Chapter 10

Ecological Validity in the Study of Human Pheromones

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Abstract. Several constituents of human axillary secretions have been proposed as candidate human pheromones, but their influence on human behaviour remains controversial. Here we briefly review the literature on the behavioural effects of candidate compounds, noting that inconsistencies in findings could be due in part to the variation in experimental context and potential lack of ecological validity. We also report results of a pilot study which attempts to overcome these limitations in an ecologically-valid experimental paradigm: a speed-dating event. We tested the effects of 4,16-androstadien-3-one within a single speed-dating evening with 25 female and 22 male participants. We found a significant effect of androstadienone on female judgments of male attractiveness, which is consistent with the proposal that androstadienone could act as a modulatory pheromone in humans.

10.1 The Case for "Human Pheromones"

Pheromones have been defined as substances released by an individual into the external environment which precipitate a particular reaction in a conspecific (Karlson and Lüscher 1959). Pheromones are used by species in a variety of phyla (see e.g. McClintock, Jacob, Zelano and Hayreh 2001), and there exist many examples of pheromone-mediated behaviour in a wide range of mammals, particularly in relation to mating behaviour and maturation (see e.g. Vandenbergh 1983). In humans however, the question of whether pheromones influence behaviour was recently listed by Science magazine as one of the top 100 outstanding questions (Anon 2005). A recent review of behavioural and anatomical studies relating to the function of pheromones in human interactions concluded that while a small number were "unambiguously supportive", none seemed ultimately conclusive (Hays 2003).

One hurdle for proponents of human pheromones is the lack of clear evidence for a functional human vomeronasal organ (VNO). Located within the nasal cavity, the VNO is used by many terrestrial vertebrates to detect pheromones (Johns, Feder, Komisaruk and Mayer 1978; Keverne 1983). Although one study (Grosser, Monti-Bloch, Jennings-White and Berliner 2000) reported measurable autonomic changes

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J.L.Hurst et al., *Chemical Signals in Vertebrates 11.*
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following direct introduction of a proposed human pheromone to the VNO, such that this chemical was prevented from reaching the main olfactory epithelium, there is increasing evidence that the system is vestigial in humans. The VNO is not consistently identified in human adults (Garcia-Velasco and Mondragon 1991; Moran, Jafek and Rowley 1991; Stensaas, Lakver, Monti-Bloch, Grosser and Berliner 1991; Trotier, Eloit, Wassef, Talmain and Bensimon 2000; Bhatnagar and Smith 2001; Knecht, Kuhnau, Huttenbrink, Martin and Hummel 2001); a discernable physiological substrate from the VNO to the brain has not yet been identified; and those VNO receptor genes which we might expect to enable pheromone detection (on the basis of comparative studies) appear to be non-functional or pseudo-genes in humans (Tirindelli, Mucignat-Caretta and Ryba 1998). However, pheromonal reception may be possible through the main olfactory system (see e.g. Dorries, Adkins Regan and Halpern 1997; Restrepo, Arellano, Oliva, Schaefer and Lin 2004; Liberles and Buck 2006), and so continuing debate surrounding the human VNO need not preclude ongoing research into the behavioural effects of potential human pheromones.

To date, work on possible human pheromones has primarily focused on the androgens androstenone, androstadienone, and androstenol, found in the human axilla (Hays 2003). All of these are found in much higher quantities in males than females (see Gower and Ruparelia 1992 for an overview), and at least in respect of androstenol, production rates rise sharply at puberty (Cleveland and Savard 1964) and fall in old age and post-menopausally (Brooksbank and Haslewood 1961), in a pattern of ontogeny and sexual dimorphism consistent with sexual signalling. Metabolites of androgens, 5α-androstenone, androstadienone and the low-odour androstadienol, are secreted from the apocrine glands (Gower, Holland, Mallet, Rennie and Watkins 1994). Androstadienol and androstadienone have been shown, *in vitro*, to be converted to the musky-smelling androstenol and the more prominent, urinous androstenone, under the influence of skin-inhabiting coryneform bacteria (Mallet, Holland, Rennie, Watkins and Gower 1991; Gower et al. 1994), although alternative biotransformational pathways have also been demonstrated, again *in vitro* (Decréau, Marson, Smith and Behan 2003).

