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# *Stinking Consciousness!*[1]

***Abstract:** Contemporary neuroscientific theories of consciousness are typically based on the study of vision and have neglected olfaction. Several of these (e.g. Global Workspace Theories, the Information Integration theory, and the various theories offered by Crick and Koch) claim that a thalamic relay is necessary for olfactory consciousness. Studies on olfaction and the olfactory system's anatomical structure show this claim to be incorrect, thus showing these theories to be either false or inadequate as general and comprehensive accounts of consciousness. Attempts to rescue these theories by claiming that there is a structure in the olfactory system that is functionally equivalent to the thalamus in the visual system, such as the olfactory bulb or the olfactory cortex, are also shown to fail. If we wish to understand consciousness, we have to wake up and smell it.*

**Keywords:** Olfaction, consciousness, awareness, attention, thalamus, olfactory bulb, neurobiological theories of consciousness

## 1. Introduction

Contemporary theories of consciousness stink, because they are unable to account for olfaction. The construction of neural models, and philosophical theories, of consciousness derive either from

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conceptual theorizing using our linguistic abilities or from empirical evidence gleaned from studies of the visual system. Olfaction has been ignored for far too long. This article begins to rectify this negligence by showing how the anatomical structure and functional organization of the olfactory system raises serious problems for some of the leading theories of consciousness. Overlooking olfaction has negatively impacted the current neuroscientific theories of consciousness to the extent that large portions of these theories are either false or inadequate as general theories of consciousness.

Olfaction is unique amongst the sensory modalities in not requiring a thalamic relay from its receptors to the cortex (Sherman and Guillery, 1996; 2001; Spence *et al.*, 2001; Gottfried and Zald, 2005; Murakami *et al.*, 2005; Shepherd, 2005). While there are other anatomical (Gottfried, 2006) and sensory processing (Herz, 2009) differences between olfaction and the other sensory systems, the lack of an intermediate thalamic relay is the sole focus of this article because it has the greatest impact upon contemporary theories of consciousness. The anatomical structure of the olfactory system presents a problem for current neuroscientific theories of consciousness, which require there be a thalamic relay or corticothalamic loops for consciousness to occur. The olfactory system's unique anatomy raises serious doubts about the adequacy of Crick's (1984; 1994) theory (Smythies, 1997), Crick and Koch's (1990; 1998; 2005) theory (Shepherd, 2007), Koch's neurobiological theory (2004), Global Workspace Theories (Baars, 1988; 1997; Baars *et al.*, 2003; Dehaene *et al.*, 2001; 2003; 2004; 2006), and the Information Integration Theory of Consciousness (Tononi and Edelman, 1998; Tononi, 2004; Tononi and Laureys, 2009). *Prima facie*, the olfactory system's aberrant anatomy falsifies these theories. Indeed, a more detailed investigation of thalamic processing within the olfactory system demonstrates these theories to be inadequate as general theories of consciousness.

It is generally accepted that the thalamus is not required for olfactory consciousness, which shows that olfaction is drastically different to all the other perceptual modalities. Moreover, it falsifies the putative necessary condition that consciousness requires thalamic connections or corticothalamic loops. However, there is a growing body of literature which suggests that olfaction employs two routes to the neocortex (reviewed in Tham *et al.*, 2009): a direct pathway leading from the receptors via the piriform cortex to the orbitofrontal cortex (Johnson *et al.*, 2000; Takagi, 1986; Price *et al.*, 1991a), and an indirect pathway that projects to the orbitofrontal cortex from the medio-dorsal thalamus (MDNT) via the piriform cortex (Price and Slotnick, 1983; Öngur and Price, 2000). The existence of these two pathways consequently requires a more nuanced approach to assess the role of the thalamus in olfaction and its impact upon contemporary theories of consciousness.

## 2. Consciousness: Arousal, Attention, or Awareness?

Theories that seek to establish the neuro-realization of consciousness have at least three basic options within the hierarchy of neural processing for a necessary condition of consciousness: subcortical activation, thalamic activation (corticothalamic loops), or cortical activation. The olfactory system, with its direct projection to the cortex, indicates that the last condition is in all likelihood necessary, but that the first two are debatable depending upon ones conception of consciousness. The brainstem and subcortical systems including parts of the thalamus are implicated in conscious arousal, but this notion of consciousness merely differentiates betweens states of wakefulness and unconsciousness. Subcortical regions such as the midbrain and pons, as well as parts of the thalamus, may play a necessary role for arousal but might not be considered a component of the neural basis of awareness. To borrow a distinction from Koch (2004), they may play an essential role in enabling awareness to occur but not be constitutive of the neural correlates of consciousness. However, the target of the article is the neuro-architecture responsible for consciousness conceived of as awareness and not arousal.[2]

