Chapter 20

# Evolutionary psychology and perfume design

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## Human olfaction: the neglected sense?

In most mammalian species, smell is an integral component of successful intraspecific communication. From aardvark to zebra, olfactory information is signalled via urinary or faecal deposits, or through emanations of specialized secretory structures evolved for this purpose. Olfaction mediates social behaviour—from the effusive sniff-greeting ceremonies of group-living species like wolves to the ritualized naso-anal and naso-genital inspections of neighbouring territorial male antelopes (Gosling and Roberts 2001). In many cases, selection has shaped such signals to have specific properties, particularly in terms of potency, robustness, and longevity, so that signals can withstand degradation in extreme climates and persist to allow unambiguous interpretation by a signal receiver, often after a considerable time (e.g. Gosling and Roberts 2001). Indeed, some of these same properties have been recognized and exploited by perfumers, so that musk, castoreum and civetone, components of the sexual and territorial signals of the musk deer (*Moschus* spp.), the beaver (*Castor canadensis* and *C. fiber*), and the African civet (*Civettictis civetta*), respectively, have also been used for many centuries as ingredients in human fragrances (Stoddart 1990).

Mammalian olfaction underpins the two arms of sexual selection—via the assessment of competitors and mates and subsequent modulation of social interactions, it regulates the processes of intrasexual competition and mate choice (e.g. Gosling and Roberts 2001). Furthermore, in some cases, specific compounds within olfactory signals, pheromones, can interfere with the physiology and behaviour of other individuals in particular ways. The boar pheromone androstenone, for example, induces lordosis in females, a characteristic mating posture (Signoret and du Mesnil du Buisson 1961). More insidiously, major histocompatibility complex (MHC) class-1 peptides present in male urinary scent marks are responsible for mediating pregnancy block in rodents (Bruce 1959; Leinders-Zufall et al. 2004), while other compounds manipulate female oestrus condition to the male's advantage (Whitten 1956).

Against this background, humans have appeared to be rather an exception, a primarily visual species in which olfactory abilities have largely been lost. Indeed, there are only about 10 million olfactory receptor cells in the human olfactory epithelium, compared to about 230 million in dogs (Schaal and Porter 1991), such reductions being partly due to changing facial architecture and reduction in size of the snout through the positioning of the eyes for depth perception, and through other changes associated with bipedalism (Jones et al. 1992). In terms of olfactory receptor genes, humans possess approximately 1000, of which two-thirds are non-functional or pseudogenes (Glusman et al. 2001; Menashe et al. 2003), compared to mice in which a much larger fraction (around 1100 of 1300 genes) are functional (Young et al. 2002).

However, the assertion that humans are especially microsmatic (that is, relying little on sense of smell) has been increasingly questioned in recent years (e.g. Schaal and Porter 1991, Shepherd 2004) on the basis that humans exhibit remarkable sensitivity to some odours (e.g. Li et al. 2007), and that odours regulate human reproductive physiology and behaviour to a greater extent than previously realized. One way in which this might occur, despite fewer receptors and functional receptor gene repertoire, is by increased cognitive power in the processing of odours through proliferation of brain areas associated with olfactory perception compared to other species (Shepherd 2004).

Furthermore, Stoddart (1990) reviews the enormous interest we invest in adorning our bodies with artificial fragrances, and recounts extensive ethnographic and anthropological evidence that demonstrates a much more prevalent role for odour in many non-industrial cultures than in modern urban societies. Here we pick just two examples: in the Ongee tribe of the Andaman Islands, odour is seen as the source of one's personality, and seasons are described according to the fragrance of the flowers that happen to be in bloom at that time (Pandya 1993). Meanwhile in Elizabethan times, it was the custom of young ladies to impregnate slices of apples with armpit odour and then to dispense these as gifts to potential suitors. Stoddart also pointed out that the human body possesses more odour-producing sources, especially apocrine glands, than those of closely-related primate species. Furthermore, the extensive development of axillary hair in humans, compared with other primates, coupled with the potential for communication via axillae as a result of acquired bipedality, led Montagna and Parakkal (1974) to muse that axillae appear to be excellent odour-producing organs. In light of all this evidence, Stoddart referred to humans as 'the scented ape'. Building on this idea, research over the past two decades has extended our understanding of the extent to which body odour is perceived by others, and particularly the kinds of information about an individual that we are able to glean (often subconsciously) from their body odour.

## Perfume use in human society

Like other animals, we make several inter-personal attributions using odour, or at least have the potential to do so, and these may influence biological processes that are visible to selection, particularly our choice of mate. Why then should we invest so much time, effort and money in attempting to get rid of our natural odour by masking it under a myriad of other fragrances?

### Origins of perfume use

A large part of the answer lies in cultural phenomena such as the practices of clothes-wearing and bathing. Historically, clothes were worn for weeks or months at a time, becoming impregnated with sweat and odour, as well as extraneous smells from cooking, fires and so on. Furthermore, the habit of whole-body bathing was very uncommon in European culture; indeed it was considered unhealthy (Corbin 1988) and people at most would wash hands and faces. Until around the 1850s in Europe and America, for example, bathing remained the privilege of the upper classes, promulgating the association between odour and low social status (Largey and Watson 1972; Hyde 1997). This association was already evident in ancient times: in his *Natural History*, the Roman naturalist and philosopher Pliny the Elder wrote:

> Perfume ought by right to be accredited to the Persian race: they soak themselves in it, and quench the odour produced from dirt by its adventitious attraction. The first case that I am able to discover was when a chest of perfumes was captured by Alexander among the rest of the property of King Darius when his camp was taken. Afterwards the pleasure of perfume was also admitted by our fellow-countrymen as well among the most elegant and also most honourable enjoyments of life.