The earliest work on 'human pheromones' focused on androstenone and androstenol, in part because of their documented function in other mammals: androstenone, for example, occurs in boar saliva and triggers lordosis (the 'mating stance') in the female pig (Signoret and du Mesnil du Buisson 1961). Yet the results of these earlier experiments do not lead to a consistent picture of the effects of these two chemicals in humans. For example, while some studies purport to show that androstenone or androstenol exposure reduces female ratings of male sexual attractiveness (Filsinger, Braun and Monte 1985), others show that androstenol increases female ratings of character or sexual attractiveness (Cowley, Johnson and Brooksbank 1977; Kirk-Smith, Booth, Carroll and Davies 1978), or that there is no effect of either chemical on judgments (Black and Biron 1982; Filsinger, Braun, Monte and Linder 1984). In terms of emotional and behavioural responses, female exposure to androstenone has been associated with a decrease in her self-perceived 'sexiness' (Filsinger et al. 1984), but with an increase in her levels of social interactions with males (Cowley and Brooksbank 1991). On the other hand, neither androstenol nor androstenone led to increased female sexual arousal in response to erotic prose (Benton and Wastell

1986; McCollough, Owen and Pollak 1981). Androstenol exposure has been linked with increased mid-cycle self-reported feelings of submissiveness (Benton 1982) and irritability during menses (Cowley, Harvey, Johnson, and Brooksbank 1980), and indeed its effects on the menstrual cycle may play a part in the reported menstrual synchrony of women who live together (Shinohara, Morofushi, Funabashi, Mitsushima and Kimura 2000). In two studies, females chose to approach areas which had been dosed with androstenone (Kirk-Smith and Booth 1980; Pause 2004); in a similar study, androstenol had no such effect (Gustavson, Dawson and Bonett 1987). The effects of these chemicals on males are sometimes, but not always, complementary: in Pause's (2004) study, homosexual men, like women, approached areas dosed with androstenone more often (heterosexual men were not tested). In another study, men (whose sexual orientation was not reported) rated other men as more sexually attractive in the presence of androstenone and androstenol (Filsinger et al. 1985). Although few of these studies on pheromones in humans are directly contradictory, they are sufficiently at odds to indicate that we lack enough understanding of the phenomenon to be able to ask coherent questions of its effects.

One insight into these sometimes inconsistent findings notes that only some of these studies have used a musk odour control: it could be that other musk odours would trigger similar responses to the potential pheromones (Gower, Nixon and Mallet 1988). Nevertheless, an attenuated conclusion from the work would merely be that some musks have behavioural effects, and androstenol and androstenone are examples of such musks. An alternative suggestion to help explain the reported inconsistencies is that these chemicals have different effects depending on the contexts in which they are experienced, and furthermore that only within ecologically valid conditions are we most likely to detect their influences. This explanation, which will be discussed in greater detail below, receives support from more recent work on the potential human pheromone androstadienone.

Androstadienone provides some of the best evidence for a chemical with the potential for some kind of intraspecific communicative function in humans. Females exposed to androstadienone have shown an increase in positive moods and feelings of focus, and a decrease in negative moods (Jacob and McClintock 2000; Lundström and Olsson 2005). Neurological studies indicate that its effects in females extend beyond the olfactory system, activating areas of the brain associated with attention, social cognition, and emotional processing (Jacob, Kinnunen, Metz, Cooper and McClintock 2001a; Gulyas, Keri, O'Sullivan, Decety and Roland 2004). Physiologically, androstadienone has been found to lower women's heart and breathing rates, and raise body temperature (Grosser et al. 2000). If androstadienone functions as a human pheromone, we might expect its effects to be sexually dimorphic, but little work has specifically compared the two sexes, concentrating instead on female response. One study which contrasted male with female response found different physiological response according to gender (Monti-Bloch and Grosser 1991), while another found no effect of gender on the psychological responses attributed to the steroid (Jacob, Garcia, Hayreh and McClintock 2002).

Claims of commercial manufacturers notwithstanding, it is evident that pheromones do not function as behavioural releasers in humans in the same way as they do in other species. Instead of searching for specific reactions to purported human

pheromones, it may be that these chemicals are better described as 'modulators' (Jacob and McClintock 2000) which influence psychological states and, thereby, also influence behaviour in a variety of fashions depending on the situation in which they are experienced, or the accompanying cues. The co-occurrence of different cues can affect their interpretation (Rowe 1999). In humans, we know that odour cues provide non-redundant information about potential mates because, while both visual and olfactory cues may be used to gauge physical attractiveness, the information in each is not equivalent (Roberts, Little, Gosling, Jones, Perrett and Carter 2005).

10.2 "Human Pheromones": Experimental Considerations

Much work on the impact of potential human pheromones has assumed them to be independent or dominant signals which should give rise to measurable and valid responses when presented in isolation, rather than interacting with the other signals normally available. Yet this assumption may be erroneous, and the importance of context on the effects of purported human pheromones receives empirical backing. For example, Bensafi, Brown, Khan, Levenson and Sobel (2004) found that androstadienone and estratetraenol elicited different affective and autonomic responses depending on the emotional context in which they were presented. Lundström and Olsson (2005) suggested that differences in reactions to androstadienone in two groups of female subjects could be due to the fact that one group was tested by a male researcher whose presence provided the ecological validity and concordant cues for the odour, allowing an effect of the odour to be detected, while the other group was tested by a female researcher and here the steroid had no measurable effect. Likewise, women exposed to androstadienone exhibited different physiological and affective responses from controls, but only in sessions run by a male and not by a female tester (Jacob, Hayreh and McClintock 2001b).