A further difficulty in assessing the thalamus's role in olfactory consciousness is that the diverse nuclei of the thalamus are involved in bringing about separate kinds of consciousness. For this reason it is important to note both the areas of the thalamus that each theorist claims to be necessary for consciousness and the kind of consciousness. For instance, it is thought, based on lesion studies, that the intralaminar nuclei (ILN) of the thalamus are required for conscious arousal but perhaps not for awareness (Bogen, 1995a,b). However, their role in awareness is far from clear, since some lesions result in a coma while others result in akinetic mutism. This suggests that while the ILN are involved in realizing motor intention, and to some extent

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[2] Merker's Centrencephalic theory is thus not considered, since it is not relevant to the debate over whether thalamic processing is required for conscious awareness. Olfaction also provides a counter-example to Merker's proposal that consciousness need not involve the cortex nor corticothalamic loops. While the claim that corticothalamic loops are not necessary for consciousness is true, the olfactory system's direct projection to the cortex without thalamic connections suggests that (at least for olfaction) the cortex is indeed required for conscious awareness.

sensory awareness, they do not realize conscious awareness (Smythies, 1997).

When we undergo a conscious experience we are aware of something happening to us or in the environment surrounding us. This awareness might come in two varieties. The awareness might be of a unified cross-modal perceptual experience or it might simply be that of a single sensory modality. Perceptual consciousness nicely displays the difference between these states of awareness. When I perceive a stimulus, such as the smell of baking cookies, my awareness might be of a few kinds. For instance, I might be aware of the cookies only in an olfactory manner — I might be aware of being in a state of a particular modality (Single Modality state of Awareness — SMA) — or I might be aware of the olfactory stimuli against the background of a host of other stimuli from other modalities (Cross-Modal state of Awareness — CMA). The distinction between these two types of awareness is essential when evaluating both what the leading theories of consciousness claim are the neural correlates of consciousness (NCC) and the methodology that can be used in inferring the neural realization of one type from the other.

It would arguably be methodologically poor to move from a claim regarding the neural correlates of SMA to one about another modality, especially if the visual system is the starting point. If initial theorizing and evidence comes from the visual system then, though the lateral geniculate nucleus (LGN) of the thalamus may in fact be necessary for vision, it ought not to be thought that such a claim will generalize to olfaction. Building a general theory of consciousness from research on a particular perceptual modality assumes that the neural basis of SMA is the same for all the perceptual systems. But such a methodology is quite dubious, since it would require that there be identical anatomical (or functionally equivalent processing) structures across the different perceptual modalities. The prevailing neuroscientific theories of consciousness would thus be foolish to claim that the thalamus and corticothalamic loops are necessary based on such a methodological assumption.

Alternatively, the theories' focal point might be the neural realization of CMA, which seems probable given the integrative role of the thalamus. However, if the SMA of olfaction does not require the thalamus, what implications are there for these theories of consciousness? If the thalamus is not required to realize olfactory SMA it might nonetheless still play a role in CMA. At worst olfaction's lack of thalamic relays shows that multimodal awareness cannot be adequately explained by appeal to the thalamus alone and that other areas, which subserve the same role for olfaction, must also be included. While this last option — of looking for similar areas within the olfactory system that play the same functional role — looks promising, the consequence if successful would be that these theories would be neurofunctionalist, as well as neurobiological, accounts of consciousness.

This article seeks to uncover the role of the thalamus in olfactory consciousness and thus its consequences for current neurobiological theories of consciousness. As such it does not concern attention. Assessing theories that seek to explain CMA requires careful consideration of whether they concern attention or awareness. Generally, while we can attend to olfactory stimuli, our ability to do so is not mediated by the thalamus (Spence *et al.*, 2001), which has been shown to be required for selective attention in all the other perceptual modalities (McAlonan *et al.*, 2000). Additionally, recent studies have shown that selective attention and visual consciousness are dissociable and each might have their own neural correlates (Tsuchiya and Koch, 2009; van Boxtel *et al.*, 2010). As such, if the claimed role of the thalamus is for attentional binding this is quite dubious when olfaction is taken into account. Thus, when considering each theory it will be important to note whether the claimed necessity of the thalamus for consciousness regards SMA, CMA, or attention.[3]