Pliny went on to note the use of perfume as appropriate tributes to the dead and to the gods, and subsequently other authors have noted the use of fragrances as a symbol of religious sanctity (e.g. Classen et al. 1994). Many traditional societies, such as the Ilahita of Papua New Guinea, also have deeply-embedded cultural associations between odour and morality (Tuzin 2006). Against this background, we see the widespread use of perfumes as a testament to the fundamental human desire to be accepted within one's society and to be viewed positively by one's peers and potential mates.

## Perfume diversity

The choice of perfumes is extraordinarily diverse—far more so than strictly necessary for any psychological or social function alone. One reason for this is that perfume choice follows the vagaries of fashion, as was the case even in the ancient world. As Pliny noted,

> … the first thing proper to know about them is that their importance changes, quite often their fame having passed away. The perfume most highly praised in the old days was made on the island of Delos, but later that from the Egyptian town of Mendes ranked the highest… the iris perfume of Corinth was extremely popular for a long time, but afterwards that of Cyzicus, and similarly the attar of roses made at Phasehs…

At one level, at least historically, the arrival of new scents was constrained by the availability of naturally occurring ingredients in the local area or within trading networks. Here is Pliny once more, describing the acquisition of the key and tremendously valuable ingredient myrrh:

> It is bought up all over the district from the common people and packed into leather bags; and our perfumiers have no difficulty in distinguishing the different sorts by the evidence of the scent and consistency.

Today, however, the design of new fragrances is largely unshackled from availability. In a global society, anything is available at a price. Many ingredients that were previously harvested, extracted and purified have now been replaced with artificial compounds which can be manufactured at relatively low cost.

A second reason for the huge diversity of perfumes is the way in which the modern perfumer searches for novel combinations of compounds and even entirely novel compounds produced for the first time in the laboratory (for an excellent account of this fascinating industry, see Pybus and Sell 1999). It is largely a subjective process, new candidates being evaluated by a 'nose', a virtuoso in the art of fragrance perception, someone trained to be adept at distinguishing individual constituents in a complex odour mixture and to label these using a dedicated vocabulary to a degree well beyond the layperson. Once a pleasing fragrance is found, it is further evaluated by panels and focus groups, always with a view to testing how pleasing it smells. Thus, in the typical design process, other than customary concerns regarding compound stability and pricing, the two main benchmarks of a marketable new product lie in its hedonic perception (simply, does it smell good?) and its novelty.

## Psychological effects

Today, we are more than ever aware of the deep psychological reach of odours. Certain fragrances, for example, are known to influence emotion and mood (Herz et al. 2004; Warrenburg 2005; Weber and Heuberger 2008), and performance in cognitive tasks (Herz et al. 2004; Herz 2009; Zucco et al. 2009) including memory (Smith et al. 1992; Herz and Schooler 2002). Unsurprisingly, the growing recognition of the power of odour to elicit deep-seated and often subconscious psychological effects has led to a plethora of applications, one of the best known being in retail marketing. For example, use of ambient odours increases product evaluations and brand name recall, particularly for unfamiliar brands, apparently through inducing longer periods of attention to the products in the presence of the odour (Morrin and Ratneshwar 2000; Morrin and Ratneshwar 2003). To some extent, congruity between the odour and the product can further increase marketing success (Spangenberg et al. 2006; Bosmans 2006).

## Effects on the wearer

In Western culture, almost everyone can afford to use some product aimed at controlling body odour. And most do, even though most also bathe regularly: amongst a sample of 176 women and 71 men in the UK (Roberts et al. 2010), 79% of women and 60% of men reported using a deodorant every day (only 4% and 8%, respectively, never used a deodorant), while 44% of women attested to use of a perfume on an everyday basis (with only 3% reporting they never did so).

Recently, research has turned to how the use of personal fragrances influences behaviour within a social context, specifically by action on the perfume wearer. In one study (Higuchi et al. 2005), women were interviewed by a female confederate while being filmed. Halfway through the interview, half the women applied a perfume while half did not. Independent and naïve participants subsequently scored silent video clips of the interviews for rates of non-verbal behaviours and for impressions of self-confidence. Women in the perfume group were found to display fewer non-symbolic movements (e.g. touching their hair or nose) than those in the controls, became more relaxed and more dominant according to subjective rating scales, and were judged by female observers to be more self-confident.

