes against a background smellscape (Young, 2016, 2019a-b, 2020; Young, Escalon, Mathew, 2020). The bonus of accepting this account is the further explanatory purchase of providing a means of individuating the perceptual modality of smell. What sets olfaction apart from the other modalities is not merely its proprietary sensory system, but the perceptible object of smell with its unique olfactory qualities that cannot be sensed using other sensory systems (Young, 2019a, 2020). We employ smell to gain access to the intrinsic olfactory qualities of a certain range of chemical stimuli in the environment. We smell odors, which is shorthand for we perceive the olfactory quality of groupings of types of chemical within the gaseous sea of chemical currents we are immersed in. Given this background theoretical framework and the overlap in shared transduction mechanisms, stimuli, and sensory processing centers the question becomes whether we employ retronasal olfaction to perceive smells?

What is known about retronasal olfaction will be surveyed to establish that despite their underlying similarities orthonasal and retronasal olfaction do not share the perceptible objects and olfactory qualities. Surveying the differences between orthonasal and retronasal olfaction in terms of their separate anatomical routes of odor delivery, stimulus transduction, sensory encoding, cortical processing, and perception provides the basis for the central argument that our sense of smell is relative only to orthonasal olfaction. The paper progresses

[3] The terminology of "intentional object" used in earlier versions of MST has been up-date with "perceptible object" throughout this chapter in accordance with the assumption of O'Callaghan's framework and conception of objects for perception (see footnote #1).

in the following sections to reach this conclusion. Section 2 introduces retronasal olfaction. Section 3 survey's how the different anatomical pathways generate further difference in stimuli transduction with implications for demarcating the perceptible objects and their sensory qualities. Section 4 continues the focuses of how the differences noted in the previous section mediate further distinctions in odorant perception as it is encoded at the receptor level. Section 5 progresses the argument further by looking at the how the two systems project into separate and non-convergent cortical processing areas. Section 6 wraps up the difference between orthonasal and retronasal olfaction by focusing on perceptual states and how these differ in the perception of sensory qualities. The paper concludes by arguing that orthonasal and retronasal olfaction do not share the same perceptible object and that the differences in stimulus transduction and encoding yield perceptually different types of olfactory qualities. Despite both transducing the same type of distal stimuli (odorant plumes), they do not share the same type of perceptible object as shown by difference in perceived olfactory qualities which is the primary means of olfactory object identification according to MST.[4] Thereby, establishing a disparity between retronasal and orthonasal olfaction on at least two of the three central questions required for a comprehensive account of "what are smells?"

2. What is Retronasal Olfaction?

It comes as a surprise to most people that what we ordinarily report as taste experiences are partially generated by the olfactory system in our nose. Yet not everything that goes on inside the nose should be considered part of our sense of smell. Somatosensory and trigeminal stimulation within the nasal cavity might play a role in our everyday experience of smelling, yet (without associative learning) they do not yield perceptual olfactory qualities, which has been argued is an essential aspect of smell (Young, 2016, 2017). What was argued elsewhere is that the olfactory system beginning with olfactory receptor neurons and projecting to cortical areas of encoding is the primary determinate of smell experiences of olfactory qualities and thereby the basis of our perception of smell (Young, 2017, 2019a). However, there are two distinct pathways for the odor plume to reach the olfactory epithelium and with them the conundrum of this paper. Do these distinct pathways yield two senses of smell (Smith, 2015), one perceptual modality of smell despite the duality (Shepherd, 2012), or perhaps two olfactory sensory systems only one of which yielding the perceptual modality of smell?