## 3. The Role of the Thalamus in Olfactory Processing

The anatomical structure of the olfactory system presents a problem for current neuroscientific theories of consciousness, which state that a thalamic relay is, or corticothalamic loops are, a necessary condition for consciousness. However, while a thalamic relay may be necessary for consciously analysing odorants (Plailly *et al.*, 2008), it is not required for consciously detecting or discriminating between odorants (Price and Slotnick, 1983; Zatorre and Jones-Gotman, 1991; Price *et al.*, 1991b; Slotnick and Schoonover, 1992; Sela *et al.*, 2009; Tham *et al.*, 2009; 2011). While most other modalities have a sensory thalamic relay between the receptors and cortical processing, the olfactory system has two pathways. There is a primary pathway that projects directly to the orbitofrontal cortex via the piriform cortex,

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[3] Smythies (1997) is careful to include olfaction and assigns the function of intramodal attention to the cholinergic nuclei in the midbrain and pons, in particular to the pedunculopontine nucleus and the lateral dorsal tegmental nucleus. However, his evidence that this system plays such a role only substantiates the conclusion that either the system is essential for arousal or it underlies attention. On either interpretation this is tangential to the scope of my claims concerning the olfactory system's thalamic processing and its impact upon the nature of SMA and CMA.

and a second pathway that has an intermediate link from the piriform cortex to the mediodorsal nucleus of the thalamus (MDNT) and onto the orbitofrontal cortex (Öngur and Price, 2000). The role this latter pathway plays in olfactory processing is reviewed in this section to demonstrate that olfactory consciousness may occur without thalamic mediation.

In rodents the role of the thalamus in olfactory consciousness is murky, but it is clear that olfactory processing occurs across dual pathways in a similar manner to humans. In rats there is a similar secondary pathway via the thalamus (Price and Slotnik, 1983), which is implicated in complex behavioural planning and motor integration. Lesion studies show that it has little or no effect on olfactory discrimination and detection (Price and Slotnick, 1983; Price *et al.*, 1991b; Slotnick and Schoonover, 1992). Additional studies of rats show that while lesioning of the thalamic pathway does not effect discrimination or detection nor result in anosmia, severing this pathway can produce sever deficits in odour reversal learning (Slotnick and Kaneko, 1981), changes in odour preferences, and male sexual behaviour in hamsters (Eichenbaum *et al.*, 1980; Sapolsky and Eichenbaum, 1980). Based on animal studies the thalamus is implicated in behavioural planning, motor integration, and is to some extent involved in motivation and attentional mechanisms. However, these latter effects are not specific to olfactory processing and the MDNT. Since olfactory discrimination and detection are unaffected by thalamic lesions, it would seem that (at least in the case of rodents) the thalamus is not necessary for the realization of olfactory consciousness whether conceived of as SMA or as CMA (with the caveat that the thalamus might be required when dealing with CMA, which involves the motor systems and attention). Thus, a quick anatomical perusal demonstrates that the thalamus is not essential for olfactory consciousness in rodents. However, matters are not quite as clear in humans.

Generally the thalamus is considered partially responsible for attention, memory formation, selective attention, and to some extent sensory discrimination (reviewed in Tham *et al.*, 2009), which explains why it is considered by so many as a necessary part of the NCC. The role of the thalamus in human olfactory consciousness is less than clear due to the sample pool that evidence is drawn from. In animal studies specific lesions may be generated, but unfortunately evidence for the role of the MDNT in humans must be drawn from a population with brain trauma or general neural deficiencies. As such, the sample size of these studies is quite small and the lesions are not always clean. In two recorded cases of bilateral dorsomedial infarctions, the patients suffered from abnormalities in perceiving odour character (Asai *et al.*, 2008), which suggests that the MDNT may have some role to play in identifying odours.

Two further research studies, conducted to study the effect of MDNT lesions on olfactory processing, show that while patients with MDNT lesions suffer from deficits in olfactory identification (as demonstrated by their inability to identify an odorant even on a forced choice task), their ability to detect and judge the intensity of odours is unaffected (Sela *et al.*, 2009). These results indicate that the thalamus may be required for a kind of olfactory awareness that requires the use of one's conceptual repertoire and access to linguistic resources for identifying odours, but not required for the awareness of the presence of an odour and ability to discriminate between odorants. Based on Sela *et al.*'s study the thalamus is not required, with the exception of cross-modal experiences involving conceptual identification, for olfaction (whether construed as SMA or as CMA).

More recently, Tham *et al.* (2011) have shown that while left-side MDNT lesions have no effect on odour acuity, hedonics, recognition, naming, and target search, they do have an effect on olfactory discrimination when compared to vision. While these findings differ with the results of Sela *et al.* (2009) on hedonic judgment and discrimination, the first might be attributed to the sample size and general patient abnormalities, while the latter might be construed as a deficit in contrast to vision. Nonetheless these deficits are not the result of a general olfactory deficit and as such are specific to the role that the thalamus plays in olfactory processing.

