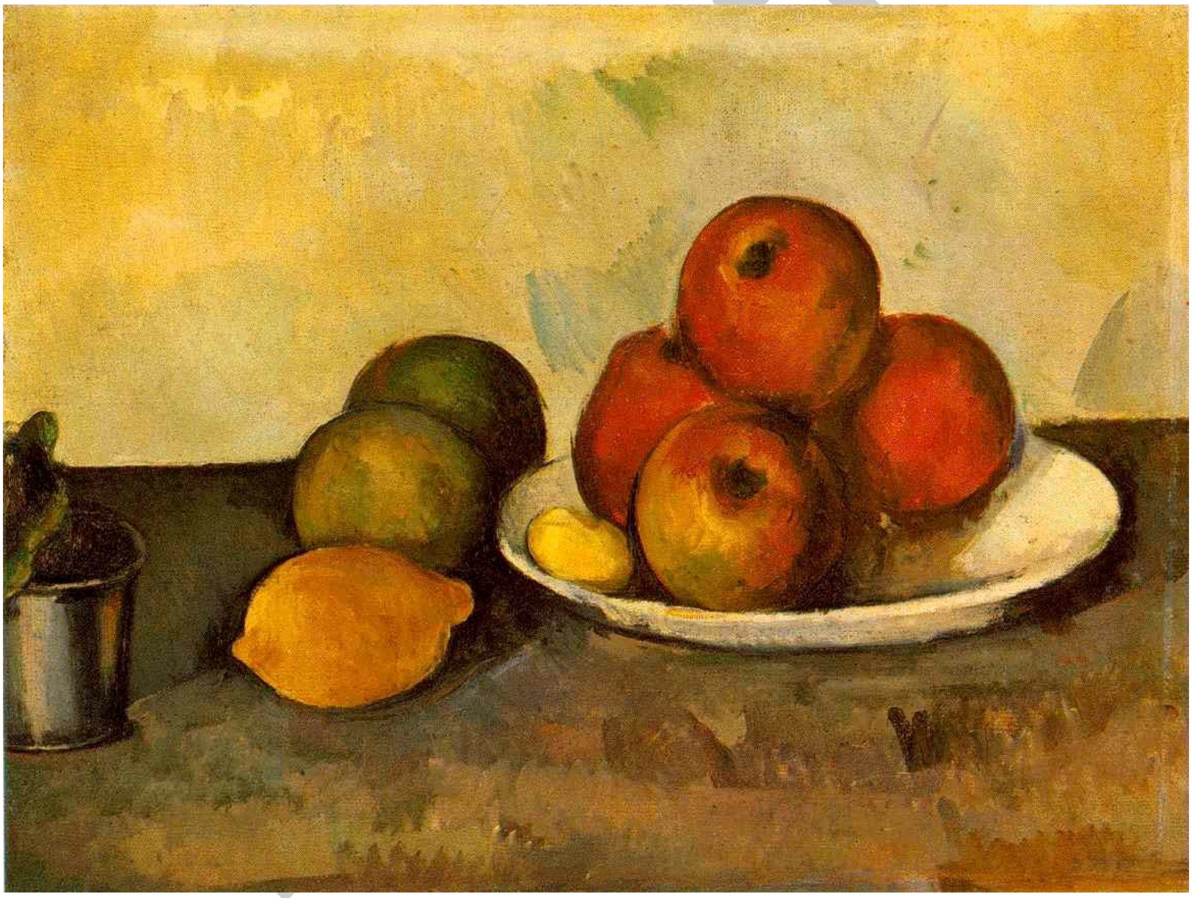
Sensation, Perception, Action – An Evolutionary Perspective

Chapter 9

Chemical Senses: Smell and Taste



‘Still Life with Apples’, Paul Cézanne, c. 1890, The Hermitage, St. Petersburg

Fruits, such as these apples, lemon and peaches painted by Cezanne, not only have the strong visual presence expressed in this still life, but are equally strongly connected to unique smell and taste sensations, which allows us to find, discriminate, and recognise them with closed eyes.

Overview

For chemical senses, the physical, or better chemical, properties of sensory stimuli are the starting point to ask the same questions which we used to understand the relevance of other sensory modalities: what is the medium carrying the stimulus, how can it be detected, what are the limiting factors of detecting, discriminating, and recognising stimuli, are there any parallels to technical applications?. The sense of smell is discussed in view of the sensor that is tasked with picking up chemicals from the air, which leads to an inherently narrow receptor tuning, and as a result of this to difficulties for a perceptual classification system for odours. The olfactory population code is explained as a highly evolved strategy to combine information from narrowly tuned receptors, allowing for the classification of a huge range of complex odours. Odour localization is discussed as a typical example of active exploration, through sniffing. The sense of taste is discussed along the same line of thought – the basic sensor function, which again hinges on chemical binding of molecules, but now retrieving taste stimuli from a liquid medium, basic taste qualities; the dimensionality of this sensory space. The similarities and differences of the two chemical senses lead us to consider some aspects of smell-taste associations that are involved in the complex sensation of flavour. The experience of spicey food highlights a peculiar cross-talk between sensory channels, which gives the label 'hot' a new meaning. The predominance of olfactory and gustatory object-related recognition and classification is at the starting point to query the nature of perceptual experience in the chemical sensory domain, trying to assess the evolutionary benefit of opening up these sensory channels for humans.

The nature of 'olfactory' perception – Smell

Imagine you are sitting at your kitchen table, eyes shut and ears plugged; without vision and hearing, you still can get some idea of what is going on. You smell the coffee, fired eggs, and burning toast – and open the eyes to rescue whatever you can. And what is the significance of smell for everyday behaviour, outside of your kitchen? The sense of smell serves as a general alarm system, when you smell, for instance, gas, fire, or smokers. Smell helps to assess the nature and quality of food, being a key component of perceived flavour. A recent discovery suggests that mammals, so far restricted to non-human species, are able to pick up the odours that signal cell damage and disease .(Munger 2009). Smell can also be part of communication systems, picking up pheromones (chemical signals involved in social communication), or recognise odours that are tokens of family, gender, or attractiveness. The scientifically rather obscure sense of smell is the basis of a multi-billion pound industry, selling fragrances to happy and beautiful customers all around the world. In many cases, olfactory communication stays completely below the radar of consciousness, so there was a lot of speculation whether humans could actually use odours to identify other individuals. In his groundbreaking experiment, M. J. Russel (1976) demonstrated that participants could recognise, by smelling T-shirts, their own body odour, and the gender of other individuals' body odour. He also provided the first behavioural evidence that human infants in their first weeks of life can recognise their mothers by means of smell (for a review of similar studies, see Doty 1981). Generally, however, such detection thresholds are high and recognition performance is low. For other tasks, like the detection of airborne chemicals, human olfaction can be much more sensitive, and it can further benefit from combination with other sensory cues, in particular vision (Gottfried and Dolan 2003). Let the odorant be subtle or bold, soft or strong, ephemeral or long-lasting in your memory, the importance of smell in a social context and nutrition is witnessed by a large industry sectors dedicated to the sale of fragrances and food!

