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Ivan Norscia, Elisabetta Palagi, Foreword by Alison Jolly,
Ian Tatterall, Afterword by Michael Huffman
Excerpt
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1 Who are you? How lemurs recognise each other in a smell-centred world

> *He approached these faces – even of those near and dear – as if they were abstract puzzles or tests. He did not relate to them, he did not behold. No face was familiar to him, seen as a 'thou', being just identified as a set of features, an 'it'. Thus, there was formal, but no trace of personal, gnosis. And with this went his indifference, or blindness, to expression. A face, to us, is a person looking out – we see, as it were, the person through his persona, his face. But for Dr P. there was no persona in this sense – no outward persona, and no person within… His absurd abstractness of attitude…which rendered him incapable of perceiving identity, or particulars, rendered him incapable of judgment.*
>
> Oliver Sacks, 1970 (p. 13)

1.1 Individual recognition: why and how

Human society is founded on individual recognition. The distinction of 'others from others' rules every aspect of a community, from the personal to the social level. In his '*The Man Who Mistook His Wife for a Hat*', Oliver Sacks (1970) stresses how the ability to discern individuals is crucial to make a judgement over them and their true identity. Understanding individuals' uniqueness is pivotal to choose partners and friends, care for family members, vote for a candidate, form political alliances, seal trade agreements, and follow rock icons or religious leaders. Individual recognition is not unique to humans. It is, instead, an ancient cognitive skill shared with other primates and rooted in humans' mammalian history. From lemurs to apes, such ability is critical, for example, to select mates and supporters, form parent–offspring bonds, establish dominance relationships, set up coalitions, exchange or interchange commodities and follow group leaders (Thom and Hurst, 2004). Individual recognition is an excellent example of the cognitive continuity that bridges humans and other primates.

Individuals can be discriminated according to their unique features, or cues. Different from signals, specifically designed to convey information beneficial to the sender (Bradbury and Veherencamp, 1998), cues carry potential information whose relevance depends on the receiver. Paradoxically, the same cue can mean something for one animal and nothing for another which does not read the cue as a cue at all! Consequently, defining a cue is not easy. In general, we can consider as a cue any sensory information (visual, tactile, auditory, olfactory, etc.) that gives rise to a sensory estimate (Ernst and Bülthoff, 2004).

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Which characteristics does a cue need to be effective in individual recognition? Firstly, a cue must possess a fixed component, a ‘fingerprint’ that can be recognised independently of other background variations. For example, a child is able to recognise the voice of their mother regardless of its volume, intonation, and/or prosody. These three elements do not answer to the question: who is she? So, they are not functional to individual recognition itself. They provide additional information of the emotional and physical state of the mother as she speaks. The child identifies a steady property of their mother’s voice (auditory cue): the tone (e.g., see Sakkalou and Gattis, 2012).

Secondly, cues must be highly diverse between individuals. For instance, if voice tones in the same family members (e.g., sisters, mother/daughters, etc.) are too similar, they are easy to be mistaken when other cues are missing (e.g., at the phone).

Finally, identity cues should stay temporally consistent or change gradually, thus allowing the receiver to update their sensory information. To stick with the previous examples, a mother can recognise her son’s voice even if they have not been in touch for a long time. Of course, it may be difficult to recognise the voice of someone we have not heard from for 50 years!

Renewing identity documents every five to ten years is mandatory in every country because the older the picture on the document gets, the more difficult is for the officer (e.g., at the airport) to match the actual face of the document owner with the old (and maybe black and white!) one. This is why new identification methods have been implemented, such as the iris scanner, based on invariant individual cues.

The presence of identity cues is not enough, per se, to ensure that individual recognition of an object by a subject takes place. The following elements are necessary: encountering the object, elaborating the cues carried by such object, making a mental connection between the object and its cues, and storing such connection in memory in order to ‘reload’ it when the same object is met again. A full mental representation of the object is built and saved. A second time, a single cue can be enough to recall the full representation of the object by the subject.

The prefix ‘re’ incorporated in the word recognition (from latin *re*=again, and *cognòscere*: to become acquainted) implies a *re*newed identification of a stimulus that has been already encountered. Thus, the memory of a previous experience is crucial.