The psychological laboratory, the usual testing ground for isolated effects, may not allow us to fully or adequately investigate the influences of pheromones. It will certainly not allow us to carry out the recommendation made implicit by Jacob et al. (2002, p.282): "If it does not function under normal, nonexperimental social conditions, then it is not a pheromone". With this in mind, we set out to test the effects of androstadienone within as normal a social context as we could.

We conjectured that a "speed-dating" event might be an ecologically valid and theoretically appropriate context to test the effects of potential pheromones involved in human mating behaviour. Speed-dating is a relatively recent form of organised social introduction. Single males and females subscribe to an independently administered event, which is organised to allow each person to interact with each participant of the opposite sex, in a face-to-face meeting, for a pre-defined, limited time period. At the end of each interaction, males and females note covertly whether they would like to meet again. If both parties select the other, their contact details are exchanged by the organisers. Since the aim of participants is to evaluate and attract potential partners, speed-dating provides a suitable arena for the testing of a chemical which might reasonably be implicated in human partner choice.

We used three experimental groups, two of which were exposed to an odour and one to an odourless condition, in order to be able to parse the effects of an odour alone from those of androstadienone. One group was given a solution containing androstadienone at a concentration of 250 μM, to be applied to the region between the upper lip and the nostrils. This concentration and application method is commonly used in such experiments (Jacob and McClintock 2000; Jacob et al. 2001a; Lundström and Olsson 2005), although an appropriate quantity of androstadienone, to reflect that which may be experienced during normal non-intimate social contact, is not clear (Wysocki and Preti 2004; Lundström and Olsson 2005). Analysis of androstadienone concentrations within the apocrine sweat of a small sample of individuals has revealed values as high as 1900 μM (Gower, Holland, Mallet, Rennie and Watkins 1994), although analysis of the quantities of androstadienone deposited upon axillary hair (excluding the skin) over a 24-hour period is suggestive of much lower quantities, up to just over 4000 pmoles of androstadienone (Nixon, Mallet and Gower 1988). Furthermore, natural production of androstadienone would not usually bring it into such close proximity to the olfactory organs, and so the concentration experienced by the women is probably higher than that which might be experienced during normal social intercourse.

Androstadienone sensitivity can vary widely; since this concentration is close to the average odour threshold of the population (Lundström, Hummel and Olsson 2003), we followed the convention of masking its odour in strongly-scented clove oil (1% clove oil in propylene glycol). It is debatable whether something may be classified as a 'pheromone' if it is consciously detected, and so this procedure aimed to prevent conscious or learnt associations with the odour from influencing its effects. The participants were exposed to the solutions by application to the upper lip, from where they were able to inhale the solutions throughout the evening. This does not exclude the possibility that the solutions were transmitted dermally rather than by odour. However, another study has noted mood effects of androstadienone which were not distinguishable according to whether exposure to the chemical was enabled by upper-lip application or passive inhalation (Jacob et al. 2002), and indeed airborne presentation of a chemical is not a necessary condition of its definition as a pheromone; Queen butterflies and salamanders both transfer pheromones directly from one individual to the next (Wyatt 2003).

10.3 Experimental Study

Twenty two males (aged 18-28) and 25 females (aged 19-24) took part in the speed-dating event. Participants were told that the study was concerned with the effects of different odours, including purported human pheromones, on social interactions and judgments, and provided informed consent. Participants applied either water, clove oil (1% clove oil in propylene glycol) or androstadienone (250 μM concentration in the clove oil solution) with a cotton wool pad to the region of skin between the upper lip and the nostrils. Interactions began at least 15 min after initial odorant exposure, and were completed a maximum of 135 min after first exposure. Previous work indicates that measurable effects of androstadienone exposure begin within 6 min,

and last for at least 2 h (Jacob and McClintock 2000). Participants noted whether they would like to meet again; females also rated males for attractiveness, on a scale of 1-7. Five attractiveness ratings were missing from the female score cards, and we excluded a further 14 out of a possible 550 ratings because, upon questioning, one or both of the participants indicated prior familiarity with the other. These 19 omitted or excluded ratings (three being the maximum from any female) were replaced by the average score given to the male in question, calculated from the remaining valid data. This is a conservative approach, reducing between-conditions variance.

