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Introduction

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Author for correspondence:
S. Craig Roberts
e-mail: craig.roberts@stir.ac.uk

Human olfactory communication: current challenges and future prospects

S. Craig Roberts[1], Jan Havlíček[2] and Benoist Schaal[3]

[1]Division of Psychology, University of Stirling, Stirling FK9 4LA, UK
[2]Faculty of Science, Charles University, Viničná 7, 128 42 Prague 2, Czech Republic
[3]Developmental Ethology and Cognitive Psychology Laboratory, Centre for Taste, Smell and Feeding Behaviour Science, UMR 6265 CNRS-Université de Bourgogne-Inra-AgroSup, Dijon, France

SCR, 0000-0002-9641-6101; JH, 0000-0003-2374-7337; BS, 0000-0002-9419-3282

Although anthropologists frequently report the centrality of odours in the daily lives and cultural beliefs of many small-scale communities, Western scholars have historically considered the sense of smell as minimally involved in human communication. Here, we suggest that the origin and persistence of this latter view might be a consequence of the fact that most research is conducted on participants from Western societies who, collectively, were rather *old* (adults), *deodorized* and *desensitized* (ODD) to various aspects of olfactory perception. The view is rapidly changing, however, and this themed issue provides a timely overview of the current state-of-the-art on human chemocommunication. Based on evolutionary models of communication, the papers cover both general mechanisms of odour production by 'senders' and odour perception by 'receivers'. Focus on specific functional contexts includes reciprocal impact of odours between infants and mothers, the role of odour in mate choice and how odours communicate emotion and disease. Finally, a position paper outlines pitfalls and opportunities for the future, against the context of the replication crisis in psychology. We believe a more nuanced view of human chemical communication is within our grasp if we can continue to develop inter-disciplinary insights and expand research activities beyond ODD people.

This article is part of the Theo Murphy meeting issue 'Olfactory communication in humans'.

1. Introduction

Communication pervades daily life in any social species. Humans most frequently use language to convey information and complex concepts, but non-linguistic communication is also a critical component of many social interactions. This can involve different sensory modalities. For example, facial and gestural expressions impart cues of an individual's emotional condition and likely future actions, the pitch and intensity of a scream or roar alerts us to imminent threat [1], and a gentle touch or slap on the back may provide reassurance [2]. However, while the use of such visual, acoustic and tactile social information is uncontroversial, the suggestion that humans also use body-based olfactory information for communicative purposes has historically been often met by scepticism, ambivalence or even antipathy.

These views are largely shaped by the conceptions of an intellectual elite, reaching back to the theories of the senses construed by philosophers, moralists and theologians since Antiquity [3,4], and according to which humans no longer rely on olfaction, not just in communication but in general. As argued by Schaal & Porter [5], and more recently McGann [6], this long-standing conception was crystallized by the neuroanatomist Paul Broca, who classified mammals as 'osmatic' or 'anosmatic' depending on the development of their olfactory bulb, hippocampus and 'great limbic lobe' relative to the rest of the brain [7]. Humans were entered into the anosmatic group, along with other primates and cetaceans, because although Broca noted that humans remain sensitive and reliant on odorants, their olfactory structures were 'considerably lessened'. This notion of

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an anatomical reduction of olfaction, despite its functional persistence in directing attitudes and behaviour, was later nuanced in considering humans as a 'microsmatic' species [8], one in which smell remains active despite it having been apparently superseded by other senses. This view has been extremely pervasive, and textbooks of human evolution relate the loss of the sense of smell to a shrinking nasal prominence as the eyes moved to the centre of the face to improve binocular vision, coupled with bipedality and ecological changes reducing exposure to, or relevance of, olfactory stimuli (e.g. [9]). The reasoning of Broca and his followers was based on inferences of functional consequences from purely anatomical observations, reflecting the biological thinking of their time. Interestingly, Darwin [10, p. 17] also asserted that 'the sense of smell is of extremely slight service, if any…' to humans. Freud went even further, suggesting that the loss of interest in odours was integral in the evolutionary advent of the erect posture and elaboration of civilized behaviour [11]. He interpreted any residual interest in body odour to be a throwback of our ancestral past and even considered such interest to be symptomatic of psychiatric disorder.

The macro/microsmatic divide of the animal kingdom has persisted and was further revived by molecular biologists, who sought to correlate the number of functional olfactory genes (or of non-functional pseudogenes) across species with the degree of olfactory reliance in directing behaviour [12,13]. However, in these studies, the nature and depth of reliance on olfaction in behaviour was rather crudely inferred, and the incidence of pseudogenization of olfactory receptors does not appear to directly link with olfactory sensitivity/reactivity processes [14]. The expanded primate brain, and particularly, the neocortical backup of the human brain, have indeed evolved sophisticated analytic processes to decode olfactory information in various functional domains, and elaborated ways to communicate about them (e.g. [15]).

