Chapter 14
The Perfume-Body Odour Complex: An Insightful Model for Culture–Gene Coevolution?

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Abstract Olfaction is involved in various human social interactions, ranging from mother-offspring attachment to mate choice; as in other species, such chemical signalling is thought to be shaped by evolution. However, across many human cultures, individuals manipulate their body odour by means of various fragrances and these may significantly affect the outcome of social encounters in a context-specific fashion. Here we employ the framework of dual-inheritance theory, which advocates that cultural practices should be incorporated into the analysis of evolution of human behaviour, to explore cultural means of olfactory signalling such as ethnic and status markers. Further, we review studies showing that perfumes interact with body odour in an individual fashion and that people tend to choose perfumes according to their genetic make-up. This indicates that biologically evolved chemical signalling might operate in concert with cultural human practices. Finally, we propose two scenarios: (1) how culturally based preferences and use of perfume might impact gene frequencies in individual populations, and (2) how evolved cognitive biases might affect selection of scents that are appropriate for body adornments. This, in our view, makes the perfume-body odour complex a potentially insightful model for culture–gene coevolution.

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14.1 Biology of Human Semiochemistry

Humans, like other vertebrates, emit from their bodies a variety of aromatic chemical compounds that can be perceived by others and thus become involved in communication processes. Body odours can be categorised as cues of: (1) individuality and relatedness; (2) reproductive state; (3) affective state; (4) individual quality; and (5) genetic complementarity. These phenomena are reviewed elsewhere (e.g. Havlicek et al. 2010; Lenochova and Havlicek 2008; Havlicek and Roberts 2009; Roberts and Havlicek 2012). Here we detail the richness of human semiochemistry in two areas: (1) how affective states may be communicated via body odours, and (2) how genetic complementarity affects body odour preferences in mate choice.

In a classic study, Karl von Frisch (1938) found that skin damage in European minnows causes a flight reaction in conspecifics. The phenomenon later described as an alarm pheromone is present in many other social species, e.g. in black-tailed deer (Müller-Schwarze 1971). Inspired by these findings, researchers have tested whether affective states might also be communicated in humans. Although there is ongoing debate about whether these should be called cues or signals, evidence supports the idea that affective states can influence body odours in a way that can be perceived by others. Axillary odours collected from individuals when they feel socially anxious induce a higher startle reflex and this reaction is specifically pronounced in individuals scoring high in social anxiety (Prehn et al. 2006). The startle reflex is used as an indicator of individual alertness. Similarly, smelling "anxious odours" increases the state of anxiety in others (Prehn-Kristensen et al. 2009). Individuals also tend to use more risky strategies in experimental games after exposure to 'anxious' odours (Haegler et al. 2010), while Adolph et al. (2010) reported that body odours collected under a competitive situation (a badminton match) tend to increase skin conductance in individuals smelling them. Communication of affective states by body odours is a fascinating and fertile area that will yield further exciting results.

Another principal context in which human chemical communication takes place is within mate choice. Studies in several vertebrates show that odour cues provide information about genetic make-up of conspecifics (Bernatchez and Landry 2003). Particular attention has focused on the link between odour and genes in the major histocompatibility complex (MHC). The MHC is extremely variable, with hundreds of different known alleles in some human loci. MHC gene products play a critical role in vertebrate immune functioning by discriminating between self/non-self molecules. Higher MHC-heterozygosity, and thus vigour, in resulting offspring is achieved by individuals often preferring MHC-dissimilar sexual partners (Apanius et al. 1997). This is also true in humans: in a pioneering study, Wedekind et al. (1995) found that women judged as more attractive the axillary odour of men whose MHC was dissimilar to their own. This finding was further supported by several other studies (Wedekind and Füri 1997; Santos et al. 2005; Thornhill et al. 2003; reviewed in Havlicek and Roberts 2009). Interestingly, Wedekind et al. (1995) also found that women using hormonal contraception showed elevated preference for

MHC similarity. Shifts in preferences due to hormonal contraception were confirmed by a more recent study in women tested before and after initiation of oral contraceptive use (Roberts et al. 2008). Although MHC studies sometimes produce inconsistent results, may be context-dependent, and may be modulated by other factors, we concluded that the evidence suggests that mate-related odour preferences are associated with one's genetic make-up (Havlicek and Roberts 2009).