Given the range of functional contexts, and the scope of information processing problems in the absence of straightforward unifying theoretical concepts, there are many questions to ask about olfactory perception, but rather few answers. Perhaps most pressingly in the quest of developing systematic experimental protocols, we need to ask, how can we classify odours? There are no simple physical dimensions for odours, like we know them from vision (brightness, colour) or hearing (loudness, pitch), and we tend to use descriptions by examples, such as 'this soap smells like Lavender'. Such challenges feed into experimental issues: how can we measure the intensity of odours, what are the lower limits of detecting them, can we localise them in space? For instance, it is very difficult to control the concentration of airborne molecules, and is even more difficult to capture the patterns of molecules floating in the air that have travelled a long distance from a source to the nose.

The sensory organ to capture olfactory information is the nose (see figure 9.1), and olfaction is the most important function of the nose: apart from filtering and humidifying the air before entering the lungs, is its role as gatekeeper of olfactory perception. Although the nose is sometimes regarded as a rather curious or crude protuberance of the face in need of embellishment, it presents a very intricate physical and biochemical design to support this dual function. The most relevant, although not the only, structure involved in converting airborne chemical signals into neural signals, are the olfactory epithelium and olfactory bulb at the roof of the nasal cavity (see chapter 23 in Roberts 2002). When the air flowing through the nose is passing the sensory epithelium, the odorant molecules need to be captured from the air, by dissolving them in the olfactory mucus which covers the epithelium. This mucus is a water-based solution of a number of biochemical substances, including enzymes to break down toxic substances, and proteins to bind odorants that would not dissolve in water (which are called 'hydrophobic'). Embedded in the mucosa are the fine nerve cell endings ('cilia'), which contain the chemo-receptors binding the odorants dissolved in the mucus. The axons of these olfactory receptors project into the glomeruli in the olfactory bulb, where the initial information processing is carried out.

From there the olfactory information travels through the olfactory tract into the brain, where it is distributed into an extensive network of brain regions, in the limbic system, the thalamus, and in neocortical areas (see chapter 24 in Roberts 2002).

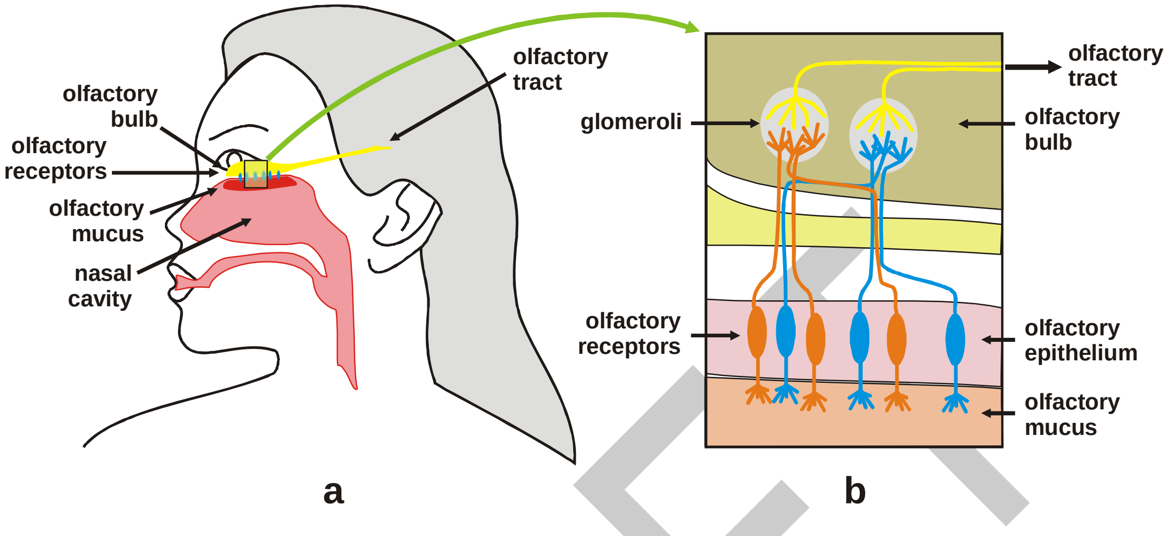


Figure 9.1: The nose is the sensory organ for olfactory perception. The olfactory epithelium at the roof of the nasal cavity (a) is covered by a mucus that contains the fine nerve endings of olfactory receptors (b) which bind odorant molecules (what makes them ‘chemoreceptors’) dissolved from the air flow passing through the nose. Chemoreceptor signals are pre-processed in glomeroli inside the olfactory bulb (b) and then transmitted through the olfactory tract into an extended network of neocortical and limbic brain regions.

At first sight the mechanism of binding chemicals to receptors seems to be rather straight forward, but it immediately throws up two rather puzzling issues about strategies to encode olfactory signals in neural systems. (i) Whereas the odorant molecules will remain in the mucosa for several minutes, we perceive odours on a much finer time scale: when you pass the espresso bar, the nice smell of coffee will fade within seconds! This suggests that in the olfactory system we should expect extensive suppression mechanisms. Interestingly, there are neuropsychological case studies of individuals who suffer from altered olfactory perception, which makes their sense of smell completely unselective and long-lasting – this rather irritating condition can be interpreted as loss of inhibition (see chapter 18 in Sacks 1998). (ii) The chemical binding between the receptor and the odorant resembles the interaction between key and lock, with only a very small group of molecules connecting to a given receptor, and as such chemoreception is much more specific than the response of photoreceptor to light, or the mechanoreceptors to sound. In consequence olfactory receptors have very narrow sensory tuning, and therefore we are not surprised that a large number of different types of chemo-receptors have been found – about over

1000 receptor types have been described in the mouse and approximately 300 - 400 in humans. The Nobel Prize 2004 was awarded to Linda Buck and Richard Axel for their work on this exceedingly complex receptor system (Axel 2005).

