Concordant preferences for opposite-sex signals? Human pheromones and facial characteristics

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We have investigated whether preferences for masculine and feminine characteristics are correlated across two modalities, olfaction and vision. In study 1, subjects rated the pleasantness of putative male (4,16-androstadien-3-one; 5α-androst-16-en-3-one) and female (1,3,5(10),16-estratetraen-3-ol) pheromones, and chose the most attractive face shape from a masculine–feminine continuum for a long- and a short-term relationship. Study 2 replicated study 1 and further explored the effects of relationship context on pheromone ratings. For long-term relationships, women's preferences for masculine face shapes correlated with ratings of 4,16-androstadien-3-one and men's preferences for feminine face shapes correlated with ratings of 1,3,5(10),16-estratetraen-3-ol. These studies link sex-specific preferences for putative human sex pheromones and sexually dimorphic facial characteristics. Our findings suggest that putative sex pheromones and sexually dimorphic facial characteristics convey common information about the quality of potential mates.

Keywords: pheromones; mating strategies; facial attraction; male–female differences

1. INTRODUCTION

Studies of human attraction framed by evolutionary theory have concluded that men and women advertise heritable mate qualities, and that their mate-choice strategies exploit these signals. While the precise roles of environment and genetic influences are equivocal, suggested visual signals of heritable mate quality include body and face symmetry (Gangestad *et al.* 1994; Thornhill & Gangestad 1994; Rhodes *et al.* 1998; Perrett *et al.* 1999; Jones *et al.* 2001; Penton-Voak *et al.* 2001), masculine and feminine face shapes (Perrett *et al.* 1998; Penton-Voak *et al.* 1999; Penton-Voak & Perrett 2000) and body shape (Singh 1993; Tovee *et al.* 1999). Non-visual signals include body odour (Gangestad & Thornhill 1998; Rikowski & Grammer 1999; Thornhill & Gangestad 1999; Singh & Bronstad 2001) and vocal characteristics (Collins 2000; Hughes *et al.* 2002). Rikowski & Grammer (1999) suggest that humans use multiple signals as a way of reducing error when assessing mate quality. Thus, humans seeking a mate should be keenly sensitive to signal concordance; and indeed, concordances have been reported. Women prefer body odours collected from men with a high degree of bilateral symmetry compared with odours from asymmetrical men (Gangestad & Thornhill 1998; Rikowski & Grammer 1999; Thornhill & Gangestad 1999). Moreover, both men and women indicate preferences for voices recorded from individuals with higher degrees of bilateral body symmetry over those from individuals with lower bilateral symmetry (Hughes *et al.* 2002).

Sexually dimorphic facial features may also signal mate quality, and Enlow (1990) has speculated that distinctly feminine features (e.g. full lips, larger eyes) in women are influenced by hormones and signal fertility. In males, features such as heavier brows and a strong jaw-line may signal increased levels of testosterone, which in turn may signal dominance (Mazur & Booth 1998) or immunocompetence (Folstad & Karter 1992).

Other possible signals of mate quality include pheromones, which are ubiquitous among animals but have only recently been seriously considered as signals in human mate choice. Indeed, the researchers investigating body odours have speculated that pheromones are key in mediating the effects. We investigate the possible roles of three putative human pheromones, the male pheromones 5α-androst-16-en-3-one and 4,16-androstadien-3-one, and the female pheromone 1,3,5(10),16-estratetrael-3-ol, as signals of mate quality. For brevity, we shall call them MP1, MP2 and FP, respectively. The two male pheromones have been found to be the most concentrated in human semen from among the androgen and 16-androstenes steroids (Kwan *et al.* 1992). Jennings-White (1995) found that, among the androstene steroids, MP2 produced the strongest response in the female vomeronasal organ (VNO), the organ mediating pheromonal signals. Previous research has tended to include only one of the male pheromones, allowing little opportunity to evaluate their similarities as mate-quality signals. Comparisons, however, between the female pheromone FP and the male pheromone MP2 have revealed sex-differentiated processing in the hypothalamus (Savic *et al.* 2001), and sensitivity of the surface potential in the VNO to opposite-sex pheromones (Monti-Bloch & Grosser 1991; Jennings-White 1995). Pheromones can prime changes in human reproductive function (Schaal & Porter 1991; Morofushi *et al.* 2000; Rekwot *et al.* 2001; Wyatt 2003); however their status in signalling human mate quality and affecting mate selection is inconclusive (Black & Biron 1982; Cutler 1988; Cowley *et al.* 1991; Jacob & McClintock 2000).

