

## The Odour, the Animal and the Plant

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**Abstract:** A review of the literature is presented that gives a background to the human sense of smell, then the importance of learnt and innate olfactory cues in animal behaviour. Some possible roles for natural products chemists interested in the interaction between animals and plants are discussed.

**Keywords:** Odour, semiochemical, sense of smell, animal behaviour, animal-plant interactions

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### Introduction: Natural products and their odours

Natural Products chemists are conspicuous when they are wandering in the bush. They habitually break pieces from plants, rub them between their fingers, and smell them. They are the people who become animated only if they detect an interesting odour; whether it be new, unusual, pleasant, or unpleasant. In the past, their chemical curiosity could only be satisfied by the use of harsh techniques such as distillation, which has not always identified the compounds that gave the interesting odour. Now, with more modern, gentle methods such as those analysing the volatile components of the headspace of living plants, chemists have more chance of identifying fragile biologically active compounds. This opens the possibility of their research being more in tune with the biological implications of the smells of their favourite plants.

In general, humans have a fascination for odours that probably arose when life began. Recorded history documents fragrances that have been used for a myriad of purposes, and until recently, natural products were the only source of these fragrances [1].

According to Pellmyr & Thien [2], odour preceded colour as an attractant. Floral fragrances may have originated from secondary metabolites, particularly monoterpenes, which had become herbivore

feeding deterrents.. It has been observed in some cases of insect preference for flowers that visual attraction does not occur unless a fragrance is present.

Odours, smells, fragrances, perfumes, semiochemicals – whatever term we use - also play an important part in modern life [1]. Some common everyday olfactory experiences are; one's favourite toiletries (and those of one's acquaintances), the distaste of the freeway or subway, the attraction of the suburban bakery, the respite of the garden, and the ritual of the evening meal (perhaps including some wine and cheese). Odours can also give information in a fourth dimension – that of time.

And yet, despite our love of fragrances, humans are considered to be “odour blind” compared with most other animals [3].

In order to survive, other living organisms rely on sensing odour cues in their environment. There are many olfactory interactions between animals (including insects) and plants, or animals and other animals, that have the potential to be exploited to manage our environment. Some of these include the pollination of plants by mammals or insects, the attraction of foraging animals for valuable plant crops, the attraction or repulsion of animals for damaged plants, the interaction of animals with those of the same species (for mating, or social organisation) and the location of prey by animals. Modern analytical methods in chemistry can help to elucidate and untangle some of these relationships. As a result, it may be possible, using odours from their natural world, to manipulate pests and beneficial organisms in the environment to our own advantage. There has been much recent work on the communication between plants and other plants, some seemingly mediated by volatile compounds, whether or not this can be considered “smell”. Some of this is alluded to in references [43-45] and there is an extensive discussion of the interesting phenomenon of induced plant defence mechanisms in the report of a recent symposium [53].

This article first presents a background to understanding the sense of smell in humans as a point of reference only, then reviews some of the literature pertaining to the importance of smell in animal behaviour. It is against this background that some natural products chemists will be interested in the further investigation of the semiochemistry and phytochemistry of animal-plant interactions. However, it is not the intention in this review to concentrate in detail on this aspect of volatile-mediated communications. In order to begin answering questions related to the biological implications of their research, chemists need some insight into the sense of smell and its importance in animal-plant interactions.

### **How do we smell?**

In order to experience the sensation we call “smell”, an odorous molecule has to waft through the air into the nose and bond with receptors in the epithelial cells lining the nasal cavity. The olfactory epithelium, covering the whole of this large, convoluted, bony area, contains nerve endings and sensory cells open to the air that enters the nose (each with up to 1000 receptors). The axons from these nerves pass through the bony structures and terminate in glomeruli in the olfactory bulbs at the base of the brain, just behind the nose. These receptors and neurons provide a continuous path from the outside air to the brain [4].

When an odour molecule binds to the cells, it docks with a particular pattern of receptors and triggers a unique fingerprint of electrical signals. These signals travel along the olfactory nerves to the olfactory bulbs which sort the signals and send them for processing to other parts of the brain – some associated with learning, some with taste, some with emotion and some with thinking or planning [8-10]. Excellent diagrams are presented in [4,5] and on the web-sites of Leffingwell [6] and Jacob [7].