One pathway for odors to reach the olfactory system is via the front of the nose. Orthonasal olfaction, as it is so labeled, is what we primarily refer to as our sense of smell. Our olfactory experiences are usually of external odors within the environment that have been brought into our nose through normal inhalation or actively sampling the surrounding air by sniffing. In addition to the orthonasal pathway, there is a second pathway for airflow from our throat via the nasopharynx upwards to the back of olfactory epithelium. A great deal of the sensory qualities that we assign to eating and drinking are transduced by the retronasal olfactory system. The activity of chewing and swallowing causes an odorant laced plume to flow from our mouths into our nose thereby traversing the olfactory epithelium and out of our nostrils. Often what we call the flavor of food and drink is not just its gustatory qualities, but a complex multi-sensory experience including retronasal olfaction, gustation, somatosensation (including thermal and nociception) and chemothesis (Stevenson, 2009; Small, 2012; Prescott,

[4] Smells, according to MST, are primarily identified and individuated based on their olfactory quality with their sensory qualities of intensity and hedonics considered to be further features of the smell (for a further discussion of concentration, intensity, hedonics, and valence of smells as properties of the odor object cf Young, 2011, 2019b).

2015). Each of these separate sensory channels provides access to the multi-phasic object for flavor perception, which compose into a unified perceptual experience of flavor. So how many senses of smell do we have? Despite sharing the same range of chemical stimuli and receptor transduction, what will be argued throughout this paper is that we only have one sense of smell - orthonasal olfaction. Under laboratory conditions we can elicit pure retronasal olfactory perception, yet normal everyday retronasal experiences are of multi-sensory flavor objects. Aside from exceptional cases, it is arguably the case that retronasal sensations do not generate perceptions of smells.

3. Background effects: airflow, mucus, and placement of stimuli contact with epithelium

The separate anatomical pathways of odorant delivery do not exhaust the full range of differences between orthonasal and retronasal olfaction. The direction of airflow, how the stimulus traverses the mucosa layer covering the olfactory epithelium, and where the stimuli makes contact with the olfactory receptor neurons along the epithelium all play a role in generating distinct perceptual states despite sharing an identical set of chemical stimuli. This section explores the background stimulus transduction effects that are operant in generating differences based on the separate anatomical pathways.

The direction of air flowing through the nostrils, and respiratory patterns determine if the chemical stimulus will be perceived orthonasally or retronasally. Whether the stimulus is being brought in through the front of the nostrils or being pushed out from the back of the nasopharynx will determine how it is perceived. Chemical stimuli that are inhaled from the front of the nostrils are perceived as orthonasally, whereas the exhalation of odorants from the back of the throat through the front of the nostril generates retronasal olfaction (Small 2005; Shepard 2009; reviewed in Goldberg 2018). Exhalation has been shown to be essential for retronasal olfaction, such that cortical areas responsible for encoding of retronasal perception are phase locked with exhalation breathing patterns (Masaoka et al 2010).

If we consider the types of perceptible each system is ordinarily stimulated by objects (odor plumes within smellscapes vs. flavorful objects placed within the oral cavity) it makes sense that each system is sensitive to a different direction of airflow. Assuming that the objects of smell perception are odorous gaseous plumes generate by environmental turbulence then it would make sense that orthonasal olfaction as an exteroceptive sense would be sensitive to airflow and odorants based on inhalation and sniffing originating from stimuli in front of our nostrils. Whereas retronasal olfaction is sensitive to the flow of odorants originating within the oral cavity via the back of the throat. The distinct pathways begin to suggest that the types of object each system is designed to sense might be used to distinguish orthonasal olfaction from retronasal olfaction. It might not only be that the systems are sensitive to a different types of objects, but also how the same set of chemical stimuli interact with the receptors based on the difference in pathways might also shift the perceived olfactory quality, such that the same type of odorant might be perceived as having different olfactory qualities based on the path of delivery.

How the odor stimulus is transported to the olfactory epithelium impacts the nature of olfactory perception. Difference in how the odorant is transported to and interacts with the olfactory receptors partially explains the perceptual differences between the systems despite being presented with identical stimuli. The olfactory epithelium is segmented into areas of different types of olfactory receptors neurons with slight shifts in sensitivity to different types of molecules (Schoenfeld and Cleland, 2005a-b). Moreover, the olfactory epithelium is coated in a layer of mucosa that increases in depth progressing away from the nostrils. The segmentation of receptor sensitivity to different chemical properties of the stimulus combined with shifts in the depth of mucosa provide further reasons for considering the olfactory system as composed of two systems for stimulus encoding and transduction (Scott et al. 2013). Smaller molecules traverse the mucous layer faster at the front of the olfactory epithelium and slower towards the back of the epithelium. Larger molecules take longer to traverse the back of the mucus layer but have a greater chance of making it through the mucus intact and being transduced at the olfactory epithelium. Even if the stimulus is held constant, odorants will have different perceptual profiles based upon where they traverses the mucosa and what area of the olfactory epithelium they interacts with. How a stimulus interacts with the anatomical structure of the olfactory epithelium might partially explain why the concentration of an odor needs to be increased from an orthonasal presentation to a retronasal presentation to achieve the same perceived intensity.