However, recent research has steadily undermined these views to the point that one review casts alleged poor human olfaction as 'a ninteenth-century myth' [6]. Although humans have lost vomeronasal chemoreception seen in other species, we now know that a neural architecture is retained that enables sensitive and complex olfactory performance [16]. Although the human olfactory bulb is smaller in size, relative to total brain volume, compared with 'supersmeller' species like mice and dogs, new isotropic fractionation techniques show that it nonetheless contains approximately the same number of neurons as those of the 'supersmellers', with more connectivity [17]. Furthermore, it is larger in absolute terms: while the rest of the brain expanded more over evolutionary time, the olfactory bulb did not shrink. An outcome of this is that, although supersmelling species respond more sensitively to certain odours, humans can match or even outperform them in detection of other odours [18]. Humans can also undertake very sensitive olfactory tasks such as tracking an odour through a field [19] or detecting the smell of a single *Drosophila* fly in a glass of wine [20].

Beyond these experimental demonstrations, we should remember that humans strongly depended on olfaction throughout their evolutionary history, and still do today. We use it to detect, select and concoct foods, and other items used as medicinal, aesthetic or domestic commodities. Odours are universally involved in practices to optimize the balance between nutritional, toxic and sensory/hedonic properties in the preparation and preservation of numerous foods and beverages. Indeed, it has been argued that odour and flavour-based expertise to control the processing of raw materials into cooked food has been a main evolutionary driver of persistent olfactory structures [21,22], but another ostensible domain of human olfactory competence relates to interpersonal communication, as it relies on attention towards body odours and perfumes. Washing away one's *sui generis* smell and replacing it with artificially crafted scents is a widespread anthropological phenomenon. Such behaviour appears to be used for multiple goals that are common to numerous cultures, ranging from body odour masking, cultivating positive mood or emotion, and protecting from parasites, to enhancing communication of one's gender, age and individuality, conforming to a group's social norms, manipulating attention of others, imposing one's power status, and displaying prestige and wealth [23]. Such expert exploitation of local odorous items into social signs may explain why olfactory bulbs are bigger in *Homo sapiens* relative to *Homo neanderthalensis* [24], although the latter also left traces of scented items, suggesting the very early emergence of odour-based social rituals [25].

If the available evidence implies that we are not the 'micro-smellers' we have been thought to be, then we may also need to thoroughly re-evaluate the efficacy and extent of olfactory communication in humans, as perhaps for primates in general [26]. The past two or three decades have generated a suite of intriguing and exciting discoveries concerning the potential involvement of bodily odours in various aspects of familial bonding, interpersonal assessment and mate choice. Much of this literature is reviewed and summarized in papers within this special issue. However, it is probably true to say that even the contributors to this issue would feel that we are still some considerable distance from determining a comprehensive picture of human chemical communication. In this introductory paper, we first address some possible reasons for this and then outline some new and promising areas of inquiry.

2. Smell in a non-Western, educated, industrialized, rich and democratic world

Much of our understanding of human psychology, in general, is based on studies in Western, educated, industrialized, rich and democratic (WEIRD) societies [27]. Henrich *et al*. [27] note that these studies are most commonly based in North America or Europe, using easily accessible local samples (e.g. of university undergraduates). Although they can be highly informative, it is problematic when findings from these samples are injudiciously extrapolated and adjudged to be representative of humans as a species. As Henrich *et al*. demonstrate, there are numerous such examples from research on a range of psychological attributes and behaviours. We illustrate this point with just one relevant example, which they draw from the field of visual perception, specifically a study that compared cross-cultural variation in susceptibility to the Müller-Lyer illusion. In a sample of 14 small-scale societies and two from westernized samples, the latter two samples stand at the extreme of susceptibility. At the other extreme, responses from San foragers of southern Africa were not statistically different from zero; in other words, this well-known 'illusion' was not an illusion for them at all [28].

It seems very likely that the widely held view of poor human olfactory perception is, at least to some extent, a further

reflection of a WEIRD bias. For example, using a standard olfactory assay, Sorokowska *et al*. [29] compared detection thresholds for *n*-butanol among 151 Tsimane' forager-horticulturalists from the Bolivian Amazon with those of 286 urban-dwelling Germans. Their results were striking: Germans were not only less sensitive on average, but even the most sensitive individual was outperformed by a full quarter of the Tsimane' sample. A subsequent study reported still lower *n*-butanol detection thresholds in Cook Island villagers [30]. A similar pattern is found in the difficulty of describing odours, with certain groups such as the Jahai of the Malay Peninsula finding it as easy to verbally label odours as they can do for colours, in stark contrast with westerners [31].

Furthermore, Broca, Darwin, Freud and their followers may not have stated that odours are unimportant in (conscious) human behaviour if they had access to the wealth of ethnographic evidence that is available today from cultures around the world. In one review of this evidence, Classen [32] describes the role of odour in social categorization across diverse cultures, and contrasts current Western societies (for European historical accounts, see [33–35]) with what she characterizes as 'olfactorily conscious' societies. Odours are at the centre of social life in these small-scale communities. For example, members of different Tukano-speaking tribes in the Colombian Amazon learn and recognize the group's characteristic odour, associate this with the spatial extent of territorial boundaries and situate themselves in relation to these boundaries by actively sniffing as they move through the forest. Similar group and social class distinctions are found in the Dassanetch of Ethiopia and the Suya of Brazil [36]. Classen goes on to describe a range of beliefs and traditions surrounding odour and spirituality, such as how personal odours are the essence of life in the Ongee peoples of the Andaman Islands, and that the stench of death is attributed to the spirit leaving the body. Because evil spirits seek out body odours, Ongee take care to walk in single file through the forest, mixing their odours so they are not isolated and therefore vulnerable [37]. To the Amazonian Desana, the odour of women's menstrual blood is so offensive that it attracts snakes and threatens crops; to the Dassanetch, it is neutral and natural, but post-menopausal women smell foul [36].

