Odour perception: An object-recognition approach

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Abstract. Object recognition is a crucial component of both visual and auditory perception. It is also critical for olfaction. Most odours are composed of 10s or 100s of volatile components, yet they are perceived as unitary perceptual events against a continually shifting olfactory background (ie figure – ground segregation). We argue here that this occurs by rapid central adaptation to background odours combined with a pattern-matching system to recognise discrete sets of spatial and temporal olfactory features—an odour object. We present supporting neuropsychological, learning, and developmental evidence and then describe the neural circuitry which underpins this. The vagaries of an object-recognition approach are then discussed, with emphasis on the putative importance of memory, multimodal representations, and top – down processing.

1 Introduction
Kubovy and Van Valkenburg (2001) define an object as "that which is susceptible to figure – ground segregation". In both the visual and auditory domains, perceiving objects such as a 'tree' or the sound of a dog's 'bark' involves the recognition of complex sets of features. By recognition, we mean the automatic accessing of a memory system which retains information on previous occurrences of sets of features—objects (eg Bregman 1990; Ullman 1996). Successful recognition provides the perceptual basis for discriminating one object from another, and, indeed, an object from its background. In addition, successful recognition may or may not be followed by successful identification, in which the name associated with the object is retrieved. The type of features used in the recognition process needs to be that which maximises the chance of successfully recognising biologically significant events in the environment (eg food, mates). In the case of vision these are spatial and temporal features, whilst for audition they involve temporal features and pitch (Kubovy and Van Valkenburg 2001). Here, we argue that olfactory perception is organised along broadly similar lines, but, as we describe below, there are some interesting and important differences.

We start by describing the nature of olfactory stimuli and the basics of olfactory information processing, and then discuss how these provide the necessary information (features) for the formation of statistically reliable patterns—objects. We then describe a rudimentary model of olfactory object recognition and present a summary of the neurophysiological, learning, and developmental data which support it. The way in which the brain instantiates this model and supporting neurophysiological evidence are also presented. Finally, we offer a broader discussion of the current shortcomings of this object-recognition approach to olfaction.

2 Olfactory stimuli
A good starting point is to consider the type of stimulus that the nose may routinely encounter outside of the laboratory. The history of olfactory research is one in which single pure chemicals have typically been employed as stimuli, whilst in the world outside

the lab most odours are composed of multiple volatile components (Hudson 1999). Of course, not all these volatiles are detectable or relevant, but we know that even apparently 'simple' smells may have scores of constituents all of which are independently odorous. A few examples should suffice (see Maarse 1991, for further examples in the food domain). Aged Rioja red wines have over 800 volatile components, of which approximately 60 have odours detectable by humans (Aznar et al 2001). Parmigiano-Reggiano cheese has around 160 volatile components with nearly 30 of those odorous (Qian and Reineccius 2002). Despite these incredibly complex stimuli, our percept is largely unitary (despite anecdotal evidence and folklore to the contrary), and we perceive a specific red wine or cheese. In sum, many olfactory 'events' are composed of complex chemical mixtures.