In a second study, 35 heterosexual men were randomly allocated to a group given a commercially available deodorant or a placebo deodorant (containing alcohol spray but no active ingredients), both of which were presented in unmarked white spray cans of different shape to the product's characteristic form (Roberts et al. 2009). The men provided subjective self-ratings of confidence and attractiveness before use, and then on two subsequent occasions over 4 days while using the provided deodorants within their daily hygiene regimen. The men were also photographed and videotaped after having been asked to imagine introducing themselves to an attractive woman. The study (see also Figure 20.1) found that men in the placebo group progressively rated themselves as less attractive and self-confident compared to men in the deodorant group, although there was no initial difference. There was no difference in the perceived attractiveness of the men in the two groups as judged from their photographs by a panel of independent female judges. However, the same judges watching the muted video clips scored men in the deodorant group as significantly more attractive than men in the placebo group. Furthermore, the more the men reported liking the allocated deodorant, the more attractive they were judged in the video than expected based on their photo-rating (i.e. suggesting relatively favourable behaviour or body language). These results show how personal fragrance appeared to have an effect on men's non-verbal behaviour in such a way that it influenced how they were perceived by others, even in the absence of odour cues.

Results such as this demonstrate the potential for incorporating evolutionary psychological studies on wearer effects of personal fragrances, allowing real evaluations of important innovations in design, beyond simple provision of a convenient marketing angle. What we would like to argue in this chapter is that the process of perfume design would be further enhanced if another critical benchmark was introduced: how does the fragrance influence the communicative value of the underlying body odour of the individual who uses it? Before we address this, however, let us first examine the nature of the biological cues available in body odour and how these might influence inter-personal attributions.

## Body odour as a biological signal

Animal and human work points to five main categories of information that are transferred using body odour. These are: 1) individual recognition cueing and kin-related behaviour; 2) cues of current state; 3) mediation of female reproductive physiology; 4) cues of underlying good-genes; and 5) cues of complementary genes in partner choice.

## Individual recognition

The similarity of body odour among twins (Roberts et al. 2005) and other relatives (Porter and Moore 1981) indicates that body odour has, to some significant extent, a genetic basis. This, coupled with ultra-high variability in odour chemistry, has led some scholars to coin the term 'body odour signature' (Porter et al. 1985) and indicates that body odour can be involved in individual recognition. A solid body of evidence suggests that adults are able to recognize their own odour (Russell 1976; Hold and Schleidt 1977; Schleidt 1980; Schleidt et al. 1981; Platek et al. 2001), the odour of their partner (Schleidt 1980; Schleidt et al. 1981) and that of relatives (Porter and Moore 1981; Porter et al. 1985, 1986; Weisfeld et al. 2003). It should be pointed out, however, that success rates in recognition vary extensively, mostly due to the experimental paradigm, and are typically far lower than facial recognition. The ability to recognize odours develops soon after birth, as newborns prefer their mother's breast and axillary odour within several days of delivery. Similarly, mothers quickly learn the odour of their offspring (Russell et al. 1983) and it is thought that smell plays a significant role in development of mother–infant attachment. This is supported by studies which show that mothers who recognized the odour of their babies behaved more affectionately toward them a month later (Fleming et al. 1995; Steiner et al. 1996).

Furthermore, odour recognition of relatives within a family, and hedonic attributions towards such odours, may be an important component of incest avoidance. Mutual odour aversion occurs between father and daughter, and between brothers and sisters (Weisfeld et al. 2003). Hedonic shifts in odour preferences away from kin and towards non-kin is expected to develop during puberty when mate choice becomes relevant. However, a recent study by (Ferdenzi et al. 2010) did not find clear support for this idea, perhaps due to the relatively small sample size, and we await more data to resolve this issue.

### Cues of current state

Body odour variability reflects not only genetic make-up but also some environmental factors which may provide cues to an individual's current state. Examples of such cues include: 1) reproductive state, 2) diet, 3) health status, and 4) affective state.

Although human ovulation is traditionally regarded as concealed, results of several recent studies show changes in hedonic ratings of female axillary odour across the menstrual cycle, peaking around ovulation (Havlicek et al. 2006; Singh and Bronstad 2001). In contrast, such shifts were not observed in women using hormonal contraception (Kuukasjarvi et al. 2004). The apocrine glands of the axillary region, which are primarily responsible for production of chemicals involved in development of body odour, initiate activity only in puberty and it is thought they are sensitive to fluctuations in steroid hormone concentration. Direct empirical evidence is scarce, but we can expect changes in body odour related to puberty, and perhaps also to menopause.

Studies on rodents show that diet affects body odours, and subsequent odour preferences among conspecifics (Beauchamp 1976; Ferkin et al. 1997). Odours of mice which had been temporarily starved were not attractive to opposite-sex individuals, but attractiveness was restored within 24h of feeding recommencing (Pierce and Ferkin 2005). In contrast to rodents, most evidence on dietary effects on human body odours is only anecdotal or indirect. For instance, communities that traditionally eat high amounts of fish are said to have a characteristic odour. Analytical studies suggest that some aromatic foods, for example plants of the *Alliaceae* or *Brassicaceae* families which are a common part of European cuisine, could affect human axillary odour (Buttery et al. 1976). However, the only direct evidence comes from a study in which consumption of red meat negatively affected subjectively perceived quality of the body odour (Havlicek and Lenochova 2006).