The findings of these studies are not completely congruent, but they do indicate that olfactory detection, discrimination, and odour recognition are possible without the thalamus. While, the thalamus does not seem to be essential for olfactory consciousness, considered as simple SMA, it does seem to be required for some cross-integration, since each of these studies suggests that the thalamus is a constituent of the olfactory motor system. Lesions of MDNT do not have drastic effects on olfactory discrimination and detection, but do affect subjects' ability to judge flow rates of odorants across their nostrils. This latter finding might be of importance if the sniff is considered as part of the olfactory percept in generating a determination of olfactory quality and odour identification (Sobel *et al.*, 1999; Kareken *et al.*, 2004; Kepecs *et al.*, 2006; Mainland and Sobel, 2006; Koritnik *et al.*, 2008). However, these results would only implicate the necessity of the thalamus in CMA involving olfactory quality and conceptual identification.

Studies on lesions of the ventrolateral thalamus further substantiate the finding that the thalamus is part of the olfactory motor system, since they have a negative effect on odour threshold due to decreased motor control and the ability to judge sniff volume (Zobel *et al.*, 2010). Additionally, deep brain stimulation of the cerebellothalamic pathways produces a negative effect on odour threshold and slight effects on discrimination, but no effect on odour identification (Kronenbuerger *et al.*, 2010), thereby strengthening the case that the thalamus is part of the olfactory motor system, but is not necessary for olfactory awareness.

The studies discussed here show that the thalamus is not required for us to discriminate between odorants nor to detect odours, but that parts of it may play a role in odour identification and motor integration. Thus, the thalamus is not necessary for SMA of some olfactory experiences nor CMA of visual, linguistic, and olfactory experiences, but is implicated — based on its negative impact on olfactory identification — in CMA involving motor integration and conceptual integration. With this more nuanced appraisal of olfactory anatomy and the role of the thalamus in olfactory processing in mind, the next section provides an assessment of the current neurobiological theories of consciousness, all of which claim an essential role of the thalamus. Though the anatomy of the olfactory system and lesion studies of the thalamic relay in olfactory consciousness provides evidence in favour of the traditional view that the thalamus is not required for olfactory consciousness, Plailly *et al.* (2008) argue that the olfactory system may be similar to the other modalities in requiring thalamic connections. *Prima facie*, their results vindicate the targeted theories of consciousness, based on the conclusion that a thalamic relay is required to consciously analyse smells. However, their study only shows that attending to odours increases the connectivity of the olfactory medial pathway, thus only licensing the conclusion that it is involved with consciously sniffing and attending.

The experimental task of Plailly *et al.* (2008) was a simple detection task that required subjects to attend to the presence or absence of an odour in one condition and a tone in a second condition. Subjects were instructed to be attentive and detect the presence or absence of the target. The tone task was used as a baseline to judge the effects of the overall connectivity of the dorsomedial thalamic connections in the olfactory task. Plailly *et al.* claim that their results of increased connectivity of the dorsomedial thalamic pathway indicate that the thalamus is required when ‘we consciously analyze smells’ (*ibid.*, p. 5257).

Given the experimental design there are multiple problems with this conclusion. The most trifling problem is that their results are overstated, which is evident from the fact that the experiment is a mere detection task from which no inference regarding the conscious analysis of smells can reasonably be made. Properly stated the results indicate only that thalamic connectivity is increased when attempting to detect the presence of odours. Their conclusion is also unwarranted because the experimental design itself required active sniffing as part of the task. Subjects were instructed to actively sniff for 3 seconds as cued by a green fixation screen, which allows for an alternative explanation of their data: the increase in the connectivity of the thalamic pathway is probably caused by consciously sniffing, which requires a convergence of motor areas. The evidence suggests that consciously sniffing odours requires thalamic connections but does not show that detecting an odour, while engaging in normal respiratory activity, is not possible without a thalamus or an increase in thalamic connectivity. Plailly *et al.*'s findings, while interesting, do not substantiate their claim, but rather serve to reaffirm the findings in animal studies, discussed earlier, that the MDNT is required for complex olfactory motor integration. Additionally, the findings converge with the previously discussed lesion studies on humans, which suggest that the MDNT is part of the olfactory motor system. Interpreted in this manner, the results do not have implications for olfactory awareness, but do suggest that the thalamus plays a role in olfactory selective attention such that there is increased thalamic connectivity when attending to olfactory perception. These results are also in line with the findings of lesion studies in animals that show a decrease in performance as the attentional demand of the task increases. Tentatively, this suggests — contrary to previous research on the thalamus's role in attention (McAlonan *et al.*, 2000; Spence *et al.*, 2001) — that olfactory selective attention might be partially mediated by the MDNT.