3 Olfactory processing

The stimulus—a chemical mixture—is either transported via the nasopharynx during eating and drinking, or is actively sniffed via our two nares. In both cases the stimulus passes over the olfactory epithelium, in which are embedded olfactory receptor cells, each of which contains only one type of G-protein-coupled receptor (Buck 2000). It is estimated that humans have somewhere around 300 different types of receptor. Each receptor is broadly tuned and is responsive to a range of chemicals (Buck 2000). When the components of the mixture arrive on the receptor surface, they bind to a range of different receptors. Even a pure chemical is likely to activate several receptor types, whilst a complex mixture will activate many more. Not only does this produce a complex signal composed of the activation of many receptor types, but the signal has a temporal component, reflecting the faster or slower binding of particular chemicals and the effect of interactions at the receptor site (Buck 2000). Information from each type of G-protein-coupled receptor is then sent to a glomerulus, a structure within the olfactory bulb. In mice, where there are around 1000 different G-protein-coupled receptor types, olfactory receptor neurons expressing a particular G-protein-coupled receptor converge onto approximately two glomeruli; thus there are about 2000 glomeruli in the mouse. These glomeruli are arranged in a two-dimensional sheet, with G-protein-coupled receptor types sensitive to similar structural aspects of the stimulus, feeding into neighbouring glomeruli. Whilst it is not clear yet if this arrangement holds true for humans, it would seem highly likely that the basic principle is the same, given the highly conserved nature of olfactory system anatomy across animal species. The output from the glomerular layer forms a spatial (two-dimensional map of activation on the glomerular sheet) and temporal (changing across time) pattern, which is then used as the input for cortical processing in the piriform (primary olfactory) cortex.

4 Olfactory features

A central component for understanding object recognition in the visual and auditory domains is to identify the features that are used to generate an object. In these domains there are potentially many characteristics that could form the basis for defining an object, but in fact there are only relatively few features, which are, in Kubovy's (1981) terminology, indispensable. Unfortunately, in olfaction it is very difficult to manipulate stimulus dimensions which are likely to be 'indispensable', in the way that it is possible to do so for visual or auditory stimuli. As a result there are no psychological data to guide our choice of indispensable features, and so we have reversed the usual process (moving from psychophysics to psychophysiology) and used instead what we know about the way the brain processes olfactory information to identify the (presumably) indispensable features for olfaction.

On the basis of our discussion of olfactory processing above, we suggest that the olfactory systems utilise two types of features: spatial and temporal. Our use of both

these concepts is different from their use in visual object recognition. By spatial, we mean the two-dimensional distribution of neural activity across the glomerular layer of the olfactory bulb. This has no strict and direct spatial correlate with events in the external world; rather it reflects the way the nervous system groups chemical information into a spatial array suitable for recognising different odours. What this spatial array does correlate with are the chemical structures that are present in the stimulus, although the structures which are important are still being actively identified (eg Araneda et al 2000). Whilst chemical structure may in some cases be predictive of what will be perceived (especially with single pure chemicals; see Rossiter 1996), in many cases, and especially with ecologically valid stimuli containing many chemicals, this relationship would be very difficult to establish.

In the same way that 'spatial' here assumes a different meaning to 'spatial' in the visual domain, 'temporal' here also assumes another form. By 'temporal' we mean the changing pattern of neural activity across the glomeruli layer of the olfactory bulb. Again, this will not always reflect events in the external world; that is, the concentration of the stimulus may remain the same, but receptor events may change. As we describe next, this spatial and temporal information appears to form the basis for extracting patterns, which in turn leads to figure – ground separation, our defining criterion for objecthood.

5 Figure and ground

Odorants are often complex mixtures. Each blend will produce a relatively unique spatial and temporal signature that the brain must recognise as an odour object. For the olfactory system to function appropriately in its natural environment, odour objects need to be recognised against a background of other odours. The brain therefore faces the task not only of having to recognise a complex blend, but often of having to extract this blend from a background of chemical noise or competing olfactory objects.

Two processes appear to accomplish this feat: rapid cortical adaptation to background odours and pattern recognition of glomerular output. We deal first with rapid cortical adaptation, which functions to identify a new object should one appear. In both humans and rodents, the piriform (primary olfactory) cortex rapidly adapts to stable odours, despite relatively maintained peripheral input (Sobel et al 2000). Both odour receptors (Zufall and Leinders-Zufall 2000) and olfactory bulb neurons (Fletcher and Wilson 2003) adapt, at least to a small extent, in response to constant odour stimulation; however, neurons in the piriform cortex can completely stop responding to stable odours within seconds.

