Oxford Reference

The Oxford Companion to Consciousness

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Publisher: Oxford University Press
Print ISBN-13: 9780198569510
Current Online Version: 2010
Print Publication Date: 2009
Published online: 2010
eISBN: 9780191727924

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The sense of smell is widely believed to be of relatively minor importance in humans. Most theories of mind and consciousness therefore build on other senses, especially visual perception. However, a growing body of research across many fields is documenting the crucial roles, most of them hidden from our conscious perception, that the sense of smell plays in human behaviour. Here we summarize briefly some of those roles that are most relevant to human cognition. It will be shown that, especially through its unconscious role in the human brain flavour system, smell is a hidden sense that is a powerful factor in shaping human lives.

The sense of smell arises from stimulation by odour molecules of olfactory receptor molecules in the nasal cavity. There are hundreds of different molecules, embedded in the membranes of tiny hairs extending from the olfactory receptor cells. Each cell expresses one type of receptor, which responds differentially to different odours. Thousand of these cells send their long fibres (*axons*) to two modules (*glomeruli*) within the brain, in a structure called the *olfactory bulb* that rests just below the frontal lobe of the brain. Here the activated glomeruli form a complex spatial pattern, referred to as an *odour image*, representing the stimulating molecules. Different molecules are represented by different patterns, and different odour objects, such as perfumes or foods, are represented by different combined patterns, and are therefore believed to be the basis for detecting and discriminating different odours, analogous to images in the visual system. The odour images are subjected to successive processing by neural microcircuits in the olfactory bulb, then the olfactory cortex, and finally the primary olfactory receiving area in the orbitofrontal cortex, where conscious perception arises. Thus, the sensory stimulus that is processed is in the form of an image, and not conscious, as in the case of the retinal image, but the conscious sensation does not retain the quality of a spatial image, as in the case of vision. How the initial spatial pattern in the glomeruli is changed into the quality of a smell is one of the greatest challenges in studies of human perception.

This is the *common olfactory pathway*, but its activation actually involves two distinct routes which, as noted by the psychologist Paul Rozin (1982), makes smell for most practical purposes not one sense, but two. One is called *orthonasal smell*, which is the sense we use when we sniff in the odours of our environment. These span a vast range, from floral scents, including perfumes and incense; alarm signals such as smoke; food aromas; and social odours such as prey/predator smells, pheromones and molecules from the major histocompatibility complex (MHC) that controls the immune response. Humans generally are aware only of the floral scents as found in our daily experience of perfumes and deodorants, unpleasant body odours, and the aromas of food. By contrast, the behaviour of most mammals is dominated by the social odours. Since the work of Martha McClintock in the 1970s, showing that there is synchronization of menstrual cycling among women living together in dormitory environments, there has been interest in revealing social odours in humans. There is evidence, for example, that sex pheromones can affect mate preferences in humans, and stimulation with these compounds can activate wide areas of the human brain as shown by *functional brain imaging. The roles of these and other social odours in humans are under active investigation. The fact that human social interactions depend on so many variables makes these investigations quite difficult.

The other olfactory sense is *retrograde smell*, which occurs when the receptors in the nasal cavity are activated by the molecules released from food and drink within our mouths. This occurs when we breath outward while masticating the food, releasing volatiles that pass from the back of the mouth through the nasopharynx and outward through the nasal cavity. This activation of the smell pathway is almost entirely unconscious, as evidenced by the fact that humans refer to the ‘taste’ of a food or drink, reflecting the fact that the perception appears to come from our mouths. However, many studies have shown that most of what we call *taste* is actually due to smell. You can show this yourself by the jelly bean test: chew on a jelly bean while holding your nose and you will sense practically no ‘taste’; open your nose and the taste floods your perception. A better term is *flavour*. Taste and smell are often believed to be the basis of flavour, but in fact flavour is a multisensory perception. It includes the five traditional tastes (sweet, salt, sour, bitter, and umami), a wide range of texture (somatosensory) submodalities, such as temperature, astringency, deep pressure, light touch, creaminess, pain, etc.; vision (shape, colour), and even hearing, as we grind our teeth (reviewed in Shepherd 2006).

This multimodal character of flavour means that retronasal smell always occurs in conjunction with all these other senses. This is confirmed by brain imaging, showing the extensive brain areas that are activated during food tasting. In addition to these areas involved in flavour perception, food volatiles also activate many areas that subserve memory, motivation, and emotion. These latter areas involve the amygdala, a key area of the brain integrating and controlling different states of emotion. There is evidence that these areas are activated when subjects are presented with foods that they crave, or even when they just think about them. Marci Pelchat, of the Monell Chemical Senses Center, has called these patterns of activation ‘images of desire’ (Pelchat et al. 2004). A key point is that these areas of desire and craving for foods overlap with those that have been shown to be involved in the addictive states related to nicotine, alcohol, and other drugs of abuse. A better understanding of how these areas are engaged during eating behaviour may thus help us to understand better how flavour is related to the abnormal feeding behaviours that underlie excessive desire and craving and that lead to obesity and other feeding disorders.