The medial dorsal thalamus's role in olfactory cognitive processing and consciousness requires further study. Yet current evidence about the anatomical structure of the olfactory system establishes that thalamic relays and corticothalamic loops are not required for all of our conscious olfactory experiences. The inessential nature of thalamic relays, connections, or loops involved in olfactory consciousness brings into doubt three major groups of neuroscientific theories of consciousness: (1) Crick and Koch's framework for the specificity of the NCC, (2) the Global Workspace Theories (GWT) of Baars and Dehaene, and (3) Tononi and Edelman's Information Integration Theory (IIT). The mere anatomical structure and functional organization of the olfactory system demonstrates that these theories do not provide adequate general accounts of consciousness.

## 4. Contemporary Neuroscientific Theories of Consciousness

### *4.1. Crick and Koch: Neurobiological Specificity of NCC*

The driving methodological assumption behind Crick and Koch's framework of consciousness is that it should be initially assumed that there are specific areas of the brain or specific neural circuits that underlie consciousness, rather than the alternative assumption that consciousness is distributed across the entire brain. The thalamus, with its central location and connections, serves as a good starting point for such specificity. The underlying idea behind the posited involvement of the thalamus is that it acts as a mechanism for the attentional binding of visual information and can create strong reverberatory connections with the cortex.

Crick (1984) claims that the thalamus and the nucleus reticularis are the neural basis of his hypothesized searchlight of consciousness, which is suggested both by the thalamus's topographical maps of the sensory modalities and cortical loops that the fact that the reticular nucleus plays a role in unifying our perceptual experiences. Crick thus claims that the thalamus, and in particular the reticular nucleus are necessary parts of the neural realization of consciousness. While Crick (1994) maintains the instrumental role of the thalamus as the 'conductor' that produces consciousness he is careful to restrict his theory to claims about the NCC of visual awareness. Furthermore, he rejects the intralaminar nuclei and the reticular nucleus of the thalamus as the key to consciousness and replaces them with LGN based on its role in the visual system. Crick admits that his claims regarding thalamic connections do not apply to olfaction (Crick, 1984), but nevertheless assumes that the theory of visual consciousness will generalize across all the modalities. The assurance that these differences need not worry us is given throughout his collaborations with Koch (Crick and Koch 1990; 1998; 2005) and indeed in Koch (2004).

Crick and Koch's (1990; 1998; 2003; 2005; Koch, 2004) general strategy is to generate a framework for understanding consciousness. One of their key assumptions, based on studies of the visual system, is that coalitions of neurons must fire together in circuits to generate enough activation to bind sensory information into a conscious percept. This implicates the thalamus as the seat of attention, since it is necessary for consciously attending to a bound unified perceptual experience. More generally they claim that the thalamus is a necessary condition of conscious awareness (Crick and Koch, 1998; 2003; 2005), as well as the reticular nucleus (Crick and Koch, 1990), the pulvinar (*ibid.*), the LGN (Koch, 2004), and the intralaminar nuclei (*ibid.*).

Given the specificity of their claimed NCC, and the central role of the thalamus therein to bind information attentively, the lack of a thalamic connection within the olfactory system creates real trouble for the claim that this approach generalizes as a theory of consciousness for the other perceptual modalities. The olfactory system's unique anatomy certainly causes trouble for these iterations of Crick and Koch's theory, since they begin as a claim regarding either the essential nature of the thalamus for attention or the role of the thalamus in generating CMA. While this second interpretation might be worth exploring, the shift of focus to vision and the assurances that while olfaction is different it will not present difficulties further exacerbates the problem. What is apparent at this stage of their theorizing is that the theory is being generated for SMA in vision and then generalized to CMA with the assumption that SMA is realized in the same way across the other perceptual modalities. The thalamus may be required for some kinds of CMA involving olfaction but, as shown above, it is not essential for SMA within olfaction. Thus, the inference from the neural realization of the SMA of vision to the CMA of vision to the neural realization of the SMA of olfaction is quite dubious. Crick and Koch's framework may generalize by jettisoning its focus on neural specificity, but only at the cost of becoming a functionalist account of consciousness. Furthermore, this strategy would only succeed if a functionally equivalent neural analogue to the posited role of the thalamus were found within olfaction.

### *4.2. Global Workspace Theories of Consciousness*

The anatomy of the olfactory system has the least impact on the Global Workspace Theory (GWT) of consciousness, according to which consciousness is functionally realized by a global workspace system (GWS) that is distributed throughout the brain. Nonetheless, as a neuroscientific theory of consciousness it does not remain neutral on the neural realization necessary for global broadcasting. Although the mere lack of thalamic relays within the olfactory system is not decisive proof against GWT as a plausible neurofunctionalist theory of consciousness, evidence is presented in section 5 that there is no functional equivalent to the thalamus in olfaction, thereby providing reason to doubt that the GWT can be even functionally generalized to the case of olfaction.