The “smell” sensation that we finally experience depends on the way that various parts of the brain interpret a complex array of signals relayed by a large number of neural messages. Sell [10] has commented that odour is a perception, not a physical quantity that can be measured objectively. R. Herz, quoted by M. Holloway [11], stated that the limbic (emotional) system evolved from the olfactory system and postulates that the emotional dichotomy between 'good' and 'bad' reflects a chemosensory one. She is quoted as saying “in the beginning there was smell: organisms used chemical sense to move towards good (food) and away from bad (predator)”.

### **How does the nose know?**

Brennan & Friedrich [12] further discussed the processes that occur from the point where an odorant enters the nose to the generation of a response (either conscious or unconscious). Small hydrophobic molecules need to cross the mucous membrane barrier of the olfactory epithelium before interacting with a receptor; odorant-binding proteins may facilitate this [10,12].

The recent studies of Linda Buck, which follow on from her earlier work with Axel [4] and reported by Holmes [13], indicated that each neuron interacts with only a single receptor; each odorant binds to several different receptors, and each receptor recognises several different odorants. Olfactory cells assemble a representation of an odour as they are stimulated by the unique pattern of receptors triggered by that particular odorant. This is described as a “map” by Ohloff [5].

An alternative theory is proposed by Turin, reported in S. Hill [14] and Sell [10]. There is some evidence that it may be the vibrational frequency of the intramolecular bonds that is important in the relaying of information from the odorant-receptor complex to the olfactory nerves. This would explain why some molecules that are quite different shapes smell similar, while others with similar shapes smell different. However, this theory is not widely accepted, and Hill [14] also quotes other authors who refute this theory.

Sell [10] and Ohloff [5] both note that there is a variety of theories on how an odorant generates a particular signal that is interpreted by the brain as an “odour”, but none of the theories so far has been able to explain all the experimental evidence.

### **How do we name odours?**

There have been various attempts to categorise “smell” as experienced by humans. The labels given to various characteristics of the bouquet of wine is a well known example. Scientists working with organoleptic properties of essential oils have also attempted to label various odours. Some of these descriptors do not convey any clear information about the odour; for example in the web-site of Acree [15] a few of the compounds are described as “green”, “paint”, “medicinal”, “fatty”, “acidic” and

“chemical”. Although these are unhelpful to the layman, some of them have their place on variations of an “odour wheel” or “odour map” adapted for their own use by professionals in various industries. A recent statistical approach has been used by Richardson [16] to develop a “map” that is useful in the perfumery industry. This is only one of several such charts adapted by professionals to help them classify odours in such industries as winemaking, beer brewing and aspects of food preparation. Ohloff [5] commented that odour recognition and characterisation is psychophysical and not subjective, which puts scientists in an invidious position when they try to develop an objective procedure to describe odours. Descriptors require multidimensional maps, whether reference to standard odours or semantic parameters are used. Various statistical treatments (cluster analysis being only one example) produce two-dimensional charts such as those mentioned above.

Many authors have also had difficulty describing odours of various plants and plant extracts.

Bat-pollinated plants in the New World tropics are commonly described as “displeasing” - but variously described as being like fermenting fruits, cabbage or garlic [17]. MacTavish & Menary [18] quote several paragraphs from researchers who attempted to describe the smell of boronia extract. There seems to be no common descriptor that is used by all these people. Chamblee & Clark [19] note that professional, trained observers experienced in olfactory analysis of lemon-type odours were diverse in their descriptions of components of lime oil. For example, linalool was described as ‘lemon-like’ by some sniffers and ‘floral’ by others.