14.2 Universal Use of Fragrances

People can modify their body odour by using fragrances. Estimated sales in the fragrance and flavour industry ($22 billion in 2010: Leffingwell & Associates 2012) show that such tendencies cannot be overlooked. Is fragrance use a relatively recent phenomenon, perhaps linked to the perception of an association between strong body odour and disease, as described by Corbin (1988)? It seems unlikely given that scented oils were used in ancient Mesopotamia and pre-Roman Palestine. In ancient Egypt, fragrances were used to anointed mummies, cult statues, and participants of religious ceremonies, and women used fragrances for secular purposes as depicted on Theban tombs (Stoddart 1990). Ancient societies did not use distillation for perfume production but instead used oils as a base material. These were heated together with specific plants and then mixed with aromatic substances of mostly floral origin (Castel et al. 2009). Depictions on Rekmirekh's tomb, for instance, show perfumers mixing oils with resin and aromatic substances crushed in mortars and then heated in a cauldron to create aromatic oil (Brun 2000). Compared to Egypt, the use of aromatic compounds in Ancient Greece was of a more secular character and commonplace in the Classical period. It flourished in the Hellenistic period, becoming a well-established industry (Brun 2000). Perfumes were also popular amongst the Romans, with Campania as the centre of perfume production. Scented oils were commonly used during bathing, which was a sophisticated and lengthy procedure during which many important business contracts were made and political discussions held. In the part of the baths called the caldarium, aromatic oils were rubbed over the body. Romans also tended to control or forbid perfume usage (as in, for example, the general edict of Rome in 188 BC) as they were seen as seductive and immoral (Stoddart 1990).

Anthropologists report that, in diverse cultures and geographically distant regions, people modify their body odour with various odorous substances. An example is the Ongees, hunter-gatherers of the Andaman Islands (Pandya 1990), who believe each living creature (including humans) emanates smell that can be traced by malevolent spirits that cause disease or kill incautious individuals by eating their smell. To avoid this, Ongees decorate their face and body with red and white clay paints. Red clay is thought to warm the body and increases smell release whereas white paint cools the body and restrict sweating. Clay paint is used by pig hunters to ensure they are not smelled by the animals they aim to kill (Pandya 2007). Ancestral (i.e. benevolent) spirits are believed to identify their descendants by the

specific smell each person produces. A combination of visual and olfactory adornment by scented body paints is also performed by the Desana of Upper Amazonia and the inhabitants of the Kiriwina (formerly Trobriand) Islands of New Guinea. Another use of fragrances is illustrated by the Nauruans of the Southern Pacific, who place fragrant herbs on hot stones to produce aromatic steam which is thought to cleanse the body of bad smells and create a lasting perfume (Classen et al. 1994). Altogether, this evidence clearly indicates that olfactory adornment has been an integral part of human cultures in historical societies as well as cross-culturally.

14.3 Social Effects of Perfumes

Some regard the use of fragrances as a form of olfactory jewellery, adding extra cachet but leaving evolved routes of biological odour communication unaffected. Certainly, psychological studies provide relatively robust evidence that fragrances affect behaviour and social processes such as interpersonal assessment. For instance, formally dressed interview candidates are perceived more negatively when they use perfume compared to informally dressed candidates who after perfume usage were perceived more positively (Baron 1981). Fragrance use may also influence perception of masculinity and hence suitability for a managerial position (Sczesny and Stahlberg 2002). Fragrance can also influence perceivers indirectly via an effect on perfume wearers themselves. Roberts et al. (2009) filmed male participants after application of fragrance or a placebo substance. Observers of the videos rated fragrance users as more attractive even though they could not smell the targets, apparently because of reduced self-confidence in those given the placebo. Similarly, Higuchi et al. (2005) found a decrease in nonverbal behaviours labelled as non-symbolic movements (e.g. self-touching) amongst women wearing perfume during a mock interview; again observers rated perfumed individuals as more self-confident. Taken together, these studies convincingly show that perfumes indeed affect the perception of others, although the nature of the effects might depend on the context of the interaction.