Box 1.1 **by Paolo Pelosi**

Speaking of which: breaking the olfactory code

Olfaction is the language of chemistry. Being a chemist, I have always been fascinated by molecular structures, first of all by their beautiful architecture, but also by their diverse properties, from physical appearance, such as colour, odour, consistency and optical properties, to their capacity of interacting with other molecules and giving birth to new entities. But molecules are also the words of a language, a language most animal species use all the time to communicate and exchange information.

Chemical communication can be so complex, as in the case of social insects, that it can acquire all the characters of a spoken language, with its own rules of grammar and syntax. Discovering the architecture of this language and breaking its code is one of the most fascinating and exciting tasks, with challenges similar to those encountered when trying to decipher an ancient scripture. Despite all the information of molecular biology, we are still far from ‘breaking the olfactory code’, but a large wealth of information, accumulated during the last three decades, has provided a solid ground and indicated clear guidelines for future research. Now the main problem is coping with the extreme complexity of olfaction, notably human olfaction.

My research has been focused for the last three decades on a class of soluble binding proteins for odorants, appropriately named for such property as odorant-binding proteins (OBPs), which I discovered by chance, while searching for olfactory receptors.

When I first approached the study of olfaction, in the late seventies, I followed the main trend, which consisted in investigating relationships between odour and molecular structure. In practice, you present different compounds to human subjects to smell and ask questions about the type and intensity of odours. By comparing structural parameters of the molecules and odour properties, you can draw correlations and formulate hypotheses on how the human nose works. This method proved troublesome and not very efficient, mainly due to the previously unforeseen complexity of the olfactory code. At the same time I wondered why most scientists were afraid of tinkering directly with this sort of ‘black box’ that was the olfactory system and were addressing indirect questions instead. In other words, this meant applying biochemical tools to olfaction. It was a very risky project, but I had nothing to lose and decided to open this mysterious black box.

The discovery of OBPs in mammals (Pelosi *et al.*, 1982), together with a parallel and almost simultaneous finding of a similar class of proteins in insects (the OBPs of insects) by Richard Vogt (Vogt and Riddiford, 1981), marked the first step of biochemical research in olfaction. After that, we experienced an explosion of interest in olfaction, with fast and still growing developments in the study of OBPs and other soluble proteins (Pelosi, 1994; Pelosi *et al.*, 2006; Leal, 2013). I think the most important outcome was that for the first time we showed that biochemistry could be applied to the study of olfaction. We therefore broke into the mysterious black box and stimulated an increasing number of scientists to peek inside. This fact gave confidence to scientists and prepared the ground for the discovery of olfactory receptors (ORs) about a decade later (Buck and Axel, 1991), which won the authors the Nobel Prize in 2004.

OBPs of mammals and those of insects proved completely different in structure (Bianchet *et al.*, 1996; Tegoni *et al.*, 1996; Sandler *et al.*, 2000; Tegoni

Box 1.1 (continued)

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Box 1.1 (*cont.*)

et al., 2004), although similar in function (Pelosi and Maida, 1990). In both cases we are dealing with small soluble proteins, endowed with extremely stable folding. Incidentally, their exceptional resistance to heat, solvents and proteolysis has recently indicated OBPs as the most suitable biosensors for an artificial nose (Pelosi *et al.*, 2013).

Their simple structure and stability has made the study of these proteins relatively easy. Moreover, thanks to genome information and more recently to transcriptome projects (Vieira and Rozas, 2011), the number of sequences encoding OBPs has exceeded one thousand and is still growing fast. Despite such wealth of structural information, the specific function of OBPs in odour detection is still elusive. Most recent studies provided convincing evidence that OBPs are required for a correct functioning of the olfactory system and are likely involved in odour discrimination. In fact, silencing the gene encoding a specific OBP in *Drosophila* produces flies insensitive to the male pheromone, while several *Drosophila* mutants each lacking one of the 60 OBP genes have shown defects in responses to various odours (Xu *et al.*, 2005; Matsuo *et al.*, 2007; Swarup *et al.*, 2011). In aphids we have found a good correlation between avoidance behaviour of several repellents and affinity to specific OBPs (Sun *et al.*, 2012). However, how the first binding of odorant molecules to OBPs might lead to the activation of membrane-bound olfactory receptors is still an open question.

