Minireview

In the nose of the beholder: are olfactory influences on human mate choice driven by variation in immune system genes or sex hormone levels?

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Abstract

The human leukocyte antigen (HLA) is the most polymorphic region of the genome, coding for proteins that mediate human immune response. This polymorphism may be maintained by balancing selection and certain populations show deviations from expected gene frequencies. Supporting this hypothesis, studies into olfactory preferences have suggested that females prefer the scent of males with dissimilar HLA to their own. However, it has also been proposed that androstenones play a role in female mate choice, and as these molecules inhibit the immune system, this has implications for the theory of HLA-driven mate preference. This review will critically analyze the findings of studies investigating olfactory preference in humans, and their implications for these two contrasting theories of mate choice.

Keywords: human leukocyte antigen, major histocompatibility complex, mate choice, olfaction, andosterone

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Introduction

Evidence from molecular studies of the major histocompatibility complex (MHC) termed human leukocyte antigen (HLA) in humans[1] has meant that the concept that variability at the HLA is maintained by balancing selection is now almost unanimously accepted.[2] Both pathogen and non-pathogen linked models for the mechanism by which this polymorphism is maintained have been proposed. The two models overlap greatly in that they both assume that a female will prefer to mate with males whose genes confer the greatest competitive advantage on her offspring.[3] The nature of the genetic haplotype best able to confer competitive offspring affects the potential decisions made with regard to mate choice, and therefore has important bearings on the conclusions that may be drawn from studies of olfactory-driven mate choice. This paper will review the evidence relevant to potentially desirable HLA haplotypes, and its implications for theories of olfactory-driven mate choice.

Mate choice at the HLA

The HLA is one of the areas of the genome best suited for the genetic study of mate choice,[4] and support for discriminative mate choice based on MHC haplotype has come from both animal and human studies[5–9] (see Piertney and Oliver,[10] for a review). However, their findings have proved inconclusive with regards to the most desirable MHC haplotype. Studies in semi-free populations of mandrills with little migration found strong dissassortative mating,[4] whereas in baboons with a higher degree of outbreeding the effect was not found.[11] Disassortative mating results in negative relatedness coefficient between partners. Ober *et al.*[6] found that this effect was pronounced among Hutterites, and suggested that it may be due to their limited outbreeding, increasing the selective pressure of finding non-related mates. Similarly Chaix *et al.*[7] proposed that the differences in relatedness coefficient found between the Yoruba and European population may be a result of cultural factors. Therefore, the effect of HLA disassortative mating, and subsequently individual female preference should be taken with the proviso that they are dependent on context and may vary over time[10,12] (see Table 1).

Which haplotype is most desirable?

In the HLA, alleles show co-dominance,[17] with the effect that heterozygotes are able to respond to a wider array of non-self pathogenic antigens as they can bind to and present twice as many foreign peptides compared with

Table 1 Summary of HLA mate choice hypotheses

Preferred mate HLA haplotype	Rationale in terms of offspring	References
Dissimilar	Most diverse HLA haplotype	Wedekind[13] and Wedekind and Furi[14]
Heterozygous	'Best of a bad job' – high-quality mate able to provide first-order benefits and reasonable offspring quality	Brown[3]
Rare	Resistant to common parasites	Potts and Slev[29]
Intermediate heterozygosity	Ensure the maintenance of locally co-adapted gene complexes along with HLA diversity.	Jacob *et al.*[15]
Complementary	Most diverse HLA haplotype	Trivers[16] and Brown[3]

homozygotes.[18] HLA molecules bind to and present pathogenic cell fragments on the cell surface membrane, where they are recognized by *T*-cells.[19] A larger repertoire of HLA molecules therefore theoretically would confer greater pathogen resistance. It has therefore been proposed that heterozygotes would be favored by natural selection. The red queen hypothesis assumes that new combinations of genes are required every generation to counter currently dominating parasite.[20] A female would therefore benefit from selectively mating with those who would provide her offspring with the best immune response to current parasitic pressures, in combination with her own genes for immune function.[21] There are various theories as to how this pressure might translate into mate choice.

To produce maximally heterozygous offspring, it has been proposed that females would preferentially mate with those most dissimilar to themselves,[14,22] which would theoretically produce offspring with the widest range of pathogenic antigens. Wedekind and Penn[23] also suggest that by producing an excess of heterozygotes a population produces a 'moving target' against rapidly evolving parasites. However, heterozygosity is not without its costs as certain HLA combinations are associated with links to autoimmune disease.[13] There are also physical constraints on the expression of HLA genes. Specifically, there is an inverse relationship between MHC diversity and T-cell repertoire;[13] an individual with all the MHC molecules required to respond to all potential pathogens would probably have no T-cells left to respond to them due to self-reactive T-cells.[21] There are also density requirements for the cell surface glycoproteins encoded by the HLA genes.[13]

Given the potential advantage conferred by HLA variability, it has been suggested that females seek to mate with those whose genes best complement their own.[16] However, to do this at the level of the HLA[3,24] would require that:

- Females have a knowledge of their own immune genes;
- There is a large variation in resistance genes in the population;
- She is able to determine the immune genotype of any potential partner;[6]
- She would also need to make decisions based on fluctuating parasitic pressures.