This cortical adaptation appears to be due to depression of the synaptic input from the olfactory bulb to the piriform cortex. During periods of intense or prolonged stimulation glutamate binds to pre-synaptic receptors, which then reduces subsequent transmitter release—a negative-feedback system. Pharmacological blockade of this feedback system prevents central cortical adaptation (Best and Wilson 2004). Furthermore, it completely blocks habituation of an odour-evoked bradycardia reflex and delays habituation of odour investigation behaviours in an open-field test (Yadon and Wilson 2005). Together, these results suggest that odour adaptation is mediated by synaptic depression within the primary olfactory cortex.

In the context of the present discussion, it is important to note that this rapid cortical adaptation is remarkably odour-specific. Thus, adaptation to a 5-carbon alkane leaves cortical responses to a 7-carbon alkane largely unaffected (Wilson 2000). Similarly, adaptation to a familiar binary mixture of odours produces minimal cross-adaptation of cortical responses to the components of that mixture (Wilson 2003). This odour-specificity of cortical adaptation could allow filtering of stable, background odours with continued responses to novel odours presented against that background. In fact, piriform

cortical neurons respond to a target odour presented against a stable background as if that target odour alone were present, despite the fact that, at the nose, a binary mixture of the target and background is present (Kadohisa and Wilson 2006a). The response of olfactory bulb neurons under the same conditions matches the response to the binary mixture (ie these are the features inhaled), while the cortical neurons, owing to their ability to adapt to the background, respond solely to the target (ie separation of figure from background). In rodents, stereotyped rapid sniffing behaviours may also contribute to background filtering, though the relevance of this mechanism to humans is unclear (Verhagen et al 2007).

6 Pattern recognition

The second central process involved in perceiving odour objects is a pattern-recognition system. The brain appears to store previous patterns of glomerular output, so that when a new output arrives it may be matched to all previous encodings (Stevenson and Boakes 2003). If there is a good match, we consciously experience a discrete odour, distinct from its background and discriminable from other odours. It may or may not be identified (named). Where the input is unfamiliar, our experience is vague and ill-formed and the odour is hard to discriminate from other unfamiliar odours. However, novel input patterns (ie novel odours) are rapidly acquired by any process that involves exposure to the target odour (passive exposure, association with a reinforcer, etc). When the now not-so-novel odour is encountered again, it can produce a more distinct representation by virtue of being recognised, making it more readily discriminable from other unfamiliar odours, from the olfactory background, and from other familiar odours. According then to this account, if the ability to match patterns is lost or, relatedly, if the store of previous encodings is damaged, one should no longer be able to appreciate odour quality—a rose would not be discriminable from diesel fumes. Is this claim sustainable?

6.1 Psychological evidence for an odour object-recognition system

The evidence favouring an odour object-recognition system of the sort described above comes from a variety of sources. Visual object recognition in particular has benefited from the study of patients with selective deficits in recognition—agnosias (Farah 2000). Before turning to consider these, it is important to consider whether we are trying to draw a parallel to either the associative or the apperceptive agnosias. Associative agnosia is assumed to reflect intact perceptual processes, but is accompanied by a failure to perceive the object's meaning. In contrast, apperceptive agnosias are presumed to reflect a failure to correctly perceive a set of features as an object. This distinction may be somewhat artificial. A central argument used to suggest intact perceptual processes for the associative agnosias is the preserved ability of patients to draw the object in question (Riddoch and Humphreys 2003). However, as Farah (2000) points out, these drawings may take hours to produce as the patient may construct them piece-by-piece as if they could not perceive the whole. For this reason we will simply be agnostic and refer to 'agnosia', rather than to any specific type.

A careful search of the olfactory neuropsychology literature points to several apparent parallels to visual-agnosia cases. The most striking is HM, who received a bilateral temporal lobectomy for intractable epilepsy. In the early 1980s he was extensively tested for olfactory functioning (Eichenbaum et al 1983). This revealed a remarkable pattern of deficit. HM's acuity, that is his ability to detect an odour, was completely intact and as good as that of people of his own age but without any brain injury. Likewise, HM was able to discriminate two different odours, when one was presented in more concentrated form than the other. Thus HM was capable of detecting stimuli: of making intensity discriminations and of performing an olfactory discrimination task.