Recognition and classification of odours

With the large number of highly specific chemoreceptors, how many different odours can we identify and discriminate? This question is difficult if not impossible to answer, because there is no continuum of odours that can be discriminated, but particular substances that are stimulating particular receptors. In a strict sense, estimating the number of discriminable stimuli in such a categorical system of different sensory experiences would require to present all possible odorants to a sufficiently large number of participants, under a wide range of experimental conditions, in a objective recognition task. Because this thought experiment is clearly not feasible in reality, and presumably also not overly exciting to carry out, nor really meaningful, we have to do some guess work. So we perhaps could say with some reason that there are quite a few different odour categories, but certainly not millions. When you want to test your sense of smell next time visiting one of the fancy soap shops on the high street, you might be surprised what a difficult task this is. Which brings us to the second question: how reliable is odour recognition? Which has a simple answer: pretty bad! In a historical and quite heroic experiment Cain (1982) asked more than 200 participants to identify 80 common substances by smell. The proportion of correct identification varied between 90% and 20%, and overall performance was better for females than for males (see figure 9.2). And contrary to what most readers might expect there are no clear patterns of olfactory experience: although men indeed tend to be better in recognizing bourbon, sherry and beer, women are almost reaching the same ‘performance’ for beer, and the other few areas of male advantage (ammonia, mothballs, banana, mustard, raspberry syrup) hardly make a group of substances that would be associated with typically male activities and experiences. If we would really like to know whether there are gender-specific differences in olfactory perception, there would be no way to avoid an even more extensive, even more systematic, even more heroic experiment – so it might be worth asking seriously why we should expect such a difference…

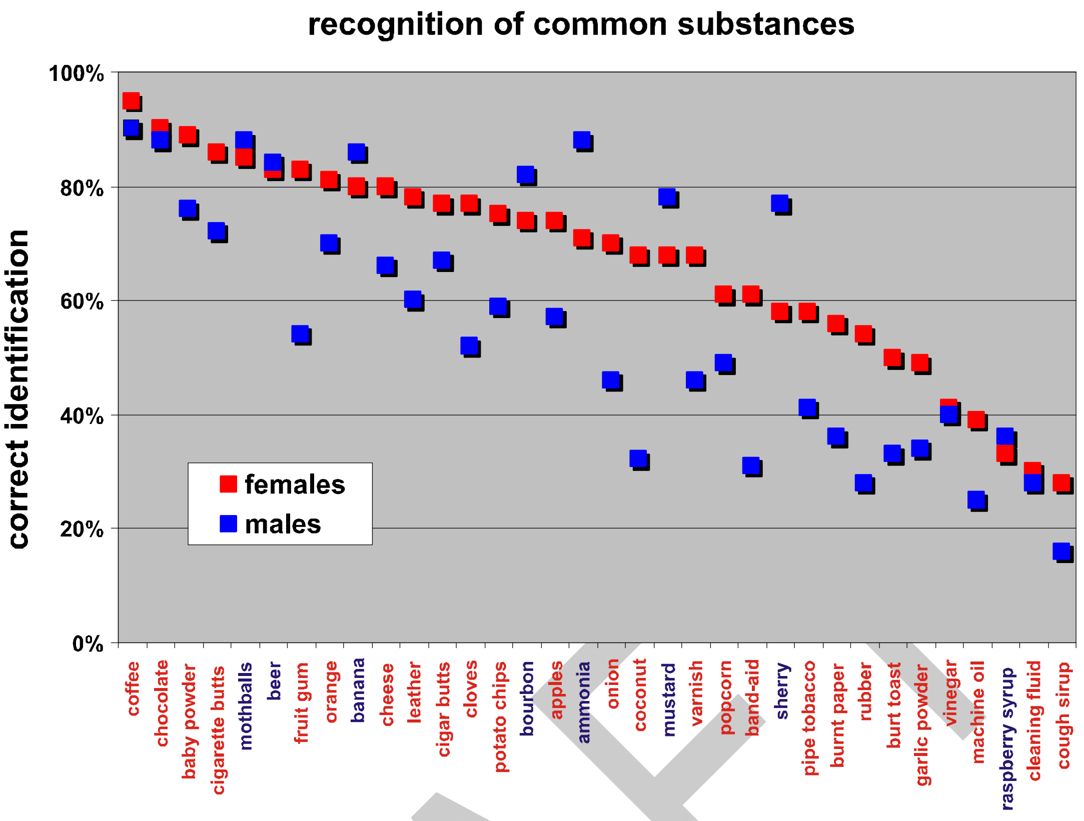


Figure 9.2: Recognition performance for 33 example substances tested by Cain (1982). The proportion of correct identification is shown for females (red symbols) and males (blue symbols). Females did perform generally better in this experiment than males.

From this type of experiments we can clearly recognise an emerging demand for some theoretical framework to study smell, which gives a rational basis for the classification of odours, similar to that of sound or colour. So can we can we identify a small basis set of fundamental odours that would generate a smell space? Usually olfactory stimuli and fragrances are described by object names, which need to be mapped onto such a smell space, where distance between any of two stimuli in a multi-dimensional map is inversely proportional to perceived similarity of these stimuli. Perhaps the most prominent attempt was made almost a century ago by H. Henning (Henning 1916), who designed a smell prism to arrange 6 primary (independent) odour qualities: fragrant, ethereal, resinous, spicy, burned, putrid. The claim then is that any odorant can be positioned on this prism in a unique neighbourhood relationship (see figure 9.3), or in other words, that any olfactory sensation can be described as combination of these 6 components (please note the similarity of this system to the colour triangle shown in chapter 4).