It is more difficult for humans to identify and name odours than colours; but smells can elicit potent memories of past events as is summarised by Axel [4]. Holloway [11] quotes Hertz as stating that although either the odour or the name of the odour can aid in remembering an event, only the odour itself can recreate the emotional reaction (such as change in heart-rate) of the original event. This appears to ignore many studies of the classic Pavlovian response which show that other senses can have similar effect. Pavlov’s study used an auditory cue to initiate salivation in dogs [20]. Cain [21] noted that three things were required for successful identification of odours: familiarity, connection between the odour and a name and some “aid” or “training” in recalling the name. Engen [22] claimed that the function of smell is to respond to odours, not recall them for cognitive reasons. This hypothesis would give support to the idea that the sense of smell is a primitive one [10,11]. Axel’s finding [4] that approximately one percent of the genetic code is devoted to encoding odour receptor proteins in several species of mammal also points to the evolutionary importance of this sense. As a comparison, there are approximately one thousand odour receptors and only three types of photoreceptors in humans. This comparison may not reflect the fact that more sophisticated analyses of the environment have evolved in humans. The perception of a sense depends in part on the neuronal mechanisms present in the brain to decode the messages. An estimate of the number and complexity of these networks is indicated by the proportion of the brain they occupy. In humans, size of the visual cortex (occipital lobe) is approximately the size and shape of the palm of a hand, whereas each olfactory bulb is barely the size of a fingernail. This would indicate that, as commonly observed, vision is more important than olfaction in making sense of the world for humans. This is not the case for many animals, whose olfactory bulb can be a substantial proportion of the brain (for example, in rats it is approximately one-third of the brain size)[8].

In Engen's subjects, odour was used to re-create past episodes – and the strength of the memory varied with any special involvement with the odour. He also showed that the link between odours and names was weak and suggested that subjects who could recognise an odour could not necessarily name it. The “tip of the nose” phenomenon (knowing the odour but not being able to recall a name for it) is not analogous to vision.

This difficulty was recognised by Livermore and Laing [23], who trained their subjects by asking them to write down life associations as an aid to recognising and remembering complex odours. These authors also commented that the mechanism by which the olfactory system extracts meaningful information from its environment is not well understood. They studied “object odours” – those such as coffee, smoke, lavender or honey that consist of many odorous compounds - and concluded that each of these complex odours was perceived as a unique and singular entity (associative or *synthetic* processing). Trained human subjects could only identify up to four of these “object odours” in a mixture of such odours. Previous studies had already indicated that this is the same as the number of pure odorants that can be easily identified within a mixture. In this respect, the neural processing appears to be similar to that for visual stimuli, where the number of easily-remembered items has previously been estimated as the “magic number” of  $7 \pm 2$  [23].

### **Different mechanisms for odour perception**

There is more than one way that molecules in the environment can connect with the brain, eliciting a response that we may call “smell”. The three best known mechanisms are described below, although there may be other odour sensing mechanisms in mammals which are less well understood, and are not discussed here [24].

#### *The main olfactory bulb*

The receptors attached to the cilia of the neurons in the olfactory epithelium in the nose provide a direct physical contact with the outside world and the brain [4]. The axons from these neurons pass through the bones at the top of the nose and terminate at a series of ganglia (glomeruli) which are part of the olfactory bulbs. These ganglia serve to “sort” the signals and send them for processing to other parts of the brain. Some signals go to the amygdala which is associated with emotional behaviour, particularly fear. From there some of the signals are sent further to the very “primitive” hypothalamus. Other signals from the olfactory bulbs are passed via the entorhinal cortex to the hippocampus, which is associated with learning and memory (particularly as regards context and place). Yet other signals from the olfactory bulb go to the pyriform cortex, which also receives signals from the stomach, and may be important in recognising taste. From here, some signals are relayed to the hypothalamus and some go to the orbitofrontal cortex, which is involved in thinking and planning [8, 9, 25].

*The accessory olfactory bulb (and the vomeronasal organ)*

The vomeronasal organ (VNO) in most animals is a pouch in the upper part of the nose containing a patch of sensory epithelium. It is connected by ducts to the nasal cavity. When an animal senses novel substances in its environment, fluid is pumped into this organ by specialised cells. It is thought that the vomeronasal organ recognises non-volatile molecules in solution rather than (or perhaps as well as) airborne molecules, and these molecules elicit behavioural responses usually associated with social order, mating and reproduction. Since licking is often associated with these behaviours, it seems that some non-volatile compounds could enter the VNO via the saliva [26].

In humans, the vomeronasal organ is reduced to small slit. There is some dispute between researchers as to whether it is vestigial or whether we respond to its stimulation at a subconscious level [10, 27, 28].