However, when presented with two different odours, matched for strength (eg coffee versus lavender), HM's discriminative performance was at chance level. Likewise, when asked to name or describe an odour, HM was not able to do so. This pattern of deficit suggests that HM could not perceive odour quality (ie from our perspective, odour objects), but Eichenbaum et al (1983) state explicitly that this is not an agnosia, because of his discriminative failures. They reach this conclusion by drawing a parallel to the visual domain. A person who could not visually discriminate between objects because they all look the same would not be termed agnosic.

We offer a rather different interpretation. In the visual system, the absence of object perception is still accompanied by conscious perception of individual features — lines, edges, colour, etc. Whilst a person may not be able to recognise them as a discrete object, two different objects could still be told apart on the basis of this feature information alone (Riddoch and Humphreys 2003). Our argument is that in olfaction this feature-based information is not consciously available. Evidence for this comes from several sources (see Wilson and Stevenson 2006), but in humans the primary finding is that intact participants are very poor at discriminating the component parts (or elements) of odour mixtures (eg Laing and Glemarec 1992; Livermore and Laing 1998). This is arguably a consequence of the way that the spatial feature is assembled, the act of assembly reduces information about individual chemical features. If then a person's memory for previously encoded patterns is damaged, as we suggest for HM, all that is left is the intact glomerular output. HM's data suggest this yields little more than olfactory sensations, which can differ in magnitude. This is an olfactory agnosia, because the stimulus cannot be perceived as an object, but, unlike vision, here the absence of object status is accompanied by the absence of feature-based information, eliminating any basis for qualitative discrimination. In this sense object perception and olfactory perception are synonymous, in a way they are not for visual (and presumably auditory) stimuli.

HM is not alone. Several other conditions also produce olfactory agnosia, although their deficits are generally not as striking as those of HM. For example, epileptic patients who have brain tissue removed to prevent further seizures may show intact acuity, but are selectively poorer at odour discrimination (Eskenazi et al 1983). A similar, but more complex picture is present in Alzheimer's patients. Here acuity is lost too, but there is an abundance of cases indicative of deficits in odour discrimination, in the absence of acuity loss (eg Morgan and Murphy 2002) and prior to disease onset (eg Calhoun-Haney and Murphy 2005). Finally, the process of ageing may also affect both acuity and discrimination independently (eg Schiffman 1992). All of these cases suggest that participants can detect odorants, but that they fail to recognise them.

A further strand of support comes from the perceptual-learning literature. Rabin (1988) observed that passive exposure to a set of unfamiliar odours resulted in improved discriminability between members of that set, relative to unexposed controls. Similar findings have also been obtained in other laboratories (Jehl et al 1995) and in naturalistic studies of olfactory perceptual expertise (eg Chollet et al 2005; Parr et al 2002). The functional value of this perceptual learning became evident in a further experiment reported by Rabin (1988). Here, participants had to determine whether a target odour was present or absent in a mixture. Targets could be familiar or unfamiliar as could the distractor odour mixed with the target. Discrimination of the target was very good when both the target and the distractor were familiar and very poor when both were unfamiliar. These results suggest that experience with an odour is necessary for it to be recognised as a discrete object and hence for it to become discriminable from other odours (ie the background).