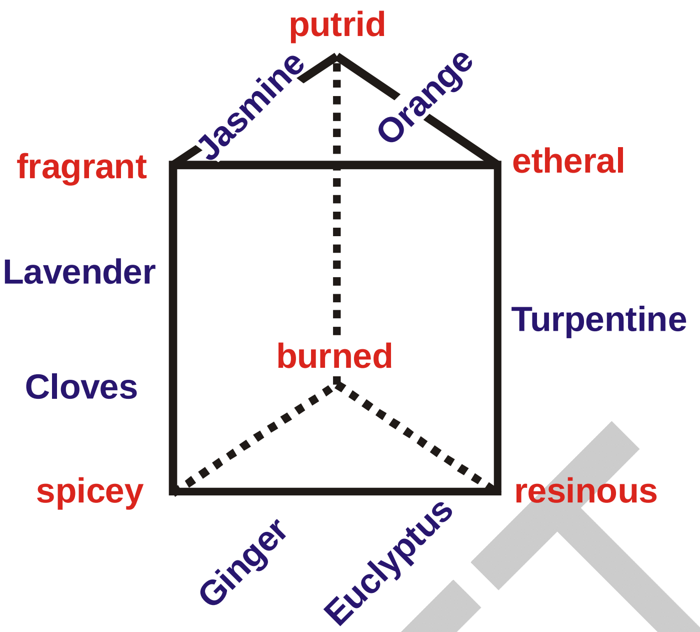


Figure 9.3: Odour prism as proposed by Henning (1916). The six primary odour qualities (red labels) occupy the corners of this prism, and real olfactory stimuli can be positioned unambiguously on any of the nine axes(blue labels).

Although the 'smell space' depicted schematically in figure 9.3 offers an elegant solution, there is debate to what extent it is supported by any experimental evidence that goes beyond introspection. What would be needed are indications that there are specific receptor types corresponding to the basic small qualities, or specific anosmias ('smell blindness', in this case the specific inability to pick up one of the 6 basic qualities), or the selective adaptation of one of these components that would not affect any of the others. However, coherent experimental evidence has been thin on the ground and there still are many more questions than answers. Amoore (1964) suggested that there 7 primary odour qualities, and we now know that there are many more receptor types than the proposed independent perceptual qualities (Buck and Axel 1991). A recent computational attempt to determine the number of independent dimensions for odour recognition estimated up to 32-64 (Mamlouk and Martinetz 2004). So the debate keeps moving on, though rather slowly.

At this stage it could be helpful to have another look at the neural systems involved in the processing of odour stimuli. If we could understand the fundamental principles of olfactory encoding, we might be able to develop a better theory of smell. So what is the olfactory code? Little is known about the physiology of olfactory processing in humans, but there are two threads of evidence from a wide range of biological systems, including mammals, about how the complex olfactory encoding can be deciphered. (i) The combinatorial matrix of activations in different receptor types and odorant molecules (Buck 2005) suggests a population code (schematically shown in figure 9.4a): a specific pattern of activity that is distributed across a group of neurons reflects a given odour, and can be decoded from the distribution of activations (e.g., Koulakov et al 2007). One of the most exciting aspects of such a population code is the fact that it joins together two prominent steps of olfactory processing, the decomposition of an odour into highly specific components at the lower level, and the completion of patterns in activity distributions at higher levels, which allows the sensory system to recognise an odour despite of the variation in the exact mix of components (Barnes et al 2008), which reflects the general feature of distributed networks to be robust and 'error-resistant' (Minsky and Papert 1988). (ii) At other stages of the olfactory processing stream, we find neuronal activity patterns that suggest the existence of an olfactory map, in which different odours are represented at different locations in the neural network (for instance, in the olfactory bulb, schematically shown figure 9.4b). This includes activations by airborne chemical stimuli like CO_2, which are not consciously perceived by humans but leads to distinct behavioural responses in animals (Axel 2005).

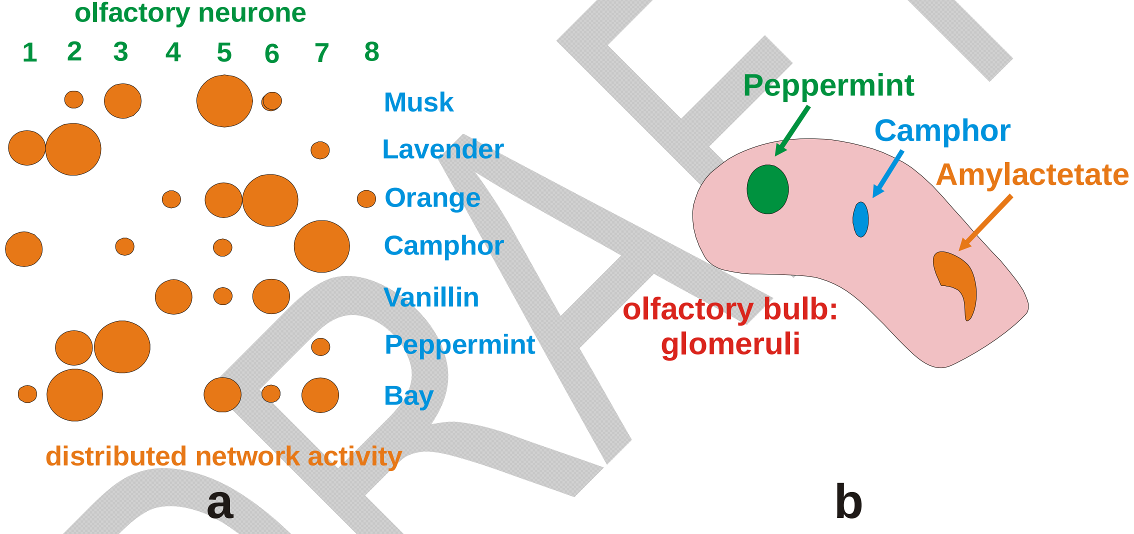


Figure 9.4: Neural code of olfaction. (a) At receptor level each sensory neuron (columns) responds to a range of stimuli (rows), and each stimulus activates a range of sensory neurons, constituting a population code. (b) At the level of the olfactory bulb, the activation of individual glomeruli reflects particular stimuli, i.e., different stimuli can be mapped to different locations. (See Colour Plate VI.3)

These two sets of observations offer no clue to support the idea that there is a reduced set of basic odorant qualities creating a simple smell space. However, they are based on evidence collected from simpler sensory systems than the human brain, and are restricted to comparatively early processing stages. So it could still be possible that the extensive redistribution of olfactory information across various structures in the human central nervous system (chapter 23 in Roberts 2002) leads to different encoding strategies at higher levels.