Baars' original model built upon the idea that information must be integrated from across the different sensory systems and have access to working memory to become conscious, and as such is primarily concerned with CMA. The integrative property of consciousness is utilized as evidence in favour of there being a global workspace in which information from across the different sensory modalities is combined to form a unified conscious percept. Baars (1988) is explicit in identifying the thalamus as a necessary element in GWS interconnectivity and suggests the Extended-Reticular Thalamic Activation System as a possible workspace realization.

Baars' more recent work still implicates the thalamus as a necessary precondition for waking consciousness in terms of the intralaminar nuclei (1997) and the role of the thalamus as a general requirement for consciousness, based on a contrastive analysis with other kinds of conscious states (Baars *et al.*, 2003). However, these areas are neutral and irrelevant with respect to the issues at hand, since they are more charitably attributed as having a role in arousal rather than awareness. The current version of the GWT takes the guise of a metaphor of 'the theater of consciousness', whose applicability to olfaction is unclear, yet Baars is still explicit in endorsing the thalamus as playing a necessary role in the realization of the global workspace. The thalamus is vital because of its centrality within the brain and its interconnections to the different sensory systems, cortex, working memory, and motor systems. Baars leaves open the possibility of other functional implementations of the global workspace within the olfactory system. However, the lack of any suggestions of what these might consist of within the olfactory system's anatomical structure remains a serious problem for his theory. Although the olfactory system's anatomical and sensory processing differences will not falsify Baars' GWT, they will need to be accommodated to yield an adequate account of the GWS responsible for CMA including olfaction.

Dehaene's version of the GWT (Dehaene *et al.*, 2001; 2003; 2004; 2006) is indirectly influenced by Crick and Koch's framework via Baars' GWT. The identity of the neural realization of consciousness is difficult to ascertain in Dehaene's account, since it is not offered as a theory of the NCC itself, but rather as an account of long-distance neural connections and bi-directional connectivity and their connection to memory, motor, and language areas as essential requirements for the neural circuitry responsible for generating a global workspace (Dehaene and Naccache, 2001). While this is not enough to implicate his version of the GWT in the anatomical crimes of the other theories, Dehaene *et al.* (2006) do in fact suggest a role for the thalamus in this regard while Dehaene *et al.* (2003) state that pyramidal neurons distributed across cortical and thalamic regions may be responsible for realizing conscious states.

The requirements of the GWT model implicate a role for the thalamus as a necessary condition for CMA. Since the olfactory system's anatomical connectivity does not meet this general constraint, the only option left to them is to retreat to a functionally equivalent model for the olfactory system. Both Baars' and Dehaene's models of the GWS might be able to accommodate olfaction by either adding those parts of the olfactory system that are required for CMA or by finding something within the olfactory system that plays a functional equivalent role to the thalamus in their GWS. Ultimately, if the GWT merely generates a functionalist account of consciousness in terms of information processing then any problems discovered with the IIT (discussed in the next section) will equally afflict the GWT.

### *4.3. The Information Integration Theory of Consciousness*

The Information Integration Theory (IIT) seeks to account for consciousness in terms of the information processing internal to a system, and is the most explicit theory with regards to its endorsement of the thalamus as a necessary condition for consciousness. The IIT was proposed by Tononi and Edelman (1998), and elaborated by Tononi (2004) and Tononi and Laureys (2009). The key claim is the dynamic core hypothesis, which states that the neural correlates of consciousness are realized by a process of dynamic integration between neural states. Evidence for the IIT derives from what Tononi and Edelman claim are two underlying properties of consciousness: (1) the integration or unification of information (i.e. each conscious experience has some manner of unified content to it), and (2) differentiation (i.e. our conscious experience can rapidly change between drastically different percepts). Tononi and Edelman identify the dynamic core with the recurrent interaction between the anterior and posterior areas of the thalamus and claim that it is required to generate information states that have the properties of integration and differentiation (the dynamical core hypothesis). While Tononi (2004; Tononi and Laureys, 2009) does not reject this earlier idea, he only endorses the view that the thalamocortical system is essential for consciousness.