How the odorant traverses the mucus impacts the difference between orthonasal and retronasal perception. Mozell (1966) and Mozell and Jagodowicz (1973) using gas chemotopography showed that different size molecules transduced by the olfactory system are absorbed by the mucosa at different rates. Their research generated the sorption hypothesis that the rate at which a molecule is absorbed by the mucus and transported to the olfactory epithelium effects the perception of smells. While there has been some debate regarding whether or not sorption yields a determination of perceive odorant identity or concentration as modulated by sniffing rates (Cenier et al. 2013), Kent et al. (2003) extends Mozell's findings by showing that the sorption rate also effects where the odorant will interact with the olfactory receptor neurons. Where the stimulus places on the olfactory epithelium further influences how it is transduced by the olfactory system. Using a range aldehydes of different carbon lengths, they showed differential rates of olfactory receptor neuron activity within the olfactory epithelium brought about by something as small as a change in a single carbon molecule. The different sorption rates for stimuli are further borne out by Wilkes et al.'s (2009) results that the rate of sorption varies even with binary mixtures. Their research shows that stimulus presentation can be distinguished using differences in concentration rates between orthonasal and retronasal perception, which is corroborated by Scott (2006) and Scott et al. (2014) that sorption and intranasal airflow shows differentiations for different types of molecular structures. Not only does mucus play a role in the rate at which the stimulus can interact with epithelium, but also the sorption rates and where the odorant comes into contact with the olfactory epithelium make a difference.

In addition to direction of airflow, sorption rate, and place of transduction on the olfactory epithelium, Nagashima et al. (2010) provide evidence that the enzymatic reactions within the mucus effect the olfactory stimuli for in vivo orthonasal olfaction. Whether this is applicable to retronasal olfaction and how it might effect perceived olfactory quality requires further research, but it seems likely that the mucus itself plays a role (in terms of its enzymatic reactions) in the transduction of olfactory stimuli, which will have a differential effect upon odorant transduction based on the depth of mucus that the odorant traverse to reach the olfactory receptor's cilia – assuming the quantity of mucus interacted with by an odorant will increase the rate of enzymatic reactions.

What is of further interest is that we can identity odorant onset relative to orthonasal or retronasal presentation, yet without training (Negoias et al, 2013) we are not able to localize the lateralization of the odorant to a nostril (Frasnelli et al 2009, 2010). We might be able to localize and identify whether or not we are having an orthonasal or retronasal experience, but we cannot differentiate odorant onset between nostrils. These results might depend upon the role of the trigeminal nerve in the nostrils, nevertheless in combination with other sensory systems these separate pathways generate a distinct capacity to identify the origin of the perceptible object. Thus, each system is tuned to transduce a different range of perceptible objects in a manner that might yield differences in the perceive olfactory quality of the same type of odorant based on how the stimulus reaches and is transduced by the receptor neurons.

Given differences of sensory transport, stimulus transduction, odor encoding, and perception it is arguably the case that olfaction has two different sensory system despite sharing the same transduction mechanisms and range of stimuli (for a review of further evidence supporting the claim that olfaction has two sensory systems see Bojanowski and Hummel, 2012; for a review with clinical data see Goldberg et al., 2018). Moreover, in reviewing differences between the two olfactory systems Goldberg et al. (2018) surveys further evidence that the olfactory quality of an odorant might depend upon the route of delivery. Aside from the differences in airflow pathways, the placement of the stimuli on the olfactory epithelium, and sorption rates, further differences distinguish orthonasal and retronasal olfaction.