After the identification of olfactory receptors (Buck and Axel, 1991), many scientists believed that there was no room left for further major discoveries in olfaction. This might be true to some extent, because the corner bricks had already been placed. Nevertheless, a lot remains to be done. There are still several questions awaiting answers, which will require long and detailed studies, but there is also need for new brilliant ideas.

Concerning OBPs, the main open question is: how do they interact with olfactory receptors? Or, in other words: how is the chemical information encoded in the structure of odorants transferred to membrane-bound receptors? Some scientists posit that odorants interact directly with olfactory receptors, others envisage a role of OBPs as carriers of hydrophobic odorants across the aqueous nasal mucus or the sensillar lymph in the case of insects, and others think that it is the complex OBP-odorant which activates the receptor. Devising experimental protocols to prove or disprove such models is highly challenging and no convincing answer has been so far provided. Besides solving the puzzle and putting all the pieces in place, it is of fundamental and practical importance to understand whether ORs or OBPs are the recognising elements and responsible for identifying the different odours. In fact, OBPs, being small soluble proteins, are much easier to study than ORs. If discrimination of odorants occurs at the level of OBPs, we can use these proteins to measure interactions with as many odorants as we like and move quickly towards the elucidation of the olfactory code. We can also use the same proteins that can be easily prepared in bacteria, to assemble artificial devices for odour detection and recognition.

Another active field with enormous possibilities of investigation lies beyond the peripheral olfactory neurons. We know almost nothing about how the brain makes use of individual signals coming from the periphery to build ‘olfactory images’, so accurate and unique that they are able to promptly recall past experiences even if not supported by other sensory modalities. Then, of course, how such ‘images’ are stored in the memory is another fascinating topic of research. The brain certainly applies a combinatorial code to olfaction, in order to meet with thousands or even millions of odours in the environment using only a limited number of receptors. In fact, we know that each kind of odour molecule is generally able to stimulate several types of receptors at different grades of intensity, while, at the same time, each receptor can produce different levels of response to structurally related odorants. Since the number of functioning human olfactory receptors is a little more than 300, we end up with virtually an infinite number of combinations.

A third area that future research is likely to explore is that of artificial olfaction. There is a strong interest in this topic and a large number of reports have been published (Persaud and Pelosi, 1992; Pelosi, 2003; Turner and Magan, 2004; Stitzel *et al.*, 2011; Manai *et al.*, 2014), but we are still very far from designing an instrument able to reproduce in some way an artificial nose.

To move from a general gas detector to an instrument capable of discriminating and measuring odours in a similar way to natural organs we need to improve our knowledge and technology along two parallel lines:

(1) A better understanding of our olfactory system. In other words how our olfactory receptors read, decode and integrate the chemical information hidden in molecular structures; we are still miles away from assigning to each of the 300+ receptors its best ligands, and we know almost nothing of how their responses are mixed and integrated in the brain.
(2) Better sensing elements. So far, the instruments for the detection of odours have been based on metal oxides or conducting polymers. The former, used in commercial smoke alarms, are virtually unspecific whereas the latter presents very broad responses to odours. Both of them are orders of magnitude less sensitive than any biological system. Most recently, the use of OBPs as specific detectors in electronic devices has attracted wide attention, owing to their better specificity of response, as compared to other sensors, and to their exceptional stability as proteins. However, the issue of sensitivity still remains and represents one of the major challenges when we want to reproduce the functioning of the olfactory system with an electronic device.

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1.2 How different sensory modalities concur to individual recognition

Humans can individually identify conspecifics by either using single cues (unimodal recognition) or combining them into a cross-modal recognition system (Joassin *et al.*, 2011; see also Chapter 2). Mothers are able to recognise their babies by using single sensory modalities, such as the odour of their infant's garment (Porter *et al.*, 1983) or the cry alone (Green and Gustafson, 1983). Humans normally rely on the visual sensory modality to identify other individuals. Face is certainly the primary identity signal (Sergent *et al.*, 1992; Kanwisher *et al.*, 1997; Rhodes *et al.*, 2004), as clearly exemplified by the face photo that must necessarily accompany identity documents. Humans are also able to discriminate individuals by using other single characteristics, such as gait or clothing, especially when the face is obscured (Bruce and Young, 1986).