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(a) Multiple signals, individual differences and mating strategies

It has been suggested that multiple signals reduce error when evaluating potential mates (Rikowski & Grammer 1999; Kohl *et al.* 2001). The strength of concordance, however, may depend upon the context in which the judgement is made. For example, an increasing number of studies emphasize individual differences in the assessment of quality signals and have found that preference for facial masculinity is affected by relationship status (Little *et al.* 2002), age of parents (Perrett *et al.* 2002) and self-rated attractiveness (Little *et al.* 2001). We test these assumptions by examining judgements of visual and olfactory signals of potential partners in two contexts: long-term and short-term relationships.

In keeping with research on mating strategies and with the good-genes theory (Andersson 1994; Gangestad & Simpson 2000), we propose that both facial characteristics and pheromones signal mate quality, and that preferences for cues to mate quality should covary across domains. Women who prefer more masculinized faces should also show an increased liking for male over female pheromones, while men who prefer more feminized faces should indicate a corresponding inclination towards the female pheromone.

It should not be assumed that the strategies used in seeking a partner are the same across individuals, or across time for any one individual, nor even that they must be rooted in the same biological function. Women might have been selected to seek 'good genes' through cuckoldry (Gangestad & Simpson 2000), to evaluate prospective 'good fathers' or to replace a current mate (Buss 1994). While the mating system of ancestral hominids is unknown, it is likely that during hominid evolution there has been at least some male investment in mate and offspring upon which natural selection has shaped modern human mating behaviours. Today's world is vastly different from the world in which our ancestors were naturally selected, and immediate psychological motivations, such as the need for self-affirmation or bowing to peer pressure, may have only the most tenuous links to Darwinian selection. Men's risks when engaging in a short-term relationship are fewer, but the strategies used in choosing a partner are no less likely to vary. Different selection pressures should be expected to affect signal preference and attention to specific signals by both men and women.

The selection pressures underlying the strategies used when seeking a long-term relationship may vary among individuals, but it is possible that for any one individual the strategies employed are more consistent across time compared with short-term benefits. Those females who were more discriminating when choosing a long-term partner achieved higher fitness than those women who were not so selective. Women in the past were, in an almost literal sense, placing all their eggs in one basket. Although women today do not face the same risks that led to the selection of the genes behind this strategy, the evolutionary legacy remains intact. Females, therefore, are selected to desire a healthy and fit partner, and expect substantial investment by him in both her and all their resulting offspring. This Darwinian function would require females to read all available signals accurately and to be sensitive to their consistency (see Møller &

Pomiankowski 1993). Selection pressures on males influence the strategies used when investing in a long-term partner, and males sacrifice time, energy and potential mating opportunities. Males' judgements across multiple modalities should be most strongly correlated when evaluating a potential partner for a long-term relationship. We therefore propose that relationship context, that is long-term versus short-term, will influence concordance of signal judgements for both men and women, though the nature and direction of these effects (particularly for women) are uncertain, and these effects should be sex specific.

2. STUDY 1

The purpose of study 1 was to investigate whether two proposed signals of mate quality, masculine versus feminine facial characteristics and masculine versus feminine pheromones, are chosen concordantly and whether these judgements are sex-specific. Do women who prefer more masculinized facial shapes also find putative male pheromones more appealing? Similarly, do men indicate an increased liking of the female pheromone if they prefer a more feminized facial shape when judging a partner?

(a) Methods
(i) Participants

Heterosexual undergraduate students (56 women, age range 17–26 years, mean 20.7 ± 2.12 years; and 56 men, age range 17–26 years, mean 21.14 ± 2.01 years), not taking hormonal contraceptives, were recruited from the University of St Andrews.

(ii) Materials

Five odorants were used: two male pheromones, MP1 and MP2; a female pheromone, FP (Steraloids Inc, RI, USA); and two filler items, clove oil and oil of cade. Solutions were made of each compound (2 mg per 1.0 ml of propylene glycol). A 20 µl aliquot of the solution was then deposited onto filter paper (Filsinger *et al.* 1985; Jacob & McClintock 2000). The filter paper was presented to the participant in a glass vial after the experimenter removed the lid. Vials were stored at 5 °C when not in use. Experimenters conducting the testing were blind to the identity of the odorants.