4. Differences in Sensory Transduction

The two systems of olfaction can be distinguished in terms of their respective activation patterns on the olfactory epithelium relative to the direction airflow, which might play a role in explaining Frasnelli's et al.'s (2009) finding that we can localize the onset of an odorant between orthonasal and retronasal presentations. However, Olfactory Receptor Neuron (ORN) sensitivity also differs between orthonasal and retronasal transduction of the same stimulus. Small et al (2005) showed that regardless of the chemical structure of the odorant, receptivity differs as measured by threshold for orthonasal and retronasal stimuli. Orthonasal olfaction has a lower threshold and greater sensitivity for the same stimuli than retronasal olfaction, which requires higher concentration levels to achieve the same level of judged intensity. Further differences regarding olfactory sensitivity relative to route and placement of presentation on the epithelium can also be found in Frasnelli et al. (2004) such that the anterior portion of the epithelium shows increased chemosensitivity whereas the posterior area shows increase sensitivity towards mechanical simulation. Even ORN sensitivity shows a direct difference as measured by ERP with decreased amplitudes and longer latency when measuring retronasal olfactory sensory transduction. Combined together these studies suggest that even if the same stimulus is presented via the two pathways the sensitivity of the olfactory receptor neurons within the olfactory epithelium yield differences in perceived sensory qualities.

There are further differences in transduction and processing at the sensory encoding stage depending upon how the olfactory stimulus is combined with a gustatory stimulus. Orthonasal and retronasal presentations of the same odorant combined with congruent or incongruent gustatory stimuli yielded differences in olfactory sensitivity and processing at the initial transduction stage of olfactory processing (Welge-Lussen et al. 2009). Incongruent gustatory stimuli combined with an orthonasally presented odorants were interpreted as possibly increasing arousal based on conflict priming, while congruent gustatory stimuli combined with retronasal odorants enhanced processing, as determined by ERPs measures. Not only does the olfactory stimulus shows differential processing, when combined with gustatory stimuli, the olfactory system shows differential responses relative to route of a presentation.[5]

[5] Further anatomical differences related to the route of delivery in sensory transduction also separate orthonasal from retronasal olfaction. Using a limited model, which did not take into account the chemodynamics of the odorants, Verhagen et al (2015) showed that lung retention might affect retronasal olfaction. Their results indicate that lung retention might cause around a 74% reduction in the concentration of the odor profile for retronasal olfaction

Sensory habituation also cleaves the systems apart. Using salivary responses, as a measure of habituation, Bender et al (2009) showed that salivary responses display a rebound effect after habituation to food odors that is different between orthonasal and retronasal stimulation. Additionally, the habituation would not occur if the odorant was presented first to one system and then the other, which indicates a lack of overlap in the encoding between the two sensory transduction systems in olfaction. Based on these results, they conclude that at least for food odors, orthonasal and retronasal olfaction should not be considered the same perceptual systems. Thus, at least relative to what we consider the perceptible object of retronasal olfaction, that is consumable entities places within the mouth, the two systems treat the same set of stimuli differently. The research surveyed thus far suggests that the same set of chemical stimuli and their resultant odor plumes might generate different perceptual qualities depending upon whether they are transduced and encoded by orthonasal or retronasal olfaction.

5. Differences in Cortical Encoding

Orthonasal and retronasal olfaction can also be contrasted based on their distinct cortical pathways and processing centers (cf Hummel (2008) who surveys both EEG and ERP differences, as well as cortical processing differences). Orthonasally presented odorants are initially transduced at the olfactory epithelium, encoded within the olfactory bulb and then processed within the piriform cortex, which then projects to the primary olfactory centers within the Orbital Frontal Cortex (OFC) (for an overview of the unique cortical pathways of orthonasal olfaction in connection with consciousness cf Young, 2012). While there is some convergence between retronasal and orthonasal cortical processing within the OFC, retronasal olfaction is mostly processed in separate cortical areas that show a sensitivity to food related odorants and convergence with other sensory systems that transduce objects placed within the oral cavity.