14.4 Dual-Inheritance Theory

Although the use of fragrances is cross-cultural and widespread and affects both wearers and perceiver, there is robust evidence that body odour may cue various biological qualities. How might such apparently contradictory evidence be reconciled? Similar issues in other domains of human behaviour have been addressed by the dual-inheritance paradigm which we believe could also be a useful framework for the study of the fragrance-body odour complex. In essence, this theory takes account of the fact that, as well as inheriting genes, people also acquire beliefs, attitudes, and values through social learning (Richerson and Boyd 2006). The capacity for culture is then seen as a distinct complex of human adaptations.

From this perspective, a full understanding of human behaviour includes knowledge of local cultural practices (Henrich and McElreath 2007). It assumes that humans evolved various cognitive adaptations to learn cultural practices and symbolic systems; or as articulated by Henry Plotkin (2007): "Mankind's natural place is in culture, and culture is a part of human biology because it is our biology that gives us the ability to enter into culture". It also embraces formation of socially constructed systems which shape social reality and are based on mutual sharing, such as marriage, money, a police force, and so on. However, the existence of socially constructed beliefs should not be mistaken for arbitrariness of constructs as is currently thought by many social anthropologists. In contrast, theorists of cultural evolution suggest that human cognition related to cultural capacity was (or is) subject to natural selection (Boyd and Richerson 2005). This manifests itself in cognitive biases in social learning processes and the perception of others. It also suggests that various ways of signalling may take on the form of cultural practices. We will first focus on cultural aspects of chemosignalling and subsequently turn to the possible interactions that may exist between cultural and biological means of signalling.

14.5 Cultural Aspects of Olfactory Signalling

14.5.1 Ethnic Group Markers

Humans live in social groups of different size and complexity. Such groups, here labelled as ethnic groups, cultures or communities, can be identified by variation in beliefs, norms, religion, and other cultural practices (Boyd and Richerson 2005). Cultural group markers include language, dress, cuisine, and adornment. Derogation of other ethnic groups can include the attribution of dubious morality and even the status of full human-ness may be restricted to in-group members. In some cultures, body odours and fragrances are implicated in these prejudices: for example, attributing foul smell to people of other cultures due to their "wrong" way of living. The Desana people of Amazonia say that each tribe emits a specific odour, traceable to the territory they inhabit, and while walking through the forest they constantly sniff to see whether people of other tribe have been present (Classen 1992). It is not uncommon to classify "we" and "others" according to their odour, which varies by ethnic origin, or culinary, hygienic, and religious practices (Low 2005, 2009). These examples indicate that body odours and related scents could be salient cues of ethnic markers.

14.5.2 Status Markers

Social hierarchies are found within most human societies and again, fragrances may denote social status. A characteristic feature of status markers is their limited availability; in complex societies, this is frequently expressed through monetary cost

(compare this concept with the idea of 'honest signals' used in behavioural ecology). At least before the advent of synthetic perfumes, fragrances were scarce commodities: ingredients were typically specific plant parts (such as rose petals), which were seasonally or climatically restricted. In addition, the technology involved in their extraction, together with the blending art of perfumers, suggests the manufacturing process was restricted to a few individuals or sites. Add to this the relative instability of ancient perfumes, due to high volatility of some of the compounds and tendency of the bases (e.g. olive oil) to go rancid (Castel et al. 2009), and it is clear how high-quality perfumes became a significant part of trading networks (Brun 2000) and were expensive goods, affordable only to the upper classes, while others used scents containing lower quality ingredients. To more limited extent, this remains true today: the most favoured scents, such as aloewood in the United Arab Emirates market (Classen et al. 1994), are also very expensive. Furthermore, both unpleasant body odour and use of "cheap" perfumes is used to characterise the lower classes in modern Western literature (Largey and Watson 1972). Fragrances are thus interpreted according to cultural constructs of a particular culture, but nonetheless provide information which is also biologically relevant, such as group affiliation and social status.