To assess masculinity preference we used interactive face-sequence trials consisting of six opposite-sex and six same-sex images (four Caucasian faces, one African-Caribbean face and one East Asian face). The same images had been used in previous studies (Perrett *et al.* 1998; Penton-Voak *et al.* 1999; Penton-Voak & Perrett 2000). The sequences involved selection of preferred face shape from a range of 50% feminized to 50% masculinized (see Tiddeman *et al.* (2001) for a full review of the technique).

(iii) Procedures

Participants were presented with six interactive face-sequence trials and were asked to select the face they most preferred. Subjects were asked to judge opposite-sex faces for two hypothetical situations: long-term and short-term relationships. As a control to assess whether preferences are sex specific, we included judgements of same-sex faces without any such mention of relationship context. If preferences are sex specific, we would expect concordance to be found only between opposite-sex faces and pheromones. They should not apply to the assessment of

Table 1. Study 1. Spearman's rank correlations between odour pleasantness and preference for masculinity in male faces or femininity in female faces.

(Opposite-sex face judgements were performed in the context of short-term and long-term relationships. Positive correlations indicate like preferences for the same sexual characteristics (e.g. male pheromone and masculine facial characteristics would be positively correlated if preference for both increased).)

	rater sex	opposite-sex faces short-term relationship	opposite-sex faces long-term relationship	same-sex faces
5α-androst-16-en-3-one (male pheromone, MP1)	F	$r_{43} = -0.060$	$r_{43} = 0.222$	$r_{43} = 0.012$
	M	$r_{48} = -0.111$	$r_{48} = -0.040$	$r_{48} = 0.040$
4,16-androstadien-3-one (male pheromone, MP2)	F	$r_{42} = 0.097$	$r_{42} = 0.379$[a]	$r_{42} = -0.184$
	M	$r_{37} = -0.225$	$r_{37} = 0.126$	$r_{37} = 0.068$
1,3,5(10),16-estratetrael-3-ol (female pheromone, FP)	F	$r_{36} = 0.170$	$r_{36} = 0.011$	$r_{36} = 0.143$
	M	$r_{34} = 0.098$	$r_{34} = 0.352$[a]	$r_{34} = -0.071$

[a] $p < 0.05$.

same-sex friend or foe. A long-term relationship was defined as a committed relationship possibly leading to cohabitation or marriage. A short-term relationship was described as one that is short, such as a one-night stand or a brief affair. Each relationship context was run as a single block of paired opposite-sex faces. Blocks and face-sequence trials were presented in random order. Participants then completed a questionnaire regarding sexual orientation and oral-contraceptive use. They were then asked to smell the five 'naturally occurring' odorants and to rate them in terms of pleasantness (seven-point Likert-type scale ranging from very unpleasant to very pleasant) or indicate that they could not detect the odour.

(iv) *Analysis*

Data from subjects anosmic for a given pheromone (unable to detect the odour) were removed from the analyses for that pheromone. Ratings of the pheromones and the preferred level of masculinity versus femininity in face shapes were compared using Spearman's rank correlation (two-tailed probability).

(b) **Results**

For women, the only significant positive correlation found was between the judgements of male faces for long-term relationships and the ratings of the male pheromone MP2 ($r_{42} = 0.379$, $p = 0.017$; see table 1). This correlation suggests that preference for facial masculinity corresponds with a greater liking for masculine smells. The corresponding judgement of faces for short-term relationships was not significantly correlated with ratings of either male pheromone.

Men's preferences mirrored these. Their ratings of the female pheromone significantly and positively correlated with preference for a more feminine face shape in long-term-relationship contexts ($r_{34} = 0.352$, $p = 0.045$) but not in short-term-relationship contexts (see table 1).

(c) **Discussion**

The prediction that judgements of facial shapes and pheromones would positively correlate was partially supported, and the results were also sex specific. Women showed a greater liking for the male pheromone MP2 the more they preferred masculinized faces when judging for long-term relationships. Men's preferences for femininity in face shape when judging for long-term relationships corresponded with their ratings of the female pheromone.

One limitation of study 1 was that the relationship context was tied only to the judgements of face, while the pheromone ratings were not bound to a relationship context. To explore these effects and pursue a possible explanation, we carried out a second study.