An early study showed variance in cortical processing by identifying activation in separate cortical systems for the transduction of chocolate odor.[6] Small et al, (2005) showed that there is an experience dependent difference between retronasal and orthonasal presentation of food odors. Unsurprisingly there are also differences in cortical activation relative to breathing patterns for inhalation versus exhalation. Employing EEG, Mishawaka et al (2010) measured differential activation patterns - different cortical areas are activated for retronasal olfaction including the Anterior Ventral Insula (AVI) that shows sensitivity to the type and direction of airflow.

Different kinds of olfactory stimulation also show differences in cortical processing. For instance, the activation of Central Sulcus (CS) for retronasal olfaction possibly indicates a mechanism for oral referral, whereby the perception of a retronasal stimulus is reported as arising from activity in the oral cavity (Small, 2005). The activation pattern in CS relative to retronasal presentation is independent from encoding the direction of airflow as this was controlled for by continuous airflow for both retronasal and orthonasal stimulus delivery. Small et al's findings also show activation of the Rolandic Operculum, at the base of the

[6] It should be noted that chocolate and possibly lavender are outlier stimuli that are reported as having the same olfactory quality regardless of presentation to retronasal or orthonasal olfaction. While seemingly counterexamples to half of the thesis of the paper that olfactory qualities differ between the two systems thereby allowing the individuation of smell from flavor perception the contradiction is only apparent as the claim should not be taken as a necessary truth that all stimuli will yield different qualities, but rather the weaker claim that in the vast majority of cases the difference in olfactory quality can be taken as defeasible empirical evidence combined with the other evidence that the system are also poised to perceive different types of perceptible objects.

central sulcus, that corresponds to the representation of the oral cavity. Activation of CS was predominantly measured during retronasal olfaction and was not apparent for orthonasal olfaction. Their study documents differential activation within primary areas of cortical olfactory processing for food odors depending upon which of the two olfactory systems is transducing the stimulus. These findings indicate that there is cortical sensitivity for the oral presentation of a stimulus relative to retronasal olfaction that does not show activation when the same stimuli are delivered orthonasally. Furthermore, their results identify key olfactory areas of the cortex that have preferential firing patterns for food odors when the stimulus is presented retronasally. Retronasal cortical processing is deeply intertwined with the encoding of sensory information from other transduction channels responsible for perceiving consumable flavorful objects, hence it seems that retronasal olfaction is primed to function as a sensory transduction system that work in cohort to track and perceive a different type of perceptible object then orthonasal olfaction. Taken together these results indicate a difference in the type of perceptible object each system transduces, as well as a differential sensitivity to ranges of chemical stimuli identified in terms of its type of sensory quality.

The Anterior Cingulate Cortex (ACC) seems to be responsible for the representation of retronasal olfaction when combined with gustatory information. In addition to the activation of the AVI there are measurable differential responses in the olfactory cortex for retronasal olfaction (Small et al 2005). The OFC and the anterior cingulate cortex show increase activation for the combination of a retronasal stimulus with a gustatory stimulus, yet decreased activation when the stimulus is presented orthonasally coupled with a gustatory stimulus. In more recent studies Small et al (2012) argue that the AVI is responsible for the representation of flavor perception, as it is the first area to show integration between gustatory, tactile, and perhaps thermal perception together with retronasal olfaction. Their results build upon research done by Cerf-Ducastel and Murphy (2001) measuring increased AVI activation for retronasal olfactory stimulants. The studies of the cortical processing center of retronasal olfaction as partially located in the AVI together with the ACC indicate that retronasal olfaction is mostly encoded and processed as different patterns of cortical activation. Further research supporting the claim that the two olfactory systems employ distinct cortical networks for their encoding and processing is reviewed in Shepherd (2012) who documents cells within the OFC that display sensitivity for the combination of tastes, odors, and touch.[7]