In addition, body odour may reflect underlying health, although similarly to dietary effects, we currently have only limited experimental evidence about this issue. However, numerous reports from the clinical literature provide strong support for this view (Havlicek and Lenochova 2008). It is known that individuals affected by some metabolic disorders such as diabetes have a characteristic smell of acetone on the breath, while the rarer maple syrup syndrome causes a distinctive odour (Monastiri et al. 1997). More commonly, changes in body odour are caused by infectious agents. For example, some skin inflammations or ulcers have a specific and foul odour (Finlay et al. 1996). It is noteworthy that rodent studies show that the smell of individuals infected by parasitic worms is avoided by their conspecifics (Willis and Poulin 2000). There is no evidence of a similar phenomenon in humans; however, in view of the significant role of parasitic diseases in human evolution, this issue is no doubt worth exploring.

Last, results of several studies point to the fact that humans are sensitive to changes in body odour caused by affective tuning (Ackerl et al. 2002; Chen and Haviland-Jones 2000). These studies evoked specific affective states in participants by showing them films of either a fearful or happy nature while they were wearing experimental tee-shirts. Subsequently, raters were asked to judge how the odour donors might have felt, based solely on their odour. Raters, women in particular, judged the odours in the fearful condition (and to some extent also the happy one) correctly at levels above chance. Further, several recent studies suggest that human odour collected under conditions of anxiety cause increases in the startle reflex and risk-taking behaviour, and induces empathy and anxiety in smellers (e.g. Pause et al. 2009; Albrecht et al. 2011). Anxiety-related body odours also enhance decoding of emotionally ambiguous human faces (Zhou and Chen 2009). The significance of these findings is further supported by brain imaging studies which show that these chemosensory cues activate neural segments, for instance the amygdala, involved in processing emotionally-laden stimuli (Mujica-Parodi et al. 2009).

In summary, body odour provides various cues about individual current state. Although this field started to expand only very recently, the reviewed evidence clearly support the notion that communication of affective states is partly mediated by olfaction.

## Mediation of reproductive physiology

More than 30 years ago, McClintock (1971) noted in her classical paper that cohabitating female students tend to synchronize the onset of their menstrual cycle. This early observation gave rise to several dozen studies on highly variable samples of cohabiting women, such as among mothers and daughters (Weller and Weller 1993a), Bedouin families (Weller and Weller 1997), kibbutz shared households (Weller and Weller 1993b) or lesbian couples (Weller and Weller 1992). A majority, but not all (Trevathan et al. 1993; Yang and Schank 2006) of the studies showed similar shifts toward menstrual synchrony. Menstrual synchrony was also found in some samples of women spending protracted amounts of time together (e.g. in women sharing offices) and this effect is modulated by closeness between workers (Weller and Weller 1995b). On the other hand, a similar effect was not shown in other samples, for instance basketball team players (Weller and Weller 1995a). It should also be pointed out that the methodology of a majority of these studies

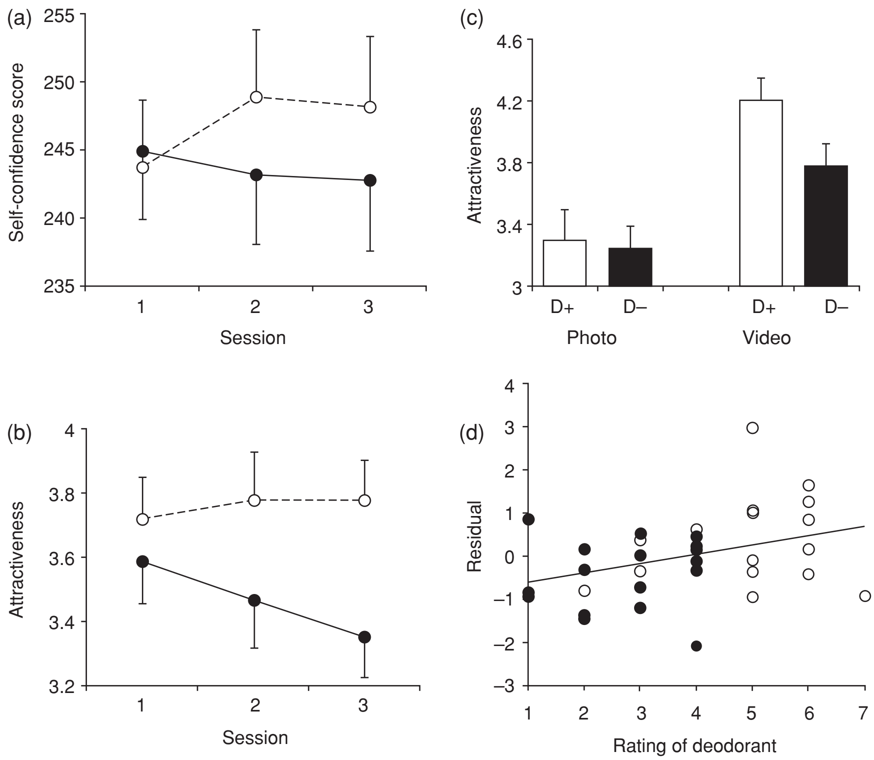


**Fig. 20.1** Effects of perfume use on wearer's behaviour and perceived attractiveness of others. (a) Mean (± standard error) self-confidence scores collected from participants using an allocated full deodorant formulation (open circles or D+) or a placebo deodorant (closed circles or D–), assessed across three sessions spanning 72 hours. (b) Self-rated attractiveness scores during the same experiment. (c) Mean (± standard error) ratings of male facial attractiveness by female judges based on either digital photos or video clips taken at the end of the experiment. (d) Standardized residuals of video-rated over photograph-rated attractiveness and male-assessed odour pleasantness, for the D+ group (open circles) and D– group (closed circles). The figure shows that men who expressed liking for the allocated deodorant were more likely judged attractive in video-ratings than expected based on their photograph-rated attractiveness.

has been questioned (Wilson 1992) and some authors even suggest that the whole effect is an artefact of convergence of irregular cycles (Schank 2001, 2006).