The female participants rated each male for physical attractiveness on a 1-7 Likert scale (1=unattractive, 7=attractive). Physical attractiveness judgments tend to be remarkably homogeneous between subjects (Langlois, Kalakanis, Rubenstein, Larson, Hallam and Smoot 2000), presenting an appropriate assay of judgment modulation within a small sample. The ability to judge the physical attractiveness of members of the opposite sex is thought to exist in order to enable reproductively successful partner choice (Grammer, Fink, Moller and Thornhill 2003; Rhodes 2006), and so requesting that people assess physical attractiveness in effect provides an insight into their mating decisions. In this regard, other factors are known to have the potential for a systematic effect on female ratings of male attractiveness. These include female hormonal status (Penton-Voak, Perrett, Castles, Kobayashi, Burt, Murray and Minamisawa 1999), self-rated attractiveness (Little, Burt, Penton-Voak and Perrett 2001) and other-rated attractiveness (Penton-Voak, Little, Jones, Burt, Tiddeman and Perrett 2003); relative age of the two participants is also likely to affect judgments. We took details of all of these for control purposes in our analyses.

Analyses were conducted with SPSS version 13.0, and data satisfied the requirements of the statistical tests used; non-normally distributed data were analysed with the Kruskal-Wallis test. We compared how highly the males were rated in terms of their attractiveness by the women in each of the three experimental conditions. Firstly, we confirmed that there were no significant differences between the three groups of women in terms of other factors which are known to influence attractiveness ratings (number of normally-cycling women in the phase of the menstrual cycle of highest conception risk, 15 to 24 days prior to her next expected menses $H_2 = 0.07$, $p = 0.97$; self-rated attractiveness $H_2 = 0.54$, $p = 0.69$; attractiveness as rated by a panel of 15 males from photographs $F_{2,22} = 0.78$, $p = 0.47$; ages of the women in each group $F_{2,22} = 0.12$, $p = 0.89$).

An ANCOVA was carried out on the average attractiveness rating given by each female to all 22 males, with other-rated attractiveness and age entered as co-variates. We could not include conception risk or self-rated attractiveness data due to non-normal distribution, but these varied little between groups; one woman from each group was at the highest conception risk, and 20 out of 25 females self-rated their attractiveness as four out of seven. The women in the three conditions gave significantly different attractiveness ratings ($F_{2,20} = 5.73$, $p = 0.01$) and androstadienone exposure co-occurred with significantly higher ratings (paired-samples t-tests: androstadienone/clove: t_{21}=-.58, p=<0.001, androstadienone/water: t_{21}=-5.41, p=<0.001, water/clove: t_{21}=-.73, p=0.47). Experimental condition (water, clove or

pheromone) was a more influential factor on female ratings than other-rated attractiveness ($F_{1,20} = 6.25$, $p = 0.021$) or age ($F_{1,20} = 3.84$, $p = 0.064$).

10.4 The Future of "Human Pheromone" Research

Our study is suggestive of chemically-induced judgment modulation. Women exposed to androstadienone, compared with both similar-odour and odourless controls, rated males as more attractive. This result is particularly interesting because a recent study (Lundström and Olsson 2005) of the effects of androstadienone on female attractiveness ratings of a set of male images, cropped from the shoulders up and presented on a computer, found no effect when comparing androstadienone in clove oil to clove oil alone, in concentrations identical to those used in our work. If, as discussed above, ecological validity is required to put into motion the "pheromonal" effects, it could be that images on a computer are not sufficient to affect reactions. Alternatively, it could be that the androstadienone was affecting how the women interacted with and assessed the men in relation to both physical traits and behaviour overall, and that this impacted upon their assessments of attractiveness. Such unavoidable generalisation of personal assessments across attributes is known as the 'halo effect'.

One of the most under-investigated aspect of human pheromone research is that of production. It is not enough to show that purported pheromones have effects; it is also necessary to show that these chemicals are secreted in sufficient quantities to influence others in normal circumstances. Although we believe we have demonstrated the efficacy of a speed-dating context as an experimental paradigm for assessing putative pheromonal effects, the question of whether the dosage and mode of presentation is in any way realistic awaits further investigation. In this sense, our experiment is a form of proof of principle, which now requires more detailed enquiry.

Acknowledgements We wish to thank Nicola Koyama, Minna Lyons, Cathal O'Siochru and Sanjeevani Perera for their help with participant recruitment; **Tom Heyes for his technical and laboratory expertise; Christopher Hassall and Alexandra Wall for their assistance with data collection; Jan Havlicek, Jane Hurst and Tristram Wyatt for helpful comments and advice on an earlier draft; and the University of Liverpool for funding this work.**

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