

Chapter 12

Is the Perception of Dietary Odour Cues Linked to Sexual Selection in Humans?

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Abstract A growing body of evidence suggests that various animal species use diet-associated cues to assess the condition of a potential mate. Such cues are not restricted to the visual channel (e.g. brightness of colouration) but could also be perceived by olfaction. Here, we first summarise current knowledge about the role of diet in vertebrate semiochemistry. Consequently, we employ an adaptationist approach to communication to explore whether cues to diet are or were subject to sexual selection in humans. These thoughts are speculative as research in this area is rather fragmental.

12.1 Introduction

The majority of research on human communication has focused on the vocal and visual domains. Comparatively little research has considered chemosignalling in humans. However, an accumulating body of evidence indicates that human odour cues provide information about the producer's sex, genetic compatibility, reproductive and emotional state, health and diet (for recent reviews see Grammer et al. 2005; Havlicek and Roberts 2009; Lenochova and Havlicek 2008). These body odour cues appear to be used for communication and formation of attributions, although sometimes on a subconscious level and/or in form of hedonic assessment.

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12.2 Adaptationist Approach to Communication

Theoretical approaches to communication vary widely, not only across different scholarly fields, but also within those taking an evolutionary perspective. Here we employ the adaptationist approach elaborated by Maynard Smith and Harper (1995) as it specifically focuses on evolution of biological signalling. According to them, a signal is any act or structure which alters the behaviour of other organisms, which evolved because of that effect, and which is effective because the receiver's response has also evolved. Such behaviours or traits are thought to be often formed through the process of ritualisation, where a behaviour originally had a different function, which has been lost, but receivers started to use it as a cue and under selection the cue evolved into a signal (Scott-Phillips 2008). In this view, a signal is differentiated from a cue: a cue is anything which affects another organism's behaviour but did not develop for that effect (Maynard Smith and Harper 1995). Under this definition there is transfer of one of two types of semantic information (information about an event or a state). The first can carry information about the sender and is often sexually selected ('self-reporting signals', which could, for instance, be represented by displays of physical quality or status, often to the opposite sex), while the second carries information about the environment ('other-reporting signals', e.g. alarm calls and the dances of honey bees) (Maynard Smith and Harper 1995).

If the signal is more costly to produce than the minimum required for effective information transfer, we may refer to cost-added signals. The excess cost evolved because receivers have been more likely to respond appropriately to costly signals. In models of sexual selection it is assumed that if signals reveal the quality of an individual's genes or potential parental care, there is a correlation between signal cost and the quality of the signaller. In mate choice, for example, the correlation exists because high-quality males can afford to produce more costly signals and females benefit from choosing higher quality males. Such signals are likely to reflect a signaller's overall condition, rather than be related to a specific disease or nutritional state (Wyatt 2003). Furthermore, such costly signals are considered to be 'honest' reflections of a signaller's quality, because poor quality cheaters cannot fake them (Maynard Smith and Harper 1995; Zahavi et al. 1999).

12.3 Nutrition-Related Signals

Numerous studies have shown that secondary sexual displays (e.g. brightness of colour) 'honestly' reveal quality via a link between signal characteristics and foraging success or diet (Maynard Smith and Harper 1995; Kirkpatrick 1996). An example is the plumage colouration of male house finches (*Carpodacus mexicanus*), which varies from pale yellow to bright red. Colourful plumage is a result of carotenoid pigmentation. The distribution of carotenoid colouration is inherited, but the intensity of pigmentation is a result of variation in the type and quantity of carotenoids ingested. This is because carotenoids cannot be synthesised *de novo* and must be derived from food. Carotenoid pigmentation therefore represents a condition-dependent trait, where

the condition reflects access to carotenoids. In experiments, female house finches prefer males with the most colourful plumage who have consumed food richer in carotenoids (Hill 1990). Pairing success has also been positively linked to carotenoid-based colouration in the American goldfinch (*Carduelis tristis*) (MacDougall and Montgomerie 2003) and golden-collared manakin (*Manacus vitellinus*) (Stein and Uy 2006). Similarly, male guppies (*Poecilia reticulata*) raised on a high-carotenoid diet were more attractive to females than males raised on a carotenoid-free diet (Grether 2000). As in bird and fish species, carotenoid colouration is a perceivable cue to human health, and may also be relevant to mate choice: people with higher dietary intake of carotenoids in fruit and vegetables have increased skin yellowness which improves their assessed attractiveness (Stephen et al. 2009). Moreover, when participants were asked to maximise apparent health of faces in photographs, they preferred increased skin carotenoid colouration (Stephen et al. 2011).