In her original paper, McClintock suggested that menstrual synchrony could be mediated by odour. More recently, her team carried out an experiment in which a group of women was exposed to axillary extracts from other women (Stern and McClintock 1998). The odour recipients tended to shift the onset of their cycle towards the odour donors, suggesting a priming pheromonal effect. The chemicals responsible for this phenomenon are currently unknown, but it was shown that women sensitive to androstenol (a steroidal compound found in axillary odour) have a higher tendency to synchronize their cycles (Morofushi et al. 2000). Although menstrual synchrony is often regarded as the best examined example of human pheromones, its potential function is rather unclear. It is also possible that its function was more significant in cooperatively breeding primate ancestors of our species, or in polygynous social settings (Burley 1979), and simply remain as an evolutionary vestige in modern humans.

Several studies have also found that regular dyadic sexual activities, but not autosexual ones, have an effect on female menstrual functions. Women with weekly sexual activity had more regular cycles and a higher frequency of ovulatory cycles (Cutler et al. 1985; Burleson et al. 1991). Again it is thought that this effect may be mediated by male odour, supported by a study showing shortenings of length between individual LH (luteinizing hormone) pulses in women smelling male axillary extracts (Preti et al. 2003). Levels of LH are involved in hormonal regulation of ovulation.

Lastly, it is known that male partners of pregnant women show changes in hormonal profiles of testosterone and prolactin, which might have an impact on their nurturing behaviour (Storey et al. 2000). The mechanism underlying these shifts is currently unclear; however, it is possible that it is again due to some chemicals produced by pregnant women. This idea is supported by an analytical study showing that pregnant women emit different chemical substances compared with non-pregnant women (Vaglio et al. 2009).

## Indicators of genetic quality

It is thought that the main role of odour communication is in mate choice and the regulation of romantic relationships. Current models of sexual selection predict that at least some cues which are involved in mate choice reflect the quality of the individual (Kokko et al. 2002). We can thus expect this would also be the case for body odour. One of the indicators which has been extensively studied in the last two decades is fluctuating asymmetry. In bilaterally symmetric organisms (including humans), we can see small non-directional imperfections in symmetry, termed fluctuating asymmetry. These fluctuations are thought to reflect the ability of the organism to cope with environmental stresses like toxins and infections (Møller et al. 1999). A number of studies on both facial and body attractiveness have shown that more symmetrical individuals tend to be perceived as attractive (Thornhill and Gangestad 1999a). It has also been shown that the level of symmetry is related to the attractiveness of body odour in both men and women (Gangestad and Thornhill 1998; Rikowski and Grammer 1999; Thornhill and Gangestad 1999b; Thornhill et al. 2003), and that women are particularly sensitive to these cues around the time of ovulation (i.e. when conception is most likely). Furthermore, there is evidence that periovulatory women prefer men with high scores of psychological dominance, which may in turn reflect their biological quality (Havlicek et al. 2005).

## Cues of complementary genes

Whilst it is expected that the above-mentioned preferences to markers of genetic quality will show a rather uniform preferential pattern across individuals, the same does not apply to cues of genetic compatibility, which follow more individually specific patterns. One of the model systems in which this mechanism is studied are the highly variable genes of the major histocompatibility complex (MHC). Products of these genes play a key role in immune system functioning by presenting peptides of foreign origin on the cellular surface. Each of the genes in the complex have several tens of different known alleles, suggesting that the region is under strong balancing selection (Apanius et al. 1997). It has been shown in various vertebrate species that females prefer the odours of potential partners with MHC genes that are dissimilar to their own (Penn and Potts 1999). Several human studies have also found that naturally cycling women prefer the odour of MHC-dissimilar (Wedekind et al. 1995; Wedekind and Füri 1997; Santos et al. 2005) or moderately dissimilar partners (Jacob et al. 2002). When men judge female odours, the results are more ambivalent, with one study (Thornhill et al. 2003) showing a preference for dissimilarity while another failed to find a significant link (Santos et al. 2005). Moreover, a pioneering paper by

Wedekind et al. (1995) suggested disruption of these preferences in women using hormonal contraception. More recently, Roberts et al. (2008) replicated this study using a more sensitive within-subject design. Although they found a shift in preferences in women who started to use contraception, they were not able to replicate preferences for the odour of dissimilar individuals (see also review in Havlicek and Roberts 2009).

## Towards biologically-informed design?

As we have shown, odour carries several important cues to biological quality. Since these cues have been shaped by selection over evolutionary time, and play a role in coordination of key social interactions, incorporation of this knowledge into perfume design could potentially provide a springboard for transforming the success of specific perfumes. Current understanding of body odour-associated effects on inter-individual perception and attribution lead us to several promising possible avenues to take this process forward.