The dynamic core hypothesis shows that the target of their theories is the neural realization of CMA and perhaps those SMA experiences that satisfy integration and differentiation. However, as noted in section 3 the thalamus is neither necessary nor essential for SMA in olfaction, and is not required for all types of CMA that involve olfaction. The IIT's failure as a general theory of consciousness is even more apparent given the unique anatomical structure of the olfactory system. The IIT may work as a theory of the other perceptual modalities, but the anatomical structure of the olfactory system simply cannot be accommodated by it.

## 5. Is there a Functionally Equivalent Analogue to the Thalamus in Olfaction?

It has been argued that the thalamus is not required for olfactory consciousness and that the most natural strategy for the theories of consciousness discussed, when faced with the evidence that the thalamus is not required for olfactory consciousness, is to claim that there is nevertheless a part of the olfactory system that has a functionally equivalent role to that of the thalamus in producing consciousness. In this section, this claim with regards to the olfactory bulb (OB) and olfactory cortex is evaluated and it is argued that there is little reason to think that either are functional analogues to the thalamus in the olfactory system. The functional role attributed to the thalamus is to bind information, as a common workspace, or to integrate information cross-modally.

Since the theories of consciousness are looking for an intermediate-level structure between the cortex and receptor cells of each perceptual modality, one suggestion would be to view the OB as functionally equivalent to the thalamus. Using research on the functional encoding of odorants in the OB, it is shown that the functional organization of the olfactory bulb is not functionally equivalent to the role assigned to the thalamus within these theories.

Kay and Sherman (2006), using the intermediate stage of processing approach, argue that the OB is functionally equivalent to the thalamus, i.e. it plays the same role in the olfactory system as the thalamus in the visual system, on the basis of three claims.

The first claim is that both the OB and the LGN are anatomically situated at an intermediate stage of processing between the receptor cells and the cortex. However, this observation does not support the claim that the OB and LGN are functionally equivalent and only supports the much weaker claim that if vision has three stages of processing projecting to the cortex, so might the olfactory system (depending upon whether the OB is considered a receptor site similar to the ganglion cells of the retina or the LGN of the visual pathway).

The second claim is that both the OB and LGN serve as a bottleneck within the informational stream that reaches the cortex. The popular metaphor of an information bottleneck is best unpacked as the claim that both structures focus incoming stimuli by decreasing the amount of information projected from the receptor sites to the cortical areas. However, this falsely assumes that the functions of glomeruli and mitral cells within the OB are to only act as relays, and thus grossly underestimates their actual functional role.

Lastly, Kay and Sherman use the structural similarity of mitral and tufted cells of the sensory input circuitry within both the OB and LGN as a means of comparison. While in general understanding structural organization facilitates a better understanding of function, it is essential in this case to take into account the actual workings of the olfactory bulb at a more detailed level.

Given these problems it is quite reassuring that Kay and Sherman admit ignorance regarding the functional role of mitral cells within the human olfactory bulb. Friedrich and Laurent (2001) use the zebra fish as an animal model for OB function in humans. Based on the convergence over time of olfactory receptor cells firing rates and, in particular, the convergence of firing patterns within the odour-coding assemblies of mitral cells in the olfactory bulb of zebra fish, they suggest that the OB encodes odorants in a combinatorial manner such that the representation of a stimuli is holistically encoded in the firing patterns of the glomeruli and mitral cells across the entire olfactory bulb itself (rather than each aspect of the stimuli being discretely encoded within it). This nicely highlights a key difference between the functional organization of the olfactory system and all other perceptual systems in terms of the variable of time. Friedrich and Laurent argue that given the slow transduction speed of the olfactory system, as compared to vision, time can be used as a computational variable in encoding the presence of an odour across olfactory bulbs within an individual circuit. Further work done in Laurent's lab further supports the claim that odours are spatially and temporally encoded throughout the glomeruli and mitral cells of the OB (Stopfer *et al.*, 2003) in a manner unlike the other perceptual systems. These results taken together with the problems raised for Kay and Sherman's three claims shows that the function of the olfactory bulb should not be equated with that of the LGN of the thalamus.

Another reason to reject the claim that the OB is functionally equivalent to the LGN is that Kay and Sherman only compare the LGN to the OB. Consequently their results are methodologically sound only if all areas within the thalamus do in fact function in the same manner as the LGN, something which needs to be demonstrated. Even if, as Kay and Sherman claim, the OB is in fact functionally equivalent to the LGN, this will only assist the neurobiological approaches of Crick (1994) and (perhaps) Koch (2004): it would be of no help for the GWT, the IIT, nor any other theory according to which the general functional role of the thalamus is to bind information cross-modally.