Stevenson and colleagues have reported a more recent literature, which directly converges with the effects described above. Several authors have noted that certain odours are reported as 'sweet' smelling (see Stevenson and Boakes 2004, for review). Sweet, however, is a sensation resulting from the activation of tongue-based taste receptors by certain classes of chemical, notably sugars. Many participants report an apparently identical sensation when they smell odours such as strawberry, caramel, or vanilla, although these substances do not taste sweet if placed on the tongue whilst the nares are occluded to prevent retronasal olfaction (eg Frank and Byram 1988; Stevenson et al 1999). Participants who were presented with a mixture of an unfamiliar odour and a sucrose solution, which they sipped by mouth, later reported that the sucrose-paired odour smelled sweeter when sniffed, than did control odours paired with either citric acid or water (Stevenson et al 1998). It appeared that the odour had acquired a 'sweet taste' by virtue of the brain encoding a multisensory representation 'odour – sweet taste', which was then accessed when the odour was later smelled alone. Note here both the procedural (passive exposure) and explanatory (passive encoding) similarity between odour – taste learning and that of exposure enhancing the discrim-inability of unfamiliar odours.

Odours can acquire attributes not only from tastes but also from other odours. Participants passively exposed to binary odour mixtures (eg cherry – mushroom) demonstrate on test acquisition of odour qualities (ie mushroom comes to smell cherry-like—Stevenson et al 2005), greater similarity between the elements of a pre-exposed mixture (ie mushroom is judged to smell more similar to cherry—Stevenson et al 2005), and reduced discriminability between the elements of a pre-exposed mixture (ie mushroom and cherry are poorly discriminated—Case et al 2004; Stevenson 2001). These findings need to be viewed from what we might expect to occur in the olfactory object-recognition system. Once an odour mixture has been encoded, presenting an element drawn from the mixture (eg cherry) should be able to activate the encoding of the mixture, to some extent at least (eg cherry – mushroom). Consequently, we might expect that the two constituents of the mixture would come to share odour qualities, be judged as more similar, and be less discriminable from one another, than equally exposed, but unpaired, controls. The results described above bear this out. It appears that the brain does encode the mixture memory—just as it appears to encode 'unfamiliar' odours and odour – taste mixtures—and this then affects perception.

If experience is necessary to perceive an odour object and hence discriminate it from other odours, we might expect changes to occur during development. On this basis we would predict that neonates, and also children, should have largely intact acuity but that ability to discriminate odours would show improvement as the infant/child became exposed to progressively more olfactory stimuli, thus having the opportunity to encode them. Children aged 6 years are poorer at learning labels for odours that adults find unfamiliar, but learn the labels for more familiar odours nearly as fast as adults (Cain et al 1995). Cain et al suggest that this results from poor discriminabil-ity of unfamiliar odours by children. Stevenson recently tested this more directly in an extensive series of investigations with 6-year-olds, 11-year-olds, and adult participants (Stevenson et al 2007a, 2007b). Not only were 6-year-olds poorer at discriminating unfamiliar odours when compared to 11-year-olds and adults (who did not differ), discriminative differences were also evident for moderately familiar and familiar odours too. In fact, the largest effect was for odours reported by adults to be moderately familiar, as this would likely represent the largest gulf in experience. These differ-ences in discriminative ability were not a consequence of the inability of 6-year-olds to perform the discrimination task, nor were they a consequence of adults using a verbal-labelling strategy during the discrimination test. Rather, the difference appears to result from children having a less-well-developed store of olfactory experience.

Difference in odour familiarity should also occur between different cultures. Ueno (1993) compared Nepalese and Japanese participants and found that whilst a range of fish-like odours was clustered into a discrete group in Japanese participants, no such discrete grouping occurred with Nepalese participants. Perhaps not surprisingly, given their Himalayan homeland, Nepalese participants have relatively limited experience with fish odours when compared to Japanese participants. Similar findings have emerged from a comparison of Japanese and German participants too, who tended to assign different odour qualities to smells that are not routinely encountered within their particular culture (Ayabe-Kanamura et al 1998). These findings again suggest that our experience of odour quality—what we perceive—is strongly influenced by experience— the opportunity to passively encode varied olfactory inputs.

Neuropsychological, learning, and developmental data all point towards the same conclusion. A store of olfactory experience underpins odour perception, and the act of recognising (perceiving) an odour relies upon matching a neural representation of the chemical stimulus to these encodings. Do neurophysiological findings concur?