### Constant fertility enhancement

The finding that there is a periovulatory peak in attractiveness of women's axillary odour, as perceived by men (Singh and Bronstad 2001; Havlicek et al. 2006), clearly suggests a change in the chemical composition of women's axillary odour associated with ovulation. This is not unsurprising, since similar fertility-associated odour cues are well-known in other species including mice (Schwende and Novotny 1982; Andreolini et al. 1987), elephants (Dehnhard et al. 2001), cattle (Dehnhard and Claus 1996), sheep (Blissitt et al. 1994), and horses (Ma and Klemm 1997).

These changes influence attraction to the odour by males (Ferkin and Johnston 1995) and also modulate their intrasexual behaviour such that aggression between males is higher when exposed to the scent of a fertile female than a non-fertile one (Dixon and Mackintosh 1975). The potential for a similar effect in humans was recently demonstrated in an experiment in which exposure of men to the odour of women at the fertile stage of the cycle elicited higher levels of testosterone after testing than men exposed to odours of non-fertile women (Miller and Maner 2010).

Given this, if the compound or group of compounds that provide cues to ovulation were discovered, it might then be possible to incorporate this into a perfume in such a way as to raise the perceived attractiveness of the wearer, throughout the menstrual cycle, to the level normally experienced only at ovulation. Even if this were only a subtle effect, it could provide a unique selling point and one that would likely prove irresistible to perfume manufacturers and marketers.

### Amplifying quality perception

In a similar fashion, perfumes that incorporate the constituents of body odour associated with any measure of biological quality should improve the attractiveness attributions of the wearer, as well as (again) providing a gift to the product's advertisement campaign. For example, Havlicek et al.'s (2005) discovery of a correlation between perceived pleasantness of axillary odour and men's relative psychometric dominance indicates a chemical basis which could be exploited in male perfume. Once again, this finding reflects similar phenomena in other species, particularly rodents, where odours of dominant males are preferred over that of subordinates (White et al. 1986; Mossman and Drickamer 1996; Kruczek 1997; for reviews see Gosling and Roberts 2001; Roberts 2007).

In mice, unlike in humans, the compounds responsible for dominance signalling are known. Within seven days of establishment of dominant or subordinate relationships, gas chromatography reveals quantitative differences in at least sixteen compounds found in male urine (Harvey et al. 1989).

Subordinate male urine shows a decrease in concentrations of ketones, dihydrofurans, and acetates, while dominant male urine increases in levels of 2,3 dihydro-*exo*-brevicomin, 2-*sec*-butyl-4,5-dihydro-thiazole and two sesquiterpenic compounds, alpha- and beta-farnesene. These compounds are androgen-dependent and are absent from the urine of castrated males, but are restored by administration of testosterone (Harvey et al. 1989). Importantly, these compounds have been synthesized and, when added to urine of castrated males, they invoke levels of aggression (Novotny et al. 1985) and restore levels of interest and attractiveness to females (Jemiolo et al. 1985) that are equivalent to those seen in intact males.

## Cueing complementary genes

There has been much recent interest in how odour might reveal genetic compatibility between potential mates. As before, the research in humans has been preceded by work in other species, notably mice, where genotype at the MHC is revealed in urinary odour and, when given the opportunity to choose, females prefer to mate disassortatively, that is, with males who are relatively dissimilar at the MHC (Yamazaki et al. 1976; Potts et al. 1991). Although the task of characterizing the chemical basis underlying MHC-correlated odours is a great deal more complex than that of determining the basis of social dominance, it appears that the cues to relative dissimilarity in mouse urine are carried by a series of volatile carboxylic acids which vary in relative concentration according to MHC type (Singer et al. 1997; Yamaguchi et al. 1981). Although the extent to which MHC-correlated odour influence human behaviour is still a topic of debate and research interest, accumulating evidence suggests the real possibility for a significant role in affecting mating preferences (see also reviews in Roberts and Little 2008; Havlicek and Roberts 2009).

The potential for interactions between perfumers and evolutionary psychologists has been neatly demonstrated in an experiment by Milinski and Wedekind (2001), in which they correlated perfume preferences with MHC genotype. They asked 137 men and women to score 36 individual perfume ingredients using the item 'Would you like to smell like that yourself?'. Two years later, a subset of 18 ingredients was scored for self (the same item as before) and also as potential ingredients for a partner's perfume, using the question 'Would you like your partner to smell like that?'. Where results could be compared across the 2 years, a high degree of repeatability in ratings indicated consistency in odour perception. Furthermore, there were significant correlations between a rater's genotype and the extent to which they liked or disliked individual perfume components as ingredients for their own use. However, the same correlation did not exist between genotype and ratings for their partner's perfume, indicating that the results could not be explained simply by generalized odour preferences. These important results raise the possibility that perfume choice might not be arbitrary or random and simply mask underlying body odour as is generally assumed, but more intriguingly, that the choice might serve to complement one's own body odour. In other words, the use of perfume might not interfere with the underlying biological signal contained in body odour as much as previously thought.