As with visually perceived traits, females also choose between males using odour. Ferkin et al. (1997) examined how varying amounts of protein in the diet (9, 15 or 25%) affect the attractiveness of odour in meadow voles (*Microtus pennsylvanicus*). Both males and females preferred odours from individuals on high-protein diets: they spent more time investigating odours of opposite-sex conspecifics on a 25% protein diet compared to those on a 9% protein diet (Ferkin et al. 1997). Furthermore, when female meadow voles were not fed for 24 h, their odour was less attractive to males compared with odour of females fed *ad libitum*, but this difference disappeared in 48 h after the food-deprived animals were fed (Pierce and Ferkin 2005). Similarly, high-quality food positively influences attractiveness of urine odour in guinea pigs (*Cavia porcellus*) (Beauchamp 1976). In the red-backed salamander (*Plethodon cinereus*), males extract information concerning territorial ownership from chemical signals in faecal pellets. Walls et al. (1989) found that they could distinguish between faecal pellets that were derived from high-quality or low-quality diets. This ability could be advantageous for females because they can quickly assess territory quality by examination of male faecal pellets alone (Walls et al. 1989). Finally, the salience of diet in regulating odour-mediated social interaction can also be illustrated by how it modulates genetically mediated odour cues. Urinary odours of mice from the same strain but fed different diets were more readily discriminated than faeces from two different mouse strains that differed at one MHC locus, but were fed on the same diet (Brown et al. 1996). Also spiny mouse pups (*Acomys cahirinus*) prefer the odour of a heterospecific females fed on the maternal diet compared to a conspecific female on a different diet (Porter and Doane 1977; Kwak et al. 2008).

12.4 Effect of Diet on Human Body Odour

Diet is also a source of environmental variability in human body odour. This statement is supported by evidence from studies of monozygotic twins. For example, trained dogs could discriminate between the odours of monozygotic twin infants fed on different diets and between the odours of twins who differed in genetic

relatedness, but were unable to discriminate between the odours of monozygotic twins on the same diet (Hepper 1988). People asked to distinguish between hand odours of two unrelated women on the same diet, monozygotic twins on the same diet, two sisters on the same diet, and between monozygotic twins on a different diet were most successful in distinguishing odours from the two unrelated women and were also able to discriminate between the odours of twins on different diet, but could not discriminate hand odours of twins on the same diet (Wallace 1977).

Body odours of new born babies are used by obstetricians as diagnostic markers for specific metabolic disorders, such as maple syrup syndrome (Monastiri et al. 1997). Unusual odours may also be caused by maternal diet. For example, one misdiagnosis of maple syrup syndrome was subsequently explained by the mother having eaten fenugreek seeds immediately prior to delivery (Yalcin et al. 1999). In other cases, babies that smelled of cumin were attributed to maternal diet before delivery (Hauser et al. 1985).

12.5 Experimental Evidence

The above-reviewed evidence suggests that diet profoundly impacts body odour and could be a cue to the quality of ingested food and perhaps to nutritional status. However, we still know relatively little about how particular dietary components shape human body odour. A first study investigated the effect of red meat consumption on male odour. A sample of 17 adult males was placed on a prescribed “meat” or “non-meat” diet for 2 weeks. During the last 24 h, they wore cotton pads in their armpits and, immediately after these were collected, adult females rated the odours for pleasantness, attractiveness, intensity and masculinity. The same procedure was repeated a month later with the same males in each experimental group placed on the opposite diet. Samples from men on the meat diet were rated as less pleasant, less attractive and more intense than samples from the same individuals on the non-meat diet. This suggests that red meat consumption had a negative effect on male body odour attractiveness (Havlicek and Lenochova 2006). Although it is often assumed that the perception of odours associated with a high meat diet would be more attractive for women as it might point to good hunting skills (in an analogous manner to the protein-rich diet of meadow voles or intense colouration of house finches as described above), the results did not support this assumption. Perhaps the consumption of relatively large amounts of meat is instead suggestive of some sort of metabolic disorder.