The differences in cortical encoding of retronasal olfactory stimuli in the AVI, inferior cingulate cortex, and OFC is echoed by research on the role of attention relative to orthonasal and retronasal olfaction, when combined with gustatory stimuli. Veldhuizen and Small (2011) showed that attentional modulation could be utilized to separate cortical systems for orthonasal and retronasal olfaction, as well as gustatory perception. Their study demarcated separate attentional areas serving orthonasal and retronasal olfaction within the cortex, as well as identifying cortical areas in the insula that are responsive to both retronasal and gustatory attentional modulation. Their results further validate the claim that the two systems employ different cortical processing pathways and centers that are sensitive to different types of perceptible objects and sensory qualities. Additionally, given the evidence surveyed above regarding cortical processing underlying retronasal olfaction, it is arguably

[7] Stevenson (2009) postulates that shared cells of this type within the OFC combine the different sensory channels of flavor perception not as the mere concatenation of kinds, but in a synthetic fashion, which he suggests might explain wine taster's difficulties in perceiving flavor components. If the cortex encodes the sensory profile of a complex stimulus as wine as a unified percept, it is quite reasonable to think that perceptually teasing the components apart might require a specialized skill set and perceptual probing Smith (2009). Additionally, it shows a similarity with the format of the smell percept that has been argued as functionally compositional, yet often not synchronically decomposable (Young, 2019c).

the case that the primary function of retronasal processing is not to perceive odor plumes independent of the other features of flavorful objects that are transduced by gustatory, somatosensory, and thermal sensory system.

6. Perceptual differences

The literature surveyed thus far suggests that olfaction has two sensory pathways that are sensitive to different types of perceptible objects, which might explain differences in the perception of olfactory quality even with the presentation of the same odorants. Until recently it was not possible to deliver an odor to the retronasal olfactory system independent of other sensory channels. As Shepherd puts it, "retronasal smell is never sensed by itself (2012, p.17)." While this might be true under naturalistic conditions whereby a stimulus must be placed within the oral cavity thereby stimulating somatosensory, thermal, or gustatory receptors, Heilmann and Hummel (2004) developed a technique for the direct stimulation of orthonasal and retronasal olfactory systems. Tubing is placed through the nasal cavity ending either at the front of the nostrils or directly below the olfactory epithelium close to the nasopharynx. By placing the tubing in the nostrils in these two locations a stream of odorant laced air can be delivered directly to each system. Even in these extreme laboratory conditions, different olfactory qualities are reported based on route of delivery. The same set of pure odorants delivered directly to each system yield differences in perceived olfactory qualities.[8]

Heilmann and Hummel's (2008) research lends supports to previous findings of a decreased threshold for orthonasal perception as compared to retronasal olfaction, which is also observed in congenitally blind individuals. Gagnon et al (2015) documents that congenitally blind individuals have increases in orthonasal perception as measured by odorant threshold, yet there is no change in thresholds for retronasal perception.[9] These difference in thresholds help explain the difference in perception of overall odorant intensity between orthonasal and retronasal olfaction. Retronasal olfaction has a higher odorant threshold, such that the same stimulus is judged as less intense as the same concentration when presented orthonasally (Heilmann and Hummel (2004). Additionally, Diaz et al. (2004) reported differences in judged concentration of an odor based on pathway of delivery. To achieve the same perceived intensity between the two systems, the concentration cannot be held constant between route of delivery but must be modulated to control for the overall concentration of the headspace of the odorant relative to route of delivery.

The disparities in intensity and threshold might explain variations in perceptual matching that indicate the olfactory percept depends upon the root of delivery[10] and familiarity of the odorant (Hannum et al 2018). The differences of perceived intensity and difficulties in matching are further supported by research on odor identification with the same set of stimuli for orthonasal versus retronasal presentations. Rozin (1982) was the first to indicate the difficulty in identifying the same stimulus with retronasal presentations that were originally learned via orthonasal delivery. His findings are corroborated by more recent research that shows odor identification is better when the stimulus is learnt and matched in the same

[8] Hummel et al. (2006) provides a fantastic review of the differences in perception between orthonasal and retronasal perception including context of presentation, airflow, trigeminal stimulation, as well as ORNs receptivity.

[9] Their results might be partially attributed to using orthonasal olfaction for spatial perception, while lack of increase in retronasal perception might be attributed to lack of food foraging behavior and range of types of food consumed by blind individuals.