The nerves associated with this organ send signals to the accessory olfactory bulb which lies behind the main olfactory bulb, and has a similar but simplified anatomical structure. From here, neural signals are sent to the medial nucleus of the amygdala. This is known to mediate behavioural responses, particularly those associated with reproduction and feeding. Some signals proceed further to the “primitive” hypothalamus [8-10, 24, 25].

Studies on cloning genes for olfactory receptors show that the receptors in the VNO have completely different amino acid sequences than those in the olfactory epithelium. Neurons from the VNO are spatially separate from those of the main olfactory bulb, and if the VNO is destroyed, animals such as mice can still smell normally but never mate. These results taken together indicate that the VNO may have evolved separately from the main olfactory system [4].

*The trigeminal nerve and pungency*

Some compounds in the environment are perceived to irritate the lining of the nasal cavity. These can be perceived even by anosmics and result from stimulation of the trigeminal nerve in the nasal cavity [29]. This is one of a set of cranial nerves which are ultimately responsible for sensations of touch, movement, pain and temperature being relayed from the facial and head areas to the brain. The neural signals are sent to the trigeminal nucleus in the very primitive brain stem [8].

Carbon dioxide, which can be sensed by insects such as mosquitoes, acts on the trigeminal nerve in humans. This association with the sense of touch possibly explains the pleasant “prickling” sensation we experience when drinking carbonated beverages.

**Importance of smell in animal behaviour**

Although it is not possible to know whether other animals experience the same sensation as humans when they “smell” an odour, it has been observed by many people that they respond to odours in their environment; [1, 24, 25], pers. obs. Among other instances of animals finding buried food, Millington [30] reported that marsupials are attracted by odour-impregnated filter papers in the laboratory.

Some of these odours that elicit a response in various animals are also potent “smells” to the human nose, some are perceived by humans to have very little odour and others none at all. A few reported instances of this phenomenon include: Bergstrom et al. [31] who discussed human perception, chemical studies and attraction of insects to flowers; Oldfield [25] who described odour preferences in bats; MacKenzie [32] who commented on the ability of dogs to be trained to find mercury and mercury salts; and Millington [30] who reported that steroids in truffles which attract pigs have a strong odour to humans but do not attract the Australian marsupials, the bettongs.

It was initially thought that birds do not have a very well developed sense of smell and that they relied almost exclusively on visual cues (Whelan, R.J.; pers. comm.). More recently, this has been shown to be an oversimplified assumption. Stiles [33] stated that “birds' sensory world is more like our own than that of insects.” Captive birds (*Anthochaera chrysoptera*), that normally visit the yellow phase of *B. ilicifolia* in WA, can be “trained” to visit the red flower phase if a sugar reward is present in the red flowers and not the yellow [34]. The birds are possibly using their olfactory sense in the initial novel location of the sugar. Various species of birds use odour cues in their environment to: direct them to a familiar place; select nest materials; locate food and find “home” from a distance. Odour cues can overshadow the visual cues in some instances in domestic chicks, which have also been shown to imprint onto an olfactory stimulus [35].

In insects, a similar phenomenon to “smelling” is exhibited when the antennae come in contact with “odorous” compounds. This effect can be measured in the laboratory by an “electroantennogram” (EAG) in which the change in electrical potential in the cells of the antennae are noted when the insect is exposed to odorous or pheromonal substances [36, 37]. Day [38] cites studies that show that an aphid's olfactory system is much simpler than that of vertebrates. It consists of only a few olfactory nerves which are very specific and possibly sense only one compound at a time.

The reflex response of the proboscis extension of cabbage butterflies *Ligustrum japonicum* has been shown to be a better indication of simulated field behaviour than EAG performed on excised antennae [39]. A synergistic effect was noted between five of the test odours; a mixture of all five elicited a greater response in attracting the butterflies than any of the five odours individually. In fact this response was as great as the total floral extract obtained by their extraction method (comprising over 30 compounds). This would seem to indicate that the olfactory system of the butterfly is more complex than that of the aphid reported by Day [38].