An interesting theme surrounds a recurring concern for preserving odour integrity. To the Batek people of Malaysia, food odours should never be mixed because this would undo the work of the deities who made them different [38]. Other groups have different beliefs resulting in the same principle, such as the Desana never cooking together 'male-smelling' meat and 'female-smelling' fish, because this would be tantamount to adultery [38]. Among other groups, there is similar symbolism regarding the mixing of individual body odours. For example, among the Yaka of Zaire, a term that means 'smelling one another' is in fact a description of sexual intercourse, while the afore-mentioned Tukano-speaking peoples, with their distinctive group odours, believe that marriage partners should come from different odour categories [32]. Furthermore, according to the Semaq Beri of Indonesia, a brother and sister must maintain a sufficient inter-personal distance so that their odours do not mix; if they do, this would be considered to be incest [39]. These latter examples appear to be consistent with current research on a role for odour in mediating disassortative mate preferences [40], as it does in other vertebrate taxa [41].

Odour clearly continues to be a central feature in these respective cultures, directing and shaping associated beliefs and behaviour. By contrast, its effects *seem* to have been significantly reduced or lost from the same behaviours in WEIRD societies. However, this is almost certainly the consequence of a lack of research on olfactory awareness and its uses in communicative contexts in societies which generally believe or present themselves as scentless. Nonetheless, when thoroughly (albeit still rarely) assessed, individuals in WEIRD societies show evidence of great attention and reactivity to body odours in communicative contexts (e.g. [42–44]).

3. Western, educated, industrialized, rich and democratic people are also old, deodorized and desensitized

We have argued above that a WEIRD bias may be partly responsible for the prevalent views that humans have poor olfactory acuity and that odour is minimally involved in human social interactions. But why this should be so is not immediately obvious, as there is nothing in any of the characteristics that constitute the acronym that directly or explicitly link to smell. We therefore suggest that views on human olfaction are based on three further characteristics that co-occur in WEIRD societies: both researchers and participants tend to be relatively *old* (i.e. prevalently adult), and they tend to live in societies that have become *deodorized* and *desensitized* to odours (ODD). That is, WEIRD people also tend to be ODD.

(a) Olfaction is critical during childhood

Experimental evidence on human olfaction is overwhelmingly based on participants who are of undergraduate age, or older. We suggest that this may lead to an underestimation of the true significance of human olfaction. This is not to say that we think olfaction is unimportant in adults; indeed, the examples from other cultures that we outline above are predominantly based on observations from adults. However, the most critical adaptive benefits of olfaction are arguably to be found during infanthood and childhood, and we suggest that these tend to be underappreciated by adult researchers who most typically study adults.

A fuller exploration of olfaction during childhood is provided elsewhere in this issue [45], but we know that olfactory learning begins *in utero*, as very young infants can discriminate odorants associated with aromatic food items to which they were exposed in amniotic fluid, having been ingested by the mother before birth [46,47]. Furthermore, odour appears to play a central role in the ability of infants to find and latch onto the nipple in the critical first hours and days after birth. It has been argued [48] that this maternal–infant olfactory signalling context represents the most likely opportunity for finding and characterizing a human pheromone, analogous to the mammary pheromone of other species [49], precisely because the selective benefit of such a signal is so clear and vital [50]. Beyond these initial vulnerable days of infanthood, it is likely that smell could continue to play a fundamental role not just in learning about novel food items, or avoiding spoiled foods and environmental hazards, but also in the development of social relationships with carers and friends and in the shaping of future preferences for sexual partners. These social effects may well reach a zenith around puberty,

as surges of sex hormones lead to sexual maturation and concurrent activation of sexual interest, as well as activation of sebaceous and apocrine glandular activity that produces sex-typical adult body odour [51].

What this brief summary makes clear is that the most potent involvement of odour in human behaviour may have already occurred before an individual reaches adulthood. Just as studying westerners may fail to provide a complete and representative assessment of any capacity or behaviour in our species as a whole, a developmental bias may paint an equally misleading picture. In the light of abundant evidence for odour being important in shaping developmental and behavioural trajectories in other mammals, and a growing body of work demonstrating analogous effects in humans [45], it seems indisputable that future discoveries in this area will contribute to a growing appreciation of the critical role of olfaction in human behaviour. However, the importance of these multiple effects is certainly challenging to study, especially in infants, and the extent of their long-term influence is also difficult to gauge.

(b) The deodorized ape

If the Ongee and other groups view personal odour as the essence of life, the embodiment of one's soul [37], then most westernized humans take a decidedly different view. It is often socially undesirable, even unacceptable, for one's body odour to be detectable by others. This is problematic for a species that produces odorous secretions from many parts of the body. Indeed, humans appear to possess more scent-secreting areas of the body than any other ape, leading the zoologist Stoddart [51] to describe us as 'the scented ape'. In consequence, at least in many cultures, we have become so assiduous in our efforts to eliminate body odour that perhaps we would be better described as 'the deodorized ape'.