Ascending the hierarchy of the olfactory system, the natural place to look next for a claim of functional equivalence is the olfactory cortex (OC). Murakami *et al.* (2005) have shown that the state dependent gating mechanism in rats, which occurs at the thalamus for all other sensory systems, can be seen to occur at the anterior piriform cortex (APC) and olfactory tubercle (OT) of the OC. This demonstrates that sensory gating occurs within olfactory processes, and that the sensory gating with the OC is in synchrony with the activity of the gating mechanisms of the other modalities located in the thalamocortical system. While this might indicate that the APC and OT are the functional equivalents of the thalamus in olfaction, this would overstate the results of Murakami *et al.* (2005). Apart from the fact that these results are only from animal models, sensory gating at best shows that the olfactory system employs the same mechanisms for information processing of incoming stimuli. While the results show that olfaction must at times work in concert with the other modalities, they do not yield the full equivalence of function to the thalamus posited by these theories.

While only two possible candidates for a claim of functional equivalence have been considered, there are no other (to the author's knowledge) extant theories which claim that there is a functional equivalence between the thalamus and parts of the olfactory system. Attempting to accommodate olfactory consciousness within the theories of consciousness considered here is an ill-advised research strategy: olfaction works differently to the other perceptual modalities and the functional organization of the olfactory system, and its encoding mechanisms from the receptor sites to the cortex, is unique in many ways. The burden of proof thus lies with those theorists who make a claim of functional equivalence either to show that all the areas of the thalamus function in the same way as the LGN or to posit an alternative structure of the olfactory system which could fulfil the claimed functional equivalence.

## 6. Conclusion

The olfactory system's unique anatomical structure and functional organization causes problems for those contemporary neuroscientific theories of consciousness which claim that thalamic connections are part of the neural correlates of, and required for, consciousness: these include the framework of Crick and Koch, the Global Workspace theory of consciousness, and the Information Integration Theory of consciousness. Furthermore, the olfactory system does not contain a structure that is functionally equivalent to the putative role that the thalamus plays in producing consciousness, thus providing an additional reason to think that these theories of consciousness cannot generate a comprehensive (and therefore adequate) account of consciousness.

Olfaction works differently to the other perceptual modalities: an olfactory SMA does not require a thalamic relay or corticothalamic loops as it is claimed in the case of visual SMA and CMA. Hence, there is reason to reject the inference from the claimed neural correlates of visual consciousness (SMA or CMA) to the neural correlates of olfactory consciousness. Moreover, generating a theory about the neural correlates of CMA, based on the role of the thalamus in general, will not provide an adequate theory, since it will not be able to account for SMA and CMA involving olfaction.

Although damage to the MDNT pathway affects olfactory performance, it is not necessary for the occurrence of either SMA or CMA involving olfactory consciousness. While this fact alone does not refute the leading neurobiological theories of consciousness (e.g. Crick, 1994; Koch, 2004), it certainly shows that they are not sufficient as general theories of awareness involving all the perceptual modalities. This, as argued in section 5, is not simply rectified by positing that there is a structure in the olfactory system that is functionally equivalent to the thalamus in the visual system.

As things currently stand, while these theories might not be falsified by the anatomy of the olfactory system, they cannot accommodate what is known about olfactory SMA and CMA.

In addition to this negative conclusion, the findings here suggest that a fecund area of future research exists exploring cross-modal awareness involving olfaction. It is certainly worth exploring how both the unique anatomy of the olfactory system yields SMA and the olfactory experiences are integrated with the other modalities to create CMA. Furthermore, the recent findings that attention and awareness are distinct indicate that they might be realized by different neural systems (Tsuchiya and Koch, 2009; van Boxtel *et al.*, 2010). One issue touched upon in this article, though not fully explored, is whether olfactory attention and awareness are mediated by different neural systems; while the thalamus may be essential for attentional binding, it may not be for awareness. Olfactory performance breaks down in subjects with MDNT lesions as the difficulty of the task increases (discussed in section 3). This suggests that it may be part of the neural correlates of olfactory attentional binding, though not of olfactory awareness. Thus, further research on the olfactory system's unique anatomy and the functional processing that yields attention and awareness could allow an easier means of exploring the relation between these types of state.

The results of this article suggest a new methodological approach to the study of consciousness by rejecting the assumption that the findings regarding consciousness of a particular perceptual modality will generalize to the other modalities. Without further argument, I propose the Multi-Modal account of Consciousness. Consciousness is best treated as a multi-faceted phenomena, each modality requiring different lines of attack with their own specialized tools. Each modality deserves independent study. This should be followed by research on the mechanism responsible for the integration of the various modalities and cross-modal interaction. Identifying what realizes CMA may only be possible once the realization of each perceptual modality's SMA has been identified, and there is an understanding of cross-modal integration and interaction. Thus, a general theory of consciousness may be produced via the use of a bottom-up methodology.

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