Odour localisation: sniffing

Given that the function of the olfactory system is an alarm system and that it is involved in social communication, the localisation of odour sources is highly relevant. You might be rather interested to identify the person standing in a group who is wearing this attractive fragrance you did smell, and if you smell gas in your house you would like to know where it would be leaking from. Because odorant molecules are carried by air that usually is in flow, however, such localisation can be quite challenging. Furthermore, because of long-term and fast adaptation in the olfactory system (Dalton 2000) the exposure to an odorant can lead to a rapid decay in the information provided, which puts time constraints on detecting the source. So how well can humans localise the source of an odour? How do the underlying mechanisms compare to those of other sensory modalities, such as vision, hearing, touch? Because of the transient and spurious character of odorants carried by air, this is a problem much less easy to approach experimentally than in vision or hearing. Some researchers invented some ingenious setups to assess the performance at close range (see figure 9.5a). Initial ideas about localisation focused on the fact that the differential information from the two nostrils could be used to localise a small, close source (von Bekesy 1964). However, it soon became clear in such experiments that a key aspect to enhance performance is active exploration. When human observers actively move their nose and inhale in bouts, possibly to maximise the number of molecules picked up and counteract adaptation effects. Still, even when employing such active exploration, as we all know from everyday experience, human performance is rather poor, and we can only observe with envy the sniffer dogs employed by Her Majesty’s Customs Service, when detecting and tracing unwanted substances in the luggage of travellers.

Behavioural strategies, such as the ‘olfacto-motor coordination’ used by such sniffer dogs actively searching in great excitement through the luggage, can help to solve the localisation problem at a larger spatial scale, when odour traces become rather faint and spatially irregular. Such scanning movements are common in various animal systems. For instance moths use odour cues for courtship navigation, and approach sources of airborne pheromone in characteristic zigzag flights (Kennedy 1983). A recent study demonstrated that humans develop very similar strategies when they were asked to trace a scent trail (such as a trace of chocolate on a sports ground, see figure 9.5b) in the absence of other sensory cues, and that they are indeed capable to stay on track (Porter et al 2007). When systematically trained for this job, just like sniffer dogs, these participants increased performance, by reducing the sideways deviations from the track, and increasing speed. It was also confirmed that sniffing patterns can support the completion of the task: the participants were moving faster when the frequency of sniffing was increased. Furthermore, when the entry points to the two nostrils was increased by small tubes attached to the nose, the performance increased; and when the both nostrils were supplied by the air from a single point, their performance was reduced. This gives further support to the early suggestion that there is an olfactory analogue to directional hearing or stereo vision. The most important conclusion from this study is the importance of active exploration (we will return to this issue in chapter 12): by moving the sensor systematically through the environment, the sensory system can improve its efficiency tremendously.

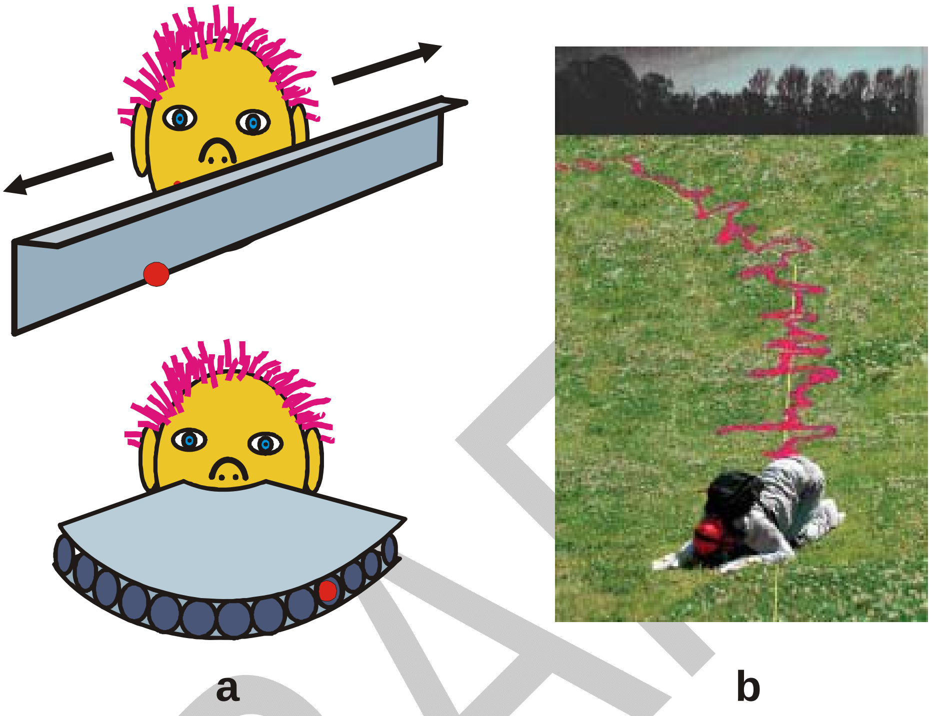


Figure 9.5: Active olfactory exploration: sniffing. (a) Boosting inhalation improves the localisation of an odour source (red sphere) hidden in one of the small tubes arranged and fan-shape with the nose in the centre (bottom panel); sidewise scanning movements of the nose can help to locate the source of an odorant (red sphere) hidden behind a ledge (top panel). (b) When humans, deprived of other sensory input, are challenged to track a scent trail, they develop behavioural patterns closely resembling those of sniffer dogs. (see http://www.nature.com/neuro/journal/v10/n1/suppinfo/nn1819_S1.html)