Strategies towards this goal are many and varied. Global consumer surveys indicate that people in urbanized countries bathe many times a week on average, and often daily. Clothes are often worn only once between washes. In many countries, it is common for men and especially women to remove axillary, leg and pubic hair, either regularly by shaving or permanently through laser depilation that destroys hair follicles [52]. Teeth cleaning and use of mouthwash is practised two or more times each day. The use of underarm bactericidal sprays is at least a daily activity for many [53]. Such sprays target the commensal skin microflora that are responsible for generating most of an individual's personal odour, altering the microbial populations present on the skin and, along with hair removal, reducing their absolute abundance. Finally, having so thoroughly removed their own natural odour, westernized urbanites then commonly attempt to 'reodorize' by replacing it with pleasing scents, using artificial fragrances based on animal, floral, herbal and similar odorants.

It is hardly surprising, then, that natural body odour is overlooked as a means of communicating social information. Indeed, it seems paradoxical to suggest that it could be. However, there are two important modulators that may help to explain how body odour remains useful in this regard, even in deodorized-reodorized populations. The first relates to the freshness and intensity of the odour: pungent breath or stale underarm odours are each associated with poor hygiene and are frequently considered distasteful, while relatively fresh personal odour has a different quality and lower intensity and may be perceived more positively [54]. Second, the social context in which body odour is perceived is critical. Even these fresher odours may be unpleasant when they emanate from strangers or where social connections are remote, but those of family and partners are more positively perceived, at least as emotionally neutral and perhaps even as pleasant. For example, parents and others appreciate the smell of an infant's head and indeed this activates reward centres in the brain [55]. Infants appear to be attracted to the odour of their mother, particularly from the breast and axillae [45,56,57]. As adults, we learn and appreciate the odour of our loved ones, especially partners [58]. Contemporary lovers may recognize the sentiments expressed by poets since highest Antiquity [59,60] and that led the sixteenth-century English poet Edmund Spenser, having compared his lover's body to a garden of various flowers [61, p. 84], to end

> Such fragrant flowres doe give most odorous smell, but her sweet odour did them all excell.

These examples of attraction, pleasure and desire require intimate experience of the other individual, as well as some learned positive association with that person. Importantly, they are often evoked by body odour alone, even when unadorned by artificial fragrances. Reodorization with fragrances might thus be expected to interfere with these processes, potentially altering the ability for any communicative functionality or re-encoding it into a semantic system conveyed by human-made odour signals. At the very least, it would seem to require the formation of a separate association between the target individual and their favoured perfume, in addition to and alongside the one formed with their underlying natural odour. This would be the case even though fragrance choice may be based on the interaction between the fragrance and the user's own odour, rather than being arbitrary or solely related to the directly perceived aroma of the fragrances themselves [62,63]. In other words, a specific fragrance may be preferred because it complements the underlying personal odour better than competitor fragrances; even though the resulting blend might not disrupt transmission of relevant social information as much as a different blend involving another fragrance, it remains a novel odour that requires additional processing with perhaps at least some loss of biological information flow.

(c) Desensitization

Westernized humans may not only be deodorized, but also desensitized, in the sense that their perceptual ability to detect, discriminate, interpret and describe important odours may be below its true potential as a result of suboptimal social and environmental conditions for the acquisition of related olfactory expertise. Many sources of desensitization may act on olfactory cognition at higher or lower integrative levels.

First, socio-cultural conditions may lead to (i) ontogenetic desensitization, through the lack of systematic educational practices involving olfaction, compared with vision (shapes, colours), audition (music), and even touch (fabrics), which are actively taught from late infancy; (ii) technological desensitization, for example through methods of food preservation and labelling (pasteurization, refrigeration, peremption dates) that abolish the need to continuously sample freshness or to test the safety of foods [64]; and (iii) normative desensitization, through repression of overt sniffing behaviour towards others or oneself, as well as minimizing the intensity of one's own body odour.

Second, an individual's biosocial condition may further aggravate or modulate this desensitization process, leading to asymmetrical effects as a function of gender. For example, women appear to be either less desensitized or more sensitized than men [65], probably because they are culturally induced to be more concerned by odour-related safety and cleanliness issues for themselves and those who depend on them [66], especially at certain stages of their reproductive career (e.g. mating, pregnancy, parenting) [44,67,68].

Third, the side effects of pollution in ever-expanding urban environments may bear massive desensitizing consequences on populations. One way in which this comes about is through direct effects of pollution on olfactory function. For example, Hudson *et al*. [69] compared long-term residents of highly polluted Mexico City with a matched sample of participants from the relatively unpolluted Mexican state of Tlaxcala. The latter group were able to detect odours at lower concentrations, were more successful at distinguishing between odours and had a lower proportion of participants (2% versus 10%) who were judged to have poor olfactory function. Individuals exposed to dust and noxious fumes following the 2001 attack on the World Trade Centre had profoundly reduced olfactory and trigeminal nerve sensitivity, two years afterwards, compared with age-matched controls [70]. Evidence may not be limited to such extreme examples of localized pollution, however. In the afore-mentioned studies by Sorokowska *et al*. [29,30], the relative olfactory sensitivities in Cook Islanders, Tsimane, and urban Germans reflect their respective levels of air quality, but none of these are nearly so extremely affected as Mexico City. Our olfactory processing may be profoundly sensitive to these environmental perturbations [71]. Indeed, we know that pollutants may not only affect the peripheral olfactory system through damage to the olfactory epithelium [72], but also processing within the olfactory bulbs [73].