In light of the complexity of determining the most beneficial partner, it may be that simple heterozygosity is desirable, as theoretically, any offspring would be able to respond to the greatest variety of parasites. Although this strategy may not produce maximally heterozygous offspring in every case, it would produce offspring that are more heterozygous on average.[25] A female may share many alleles with her heterozygous mate but a preference for HLA-dissimilar mates would ensure that she gives her offspring the most diverse immune system.[21] The female would also accrue direct advantages in that a heterozygous partner would be the least susceptible to illness and so more likely to be able to support offspring himself.[3,24]

Animal studies have found that maximum heterozygosity is not always desirable as resistance can be recessive[26] or that no heterozygote advantage exists.[27] Rather, intermediate numbers of allele matches conferred the greatest fitness, with females choosing optimal rather than maximally heterozygous partners.[15] These intermediate heterozygotes retained locally co-adapted gene complexes, MHC alleles that had co-evolved with local parasites, yet were able to respond to a wide array of pathogens, and it has been proposed that this might also be the case in humans.[15]

An alternative hypothesis rests on the argument that pathogens are more likely to have developed mechanisms to evade the immunity conferred by common HLA genotypes,[28] since it is these hosts in which they will most often find themselves.[29] As specific parasites are detected by specific HLA molecules, having maximum heterozygosity does not necessarily guarantee immunity from a parasite, as it may be that an individual does not necessarily possess the resistance allele. By this logic, rare HLA haplotypes should be favored.[18,29] However, rare alleles would only be beneficial if they conferred a resistance that others did not. Another argument would be that while heterozygosity provides the greatest range of resistance, homozygous individuals may have higher resistance against specific infectious diseases.[21] In humans, these hypotheses have been tested in the context of studies investigating olfactory influences on mate choice, which we explore in the next section.

Olfactory HLA signals

In terms of number and size of sebaceous and apocrine glands, humans are the most highly scented of all apes, and it has been suggested that the axillary apocrine gland aggregation is in fact a scent organ.[30] In men, the axillary apocrine gland is larger, and as such, men are more pungent than women.[31] There is good evidence that animals choose mates with regard to immune function through odor[32–35] and it has been proposed that humans may also be able to discriminate potential mates based on HLA-derived odors.[21] For body odor to be an effective

signal, certain criteria must be met: first, the signal must be honest, meaning that, in the case of body odor and the HLA, scent must be a reliable indicator of immunocompetence; and second, different individuals must be able to produce uniquely different odors, so we should all have a unique odor 'fingerprint.'[14]

Twin studies have been used to show that body odor has a significant genetic component,[36] and it has been proposed that the MHC may be able to produce individually unique body odors.[37] Rats have been shown to be able to distinguish between the odors of humans with different HLA haplotypes.[38] Although humans have long been thought of as microsmatic[30] ('poor smellers'), in fact, the olfactory system has been shown to be responsive to picograms of an odorant.[39] Gilbert *et al.*[40] demonstrated that humans are also extremely sensitive to differences in MHC, and able to distinguish between the odors of MHC congenic mice. Such findings have led to a number of studies into the responsiveness of humans to olfactory cues, and the influence of these cues on mate preference.

Studies into olfactory preferences

Wedekind *et al.*[22] were the first to study the concept of odor as a secondary sexual trait. Although their initial study has been criticized on the basis of experimental design,[41,42] Wedekind and Füri[14] subsequently replicated the results, altering the experimental design to address some of these concerns. Wedekind *et al.*[22] recruited 49 female and 44 male students who were typed at three loci, HLA-A, HLA-B and HLA-DR. The men were asked to wear a t-shirt for two days and women were then asked to rate the odors worn by both MHC-similar men and MHC-dissimilar men. Both the stage of the menstrual cycle and whether the women were on an oral contraceptive pill (OCP) were assessed. The latter control is important, since it has been proposed that the OCP reverses mate preferences by tricking the body into believing it is pregnant, leading women to seek similar HLA-based odors (associated with kin) over dissimilar odors (associated with non-kin).[43] Women were then asked to rate the odors between 0 and 10 for three factors: intensity, pleasantness and sexiness. Wedekind *et al.*[22] found that odors from HLA dissimilar men were rated as more pleasant and sexier than those of HLA similar men.