The nature of ‘gustatory’ perception – Taste

In many ways, taste, or ‘gustation’, is the sibling of smell – it is another type of chemical sense, that helps us to discover dangers, such as poisoned or rotten food, and it is much more difficult to study than other senses such as vision or hearing, and therefore less is known about it. In other ways, taste is rather different from smell, because it picks up chemicals in solution, and therefore is sensitive to close sources but not to stimuli originating from a distance. It also appears to be possible to classify all tastes by a comparatively simple scheme of four basic components. So let us go through our standard set of questions that we ask for each sense, to portrait a quick profile of gustatory perception. Why is it important to have a sense of taste? Taste serves as security system, making use of the fact that food that contains poisonous substances tastes different (because it might have been tampered with, or contaminated by random exposure, or simply changed through decomposition). Taste is vital for 'homeostasis', keeping a delicate balance of nutrients, minerals, fluids and acidity in the body, which can be controlled, mostly without being conscious about this at all, by selective eating and drinking. Obviously, and most prominently, taste is important for enjoyment and pleasure, an integral part of civilization, and in specific cultural contexts an instrument to guide compliance with social conventions: the symbolical meaning of 'good taste' can be directly related to the expression of some well-trained sensory schemata. And why is taste an interesting scientific topic? Many aspects of taste perception so far remain rather obscure if not mysterious, and in particular there is need of a unifying theoretical framework, similar to olfaction, but possibly less desperate because of a much reduced number of receptor types. The sense of taste is less extensively investigated than visual or auditory system perception, and offers a wide range of questions for important discoveries, in particular because it is of immense everyday relevance being so closely related to food. Finally, there is a lot of financial interest because of the high economic relevance of gustatory perception – imagine how many extra tons of nasty junk food can be sold to happy customers, if there were a reliable method to get a grip on their taste perception!

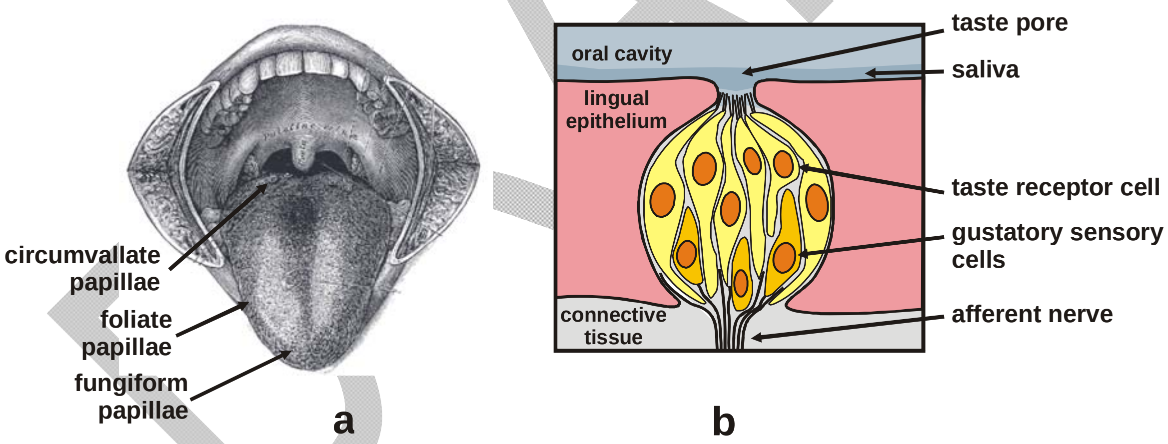


Figure 9.6: Taste sensors. (a) The tongue shown in this anatomical drawing (from 20th U.S. edition of Gray's Anatomy of the Human Body, 1918) is covered with thousands of small papillae, which contain taste buds to pick up chemical signals dissolved in saliva when eating or drinking. (b) In taste buds, chemoreceptors are aggregated in groups, sending their axons through the cranial nerves into the brain.

The sensory system supporting human taste perception resides mainly in the tongue (chapter 26 in Roberts 2002). The microscopic image of the surface of the tongue shown in figure 9.6a show, in a field of small cone-shaped ('filiform') papillae that serve tactile function, some prominent large (‘fungiform’) papillae, which carry the taste buds that are made up of a number of chemoreceptors (see figure 9.6b). Additional taste buds are found in other regions of the mouth, such as the soft palate and pharynx, the entrance to the oesophagus. These sensory cells are in contact with the saliva, which carries the flavour molecules contained in food that will stimulate the receptors. The information captured by the chemoreceptors is transmitted by gustatory neurons through cranial nerves to the solitary nucleus in the brainstem and from there to various other brain regions, including hypothalamus, thalamus, and the sensory cortex. Here the information is further processed, possibly in form of a distributed population code (as discussed above) and is also interacting with olfactory information and other information to create the sensation of flavour. One interesting aspect of gustatory perception is that the highly sensitive taste buds are constantly exposed to many inadequate stimuli, including heat or aggressive chemicals, leading to substantial cell death and continuous regeneration. Note that this requires continuous rewiring of the connection between sensory cells and cortical projection areas to maintain reliable encoding of taste and subsequent sensory information processing.

Classifying taste: is there a gustatory space?

There is a long tradition in assuming that there are four basic qualities of taste: sweet, sour, salty and bitter (Hänig 1901). These perceived taste qualities they can be roughly related to four different types of chemoreceptors that pick up the chemical signals from sweet, sour, salty and bitter substances (see figure 9.7a), and are commonly believed to be picked up preferentially at different locations of the tongue (see figure 9.7b), although it is unclear what such a spatial representation would imply, because taste stimuli are carried by the fluid medium passing the tongue and therefore should be distributed rather evenly in the mouth. More recent experiments to estimate recognition thresholds and response magnitudes as function of stimulus concentration for the four different taste categories found different patterns of preferred locations than the initial studies (Collings 1974). Furthermore, it has become clear in the last decade that, at east for various non-primate mammals such rats, cats, and rabbits, the receptor tuning to such chemical agents is much broader and not categorial as suggested by this classification (Pfaffmann 1955). Also, new evidence suggests the existence of a fifth taste category for certain amino acids which can be found in such food as mushrooms or cheese: ‘umami’, which sometimes is also called ‘savoury’ (Nelson et al 2002). Very recently, another taste receptor, for fatty acids, has been discovered (Laugerette et al 2005).

Although current research, using behavioural, electrophysiological, and molecular biological techniques suggest that the design of taste space, or in other words the sensory encoding of gustatory information, is more complicated than the initial picture might suggest, the representation of tastes in terms of four to six basic qualities still stands as a good first approximation (Scott and Chang 1984), if we do not expect that all possible experiences can be composed by combinations of the basic qualities (which was, for instance, possible for the encoding of colour from three primaries, as described in chapter 4). The key observations to support the simplified image of four basic taste qualities are: (i) Mixtures of categories cannot be perceived, which means that a well-defined substance either tastes salty or sweet, but nothing in between. (ii) There is no cross-adaptation, so that after the adaptation to a sweet stimulus there is no change in sensitivity to bitter, for instance. (iii) Nevertheless, we can experience after-effects that suggest some more complicated kind of opponency processing. For example participants report that pure water tastes sweet after they had been adapting to bitter/sour stimuli (Breslin and Spector 2008).