The concurrent use of different sensory modalities becomes important to optimise individual recognition under certain circumstances. In the forest, our primate ancestors would cope with faces partially or totally covered by the canopy; communication calls distorted or deviated by trunks, branches and twigs; and odours whose perception could be prevented or weakened by distance, or altered by the exposure to natural elements, such as heavy rain and wind. In the urban forest, the city, today's people have to deal with faces mingling in the crowd, voices covered by other voices, traffic noise, advertising announcements, music, and body odours mixed with artificial pheromones (perfumes), flue gas, and garbage smell. Hence, combining different pieces of information coming from different sensory modalities can be advantageous under less than optimal viewing or hearing conditions to determine individual identities (Blank *et al.*, 2011). Such a cross-modal process, which combines and integrates different cues, has been favoured by natural selection because often, under natural conditions, no one cue carries complete information on individual identity.

The human brain cortex possesses both unimodal and multimodal processing areas. Unimodal regions (e.g., olfactory/piriform, auditory and visual areas) elaborate single cues and multimodal regions (mainly located in the hippocampus and adjacent areas) combine and integrate single cues leading to cross-modal recognition (Gottfried *et al.*, 2004; Joassin *et al.*, 2011). Sensory combination allows maximising the information delivered by single sensory modalities whereas integration allows reducing the variance in the sensory estimate to increase its reliability (Ernst and Bülthoff, 2004). The recognition process is optimised by direct structural connections existing between single-cue processing areas (Blank *et al.*, 2011).

Cortex areas for multimodal processing are present in non-human primates (Gil-Da-Costa *et al.*, 2004; Romanski, 2007; Ghazanfar *et al.*, 2008) and other mammals, in which the response elicited by multisensory cues is greater than unisensory responses and sometimes greater than their arithmetic sum (Alvarado *et al.*, 2007). In macaques, the audiovisual integration neural circuitry corresponds closely to areas in the human brain that support cross-modal representation of conspecifics (cf. Gil-Da-Costa *et al.*, 2004; Campanella and Belin, 2007).

Neurophysiologic evidence of cross-modal recognition is supported by behavioural results. Both monkeys and apes can associate the sound of different call types with images of conspecifics and heterospecifics producing these calls (rhesus macaques, *Macaca mulatta*: Ghazanfar and Logothetis, 2003; tufted capuchin monkeys, *Cebus apella*:[1] Evans *et al.*, 2005; chimpanzees, *Pan troglodytes*: Parr, 2004). Squirrel monkeys (*Saimiri sciureus*) have been shown to spontaneously integrate auditory and visual identity cues from their one highly familiar human caretaker (Adachi and Fujita, 2007). Chimpanzees can, through intensive training, learn to associate calls from known individuals with images of those individuals (Bauer and Philip, 1983; Kojima *et al.*, 2003; Izumi and Kojima, 2004).

Olfaction is rarely considered in cross-modal recognition studies on primates. In their evolutionary history, haplorrhines have developed acute vision (trichromacy) and retained or improved their acoustic capacity (Fleagle, 2013). In contrast, olfactory abilities have been put in the corner. Social primates are mostly represented by acoustic- and vision-oriented species and, consequently, the studies on multimodal communication have focused more on these sensory modalities than on smell, considered as less relevant than other senses to monkeys' and apes' communication.

For most mammals olfaction is the dominant sense, with their behaviour being heavily influenced by the social chemosignals secreted by individual conspecifics (Wyatt, 2014).