Jacob *et al.*[15] studied odor preferences and HLA matches across five loci among the Hutterites, an inbred American population. Sampling in such small, isolated communities ensured that the number of HLA alleles was low, which should increase selection pressure at the HLA. The male scent samples, again in the form of t-shirts, came from both Hutterite and non-Hutterite males. No one man was rated more attractive on the basis of scent than any other overall; however, individual women varied significantly in whose odor they preferred, tending to choose men with dissimilar HLA genotypes. Jacob *et al.*[15] interpreted their results as suggesting that women are attracted to a small, intermediate number of HLA matches, which prevents the loss of locally adapted gene complexes and provides the optimal balance between inbreeding and outbreeding.

Some investigators have failed to replicate the above results.[44,45] For example, Santos *et al.*[44] sought to replicate the finding of Wedekind *et al.*[21] and Wedekind and Füri,[14] but found no evidence that perceived pleasantness of odor correlated with HLA-dissimilarity in either men or women. However, their experiment did not control for OCP use or menstrual cycle phase. Furthermore, they collected scent from their subjects by having them wear a necklace with a sachet of absorbent cotton. This would mean that only sweat from the sternum was collected, whereas most of a healthy person's body odor is produced by the apocrine glands of the axillae.[30] It is also possible that some studies reporting negative results lacked statistical power to detect associations of this type, since the effect sizes reported tend to be in the small to medium range.

Thornhill *et al.*[45] found that the commonness of an allele significantly predicted the attractiveness of a scent, consistent with the idea of complementary and heterozygous mating; as found by Jacob *et al.*,[15] rare alleles were not preferred. However, they found a different result to Jacob *et al.*[15] where male heterozygosity was positively correlated with scent attractiveness. Studies into fluctuating asymmetry, and its presumed links to immunocompetence, have similarly found that symmetrical men, theoretically those with the most effective immune defenses, produce the most attractive odors.[45–47]

Some studies have reported that the scent of HLA-dissimilar men reminded woman more often of previous partners than that of HLA-similar men,[21,48] suggesting that women preferentially mate with men who share common features at the level of the HLA. The degree of HLA allele sharing may also influence behavior within a relationship; Garver-Apgar *et al.*[47] found that women with HLA-similar partners are more likely to find their partners sexually unattractive and to engage in infidelity. Roberts and Little[43] also found differences in HLA-associated odor preferences between married and single women. Those women who were married found the scent of HLA dissimilar men more attractive than single women. Roberts and colleagues interpret these results as evidence that women seek attributes in extra-pair partners as a means to increase heterozygosity in their offspring.

These results are consistent with the hypothesis that humans discriminate at the level of the HLA with regards to their partners and seek out a partner with complementary HLA genes to their own. However, it is too early to reach a firm conclusion on what would be the most desirable HLA haplotype as studies have shown mixed results. That said, if women were mating for a rare HLA haplotype, we would expect to find a particularly rare man being more attractive than others; since this is not the case in any study thus far, then this theory would seem unlikely. Of the remaining hypotheses, it is difficult to disentangle the differences in results as the variation is subtle; whether women prefer an intermediate amount of matches, choose partners for specific MHC combinations or make the 'best of a bad job' with maximally heterozygous men remains unclear.

Androstenes as sexual signals of immunocompetence

An alternative theory suggests that the androstenes, androstenol and androstenone, sex hormones similar in structure to testosterone, are indicators of immunocompetence.[45] Androstenes form a large component of human sweat, with androstenone producing the characteristic sweat odor while androstenol produces a musk-like odor.[30] Men produce more androstenes than women and they have an inhibitory effect on the immune system; it has therefore been suggested that androstenes are an honest signal of mate quality. Grafen[49] elaborated Zahavi's handicap principles with the strategic-choice model whereby males adaptively allocate energy and resources between sexual displays (in this case androstenes) and immunological function.[50] The suppression of immune function due to androgen production satisfies this constraint: males who were ill or immunoincompetent could not fake such a signal without placing themselves at considerable risk. Only those with a very fit immune system can therefore afford to produce large amounts of androstenes and thereby inhibit their immune system. The production of androstenone is also highly sexually dimorphic, which suggests that it is linked to sexual selection.[45]

The brain retains a pheromone-sensitive region known as the vomeronasal organ (VNO); previously thought to be vestigial in primates, it has since been reported that the VNO is functional in humans, responding to pheromones in picogram amounts.[39] Information from the VMO travels directly to the amygdala and the hypothalamus, areas implicated in sexual behavior.[39] Moreover, a pheromone receptor gene expressed in the olfactory mucosa has been identified.[51]

Pheromones are able to produce both short-term and long-term behavioral changes.[39] Female odors have been shown to produce menstrual synchrony[42,52] while male odors have a regulatory effect on the menstrual cycle, known as the Whitten effect.[53] Responsiveness to androstenone in women also varies during different phases of the menstrual cycle, reaching its peak at ovulation.[39] Pheromones have also been found to influence behavior in experimental studies. Both men and women rate stimuli, such as faces, animals and buildings, as warmer and more friendly in the presence of androstenol,[54] and male faces are rated as being significantly more sexually attractive by women wearing androstenone-impregnated masks.[55]

If the attractiveness of a potential mate is indeed related to androstene production, this would mean that those with the fittest immune systems would be the most attractive as they should be best able to produce androstene-derived compounds. This would appear to preclude the hypothesis that women choose mates with complementary HLA haplotypes to their own, since HLA dissimilarity in itself is no guarantee of immunocompetence. However, those who are heterozygous or retain an intermediate amount of heterozygosity could conceivably satisfy this constraint.