In a study led by our colleague Pavlina Lenochova, and with several other researchers, we recently tested between these ideas in a series of experiments in Prague and Vienna. We hypothesized that if perfumes act by simply masking body odour, we should find uniformly higher ratings of perfumed axillary samples compared with non-perfumed samples from the same individuals, as well as reduced individual variability in odour pleasantness across individuals. Although we found in two experiments that naïve smellers rated perfumed samples more positively than non-perfumed samples, significant interactions with perfume wearers indicated that the perfume acted differently on different individuals (Figure 20.2a). This suggests that the application of perfumes to existing body odour produces an odour mixture with an emergent

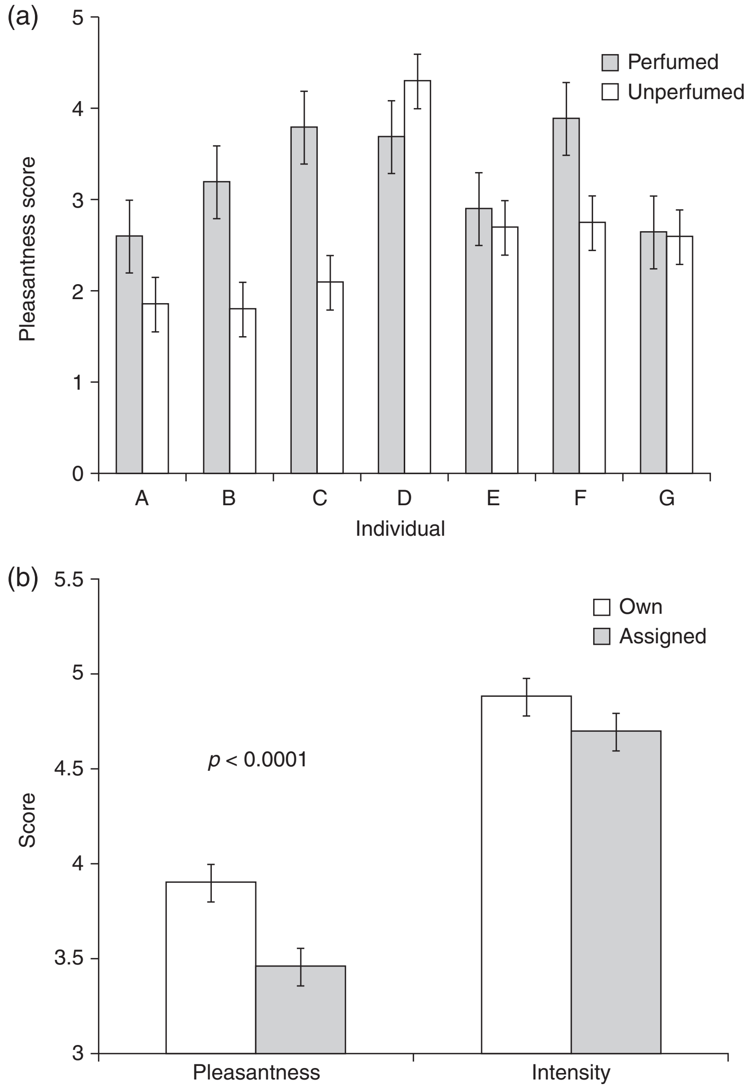


**Fig. 20.2** Effect of perfume on perception of body odour. (a) Mean (± standard error) pleasantness scores of body odour from perfumed and non-perfumed axillae of the same individuals (A–G). Perfumed odours are perceived as more pleasant on average, but not in all cases and there is a significant odour donor × perfume condition interaction. (b) Mean (± standard error) pleasantness and intensity scores of body odour and perfume blends. Participants applied their own perfume to one axilla, and one assigned by the experimenters to the other. The body odour/perfume blend is more pleasant when composed of the individual's preferred perfume.

quality that is perceptually different from either constituent. We took this further in a third experiment, in which we compared ratings of axillary samples collected when the odour donors were wearing either their own perfume or another perfume assigned by the experimenters. In subsequent rating sessions, smellers perceived the body odour-perfume blend to be more pleasant when the donors wore their own perfume, compared with the body odour blend with the assigned perfume (Figure 20.2b). These results challenge the conventional view that perfume use acts to simply mask underlying odour. On the contrary, they support the view of Milinski and Wedekind (2001) and suggest that perfumes blend with body odour in a complementary manner, working with rather than against the underlying odour. The results show that perfume use can thus potentially enhance the communicatory significance of body odour, as well as providing an explanation for the highly individual nature of perfume choice.

The implications of these results for perfumers are potentially revolutionary. First, it is equally relevant to both males and females; in contrast, the constant fertility enhancement is restricted to the female market and amplifying quality perception is likely to be mainly male-oriented. Second, it emphasizes the individuality of perfume preferences, providing a firm scientific basis for further development of a niche market in customized designer products. Third, it carries implications for the ways in which perfumes are purchased. Perfumes are often bought as presents for others. However, the research suggests that one is more likely to choose a perfume that suits oneself than the intended beneficiary. Possibly this effect would be ameliorated by buying for relatives, but, according to this study at least, one should avoid buying a perfume for an unrelated sexual partner.

## Some caveats

Although there appears to be ways in which insights from evolutionary psychology can inform perfume design and marketing, there are also some important considerations which urge for a cautious approach, and it is to these that we now turn.