Recently, we conducted similarly designed experiments to test whether consumption of garlic has an effect on human axillary odour as it has previously been reported to influence body odour (Borrelli et al. 2007; Amagase et al. 2001) and breast milk and amniotic fluid (Mennella and Beauchamp 1991; Mennella et al. 1995). The consumption of garlic is often prohibited in studies employing body odour sampling (Kuukasjärvi et al. 2004; Lenochova et al. 2009; Havlíček et al. 2005, 2006; Roberts et al. 2011).

To test the effect of garlic on body odour we performed two experiments and used a balanced within-subject experimental design (i.e. we compared hedonic ratings of the samples taken from the same odour donors in the garlic and control conditions). In the first experiment, 10 male odour donors participated (mean age 25.2; range 18–31 years), with 16 male donors in the second (mean age 25.1; range 20–34 years). All received instructions to refrain from eating spicy food, from using soap and perfumes, and to avoid demanding physical activities both on the day before sampling and during the sampling day.

In both experiments, males were randomly divided into two groups (A, B). Males in group A were given bread and cream cheese spread blended with garlic (experiment 1: 6 g and experiment 2: 12 g of garlic, this roughly corresponds to two and four cloves of fresh garlic, respectively), while men in group B were given bread and plain cream cheese spread. The procedure was reversed 1 week later. Cotton pads worn in the armpits for 12 h following ingestion served as stimuli. To avoid odour contamination from external odours, they wore new white 100% cotton T-shirts as a first layer of clothing.

Stimuli were rated by 14 female raters (mean age 24.6; range 20–35 years) in the first experiment and by 40 female raters (mean age 22.5; range 19–32 years) in the second experiment. Raters assessed odour pleasantness, attractiveness, masculinity and intensity on 7-point scales anchored by verbal descriptions (e.g. 1—very unpleasant and 7—very pleasant). Female participants were all using hormonal contraception to avoid fluctuations in olfactory perception across the menstrual cycle (Doty 1981; Navarrete-Palacios et al. 2003). The samples from each donor were presented in pairs and raters were instructed not to use same value within each pair. The ratings were written down immediately after sniffing each stimulus, but the time spent sniffing was not restricted. Each rater assessed both sets (i.e. 20 stimuli in the first experiment, 32 stimuli in the second experiment).

The statistical package STATISTICA 7.0 was used for all testing. As our design was within-subjects, paired *t*-tests were used. The results of the first experiment showed that assessments of attractiveness and pleasantness of the samples taken in the experimental (garlic) condition were higher compared to the control (non-garlic) condition; however these differences were not statistically significant. In the second experiment, the odour of donors in the experimental (garlic) condition was judged as significantly more attractive, more pleasant and less intense than in the control (non-garlic) condition (Fig. 12.1). These preliminary results unexpectedly suggest that garlic consumption positively influences body odour.

There could be several explanations of this effect. Garlic could influence armpit odour indirectly through the well-documented antioxidant properties of garlic: sulphur-containing compounds help protect blood cells and vessels against oxidative stress (Borek 2001) which is caused by highly reactive oxygen molecules, possibly by decreasing production of these molecules and/or their metabolites by axillary glands. Garlic enhances levels of two antioxidant enzymes, catalase and glutathione peroxidase, key enzymes in the cell's defence mechanism against oxidative stress (Kemper 2000). Garlic has also bactericidal properties against various bacteria that contribute to the production of armpit odour. If the quantity of bacteria