The first evidence that animals can integrate multiple cues to build a representation of an individual came from a study on smell use in hamsters (Johnston and Bullock, 2001), which produce at least five different individually distinctive odours. The experimenters exposed a male familiar with two females, A and B, to the vaginal secretions of female A. Once habituated to the vaginal secretions, the male was tested with either A's or B's flank secretions. Males exposed to A's flank secretions investigated them less than males tested with B's flank secretions. This phenomenon, known as across-odour habituation, led the authors to conclude that 'when a male was habituated to one odour he was also becoming habituated to the integrated representation of that individual'. However, direct physical contact, not just odours, is necessary to establish in a subject the full representation of the object, whose identity will be recalled using multi-cue odour memory (Johnston and Peng, 2008).

Box 1.2 **by Eckhard W. Heymann**

Speaking of which: odour communication in tamarins

I got in touch with olfactory communication early on during my studies at the University of Giessen. One of my teachers and then later supervisor of my PhD thesis, Heinrich Sprankel, had done research on the histology of scent and other skin glands of tree shrews and tarsiers (Sprankel, 1961, 1971), and he was treating olfactory communication both in his ethology

Box 1.2 (continued)

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[1] *Cebus apella* has been reclassified as *Sapajus apella* (Lynch Alfaro *et al.*, 2012). In this book we use *Cebus apella* because this species is mentioned as such in the cited articles.

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Box 1.2 (*cont.*)

and primatology classes. This and my behavioural observations in the course of my diploma thesis on tree shrews, where sternal scent marking is a very prominent behaviour, primed my interest in the subject.

When I started to study the behaviour of tamarins in 1982, it was obvious from the very beginning that any attempt to understand the social life of these creatures would fail if their olfactory communication was not considered. My interest was additionally fomented by Gisela Epple who came to the German Primate Center in 1983. Her work on the chemical composition of scent marks in callitrichids and on the proximate mechanisms of callitrichid olfactory communication (e.g., Epple, 1979, 1980; Epple *et al.*, 1981) had answered a number of questions. But it was also clear that there was a wide field of unanswered questions and unresolved problems. Furthermore, except for some anecdotal information (Izawa, 1978; Lindsay, 1979) nothing was known on callitrichid olfactory communication from the wild. What further increased my interest and triggered my ambitions to contribute to filling this huge gap of knowledge was the complete neglect of olfactory communication in the first detailed and systematic field studies on tamarins that emerged in the late 1970s and early 1980s (Dawson, 1977; Neyman, 1977; Terborgh, 1983; Terborgh and Goldizen, 1985). Obviously, here laid a field in front of me that was worth being ploughed.

Finally, what certainly also contributed to my interest in olfactory communication was the fact that – from my point of view – this topic requires 'square thinking', leaving trotted paths and mainstream reasoning – things that I increasingly like(d) to do. For example, the widespread hypothesis of pheromones from scent marking as a mechanism of reproductive 'suppression' of subordinate callitrichid females (e.g., Abbott, 1984) had never convinced me. This hypothesis could *not* explain why male callitrichids scent mark, why non-reproductive females sometimes show higher rates of scent marking than breeding females, etc. Maybe scent marks could work to suppress other females' reproduction in a 2 m^3 cage, but how should this work in a 40 ha or more home-range area?

The occupation with the topic led me to recognise that olfactory communication (and more generally olfaction) in primates is a hugely neglected field (Heymann, 2006), something that is now slowly changing.

There are three outcomes of my research that I should like to emphasise. The first one is the female bias in rates of scent marking and the recognition that this bias may have been shaped through sexual selection (Heymann, 1998, 2003). While I had already seen such a bias during my very first observations of tamarins, I could not actually make sense out of it until I came across Darwin's (1871, p. 131) statement that 'odoriferous glands [have] been acquired through sexual selection' and Blaustein's (1981, p. 1007) suggestion that odours 'are probably functionally equivalent to secondary sexual characteristics' and that 'sexual selection should act upon these odours just as it acts upon visually conspicuous characters'. Having read this, things became clear to me: in animals where females strongly compete for the single reproductive position in a group, and where males take the largest share in infant care apart from lactation – i.e., where there is a partial reversal of sex roles – the female bias in rates of scent marking (and the size of scent glands) could be interpreted as secondary sexual characteristics, possibly subjected to sexual selection. That sexual selection can strongly act upon females as well is now widely accepted (see Clutton-Brock, 2007), but that sexual selection shaped patterns of olfactory communication in tamarins and other callitrichids (Heymann, 2003) must remain a hypothesis for the moment, albeit a plausible one.