14.6 Interaction Between Biological and Cultural Chemosignalling

So far, we have shown how socially relevant information is communicated either through body odour itself or through cultural practices of artificial fragrance use. Although we can intellectually distinguish between biological and cultural contributions, these cannot be separated in everyday experience because they are mutually interwoven, often in a highly complex manner. Here we present several scenarios for how cultural practices might interact with biologically evolved signals/cues.

Firstly, cultural practices might disrupt evolved preferences. In this scenario, cultural practices follow a different pattern than evolved preferences. For instance, men's judgments of women's facial (Roberts et al. 2004) or odour (Havlí ek et al. 2006) attractiveness varies across the menstrual cycle, peaking around ovulation. These changes are thought to reflect selection on male cognition; namely sensitivity to cues of female fertility. Cultural practices such as facial cosmetics and perfume may disguise or alter such cues, and hence disrupt male assessment of fertility cues (see Roberts et al. 2010).

Secondly, biologically evolved preferences might shape cultural practices. For example, some aspects of cosmetic use might exploit evolved perception/cognitive biases, such as the use of lipstick to enhance redness of lips, and foundation to obscure poor skin health or rouge to simulate it. Perhaps surprisingly, it might also shape an individual's perfume choice. It is frequently assumed that perfumes mask or obliterate underlying body odour, which would in turn lead to disruption of preferences as reviewed above. However, the only empirical evidence supporting this view is that perfume blurs accuracy in identifying the wearer's sex (Schleidt 1980). Furthermore, if this were the sole function of perfume use, it could not explain the

huge diversity that exists in individual perfume preferences. Such considerations have led to the idea that individuals might select perfumes which in fact complement their own body odour (Milinski and Wedekind 2001), raising the intriguing possibility that cultural practices might work in conjunction with, rather than in opposition to, evolved preferences.

Recently, we studied the perception of perfume-body odour blends, testing whether perfumes might mask or interact with body odour (Lenochová et al. 2012). We reasoned that if perfumes mask body odour, the same perfume applied to different body odours would result in a set of odours that were perceptually similar and characterised by the perfume itself. In contrast, if the perfume interacts with individual body odours, then it would have positive effects in some individuals and negative effects in others, while odour variability should be maintained or even enhanced. In two studies, male participants applied perfume to one armpit (the other was left untreated). They wore cotton pads in both armpits, and these were subsequently rated by women for their pleasantness, attractiveness, and intensity. Not surprisingly, the perfume-body odour blends were generally judged as more positive than untreated samples, but analysis also showed a significant interaction between individual odour and perfume treatment (perfume had no effect, or adversely affected odour perception, in some individuals) and treatment did not alter variability among samples. Not only do these results support the interaction hypothesis, but they also indicate that people may choose perfumes in an individual fashion to complement their own body odour. Thus, we then tested the prediction that an individual's body odour would be judged more positively when blended with the wearer's preferred perfume compared with one assigned by the experimenters. This turned out to be the case, even though there were no significant differences in the perceived pleasantness between the assigned and the preferred perfumes. Together, our experiments support the idea that fragrances, rather than simply masking body odour, interact with it in a complementary manner. This is consistent with Milinski and Wedekind's (2001) pioneering work which found an association between MHC-genotype and preference for perfume ingredients for a perfume to be worn by oneself (see also Hämmerli et al. 2012). In contrast, there was no link between assessors' MHC and perfume preferences when they selected perfumes for their partners. Anecdotal complaints by customers of perfume shops indicate it is difficult to buy perfume for someone else and perfumes received as a gift often remain unused, supporting the advice of professional perfumers that perfumes must be tried on for fit (Burr 2007). Our guess is that choosing a perfume for a partner may be more difficult than choice for relatives, who share similarities in body odour (Porter et al. 1985).