### The product works too well

There are at least two possible undesirable side effects on the behaviour of the perfume wearer and those with whom the wearer comes into contact. First, imagine a perfume which contained some presently-unknown compound with attractant properties akin to bombykol and other classic pheromones of the insect world. We think this very unlikely but, according to marketing hype, this is the dream offered to young men by at least one well-known commercial product, where one spray results in a stampede of beautiful women converging from all directions towards the lucky consumer. Undoubtedly an amusing idea and excellent marketing device, in reality, such a product would generate undesirable levels of attention. Even if we assume a product existed which exerted a much more subtle effect, a user would have no control over who approached, or when. In general terms, it might be expected that it would be more popular with men than women (according to views of sex-typical evolved strategies) but even amongst young men, it might eventually become too much.

Second, one could also imagine a design which built upon the association between odour chemistry and male dominance, or one that boosted a wearer's self-confidence. While this might attract attention from potential mates, the intended receivers of the signal, it could also attract unwanted attention from others, notably other males. In the mouse studies described above, addition of synthetic compounds associated with dominance to the odour of target males increased levels of aggression from other males. Such a fragrance might also elicit higher levels of aggressive behaviour in wearers than would be normally experienced.

### Disruption of function

Another issue with a perfume that included analogues of active body odour components is that it might often disrupt the underlying signalling interaction on which it was based. The most obvious way in which this could occur is simply if detection of the signal is precluded by the overpowering nature of the fragrance. Although Milinski and Wedekind's (2001) study suggests that the masking of the biological signal by artificial fragrances (at least those made from ingredients not occurring in body odour—their study did not examine compounds of human origin) may be less problematic than previously thought, any such masking that did occur would be likely to disrupt evolutionarily stable patterns of mate selection. A more targeted manipulation of a perfume by manipulating or mimicking elements of the underlying biological signal would likely exacerbate this disruption. For example, addition of compounds associated with attractiveness, dominance, or some other trait associated with high quality, would disproportionately favour relatively poor-quality individuals and this might influence their chances of being selected by a higher quality opposite-sex partner than would otherwise be the case. This may be to the benefit of the perfume user, but could come at a cost to the partner since s/he would potentially have been deceived about the partner's quality.

A further problem could arise in the use of compounds that mimicked a woman's periovulatory state in a perfume aimed at promoting a constantly high perception of attractiveness. While at first sight this might seem to be an effective design solution to the problem of cyclical variation in odour perception by others, careful attention would need to be paid to possible disruptive effects on the user's (or others') own menstrual cycle.

### Ethical concerns

Some of the potential design improvements we have outlined also carry certain philosophical concerns surrounding the manipulation of the perception of another person through use of a biologically-manipulated perfume. In essence, the issue boils down to this: is it acceptable to subliminally manipulate Y's perception of X in order to make Y fall in love with X? How would Y respond to discovering s/he has been chemically duped?

Our current view is that this is likely to be of trivial concern, and is no more problematic than use of, say, a facial cosmetic that enhanced eyelid or lip colour to alter perception of a woman's attractiveness, a foundation make-up that disguised poor underlying skin condition, or even cosmetic surgery (e.g. breast augmentation). Sooner or later, these minor deceptions tend to come to light within a developing relationship, and may or may not play a part in its continuance.

However, we raise the point mainly because it could become relevant should there be in the future any discovery and use of a compound that has the property, in the sense of a classical insect pheromone, of insidiously triggering a specific behaviour which is beyond the control of the signal receiver. No such compound (or behavioural response) has yet been found, however (nor do we think personally one will be found, but as we have said, this is common advertisement hype). The closest we do come to this scenario are the androgen steroids which occur in the axillary sweat of both men and women and which are already known to alter physiology and behaviour, although these effects appear to be dependent on context and experience, and modulate existing behaviour in subtle ways rather than altering or dictating behavioural responses. Compounds such as androstadienone and androstenol, for example, induce changes in hormonal levels of exposed participants, along with induced moods and affective states (reviewed in Havlicek et al. 2010) and can even modulate attractiveness attributions in certain situations (Saxton et al. 2008a,b). If a still more potent compound does come to light, perhaps its use would come to be treated as seriously as mind-altering drugs like flunitrazepam (rohypnol).

## Conclusions

Although we have highlighted some cautionary issues, we believe there is at least potential for a beneficial relationship between evolutionary psychologists and designers and marketeers in the perfume industry. Evolutionary psychology has already and will continue to produce insights into the informative capacity of body odour in human perception and its role in social interactions, particularly in partner preferences and mate selection. These insights could increasingly be harnessed to increase both the potency of perfume function and the strategies employed in its marketing.

We think one of the most interesting approaches would be to address in more detail the relationship between an individual's perfume preference and their genotype, particularly at the MHC. The possibility that the two are linked has already been demonstrated, although this deserves further work and replication. If true, the connection provides a further clue for explaining the diversity of perfume preferences and choice, since MHC genotype is so variable. For the perfume industry, it has the potential to open up a new realm of individually-customized perfumes—uniquely tailored and bespoke, and thus profitable.

More work is needed particularly to understand the ramifications of perfume choices on social relationships. The past two decades have demonstrated how body odour plays a more critical role in intimate social decision-making than ever before realized. Yet issues such as how individuals choose specific perfumes, how perfumes interact with body odour, and how perfume-body odour blends are perceived, have scarcely been addressed. What is most needed, for both evolutionary psychologists and perfumers, is greater understanding of the chemistry of body odour and the chemical basis for specific biological cues. With this knowledge, some of the possibilities we have described become truly real.

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