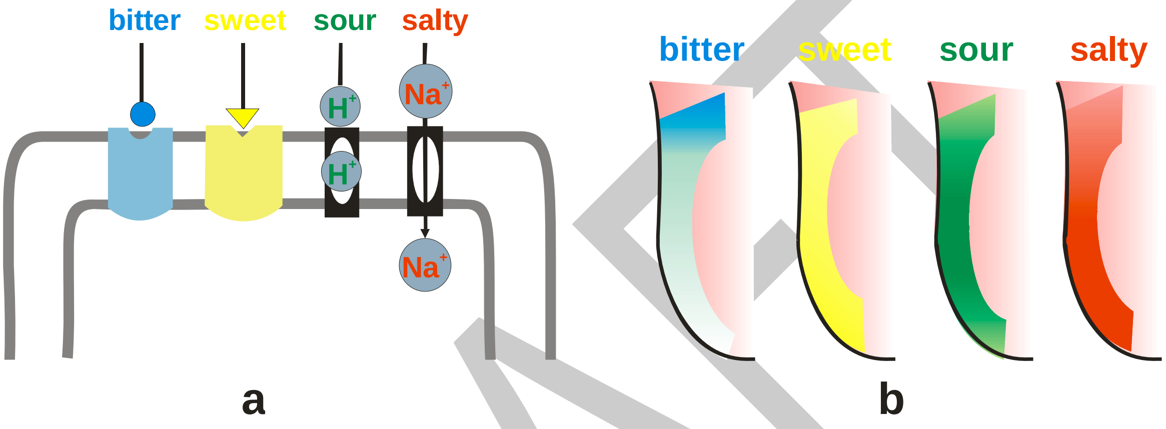


Figure 9.7: Taste sensors. (a) Four types of chemoreceptors in the taste buds, binding to four classes of chemicals, are believed to underlie the four basic taste qualities, bitter, sweet, sour, and salty. (b) The sensitivity for detecting the four basic gustatory categories varies considerably for different regions of the tongue (shown schematically for the right side of the tongue for bitter=blue, sweet=yellow, sour=green, and salty=red taste, respectively: more saturated regions indicate more sensitive regions (after Hänig 1901)).

One of the more puzzling aspects of gustatory perception is related relates to individual differences. It is a commonplace to say that taste can be a very individual sensation, in two ways. (i) Taste is a private experience, which is almost impossible to talk about – you know how a strawberry does taste for you, but can you describe it to someone else and find out whether it tastes the same for them (without diving into the fanciful poetry of food journalists who mostly rely on similes from other sensory domains)? (ii) The perceived gustatory strength of a particular substance can vary considerably between individuals. One aspect that is investigated extensively is the bitter taste of the chemicals phenylthiocarbamide (PTC) and propylthiouracil (PROP), which can be famously detected as bitter by parts of the population ("tasters"), but not by others ("non-tasters"), and in another group has very intense, and often repellent effect ("super-tasters"). These different groups are distinguished by differences in the density of taste receptors (Bartoshuk et al

1994), and there are indications that these anatomical differences as well as the specifically enhanced sensitivity, and food preferences resulting form these differences, are genetically mediated (Drewnowski and Rock 1995). It could be interesting to speculate whether the bitter, metallic taste experienced by some people for a couple of days after eating pine nuts of South-East Asian origin that contain certain triglycerids (Mostin 2001) could be related to such differences in the taste receptor inventory. Recent research seems to indicate that there also more general variations in the sensitivity to a range of taste stimuli which might be related to overall taste receptor density (Reed 2008).

In everyday life, however, gustatory perception tends to be rather more complicated. Still at the level of basic categories, we find the perceived intensity for different qualities to develop differently in time, such that mixtures of two stimuli can be perceived first as one quality, and then as the other (Kelling and Halpern 1983). This could be the physiological and perceptual basis of what the food and drink industry calls a taste profile. Such dynamic changes of the taste sensations while eating or drinking a single substance can be the result of multiple interactions between a range of different aspects of the complex information contained in food, at various levels of subcortical and cortical processing (Katz et al 2002). Unfortunately, this phenomenon is very difficult to investigate psychophysically, because the description of the dynamic changes of perceived taste under real-life conditions depends largely on careful introspection, which obviously is subjective and easily to be misled. You can try this yourself and will see how difficult it is to describe precisely the sensations you experience one after the other when you drink your next cappuccino. Most importantly, indicating massive reorganisation of the perceptual representation of tastes, we tend to use qualitative descriptions and refer to objects when try to characterise tastes, and you would say something like ‘this jelly bean tastes like strawberry’, rather than listing the combinations of basic qualities, and how they might change with time while you are chewing your treat.

Finally, we should have a brief look at the interaction and crosstalk between the chemical senses, and with other senses. In general, there are very close interactions between different sensory modalities when enjoying food, and the term ‘flavour’ is used to describe the combination of different sensory modalities, including taste, smell, temperature, softness, tactile texture, etc. (chapter 26 in Roberts 2002). There are complex interactions between such different sensory cues in the representation of olfactory information in the primate orbitofrontal cortex, which could provide hints about the mechanisms of encoding flavour relationships in the nervous system, and its relationship to perceived pleasure (Rolls 2000). Because it has been shown that smell-taste associations**,** for instance, can be learned, it can be assumed that perceived flavour is the product of life-long experiences with food (Stevenson et al 1998). More direct interaction of chemical senses with other perceptual modalities can be observed as direct sensory crosstalk, which corresponds to in-adequate stimulation at the receptor level. A well investigated aspect of taste perception demonstrating such an effect is hot food, which suggests that sensory boundaries can be crossed at a the earliest processing level. Hot chili peppers contain a chemical called ‘capsaicin’, which activates nociceptive C fibres, pain receptors that usually would respond to heat (Caterina et al 1997). The effectiveness of this chemical in truly activating a different sensory system is demonstrated by the fact that capsaicin can elevate pain thresholds by adaptation of pain receptors!