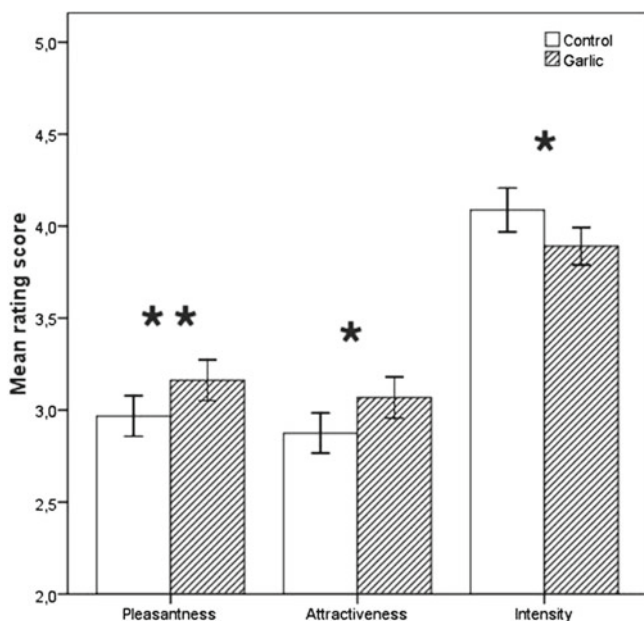


Fig. 12.1 Mean ratings (\pm SE) of 16 pairs of axillary odours on pleasantness, attractiveness and intensity in the experimental (garlic) condition (*shaded bars*) and control (non garlic) condition (*white bars*) by 40 women. Ratings were on 7-point scale (e.g. 1—very unpleasant and 7—very pleasant). Asterisks indicate level of significance in paired *t*-tests. * $p < 0.05$ level; ** $p < 0.01$ level

is reduced, the intensity of armpit odour could be reduced; the intensity of odour is often negatively correlated with pleasantness and attractiveness.

The results on perception of axillary odour after garlic consumption are consistent with the above-reviewed findings on odour-based mate preferences affected by diet in other species. The health benefits of garlic consumption are well established and far-reaching. They include antidiabetic, antithrombotic, antiplatelet, antihypertensive, antioxidative and neuroprotective effects. It is thus plausible that human odour preferences were shaped by sexual selection to be sensitive to odour cues of current metabolic functioning in potential mates. These cues are affected by the amount and quality of food such as garlic digested by the producer. At this point, our knowledge of the mechanisms underlying how garlic consumption shapes axillary odour is highly limited. Therefore, we find it premature to refer to garlic-related odours as quality signals and we conservatively refer to them as cues. To label these as signals, it should be first demonstrated that a particular mechanism has been selected for. Such criteria would, for instance, include condition-dependent production of specific chemical compounds or mixtures of compounds. Furthermore, to avoid deception, production of such compounds should be restricted only to individuals on a high-quality diet.

Finally, all empirical studies testing the effect of diet on human body odour have so far focused on specific dietary compounds. However, perceivers might be more sensitive to cues related to general nutritional status, as has been neatly shown in voles (Ferkin et al. 1997; Pierce and Ferkin 2005). In an analogous study in humans, we might expect people who are starving or on a low nutrition diet to smell less pleasant than those whose food consumption is roughly equal to their caloric expenditure. If this were the case, the mechanism would probably involve catabolic processes which include production of, for instance, acetone, which one can detect in the breath odour of starving individuals or those suffering from diabetes (Laffel 1999).

12.6 Conclusions

We aimed to assess the role of diet in the production of chemical cues involved in communication processes. In particular, we asked whether diet-related odour cues are used in assessments of condition and quality of potential mates. This idea is exemplified in the case of eating garlic, which is known for its antioxidative properties and consumption of which, we have found, increases the pleasantness of axillary body odour. This suggests that perception of odour cues linked to diet and/or nutrition may be subject to sexual selection in humans, as in animals. Having said this, the number of studies focusing on this issue remains very limited and we strongly advocate more empirical work in what we see as a fascinating area of semiochemistry.

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