3. STUDY 2

The purpose of study 2 was to investigate further the influence of relationship context on the perception of olfactory and visual signals of mate quality. In study 1, the pheromones were presented as naturally occurring odours with no mention of an association with humans. In study 2, subjects were explicitly told that the odours were related to humans and asked to what degree they would like a partner to smell of the odour within the context of a long-term or short-term relationship. As with the previous study, subjects of both sexes were asked to select the face they would most prefer for a long-term and a short-term relationship. From study 1 it was expected that naturally cycling women who indicate preferences for more masculinized faces would rate the male pheromones more favourably than would women who prefer more feminized faces. Men should also rate the female pheromone as more pleasant if they prefer more feminized faces when selecting for a long-term but not a short-term relationship.

(a) **Methods**
(i) *Participants*

Subjects were 146 heterosexual undergraduates (96 females, age range 17–26 years, mean 20.40 ± 1.76 years; and 50 males, age range 18–25 years, mean 21.18 ± 1.61 years). All women included in the study had natural menstrual cycles (neither taking hormonal contraceptives nor reported to be pregnant).

(ii) *Materials*

The three pheromones (two male and one female) were the same as those used in study 1 and prepared in the same manner. As before, the experimenters conducting the experiment were blind to the identity of the odours.

To examine the generality of the results the stimuli used for the facial-attractiveness ratings were created from a new set of original images, but in the same manner as for study 1. Twelve Caucasian images were created (six of each sex). Each image was then morphed into 50% feminized and 50% masculinized

Table 2. Study 2. Spearman's rank correlations between ratings by naturally cycling women (F) and men (M) of odour pleasantness and preferences for facial masculinity or femininity when judging attractiveness of opposite-sex faces in the same context (short-term and long-term relationships).

(Positive correlations indicate like preferences for the same sexual characteristics. Conventions as table 1.)

	rater sex	opposite-sex faces long-term relationship	opposite-sex faces short-term relationship
5α-androst-16-en-3-one (male pheromone, MP1)	F	$r_{88} = 0.093$	$r_{83} = 0.067$
	M	$r_{37} = 0.068$	$r_{35} = -0.269$
4,16-androstadien-3-one (male pheromone, MP2)	F	$r_{80} = 0.240^a$	$r_{86} = 0.170$
	M	$r_{35} = 0.312$	$r_{35} = 0.096$
1,3,5(10),16-estratetrael-3-ol (female pheromone, FP)	F	$r_{71} = -0.039$	$r_{76} = 0.044$
	M	$r_{34} = 0.466^a$	$r_{34} = 0.214$

[a] $p < 0.05$.

face shapes, creating a total of 24 images (12 male, 12 female) (see Tiddeman *et al.* (2001) for a full review of the technique).

(iii) *Procedures*

Participants were presented with six pairs of opposite-sex faces, with one face 50% masculinized and the other 50% feminized (in face shape). The face pairs were presented in blocks and the subject was asked to choose the preferred face for either a long-term or a short-term relationship and indicate a strength of choice from four categories: (a) guess (i.e. completely unsure), (b) slightly prefer, (c) prefer or (d) strongly prefer. This created an eight-point preference range for masculine face shape. The blocks were counterbalanced and the order of the pairs and side presentation were randomized. Subjects were presented with only opposite-sex faces. Following the face-choice task, the pheromones were presented in two blocks, with vials containing each of the three pheromones (two male, one female) in each block. Each of the six vials was uniquely labelled. The blocks were counterbalanced for long-term and short-term partnerships. The subjects were told that the odours they smelt were related to humans (the term pheromone was not mentioned) and asked whether they could detect the odour and then to rate each odour in terms of how much they would like a partner to smell of the odour within the given relationship context. The scale was a seven-point Likert-type scale ranging from 'not at all' to 'very much so'.

(iv) *Analysis*

Data from anosmic subjects (as with study 1) were removed from the analyses for each pheromone. Ratings of the pheromones and the judgements of face shapes were compared using Spearman's rank correlations, two-tailed, within the same relationship context, i.e. short-term versus long-term.

(b) ***Results***

For women, a significant positive correlation was found between preferences for masculine face shape and the ratings for the male pheromone MP2 when judging in the long-term context ($r_{80} = 0.240$, $p = 0.032$; see table 2). A positive correlation was found between men's ratings of the female pheromone and their preference for a feminine face shape when judging for a long-term partner ($r_{34} = 0.466$, $p = 0.006$), with men who rated the female pheromone more positively also indicating a preference for a more feminized face. No other significant correlations were found (see table 2). Individual correlations may not

withstand corrections for multiple tests. The findings, however, are consistent across studies 1 and 2.