Take home messages

- the two chemical senses, smell and taste, share some properties, like their ecological significance and highly variable sensitivity, but respond to different (airborne or dissolved, respectively) stimuli, which can correspond to distant or close sources
- olfactory perception (smell) is characterised by a complex dimensionality based on a large number of specific chemoreceptors in the nose, which is best accounted for by population coding of odorants
- active exploration strategies, such as sniffing patterns, are employed to improve the localisation of odorant sources
- gustatory perception (taste) is understood to rely on a small number (4-6) basic qualities, which roughly correspond to the filter properties of the chemoreceptors in the mouth
- smell and taste interact with each other, and with other sensory modalities, in the perception of flavour

Discussion Questions

- Describe the attempt to classify different odours in a simple ‘smell space’.
- Why is sniffing like sniffer dog such a successful strategy to localise the source of a odour?
- Discuss the evidence for and against the common assumption that there are four basic components of taste perception.
- What make hot chilli peppers hot?

References

Amoore J E, 1964 "Current status of the steric theory of odor" *Annals of the New York Academy of Sciences* **116** 457-476

Axel R, 2005 "Scents and Sensibility: A Molecular Logic of Olfactory Perception (Nobel Lecture)" *Angewandte Chemie International Edition* **44** 6111

Barnes D C, Hofacer R D, Zaman A R, Rennaker R L, Wilson D A, 2008 "Olfactory perceptual stability and discrimination" *Nature Neuroscience*

Bartoshuk L M, Duffy V B, Miller I J, 1994 "PTC/PROP tasting: Anatomy, psychophysics, and sex effects " *Physiology & behavior* **56** 1165-1171

Breslin P A S, Spector A C, 2008 "Mammalian taste perception" *Current Biology* **18** R148-R155

Buck L, Axel R, 1991 "A novel multigene family may encode odorant receptors: a molecular basis for odor recognition" *Cell* **65** 175-187

Buck L, B., 2005 "Unraveling the Sense of Smell (Nobel Lecture)" *Angewandte Chemie International Edition* **44** 6128-6140

Cain W S, 1982 "Odor identification by males and females: predictions vs performance" *Chem. Senses* **7** 129-142

Caterina M J, Schumacher M A, Tominaga M, Rosen T A, Levine J D, Julius D, 1997 "The capsaicin receptor: a heat-activated ion channel in the pain pathway" *NATURE-LONDON-* 816-824

Collings V B, 1974 "Human taste response as a function of locus of stimulation on the tongue and soft palate" *Perception & Psychophysics* **16** 169-174

Dalton P, 2000 "Psychophysical and Behavioral Characteristics of Olfactory Adaptation" *Chem. Senses* **25** 487-492

Doty R L, 1981 "Olfactory communication in humans" *Chem. Senses* **6** 351-376

Drewnowski A, Rock C L, 1995 "The influence of genetic taste markers on food acceptance" *American Journal of Clinical Nutrition* **62** 506-511

Gottfried J A, Dolan R J, 2003 "The Nose Smells What the Eye Sees: Crossmodal Visual Facilitation of Human Olfactory Perception" *Neuron* **39** 375-386

Hänig D P, 1901 *Zur Psychophysik des Geschmackssinnes* (W. Engelmann)

Henning H, 1916 *Der Geruch* (Leipzig: J.A. Barth)

Katz D B, Nicolelis M A L, Simon S A, 2002 "Gustatory processing is dynamic and distributed" *Current Opinion in Neurobiology* **12** 448-454

Kelling S T, Halpern B P, 1983 "Taste flashes: reaction times, intensity, and quality" *Science* **219** 412-414

Kennedy J S, 1983 "Zigzagging and casting as a programmed response to wind-borne odour: a review" *Phys.Entom.* **8** 109-120

Koulakov A, Gelperin A, Rinberg D, 2007 "Olfactory Coding With All-or-Nothing Glomeruli" *J Neurophysiol* **98** 3134-3142

Laugerette F, Passilly-Degrace P, Patris B, Niot I, Febbraio M, Montmayeur J P, Besnard P, 2005 "CD36 involvement in orosensory detection of dietary lipids, spontaneous fat preference, and digestive secretions" *Journal of Clinical Investigation* **115** 3177

Mamlouk A M, Martinetz T, 2004 "On the dimensions of the olfactory perception space" *Neurocomputing* **58** 1019-1025

Minsky M L, Papert S A, 1988 *Perceptrons: expanded edition* (MIT Press Cambridge, MA, USA)

Mostin M, 2001 "Taste disturbances after pine nut ingestion" *European Journal of Emergency Medicine* **8** 76

Munger S D, 2009 "Olfaction: Noses within noses" *Nature* **459** 521-522

Nelson G, Chandrashekar J, Hoon M A, Feng L, Zhao G, Ryba N J P, Zuker C S, 2002 "An amino-acid taste receptor" *Nature* **416** 199-202

Pfaffmann C, 1955 "Gustatory nerve impulses in rat, cat and rabbit" *J Neurophysiol* **18** 429-440

Porter J, Craven B, Khan R M, Chang S-J, Kang I, Judkewitz B, Volpe J, Settles G, Sobel N, 2007 "Mechanisms of scent-tracking in humans" *Nat Neurosci* **10** 27-29

Reed D R, 2008 "Birth of a New Breed of Supertaster" *Chem. Senses* **33** 489-491

Roberts D R, 2002 *Signals and Perception: The Fundamentals of Human Sensation* (Palgrave Macmillan)

Rolls E T, 2000 "The Orbitofrontal Cortex and Reward" *Cereb. Cortex* **10** 284-294

Russell M J, 1976 "Human olfactory communication" *Nature* **260** 520-522

Sacks O W, 1998 *The Man Who Mistook His Wife For A Hat* (Touchstone)

Scott T R, Chang F-C T, 1984 "The state of gustatory neural coding" *Chem. Senses* **8** 297-314

Stevenson R J, Boakes R A, Prescott J, 1998 "Changes in Odor Sweetness Resulting from Implicit Learning of a Simultaneous Odor-Sweetness Association: An Example of Learned Synesthesia" *Learning and Motivation* **29** 113-132

von Bekesy G, 1964 "Olfactory analogue to directional hearing" *J Appl Physiol* **19** 369-373