As a result of each of these influences, people in westernized and industrialized societies might simply use the sense of smell to a lesser extent. In turn, they may be less sensitive to odours through lack of exposure and lack of practice in responding appropriately to them. This is in line with the argument that there is a strong cultural component to reliance on olfaction [74], and that was brought to explain markedly better odour-naming ability in hunter–gatherers compared with neighbouring horticulturalists who share a similar language [39].

If this argument has merit, then increased practice in olfactory laboratory tasks should lead to improved performance. Earlier work reported evidence both for and against this claim, perhaps owing to widely variable methodologies. However, a meta-analysis of 13 studies, all using a standardized form of testing and with a combined total of over 1000 participants, found evidence for large effect size improvements in odour identification and discrimination, and small-to-moderate improvements in sensitivity threshold (e.g. [75,76]). Other studies report training effects using other odorants and other tasks; for example, several days of practice improved the ability of adults to detect and follow a trail of chocolate odour across a grass field, as assessed by both increased movement speed and reduced lateral deviation from the trail [19]. It is important to note, however, that although training effects appear to be relatively strong and can take effect very rapidly, they influence detection and discrimination only of the specifically trained odorants and do not generalize to an improvement in overall olfactory performance [77,78]. We will return to this point below.

(d) Chemical communication in old, deodorized and desensitized people

Recognizing that WEIRD people are also ODD has several implications for appraising the nature and extent of human olfaction. In general terms, each of the three primary characteristics of ODD people directly compound the impression that humans have relatively poor olfactory function, and each also provides a mechanism for understanding why poor olfactory functioning might be seen as a WEIRD phenomenon.

More specifically, these three primary characteristics—old, deodorized, desensitized—contribute to the impression that social communication via odours produced by the human body is of minimal importance. If such communication does occur, it is likely to be especially critical in infants and children relative to adults, even if it is also important in adults, both because it might have immediate life-and-death consequences for vulnerable infants and because it may influence long-term developmental trajectories or future behaviour. Yet, olfaction in younger people is much more challenging to observe, study and appreciate. Then, the trend towards deodorizing–reodorizing bodies to conform with culturally acceptable local norms reduces the salience of body odour, possibly leading to momentarily less pervasive or potent odours. Finally, desensitization means that we are less able to detect and respond to such odours, even when they are present in the appropriate context.

The three ODD characteristics may also interact to further compound the overall effect. For example, reduced sensitivity to odours via lack-of-practice effects may be exaggerated by bodily deodorization–reodorization. People may therefore have insufficient experience with natural body odours to make the kinds of nuanced social judgements that we might observe in other societies or other species, even if they would otherwise have that potential in different cultural settings. Meanwhile, the fact that both these effects may be in operation early in life might hide even further from view the role of odour in children's development, perhaps especially at puberty when the hygienic processes involved in deodorization–reodorization start to become a daily ritual [79].

Lack-of-practice effects for body odours may perhaps be further overlooked because we do continue to place value on and attend to other kinds of common smells that are associated with food, beverages or environmental hazards. Bearing in mind the odour-specificity in training effects noted above [77,78, but see 76], even significant experience and expertise with such other odours may not necessarily transfer to the kinds of compounds found in body odours. This might again lead to a wide and biased under-appreciation of the communicative value of body odours: we might feel we can appreciate the delicate differences between the fragrances of different flowers, perfumes or wines because we sample them often, while at the same time we struggle to distinguish even between members of our own species, because we sample so few of them and so infrequently. Indeed, it is interesting that while experienced 'noses' in the fragrance industry are capable of transferring their wide vocabulary of fragrance descriptors to describe axillary odours in a way that untrained people would find impossible, they appear to be no better at the

apparently more simple task of identifying the sex of those whose odours they describe [80].

These points highlight important questions regarding human social olfaction. To what extent do body odours influence human social interactions? Is the potential for olfactory communication limited to certain cultural settings or social contexts? What are the mechanisms involved in both emission and perception of naturally produced body odours? What kinds of information might be communicated and what are the limits of such communication? How do such chemocommunicative processes interact with information mediated by the other senses? Are there practical applications that could be developed using answers to these questions?

4. Current perspectives on human chemical communication

We are still some considerable way from providing a comprehensive answer to any of the questions posed above. The papers in this theme issue provide a unique overview of the current state-of-the-art, drawing on a range of inter-disciplinary perspectives and expertise, and highlighting the kinds of approaches and opportunities that might in the future be exploited to provide the necessary answers.