The hidden role of smell in flavour is no better demonstrated than in Proust's iconic tale of the madeleine. Proust's hero Marcel is despondent, and is given tea and a cookie to cheer him up. At the first ‘taste’ of the tea-soaked madeleine, Marcel is immediately (according to the myth) transported back to scenes of his childhood in Combray, thus demonstrating the power of smell in evoking ‘pure’ memories. Closer examination, however (Shepherd-Barr and Shepherd 1998), reveals that Marcel's experience was much like our own: it involved stimulating his olfactory pathway by the retronasal route, and rather than coming back instantly, it took great mental effort over many minutes (some one and a half pages in the book) to recover the memory, and the emotional experience must have involved the areas mentioned above that are indicated by current brain scans.

The intensity of an olfactory memory may reflect two factors. First, the olfactory pathway feeds directly into the limbic system forebrain areas for memory, including the hippocampus, amygdala, and frontal lobe. Second, smell is distinguished from the other senses by having its primary neocortical receiving area, the orbitofrontal cortex, within the prefrontal cortex of the *frontal lobe, well known for containing the highest brain centres for cognition. This may give a higher potential intensity to the perception, emotional quality, and memory of smell than the other senses, which would be of adaptive value because of the dominant role of smell in mammalian behaviour.

Thus, the location of the smell area within the prefrontal cortex has many consequences. Within the orbitofrontal cortex, multimodal integration of all of the senses involved in flavour takes place (see Ongur et al. 2003). It means on the one hand that smell has direct access to these highest centres, so that it can strongly affect not only abstract thought and planning, but also the control by these centres of the limbic system centres for motivation and emotion. One the other hand, these higher centres can in their turn affect the primary smell perceptions, exerting a kind of top-down control or modulation of the perception of a smell. This makes smell highly contingent on its behavioural state and sensory modulation (Rolls 2006). As an example, in double-blind testing it has been shown that if a white wine is coloured red, it will be judged to have qualities of a red wine.

Another common belief about the olfactory system is that it is poorly connected to our language centres, as evidenced by our difficulty in describing a smell perception in words. However, the situation is more complicated than this. There is evidence that naming different smells is difficult because smell perception and language processing use the same neural substrates. It can also be shown that verbal cues can change odour perception; the same odour molecule was shown to be attractive or repulsive depending on whether the word 'cheese' or 'body' was flashed on a monitor half a second before the stimulus was presented.

Insight into our difficulty in using words to describe smells may be gained by recognizing that the stimulus being described is a neural representation that starts in the olfactory glomerular layer in the form of a complex spatial image (see Shepherd 2006). The nearest analogy in other sensory systems may be pattern recognition in vision, as exemplified by the complex pattern of a human face. Humans are extremely proficient in recognizing a human face, even though we have great difficulty in describing it in words. The same must apply to the odour images. With training and experience we become good at it, as any perfumer, wine taster, or chef can testify. Understanding smell identification as an example of pattern recognition may suggest strategies for further analysis.

In daily life, language is particularly important in characterizing the patterns elicited by retronasal smell as components of food flavours. Flavours produced by cooking played a central role in human evolution. Social anthropologists regard the shared common meal as the defining social activity of early humans. This required the emergence of language as the means to organize the activities of hunting and gathering, and also as the necessary means to communicate about the preparation of the meal and its communal assessment in terms of desirable flavours. The advantage of language enabled humans to put verbal labels on the novel flavours produced by cooking. Language is therefore an integral part of the human brain flavour system, making verbally specific the conscious appreciation of the perception of flavour.

This leads to the final point, that the sense of smell is interesting from the point of view of the neural mechanisms underlying consciousness. Most of the interest in this problem has been focused on the visual system, for example, at what stage in the successive stages of visual processing, from thalamus to the primary and secondary cortical areas and beyond, does conscious perception of a visual stimulus arise.

The interesting aspect of the sense of smell is that the pathway goes first to a three-layer cortical region, the olfactory cortex, and then projects to neocortex through two routes. The main route is direct to the orbitofrontal cortex, as described earlier. It is therefore an exception to the rule that conscious perception in sensory systems requires a relay through the thalamus to the cortex. It is not even known yet whether conscious perception of smell can arise at the level of three-layer olfactory cortex, independently of both the thalamus and the neocortex. However, there is also in most mammals a smaller pathway from the endopiriform nucleus just deep to the olfactory cortex to mediodorsal thalamus and on to orbitofrontal cortex. Joseph Price (personal communication) has suggested that the endopiriform nucleus collects inputs from broad areas of olfactory cortex, and thus may be involved more as a general arousal mechanism, leaving the specific identification and discrimination of odours to the direct pathway. It is a hypothesis worth testing, and worth including in theories of the neural basis of consciousness.

The sense of smell thus adds some novel puzzles to the *consciousness problem. All olfactory input, in the form of images, passes through olfactory cortex, yet some of these patterns due to ordinary odours are relayed on to the neocortex for conscious perception, as we have described, whereas others due to pheromones are directed to subcortical limbic regions for unconscious control of feeding, sexual maturation, and mating. It has been suggested that an intermediate level of consciousness may arise in relation to these subneocortical activations, called *vasana* (see McClintock et al. 2001). Recent studies make clear that many of these functions traditionally ascribed to the vomeronasal, accessory olfactory, pathway are in fact mediated by the main olfactory pathway, and this must be the case for any pheromones acting in humans. In addition, the olfactory cortex also contains a mechanism for sensing the absence of essential amino acids in the diet. The olfactory cortex is thus an extraordinary clearing house for different types of input patterns destined for conscious, intermediate conscious, and subconscious roles in behaviour. How it accomplishes this is a challenge for future study.

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