Dobson et al. [40] state that flower odours are important as one stimulant (others being visual, tactile and gustatory) that aids the location and selection of flowers by insects. In some species of flowers, pollen volatiles are more important than colours in enabling bees to discriminate between flowers.. In other studies, it has been reported that whole-plant volatiles are important in attraction of honey bees to orchids [41, 42].

The phenomenon of following food cues or avoiding danger is seen in single-celled organisms [11]. The early evolution of a rudimentary olfactory sense may be evident in the phenomena of chemotaxis in bacteria. This is the process by which some bacteria are attracted to molecules representing food but repelled by those representing danger. There is also evidence of more complex chemical communication between bacteria that may be important, for example, in colony formation [43, 44].

Even plants have sensors on their root hairs which can cause the root to grow towards a source of nutrients [45].

### *What are semiochemicals?*

Semiochemicals are chemical signals that convey information between organisms. The definitions below are from Tumlinson, Turlings & Lewis [46]:

- *pheromones*: convey information between two members of the same species
- *allelochemicals*: convey information between different species
- *kairomones*: are allelochemicals that are beneficial to the receiver but not the emitter
- *synomones*: are allelochemicals that benefit both receiver and emitter.

The same semiochemical can sometimes function in more than one way, for example when a pheromone also functions as a kairomone in attracting a predator. It is not always clear from chemical analysis which organisms are emitting what semiochemical, particularly when animals sequester plant volatiles in their bodies and subsequently use them as their own attractants or repellants!

The term “pheromone” was first coined in 1959 when researchers realised that chemicals were involved in insect communication – in particular in effecting mating and reproductive behaviours. The term “pheromone” was used to describe any such chemicals, whether steroid, alkaloid, protein or something else. Taylor [27] states: “Most pheromonal conversations are blatant sexual boasting”.

Subsequently, when it was noted that chemical communication also occurred between vertebrates, there was discussion about whether the term “pheromone” was an appropriate term to use. The range of behaviours mediated by odours is far more complex in vertebrates and depends on the physiological, social and physical environments of the animal [47].

The terms defined above are now applied to animals of all classes and can even include substances emitted by plants if they affect the behaviour of animals.

### **How does smell influence feeding behaviour?**

The importance of odours and olfactory sensations in feeding behaviour of vertebrates has received little attention [25]. In his review, Doty [24] described situations where animals use odour trails put down by conspecifics to find food, or use the odour of the food on the breath of a conspecific to guide their search. No mention of studies using the odour of the food itself was made. Recently, the odour-guided feeding behaviour of various species of bats has been studied using the odour of the preferred foods. Oldfield [25] gives evidence that odour perception must be involved in both short-range and long-range orientation of bats to a food source, although different types of bats show a wide variety of sensory mechanisms to assist them in finding food. Acharya et al. [48] concluded that the Indian fruit bats *Cynopterus sphinx* use odorous cues to detect food, at least from a distance of 20-40 cm, and that non-olfactory cues were insignificant.

*Learnt or innate behaviour?*

Animals are surrounded by an olfactory world – not just of “natural” odours, but of odours they (and their conspecifics) secrete into the environment [25, 26]. The animals’ perception of the environment also depends on sound and vision – but it is odour alone that can provide cues in both space and time [24].

Various studies have shown that animals can learn to associate particular odours with an important event or substance (such as food) in their environment. Doty [24] cited many examples to support his view that only a very few mammalian odour-guided behaviours are innately associated with specific odorants. Some selected examples show the variety and complexity of behaviours initiated by either learnt or innate olfactory responses in animals.

Indian fruit bats change behaviour when presented with a novel odour such as cedar oil [48]. Although they initially avoided fruit presented with this strange smell, within two days they approached the novel-smelling fruit as familiar food. Subsequently, the bats actively investigated cotton soaked in the cedar oil when foraging for food. These same bats, who normally do not eat grapes, consumed grapes coated with banana (which they like) without any subsequent ill effects.

Domestic chicks can be trained to avoid foods that are associated with a particular odour, although the presence of this odour initially does not produce any avoidance behaviour [35].