(a) Situating human chemical communication

The first paper highlights the extraordinary potential for social olfaction. Imagine, if you will, a diurnal species of primate that is mostly terrestrial, lives in relatively large mixed-sex groups, and regularly mixes scents and applies them to its body with the purpose of influencing others. We refer, of course, not to humans but to ring-tailed lemurs (*Lemur catta*). As Drea [26] describes, their exquisitely elaborated repertoire of chemical signals greases the wheels of lemur society, providing critical information about identity, genetic diversity, relatedness, health, social dominance and sexual receptivity and history. This information is deliberately broadcast both by scent-marking on vegetation and during 'stink fights' by wafting scents into the air via secretion placed on their striking tails. It is also actively sought out by others: scent signals are rapidly approached and carefully investigated. Drawing further on a comparative review of 19 species, Drea [26] constructs an evolutionary framework to account for the diversity of olfactory specializations across the strepsirrhine primates. She also outlines current knowledge on the mechanisms involved in olfactory communication, including the underlying chemical variation in certain odour signals and the involvement of cutaneous microflora in shaping these signals. In doing so, she introduces us to a world in which olfaction is socially critical, providing a stimulating picture of what is *possible* in the olfactory signalling system of a group of primates.

By contrast, the paper by Arshamian *et al.* [81] charts a limitation in human olfactory experience, which is that we often appear to find it especially hard to describe things we smell, compared with things that we see or hear. This is despite recent evidence from Majid herself that certain communities have far richer olfactory language than others [39]. The paper proposes a novel explanation, that labelling odours is difficult in humans largely because olfactory imagery is limited by a lower degree of embodiment of the olfactory sense compared to vision and sound, and because there is lower access to olfactory sensory primitives, the shared descriptors we use to communicate about sensory stimuli without referring to the source of the odour. As a result, olfactory representation and imagery are lower because people have reduced opportunity to learn how to do this across the lifespan, compared with other senses. The proposal receives support from data in Dutch adults and children aged between 9 and 12 years old, which shows that while the vividness of visual and auditory imagery develops with age, there is an absence of comparable development in olfactory imagery.

Talking about smell, then, may be especially difficult, but to what extent is smell involved in non-verbal communication? Evolutionary models of communication [82] incorporate the transfer of information between a 'sender' and a 'receiver', even if the behavioural actions involving in sending and receiving the information are not manifested as obviously as in ring-tailed lemurs. Accordingly, the issue includes three papers that focus on odour production by 'senders', followed by three papers on issues of odour perception by 'receivers'. We then turn to specific functional areas of inquiry, with 10 papers on different aspects of maternal–infant communication, on the potential role of odour in human mate choice, and on how odour might communicate emotion and disease. Finally, a position paper outlines pitfalls from the past and prospects for the future in human chemical communication, against the wider context of the replication crisis in psychology and other disciplines.

(b) Odour production

To begin the section on odour production, Natsch & Emter [83] outline what we currently know about the source and initial production of human body odours. Secretions from apocrine and other cutaneous glands in the axillae or elsewhere do not usually have an intense odour when they are first emitted; their characteristic odour derives from their breakdown by the skin's commensal microflora. The paper describes the biochemistry of odour production through the action of bacterial enzymes, which has become clear only in recent years, and presents for the first time, to their knowledge, the crystal structure of *N*α-acyl-aminoacylase, revealing some of the intricacy of bacterial adaptation to their human hosts. In addition, by exploring results from twin pairs, individuals genotyped at genes in the major histocompatibility complex (MHC), and individuals from East Asian populations lacking a gene associated with characteristic armpit odour, they address key mechanisms underlying potential for revealing genetic information via body odour.

Understanding and describing the chemical composition of any given odour signal has proved remarkably challenging in the past. The next two papers introduce very different approaches from entirely separate disciplines that offer novel potential for the future. Radadiya & Pickett [84] draw on insights and techniques from research on insect pheromones, where there is a long track record of successful identification of specific chemical compounds responsible for eliciting defined behaviours. One such approach is to use live electrophysiological recordings from the antennae, or even single neurons, of haematophagous insects (e.g. mosquito) to detect and respond to components of human odour. They further speculate that human olfactory receptor proteins might be transferred into 'empty' neurons of *Drosophila* to study responses to given human odours, potentially enabling identification of functional

chemical signatures. Finally, they outline ways in which biosynthetic approaches currently used in insects might be used to manufacture functionally active compounds in humans.

By contrast, Roberts *et al*. [85] introduce techniques that are routinely used in atmospheric and environmental chemistry for quantifying ambient airborne volatile organic compounds. They first describe how proton transfer reaction time-of-flight mass spectrometry (PTR-TOF-MS) may be used to record changes in odour chemistry in real time, and then outline how analytical solutions such as positive matrix factorization may be employed to cope with the rich multivariate datasets that PTR-TOF generates. As they discuss, these techniques have enormous potential to transform our ability to characterize functional odours as they respond rapidly to external stimuli and changes in social context.

(c) Odour reception

Turning from the source of odours, three papers cover different issues from the receiver's side. First, Williams & Ringsdorf [86] bring further insights from atmospheric chemistry to suggest a new hypothesis for variability in human sensitivity thresholds across different volatile organic compounds. They propose that the threshold for a given compound may be primarily explained by its atmospheric lifetime, such that compounds with short lifetimes are more easily detected by the nose. They suggest that this could be an evolved relationship because, for example, compounds of anthropogenic origin do not fit the pattern as well as might be expected. Their idea produces testable predictions regarding human chemosignals: those that communicate information over great distance or that need to persist for longer (e.g. a signal of fear) should have longer atmospheric lifetimes and thus higher thresholds compared with those that operate at very close range and have shorter lifetimes (e.g. between mothers and infants, between intimate partners).