Further analysis revealed that the correlation between preferences for MP2 and facial masculinity was present in women in the follicular ($r_{34} = 0.358$, $p = 0.038$) but not in the luteal ($r_{35} = 0.068$, $p = 0.697$) phase of the cycle. Thus, menstrual-cycle phase influences the relationship between face and pheromone preferences, but does not account for it.

4. GENERAL DISCUSSION

The aim of the two studies was to illuminate the inter-relationship of signals relevant to human mate choice across two discrete sensory modalities, olfaction and vision. In both studies, concordance was found in the preferences for facial characteristics and pheromone odour, and was specific to opposite-sex signals. A strong correlation was found between men's ratings of the female pheromone FP and their preferences for feminine face shapes. Women mirrored this finding: a significant correlation was found between the rating of the male pheromone MP2 and preferences for masculinity in male face shape.

We did not expect to find, as we did, the differences between the two male pheromones. Women who preferred one tended to prefer the other (long-term: $r_{75} = 0.399$, $p < 0.001$; and short-term: $r_{79} = 0.527$, $p < 0.001$), yet there were no significant correlations between preferences for MP1 and faces in study 1 or 2. The lack of significant correlations for MP1 means that the statistics for the two pheromones cannot be usefully compared. Thus, we are presently unable to conclude that the actions of the two substances are similar or dissimilar. Concordant preferences for pheromones and facial shape could imply corresponding mate characteristics, which are subject to the same genetic, hormonal and environmental influences. Concentration of MP2 and degree of masculinity in face shape could independently and simultaneously signal traits such as testosterone level, dominance, 'good genes' or likelihood of desertion. MP1 appears to signal additional or alternative characteristics.

While these pheromones are structurally similar, they have different concentrations in bodily secretions: compared with MP1, MP2 is more abundant in men's

underarm hair (Nixon *et al.* 1988) and semen (Kwan *et al.* 1992). MP2 is also found to produce a stronger response than MP1 in the female VNO (Jennings-White 1995). These and the current findings suggest that the two pheromones may have different consequences for behaviour.

Both of our studies showed concordance between olfactory and visual signals when participants judged partner characteristics in the context of a long-term relationship. In study 1, subjects were asked to judge faces within a relationship context while odours were judged as naturally occurring substances and were not specifically linked to humans. Despite the lack of relationship context in study 1, studies 1 and 2 produced similar results. One possible explanation is that individuals' judgements default to a long-term as opposed to a short-term context (Buss 1994). Concordance, it must be noted, does not imply a preference for either masculine or feminine characteristics, only that the individual preferences are apparently consistent across multiple modalities. The perplexing question remains as to why individual differences exist at all. In other words, why would some men and women choose lower-quality markers over higher-quality markers? Speculation as to how individual differences develop include learning and differences in life history (Penton-Voak & Perrett 2001; Perrett *et al.* 2002), self-perceived attractiveness (Little *et al.* 2001) and hormonal shifts (Penton-Voak & Perrett 2000). Our findings do not elucidate the mechanisms influencing individual differences, rather they offer more enticing evidence for their existence and appeal for further investigation.

When a male or a female is choosing a partner for a short-term relationship, a variety of evolutionary functions may be relevant, such as partner replacement or assessment of mate potential (Buss & Schmitt 1993), cuckoldry (Gangestad & Simpson 2000), or perhaps intrasexual competition. Psychological motivations influenced by the vagaries of modern life, such as gaining sexual experience or peer pressure, may complicate the picture as we see it today. Diverse strategies could lead individuals to react to opposite-sex signals differently. Long-term investment carries quite different risks and costs, compared with short-term investment. Thus, as mating strategies shift between the two, we might expect people to react to different signals of mate quality. For males, the cost of investment in a long-term as opposed to a short-term relationship is much higher. A female risks pregnancy whether she engages in a long-term or a short-term relationship, and thus she must always be particular about whom she chooses as a sexual partner. The data suggest, however, that across two discrete signals, olfaction and vision, women's preferences are more consistent when judging for a long-term partner than when judging for a short-term partner. Therefore, for both men and women the implications of a long-term relationship, which must include limiting if not excluding other mating opportunities, may increase the need to find concordance between signals of mate quality.

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