6.2 Neurophysiological evidence for an odour object-recognition system

The piriform cortex is hypothesised to be the site of odour object synthesis, merging information about odour features extracted by the receptor sheet and refined by the olfactory bulb into unique perceptual odour objects (Haberly 2001). The mammalian olfactory pathway is unique among sensory systems in that there is a direct projection from the first central relay (olfactory bulb) to the primary sensory cortex (piriform cortex) without a thalamic relay. The olfactory system also includes a thalamocortical component—the dorsomedial nucleus of the thalamus projection to the orbitofrontal cortex—but the piriform cortex lies upstream of this pathway. Through interconnections with the orbitofrontal cortex and limbic structures, the perceptual objects synthesised within the piriform cortex may include multimodal or contextual aspects. This synthesis goes beyond simple spatial convergence of temporally co-occurring features to include a relatively permanent record, or template, of familiar odour objects which allows both enhanced discriminability of those familiar objects and the ability to reconstruct complete objects from partially degraded inputs.

This model of piriform cortical function relies on two aspects of piriform cortical circuitry. First, input from the olfactory bulb, conveying information about specific odour features, terminates in overlapping patches, presumably allowing spatial convergence of multiple-odour feature information onto single piriform cortical neurons (Zou et al 2005). A single odour composed of multiple odour features (eg a hydrocarbon chain of particular length, an ester group in a particular location, an aldehyde group combined with a hydrocarbon chain, etc) will activate multiple odour receptors, each binding different submolecular features (Araneda et al 2000). This feature information is further enhanced through local circuits within the olfactory bulb to create a spatial and temporal representation of the odour features present in a given inhalation (Takahashi et al 2004). While some interaction and blending of these features may occur at the receptor and/or within the olfactory bulb, the overlapping terminations of olfactory bulb output neurons within the piriform cortex allow feature combinations, rather than individual features, to be the more salient driving force in piriform activity. With just this simple anatomical convergence of feature input and coincidence detection the cortex can begin to process complex odour information (Zou and Buck 2006).

However, anatomical convergence and coincidence detection are not sufficient to account for odour object perception. For example, as noted above, neurons within the piriform cortex are able to discriminate (show minimal cross-adaptation) between a familiar binary odour mixture and the components of that mixture. However, if the

binary mixture is not familiar, but rather a novel combination of odours not smelled before, the piriform cortex discriminates very poorly between the components and the mixture (Wilson 2003). In more recent work it was found that, as animals learn a triple odour mixture, the population response of anterior piriform cortical neurons becomes more distinct (decorrelated) from the response of that same population to the components (Kadohisa and Wilson 2006b). These results suggest that experience with a mixture enhances the ability of the anterior piriform cortex to treat that mixture as a new, unique object, distinct from its components.

Electrophysiological and computational-modeling work suggests that cortical learning of odour objects occurs through the second important aspect of piriform cortical circuitry which is an extensive, intracortical association-fibre system capable of long-term synaptic plasticity (Haberly 2001; Hasselmo and Barkai 1995). Individual piriform cortical pyramidal cells, which are the target of convergent odour feature input from the olfactory bulb, have broadly ramifying axons that form an association system among widely dispersed piriform cortical neurons (Johnson et al 2000). Given the placement of these association-fibre synapses within piriform pyramidal cell dendritic trees, and electrical characteristics of pyramidal cell dendrites, these association-fibre connections are at least as effective at driving cortical neural activity as afferent synapses from the olfactory bulb (Neville and Haberly 2004). The association fibres thus greatly expand the opportunity for multiple feature convergence onto individual neurons. Importantly, association-fibre synapses are also capable of associative long-term potentiation (Kanter and Haberly 1990), suggesting that patterns of co-occurring odorant feature input could be memorised through synaptic change.