Then, Perl *et al*. [87] examine olfaction at very close range, namely the act of self-sniffing hands. They argue that very high rates of face-touching provide a way in which humans sample the odour of their own bodies and of those they have touched. While they have previously focused on the latter, how smelling one's hand after a handshake may be a form of individual assessment during greetings [88], here they speculate on the potential benefits of smelling oneself. Based on preliminary data, they argue that humans self-sample often, from different parts of the body. Although we are aware that we do this, such behaviour may covertly or subconciously provide continual updates on our emotional and physiological state, and be used to compare with the odours of people we interact with.

In the final paper of this section, Oleszkiewicz *et al*. [89] examine the consequences of olfactory loss. There is existing evidence that olfactory impairment affects individual well-being, but it is usually difficult to be certain that reduced functioning is directly responsible because the evidence is based on those who have already been clinically diagnosed. Here, data are presented from a German sample of about 200 individuals that included those with both normal and impaired smell, but where all believed they had normal olfactory function. There is no between-group differences in self-reported wellbeing, suggesting that wellbeing is only measurably affected in those who note their sensory impairment and seek treatment for it. However, there were between-group differences in reported awareness of how odours trigger emotions, memories and evaluations. Those with impaired smell formed fewer odour associations with feelings and memories. This included the formation of associations between body odour and their liking for partners, meaning that it could potentially have consequences also for their social relationships.

(d) Communication between mothers and children

In this and the following two sections, papers explore odour communication in specific social contexts. Schaal *et al*. [45] begin, providing a thorough review of the rapidly expanding literature on how maternal odours are central to the life of the developing infant. The relationship with the mother's odour starts even before birth, as babies learn the smell of the amniotic fluid and of foods she ingests, and becomes especially critical in the hours following birth, facilitating the process of finding and latching to the breast and accessing colostrum. As they argue, the relationship between mother and child is an ongoing olfactory process wherein learning at one life stage prepares the groundwork for the next, so that odour learning at the breast represents only the beginning of a continuing role of scent in the child's relationship with the mother, as well as its social relationships with others, across its childhood and beyond.

In their paper, Schäfer *et al*. [90] focus rather on the maternal perception of their child's odour. They present new data from a large sample of mothers and children, all of whom had been human leucocyte antigen (HLA) genotyped. Mothers were tasked with rating five body odours from children, one of which was their own. The other four were sex-matched unfamiliar children, varying systematically in HLA-similarity (two dissimilar to their own child, two similar) and age (two the same age, two of a different age). The results show that mothers could identify their own child's odour at rates better than chance, and rated their own child's odour as more pleasant. Interestingly, HLA appears to be involved in odour preference judgements—the HLA-similar, age-matched child tended to receive the next-highest pleasantness scores—but not identification, which thus appears to be determined by other factors. Preference for their own child's odour was highest in those mothers whose child was still very young, and decreased across the age range. Mothers of pubertal boys rated their own son's odour as less pleasant and this reduced pleasantness was predicted by their son's testosterone levels, whereas this correlation did not hold for unfamiliar boys or for ratings of girls. This latter result emphasizes how body odours may influence social interactions in complex and context-dependent ways, perhaps especially as individuals transition across puberty and odours begin to become relevant for mate choice [79].

(e) Communication between potential partners

As Ferdenzi *et al*. [91] suggest, choosing between partners is the most widely researched context for human olfactory communication to date. However, they argue that, even here, there remain significant limitations in our understanding. In light of this, they outline five key challenges for future research in this area. First, they suggest that we need to expand our scope of inquiry from axillae to odours from other parts of the body, and they present preliminary evidence to suggest that odours from the head and face may be perceived differently from axillae, at least in men. They also advocate further focus on addressing the chemosensory mechanisms underlying inter-personal judgements, testing and investigating in different cultures, and accounting

for cultural practices such as fragrance and hormonal contraceptive use. Finally, they call for an increasingly inter-disciplinary approach, drawing on expertise from neuroscientists, microbiologists and others. Their paper therefore stands as an excellent and wide-ranging summary of current knowledge as well as providing a stimulating roadmap for the future.

Havlíček *et al*. [40], in contrast, concentrate on a specific putative role of MHC-associated odours in mate choice, the possibility that odour preferences influence disassortative mating patterns. Although such an effect is widely posited, evidence remains mixed and controversial. In their paper, they assess this evidence in a series of meta-analyses, separately addressing available evidence for disassortative mate selection in actual couples, effects on relationship satisfaction, and experimental studies of odour preference as the mechanism underlying the previous two effects. These analyses suggest no consistent detectable effects of MHC on human mate selection. However, as with Ferdenzi *et al*. [91], they also provide a set of recommendations for future studies to more conclusively address outstanding questions. In particular, they point to a geographical bias of previous studies and call for more diversity in sampled populations, as well as for more work on potential mechanisms of preference and on more sensitive measures of outcome such as MHC-associated pregnancy loss.