[10] There is some limited evidence suggesting that olfactory adaptation might also depend upon route of delivery. Pierce & Simons (2018) provide experimental evidence that orthonasal adaptation occurs at a different rate than retronasal olfaction and that there is no cross adaptation between each route of delivery.

pathway of delivery and decreases for heterogeneous pairings of perceptual presentations (Sun and Halpern, 2006).

Orthonasal and retronasal olfaction show further dissociations in clinical cases involving the loss of smell. Both Hummel (2008) and Smith (2015) have interesting discussion of clinical dissociations that provide reasons to think olfaction has two independent sensory systems. Furthermore, Landis et al (2005) documents eighteen patients with no complaints of taste (including flavor) dysfunction, yet they display a deficit in orthonasal olfaction. Using an identification task, the average subject failed the orthonasal task at 36%, as well as having no ERPs recorded for the orthonasal presentation. Contrastively, the retronasal identification test yielded 56% correct identification with recorded ERP's of olfactory receptor neurons. Based on these findings Landis et al. argue that the two systems might not just be functionally distinct, but possibly structural distinguishable. They hypothesize that the olfactory epithelium is structurally organized to be sensitive to orthonasal presentations versus retronasal presentations of the same set of odorants, which would both explain their clinical data, as well as substantiate previous claims (section 3) that the direction and placement of the odorant on the epithelium based on route of delivery generate differences in perceived olfactory quality.

The differences in perception between orthonasal and retronasal perception include context of presentation, airflow, trigeminal stimulation, as well as ORNs receptivity (for a full review cf Hummel et al. 2006). However, for the purposes of the thesis of the paper what needs to be noted is that the perceptible object of each system is different and that the further pathways of delivery of the odorant to the olfactory system generate up-stream changes in the way the molecular structure of the chemical compounds that compose the perceptible object are transduced at the receptor level, encoded by the receptors, processed within the cortex, and perceived by the individual. Given all of these differences it seems safe to conclude that for at least two out of the three questions involved in answering the question “what are smells?” that the answers will differ with regard to retronasal olfactory stimulation. We don’t use retronasal olfaction to perceive the same type of perceptible object nor do the same set of stimuli transduced by the two systems yield the same olfactory qualities.

7. Conclusion

The dissociation between the olfactory sensory systems combined with pure retronasal olfactory perception only occurring under laboratory conditions makes it reasonable to think that retronasal olfaction does not independently give rise to conscious percepts. Rather, retronasal olfaction plays a dominant role in generating our uniformed perception of flavor (Stevenson, 2009). Retronasal olfaction is sensitive to food related odorants, which are bound into a uniform conscious perception based upon experience dependent learning of congruent stimulus presentation (Bender et al. 2009).

Flavor is its own perceptual modality that synthetically binds multiple sensory channels. Small (2012) and Prescott (2015) each argues that the uniform perception of flavor is generated by the brain based upon superadditive responses in the cortex, as indicated by research identifying cortical activation within processing centers sensitive to gustatory qualities, retronasal odors, somatosensation, and thermal properties of perceptible objects that we consume. The most compelling evidence to support this line of argument is that oral referral (the phenomena whereby we locate the flavor experience in the mouth despite predominantly being generated from retronasal sensation) is based upon the congruent presentation of gustatory tastes together with retronasal olfactory sensations (Lim and

Johnson, 2012).[11] While other perceptual modalities, such as vision might influence our experience of flavors, vision might not be considered an essential part of the flavor perception (Small, 2012). Similarly, Prescott (2015) argues that while gustatory, retronasal olfaction, and somatosensory stimulation in the oral cavity are all essential to flavor perception, vision, audition, and orthonasal olfaction are not essential and merely influence our perception of flavor.[12]

Orthonasal perception allows us to smell whereas retronasal olfaction is a sensory channel used for perceiving flavorful entities. Only under experimental conditions can we experience pure retronasal perception. Even in situations in which we use experimental methodologies to present odorants to the retronasal system independently of sensations in the oral cavity, these odorants do not generate the same olfactory qualities. Orthonasal olfaction should be considered the modality of smell, while the retronasal system is best thought of as a sensory pathway bound together with other sensory systems that when combined in the right sort of way yield our unified perception of flavorful objects.