In the insect world, both honey bees, *Apis mellifera L.*, and bumble bees, *Bombus terrestris L.* can be conditioned to learn a novel odour when it is presented in a paired association with a sugar reward [49]. Parasitoid wasps, *Aphytis melinus*, were shown [50] to orient towards lemon fruit if they had previous experience of their preferred food, California red scale, growing on lemons. Since they did not orient towards the scale insects growing on other vegetables, it is suggested they have learnt to associate their food with a particular plant and have no innate preference for the odour of the scale insects on their own.

Some olfactory learning may occur very early in an animal’s life. It is even possible that *in utero* exposure to odorous chemicals can modify odour-guided behaviours in the future [24]. Preweaned rats exposed to ethanol vapour have been observed to show a greater preference later in life for both the odour and taste of ethanol than controls [51]. Rat and rabbit pups begin “nipple searching” behaviour when exposed to the smell of their mothers, however they can be trained to initiate the same behaviour with a novel perfume presented to them on the mothers’ fur within 2-4 days of their birth [52].

Olfactory learning in animals may be more fundamental to their behaviour than merely being able to “learn” about a new smell and its associations. In their review paper mentioned above, Brennan and Keverne [52] give two more examples of olfactory learning that occur only within a particular “window” of time associated with a major life event of the animal. They discuss the structural and functional neuronal changes that occur during these learning events. A different mechanism is involved in each case. Female mice will “block” a pregnancy if exposed to the odour of another male rat during a few hours after mating; this is mediated by the vomeronasal organ and the accessory olfactory bulb. Sheep learn to recognise the odour of their own lamb during a specified time between 2 hours and 24 hours after parturition; this is effected through the normal nasal olfactory sensors and the main olfactory bulb.

Doty [24] comes to the conclusion that complex relationships exist between odour-guided behaviour, hormonal state and experience. He gives examples where experience can override hormone-mediated behaviour which may have seemed “obviously” innate. The plasticity of the mammalian olfactory system is such that mammals can learn to attach meaning to novel and purely synthetic odours. He also comments that rats can learn complex behaviours purely on the basis of olfactory cues.

Livermore and Laing [23] speculated that the way in which a complex sensory event is presented may influence the way animals (including humans) learn about and perceive the components of that event. They cite a study which indicated that spiny lobsters can be trained to perceive the same odour mixture either associatively or dissociatively, depending on the order in which the mixtures were presented to them.

The importance of “learnt” olfactory responses in several genera of predatory insects was a point of discussion between several researchers at the recent Novartis Symposium on insect-plant interactions and induced plant defence [53].

The relative importance of “innate” and “learnt” behavioural responses to odours has not been established; in fact, it may not even be valid to try to distinguish between the two perceived effects. For example, Oldfield [25] discussed the large differences between different species and genera of bats in the way each animal apparently uses olfactory cues in foraging. This can be correlated to some extent with the anatomical structures of the olfactory mechanisms in each individual animal, but may also depend on the foraging experience of each bat during its lifetime.

### **Interaction between animals and their “natural” world**

It may seem there “should” be a neat and orderly relationship: the “pheromonal” semiochemicals would act through the vomeronasal organ and the accessory olfactory bulb initiating “innate” behavioural responses such as those concerned with mating and reproduction (and perhaps some aspects of feeding); whereas the main olfactory system would be concerned with sensing the total environment in a more conscious way, involving “learnt” behavioural responses or decision-making behaviour. As the literature reviewed here has shown, Nature does not always put her secrets into these tidy compartments for the convenience of researchers. There is still a puzzling array of interactions, cross-relationships and enigmas in the semiochemical world of animals, plants and their environment. The researcher needs to be gentle in teasing out these secrets.

Modern analytical methods enable the use of sampling and extraction methods that may be closer to the “natural world” than the harsh laboratory-based techniques used in the past. Natural products chemists have a valuable role to play in using these in an innovative way to help solve some of these puzzles. Chemists interested in the relationships between plants and animals also need to be mindful of the current biological and ecological research in this area, and should be aware of the contribution experienced biologists can make to the long term value of their research.

*“The best that can be achieved in the advancement of knowledge is to use whatever imperfect tools are at hand, to pursue a chemical image strategy knowing that our descriptions must be limited and to*

*a pursue a response-guided strategy knowing that our descriptions must be limited and large areas of mammalian semiochemistry will be beyond its scope” Albone [26].*

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