This cortical circuitry, consisting of patchy afferent input and plastic, broadly distributed association fibres, is an ideal substrate for an autoassociative content-addressable memory system (Haberly 2001). Content-addressable memory allows the entire memory array circuit to be searched to determine whether a specific input pattern exists in the stored memory, and in some cases identifies other items associated with that pattern. This process differs from computer random-access memory where the input consists of an address or storage site and the output is the content of that site. Thus, content-addressable memory allows familiar input patterns to be recognised, completed, and elaborated upon, even if those inputs are partially degraded (eg through changes in stimulus intensity). As input patterns become more divergent, they activate different memory templates, and thus return different outputs (ie odour objects). In contrast, two well-learned representations can involve very similar inputs and yet evoke distinctly different outputs (increased perceptual acuity for learned stimuli).

The associative plasticity of intracortical association fibres plays a crucial role in content-addressable memory. As combinations of odorant features co-occur, association fibres conveying information about these features and their combinations are strengthened through synaptic plasticity (Haberly 2001). On subsequent presentations of the learned pattern, circuits containing these now strengthened synapses are more easily activated—indicating a template match. If the input pattern is slightly modified through adaptation to a subset of features or changes in stimulus intensity, the template pattern may still be completed because of the enhanced synaptic strength (Hasselmo and Barkai 1995).

Interestingly, neurons in the posterior piriform cortex, a region of enhanced intra-cortical association-fibre connectivity, respond completely differently to odour mixture experience compared to the anterior piriform cortical neurons described above. Thus, while neurons in the anterior piriform cortex decorrelate responses to familiar mixtures with experience to form unique odour objects, neurons in posterior piriform cortex respond to a familiar odour mixture and its components more similarly, in effect reducing the distinctiveness between encoding of two components that have been

experienced together (Kadohisa and Wilson 2006b). These results from the posterior piriform cortex are highly reminiscent of the human psychophysical results described above, wherein the experience of two odours together begins to merge their perceptual qualities. It has been hypothesised that anterior piriform cortex may encode information about configural odour objects, while posterior piriform cortex may encode information about broad odour quality or learned similarities (Kadohisa and Wilson 2006b; Li et al 2006).

In support of this model, pharmacological manipulations known to disrupt normal synaptic plasticity of piriform cortical association fibres impair odour discrimination of cortical single-units and disrupt olfactory perceptual learning (Wilson 2001). Furthermore, when content-addressable memory is combined with the highly specific synaptic depression of olfactory bulb inputs to the cortex, both odour object formation and background odour filtering can be accounted for. In sum, the neurophysiological data are strikingly convergent with the psychological data reviewed above.

7 Discussion

The object-recognition viewpoint that we have presented here is a new one. However, this is not to say that those before us have not reflected upon higher cortical/cognitive processes in olfaction (eg Freeman 2000). Rather, there has been a major shift in thinking, particularly in the past decade, which has made consideration of higher-order processing integral to understanding how the brain forms an olfactory representation. Part of this shift has come from biology, with Buck and Axel's (1991) discovery of the combinatorial nature of olfactory receptors, and from psychology, with the consistent failure of olfaction to yield to the 'stimulus problem' approach (Amoore 1982). These types of findings have led a number of people to consider whether a focus on receptors will ever satisfactorily explain olfactory perception (eg Hudson 1999; Stevenson and Boakes 2003). In terms of critically appraising the object-recognition approach, the best place to start is to consider how fundamental odour object recognition may be to olfactory perception.

An olfactory object-recognition model can be presented in a variety of formats, from weak, in which object recognition is seen as the top end of a bottom–up driven process of identifying chemical features, to strong, in which odour perception (ie discrimination and the experience of odour quality) is completely lost if the system is disabled. In humans at least, the system appears to be at the stronger end of the spectrum, but crucial evidence in this respect is missing. We know little about neonate's and infant's ability to discriminate odours. HM is the only strong case of olfactory agnosia that we are aware of. In animals, selective lesions of the olfactory structure we presume to underpin the object-recognition process do not appear to incapacitate the olfactory system in the way one might expect (Slotnick and Schoonover 1992). Part of this uncertainty comes from lack of evidence. The other part may imply that in macro-osmic animals such as rats, the olfactory system is at least in part capable of qualitative discrimination based solely upon receptor output.