Our everyday experiences of odors as individuated in terms of the perceptible object of smell and olfactory qualities derives from orthonasal olfactory perception, whilst those that might be derived from retronasal olfaction not only differ in olfactory quality but are also not attributed to smell but to the perceptual activities in the oral cavity. We don't claim to smell retronasal olfactory qualities. Even when attention is brought to the dominant role of olfaction in generating our experience of consuming food or drink, we are more likely to refer to these as parts of our flavor experience. We don't smell flavors.

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[11] Lim and Johnson (2011, 2012) across two studies show that oral referral might not be mediated by simultaneous tactile stimulation when an odorant is present to the retronasal system, but more predominantly by taste sensations on the tongue. Their initial study showed that it is not necessary to thread tubing through nose to generate retronasal olfactory perceptions of odorants localized as occurring within the nose, but also that tactile stimulation on its own is not always sufficient to generate oral referral. In the later study they further showed that the congruency of a tastant with the odorant modulated oral referral. What is of further interest for the purposes of the argument of this paper is that in more than 50% of the participants reports they localized the stimulus location of a pure odorant present retronasally as occurring within the nose, which might be taken as indicating that retronasal olfaction under some experimental conditions transduces the same perceptible object as orthonasal olfaction. Yet, this conclusion might not be warranted given their studies focus and design. In the first study, while the stimulus was sometimes localized to nose, this might be attributed both to method of report (chart with options) and learnt association as borne out by role of congruency of tastants. In fact, their study seems to support the claim that under normal perceptual conditions we treat the tactile, gustatory, and retronasal olfactory sensory channels as contributing to the perception of a unified flavor object. And in the later study about half the time the participants reports could also be explained as the authors note in their discussion based on learnt association, such that under normal naïve conditions the participant might have always localized the stimulate to the oral cavity or tongue, but given that in this instance there was a tasteless jelly on their tongue they inferred that the perceptible qualities of the aberrant stimulus could only be transduced by the olfactory system.

[12] The argument on offer throughout this chapter is in keeping with O'Challaghan's framework with its distinction between object for perception and object of perception, but does not explicitly frame the argument as such. What follows explicates this fit, since the evidence offered suggests that it is not clear that retronasal olfaction under naturalistic conditions has an object for perception. Moreover, retronasal olfaction's suite of perceptual abilities required to track even an object of perception is not the same as those required for orthonasal object perception. Furthermore, it is speculatively the case given the convergence of cortical processing from a host of different sensory systems that track consumable entities within the oral cavity/headspace that flavor perception is objective in the stronger sense of having an object for perception. Thus, retronasal olfaction does not share the same perceptible object as olfaction despite sharing the same type of distal stimulus. With this part of the argument in place it then become apparent that flavor perception would not be multi-modal as each sensory system would not be providing its own proper parts, but rather it would be considered as having a uniform object of perception that can only be perceived as such by multi-sensory channels each transducing features of the flavorful entity conceive of as multiphasic dynamic entities placed within our mouths and permeating our headspace.

Employing orthonasal olfaction we perceive the olfactory quality (i.e. smell) of odorous objects (conceived of as the molecular structure of chemical compounds within odor plumes), which can be corroborated based on our everyday experiences of smells (with some slight modulations to our naïve assumptions concerning ordinary objects). Retronasal olfaction neither allows us to perceive the olfactory qualities or objects of smell in this sense, but rather forms a sensory system that provides a constitutive component of flavor perception. The retronasal olfactory system can be differentiated based on its difference in both olfactory qualities and perceptible object. Having established that retronasal olfaction can be distinguished from orthonasal smell based on anatomical pathways, sensory transduction, cortical encoding, and conscious perception, as well as the perceived olfactory quality of the same stimulus differing between modes of delivery it seems reasonable to conclude that retronasal olfaction doesn't smell.

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