14.7 Body Odour-Perfume Coevolution

The sections above point to the idea that perfume and body odour create a mixture with an emergent perceptual quality, which is difficult to predict based on how they smell separately. While this interaction is itself fascinating for researchers in human

chemical ecology, we believe we can go even further and argue that it might also help us to understand underlying general processes in gene–culture coevolution.

As we have mentioned, individual communities vary considerably in the substances they employ for perfume production (in most of the speculations below we deliberately ignore recent trends such as technological advancement in global transfer of goods and production of synthetic chemicals used in perfumery: these phenomena appeared only very recently and one might not expect their immediate effect on biological evolution which operates on a much longer time scale). The absence of a specific ingredient in the perfumes of a particular community could be due to the following reasons: (1) the source of the odour is unavailable in the area and is not traded from neighbours. For example, we know that aromatic plants were an important commodity in trading networks in Ancient Egypt or Greece, but some of the scents routinely employed in that era in India were rare or absent in Mediterranean cultures. (2) The community is constrained by a technology. Some of the aromas can be extracted only using a specific technology which might not be available for or discovered by the particular community. In ancient Greece, for instance, ethanol distillation was not used and perfumers instead used mechanic extraction or enfleurage (Brun 2000). (3) Particular scents or their source (e.g. a particular plant) are believed to be inappropriate for body adornment. Such beliefs might stem from religious considerations.

Of course, there could be other reasons for a community not using particular ingredients, and the three we have described are not mutually exclusive. However, considering that only some scent ingredients will complement particular body odours (i.e. particular genotypes) and that a particular community employs only a restricted variety of scents for perfuming, it is plausible that some individuals may not be able to select a perfume which complements their body odour and may therefore suffer a social disadvantage. In the long run, the frequency of genotypes of such individuals would decrease in the particular community. This model of course assumes stability of preferences across generations which might not always be the case. However, as noted above, preferences for particular scents are not incidental and they are frequently part of broader beliefs and might thus be relatively stable. Furthermore, especially if there is preferential in-group mating, we might in consequence observe the differences in frequencies of genes linked to body odour as a result of culture-based processes.

In contrast, evolved cognitive biases in odour preferences might affect cultural beliefs about which scents are used for perfuming. Humans inhabit a world of an almost-infinite number of aromas, and in spite of relatively high cross-cultural variability, only a fraction of them are used for body fragrances. Aside from availability or technological constraints, this could be the result of evolved cognitive biases in formation of olfactory hedonics, restricting the pool of ‘acceptable’ scents (it is unlikely that any culture would use human excrement-resembling odours such as skatole, for example). Currently, most psychologists regard development of odour preferences to be the result of Pavlovian conditioning or associative learning (Herz 2006), but based on the kinds of evidence reviewed above, we find this overly simplistic and we predict that some biologically relevant odours will be conditioned

more easily than others. An example of this would underpin the preference for the odour of human milk in either breastfeeding or formula-fed infants, independently of previous experience with such odour (Marlier and Schaal 2005). If cognitive biases were at work, they might in the long run shape cultural practices.

What we hope to have shown here is that use and choice of perfume, a cross-culturally prominent behaviour which at first sight is largely culturally driven, is also strongly influenced by biology. Patterns of perfume use cannot therefore be fully explained if considered solely in the light of either genetic or cultural evolution. Both influences need to be taken into account because the substrate for selection is likely to be neither body odour in isolation, nor the perfume itself, but the blend of the two odour sources. This blend appears to have dynamic and individually variable emergent properties and is amenable to experimental manipulation. On this basis, we believe the perfume-body odour complex could become an insightful model for biology-culture coevolution.

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