A further problem is how the object-recognition system re-integrates experiences from other sensory systems, when the stimulus is purely an olfactory one. Both piriform and orbitofrontal cortices (OFC) have multimodal inputs, and at least in the OFC there are cells that are only responsive to such inputs (eg odour and taste—Rolls and Baylis 1994). Does the olfactory system then activate areas of sensory cortex that are typically associated with sensation from other sensory domains such as the insula? In this case, patients for example without intact insular cortices, the basis for taste quality perception, would presumably find that sweet-smelling odours do not smell sweet. Alternatively, does the information necessary for experiencing taste, when only an olfactory cue is presented, reside in purely olfactory areas, or in multimodal brain areas?

This very basic question offers an intriguing line of enquiry into the way in which the brain supports different sensations.

The role of 'top–down' processing in odour object recognition is also little understood. Outside the laboratory, the source of an odour is typically apparent—a pizza on the table, or something nasty on one's shoe. Our hedonic reaction to smells appears to be strongly influenced by what we believe the smell is (eg Herz and von Clef 2001) and, indeed, these beliefs do appear to influence brain activity in regions primarily concerned with olfactory processing (de Araujo et al 2005). However, findings such as the apparent misperception of white wine coloured red as red wine raise the possibility that visual (or other multimodal) cues may powerfully shape olfactory perception (Gottfried and Dolan 2003; Morrot et al 2001). On the one hand, such observations could result from purely semantic knowledge; on the other, they could result from the tuning of olfactory perception by top–down means. There is as yet no definitive evidence as to which may be correct.

A further issue is the olfactory–verbal 'gap'. Whilst most participants may readily identify pictures of objects, identification of even the commonest olfactory objects is notoriously hard (Cain 1979). Why should this be so? Three possibilities have been canvassed. One is that the neuroanatomical links between olfactory sensory processing and semantic memory are impoverished in some as yet undefined way. The second is that olfactory information processing shares common cortical resources with verbal information processing, resulting in interference between the two (Lorig 1999). The third is that it reflects a general disinclination to learn associations between olfactory inputs and semantic labels, compounded by the stochastic nature of the recognition system (which, to borrow Cain's phrase, may be termed 'noise at the nose'). Such links between olfaction and language, and, more generally, between olfaction and visual objects, are important because of the role that they might play in mediating top–down processing; but, again, we lack definitive evidence which of these explanations, if any, may be correct.

Finally, many odours are described not just by reference to their source (eg cheese or tea) but by the effect they exert on a person (Dubois 2000). This effect is typically characterised by emotive terminology, from outright repugnance to nuanced changes in mood wrought by smells that are evocative of other times and places. To what extent do these effects depend on the object-related processing that we have outlined here? One argument, that we have advanced elsewhere (see Wilson and Stevenson 2006), is that object-related processing is an obligatory first step and that these emotive meanings cannot be accessed until this has been accomplished. Although there is very little evidence to go on, it may be that separate brain systems deal with the evocation of emotive responses to odours and these may be independent of the processes we have described here (see Mendez and Ghajarnia 2001; Perl et al 1992). As the hedonic dimension of odours is highly salient, how this integrates with the processes described in this paper is a significant and poorly understood problem.

Although many details remain to be identified, we believe that sufficient evidence exists for us to conceive of olfactory perception as an object-recognition process. It may also illuminate the study of visual and auditory object recognition which in evolutionary terms it likely predates. Needless to say, the main purpose must remain understanding how we can perceive such a rich array of olfactory experiences.

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