(f) Communication of emotional state and disease

Moving beyond mate choice, four papers address ways in which odours may have influence in other types of social interactions. In particular, the possibility that odours communicate underlying emotional state is receiving increasing levels of attention. In their paper, de Groot *et al*. [92] explore fearful odours. Unlike previous studies, which tend to compare odours from the same individuals in different emotional states, here they provide new data to investigate whether and how odours may inform receivers about the relative intensity of the experienced emotion. Based on both physiological measures and subjective reports, those who experienced relatively high levels of fear while watching scary scenes also produced more sweat and higher quantities of volatile organic compounds. This demonstration of a dose–response relationship between the intensity of experienced emotion and intensity of odour paves the way for much more detailed studies in future across the range of emotions.

Pause *et al*. [93] examine odours of people in aggressive contexts. Participants provided odours while being tested in computer games in which responses were linked to overt aggression and resulted in higher testosterone levels, and during game-playing in a control condition. These axillary odours were then presented to receivers while brain activity was recorded using electroencephalography and source localization. Following exposure to the aggressive odours, increased activation in the dorsomedial prefrontal cortex was observed, an area that appears from previous work to be involved in social cognition, especially evaluation of others and response to threat. Responses were higher to male odours than female odours, and in female than male receivers. Such a pattern is striking and consistent with expectation in finely tuned responses to levels of perceived threat.

The paper by Fialová *et al*. [94] follows neatly on that by Pause *et al*. [93] by investigating the odour of winning and losing fighters in mixed martial arts contests, arguably the most aggressive sport in existence. Odours were sampled from fighters about 1 h before and after a contest, and subsequently rated by unfamiliar individuals on several hedonic scales. The general prediction is that winners should have more pleasant odour than losers, an expectation arising from the animal literature in which conspecifics tend to prefer the odours of dominant individuals, who by definition have a track record of winning aggressive encounters. In the fighters, odours were judged to be more masculine, but less pleasant, attractive and intense, after the contest, regardless of the outcome. However, the results suggested that losing may lead to a particular reduction in ratings of odour pleasantness, as predicted, and is a further demonstration that human raters are capable of discriminating socially relevant cues from odour.

The last paper in this section, by Sarolidou *et al*. [95], addresses a similar question, this time whether people can discriminate cues of illness from body odour. To do this, Sarolidou *et al*. collected axillary odours from 22 individuals before and after a systemic and transient inflammation was induced through injection of an endotoxin lipopolysaccharide (LPS), and before and after a placebo injection, with each treatment being carried out a month apart and in counter-balanced order. Subsequent assessments demonstrated that receivers attributed lower 'liking' scores for odours of individuals following the LPS injection, and that the observed pattern of responses was comparable with that recorded for ratings of facial images collected concurrently with the odour samples: olfactory cues were as good as visual cues in discriminating ill health. As such, olfaction may form an important factor in behavioural immunity.

5. The way forward

In the final paper of this issue, Wyatt [96] reflects on the state of human chemical communication research and the way forward. As in other disciplines, there are some salutary tales of research built on unstable foundations; Wyatt briefly outlines and critiques some of these, picking up particularly on the line of research focused on androgen steroids as putative human pheromones which he has dealt with more thoroughly elsewhere [48]. He goes on to describe the reproducibility crisis in psychology, the steps that have been recently taken to address it, and how human chemical communication research, in particular, might learn from these lessons and improve the quality of research in the coming years. Some general recommendations would apply across fields, including pre-registration of planned studies, and meta-analysis and replication of previous studies to verify earlier published conclusions. Others are peculiar to chemical communication research, such as more careful consideration of the ecological validity of odour experiments, the use of realistic stimulus concentrations, novel approaches used to analyse odour chemistry and focus on the right kind of molecules. The latter, as he points out, also means withdrawing focus from the wrong kind, such as 16-androstenes and copulins, attention towards which may have been uncritically extrapolated from non-human species.

We wholeheartedly agree, but we would also add two further points that emerge from a wider consideration of the papers that incorporate this special issue. The first is to echo the call by Ferdenzi *et al*. [91]—their fifth challenge—for further inter-disciplinary efforts to address key outstanding questions. The nature of human chemical communication means that

insights from multiple disciplines are needed, including chemistry, genetics, microbiology, neuroscience, physiology, psychology, anthropology, ethology, zoology and evolutionary biology. Indeed, these disciplines are all represented in the papers that make up this special issue, and many individual papers draw insights from more than one specialist area. We think this is exciting and holds great promise. Not only will such collaborative effort help us to address the outstanding research questions in olfactory communication (e.g. [97]), but it will also be directly useful in developing other non-signalling applications of an understanding of human odour. For example, these include aspects of medical diagnostics (e.g. detection of tumours and other diseases), in the behaviour of parasite vectors (e.g. mosquitoes, ticks) that use body odour to find and select potential hosts, in the potential for using odour to develop new biometric applications, and in the interactions between odour and artificial fragrances to promote individual-tailored perfume and cosmetics.

The second point is to return to the one that we made at the outset, that most research to date has focused on people who are ODD. While the papers in this special issue capture the diversity and excitement of recent advances in human chemosignalling, it has not escaped our attention that many of the papers in this issue have the same focus on ODD societies, although some also make the same point as we do (e.g. [40,45,81,91]). It has become abundantly clear that this is an essential issue but addressing it will require a considerable effort and investment from researchers and funding bodies. Only then will we be able to assess the full nature and value of human olfactory communication.

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