The second interesting outcome is the finding that scent marking in tamarins bears little relationship with territoriality (Heymann, 2000; Lledo Ferrer *et al.*, 2011, 2012), although this has created some debate and opposition (Gosling & Roberts, 2001; Roberts, 2012). Given a university training oriented towards classical ethology, I had too long been sticking to the hypothesis of a territorial function of scent marking. Only after I had found a plausible answer for the sex bias in tamarin scent marking could I also make a different 'sense out of scents' (to quote the title of a review by Epple and coworkers [1993]) with regard to the spatial patterns of scent marking.

The third interesting finding is the striking difference in patterns of scent marking between the sympatrically living *Saguinus mystax* and *Saguinus fuscicollis*, particularly the lack in the former and presence in the latter of allomarking (Heymann, 2001). Since the two species have a long separate phylogenetic history (Matauschek *et al.*, 2011; Heymann *et al.* unpublished data), it is most unlikely that these differences relate to reproductive isolation. Rather, I would speculate that the differences are linked to subtle differences in the social system, particularly in the mating system, of these sympatric species, although admittedly at the moment I do not yet have any clue how this relationship is structured.

The main future directions of this investigation domain are the following:

(1) Comparative analyses of the factors that influence the relative importance of life-history traits, social systems, activity patterns, ecology and phylogeny for shaping patterns of olfactory communication (Heymann, 2009; Delbarco-Trillo *et al.*, 2011). Such analyses will help identify specific factors and traits that can then be examined in more detail in both observational and experimental studies. However, since for many primate species, data on their olfactory communication are lacking or scanty, such analyses will remain preliminary until a broader database becomes available.

Box 1.2 (continued)

Box 1.2 (*cont.*)

(2) An understanding of the olfactory 'vocabulary'. So far, studies report rates of scent marking and other olfactory behaviours and/or the chemical composition of olfactory signals. But whether, for example, the combination of different olfactory signals (such as secretions from different scent glands and urine) conveys a message different from a single mark, or the addition of visual signals, is largely unknown, and relevant studies are only slowly emerging (Palagi and Norscia, 2009). It will also be interesting to know whether primates are capable of modulating the amount (or even the chemical content) of scent gland secretions or urine to convey different messages in relation to different behavioural contexts. Such studies will, however, be technically very difficult and require the development both of devices with which to measure olfactory signals with much precision and of clever experiments to 'playback' different olfactory signals and measure the response of potential receivers.

(3) More baseline data for a broader range of species from the different primate radiations, collected within a theoretical framework (e.g., sexual selection theory (e.g., Jannett, 1986; Heymann, 2003)). Such studies must include not only signal emission, but also reception and response to olfactory signals on the behavioural ('to whom it may concern' (Kappeler, 1998)) and the neurophysiological level (Ferris *et al.*, 2001). Furthermore, information on the chemical composition of scent marks and their longevity/degradation under natural conditions is needed.

(4) Challenge of the paradigm of scent marking as being a cheap way of communication (e.g., Krebs and Davies, 1993). This will involve metabolic studies to identify production costs, for example the question of where proteins and unsaturated fatty acids found in scent gland secretions (e.g., Epple *et al.*, 1993) are derived from. Also, detailed behavioural studies on the 'broadcasting costs' under natural conditions (e.g., how many scent marks have to be placed to reach a receiver) will be needed.

(5) Examining whether olfactory signals are related to individual quality (Endler, 1993; Zala *et al.*, 2004; Charpentier *et al.*, 2010). This will include exploring the link between intrinsic factors like the Major Histocompatibility Complex (MHC) (Setchell *et al.*, 2011) or extrinsic factors like diet (Ferkin *et al.*, 1997) and individual scent profiles, and examining variation of scent profiles over individual life trajectories. Apart from genetic and chemical analyses, dietary manipulation and its effect on the composition and attractiveness of scent marks will be necessary.

As becomes clear even from these few selected points, future studies on primate olfactory communication will have to be even more interdisciplinary