Conclusion

Much of literature has thus far treated these two components of body odor, HLA-derived compounds or androstene-derived compounds, separately. However, there is no clear reason why the two should be mutually exclusive. Much as body odor and fluctuation asymmetry are posited to work in conjunction, it may be that androstene acts as the primary determinant of mate quality, acting as an overall signal of mate quality, while HLA-derived scents provide a 'fine-tuning' of the compatibility of a potential partner. This would allow both the selection of a mate who provides direct benefits,[16] and also one whose HLA genotype provides reasonably fit offspring. If this were the case, it would be predicted that studies including sufficiently large samples of men should find that the scent of several men, with more effective immune defenses, would be rated as more attractive, based on their ability to produce higher levels of androstenes. However, female preferences would be spread across these more immunocompetent men, as different women sought different complementary HLA genotypes with regards to their own. Whatever the explanation, it is clear that olfactory cues play an important role in mate preference. However, studies assessing both andosterone levels and HLA haplotypes are necessary in order to clarify whether one of these mechanisms is dominant, or whether they act in tandem.

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REFERENCES

1 MHC Sequencing Consortium. Complete sequence and gene map of the human major histocompatibility complex. *Nature* 1999;**401**:921–3
2 Black FL, Hedrick PW. Strong balancing selection at HLA loci: evidence from segregation in South Amerindian families. *Proc Natl Acad Sci USA* 1997;**94**:12452–6
3 Brown JL. A theory of mate choice based on heterozygosity. *Behav Ecol* 1997;**8**:60–5
4 Setchell JM, Charpentier JE, Abbott KM, Wickings EJ, Knapp LA. Opposites attract: MHC-associated mate choice in a ploygynous primate. *J Evol Biol* 2010;**23**:135–8
5 Yamazaki K, Boyse EA, Mike V, Thaler HT, Mathieson BJ, Abbott J, Boyse J, Zayas ZA. Control of mating preferences in mice by genes in the major histocompatibility complex. *J Exp Med* 1976;**150**:755–60
6 Ober C, Weitcamp LR, Cox N, Dytch H, Kostyu D, Elias S. HLA and mate choice in humans. *Am J Hum Genet* 1997;**61**:497–504
7 Chaix R, Cao C, Donnelly P. Is mate choice in humans MHC-dependent. *PLoS Genet* 2008;**4**:1–5
8 Landry C, Garant D, Duchesne P, Bernatchez L. 'Good genes as heterozygosity': the major histocompatibility complex and mate choice in the atlantic salmon (*Salmo salar*). *Proc Biol Sci* 2001;**268**:1279–85
9 Aeschlimann PB, Häberli MA, Reusch TBH, Boehm T, Milinski M. Female sticklebacks *Gasterosteus aculeatus* use self-reference to optimize MHC allele number during mate selection. *Behav Ecol Sociobiol* 2003;**54**:119–26
10 Piertney SB, Oliver MK. The evolutionary ecology of the major histocompatibility complex. *Heredity* 2006;**96**:7–21
11 Huchard E, Knapp LA, Wang L, Raymond M, Cowlishaw G. MHC, mate choice and heterozygote advantage in a wild primate. *Mol Ecol* 2010;**19**:2545–61
12 Hedrick PW, Black FL. HLA and mate selection: no evidence in South Amerindians. *Am J Hum Genet* 1997;**61**:505–11

13 Wedekind C. Handicaps not obligatory in sexual selection for resistance genes. *J Theoret Biol* 1994;**170**:57–62
14 Wedekind C, Füri S. Body odour preferences in men and women: do they aim for specific MHC combinations or simply heterozygosity? *Proc: Biol Sci* 1997;**264**:1471–9
15 Jacob S, McClintock MK, Zelano B, Ober C. Paternally inherited HLA alleles are associated with women's choice of male odor. *Nat Genet* 2002;**30**:175–9
16 Trivers RL. Parental investment and sexual selection. In: Campbell B, ed. *Sexual Selection and the Descent of Man*. Chicago, IL.: Aldine, 1972
17 Thornhill R, Gangestad SW, Miller R, Scheyd G, McCollough JK, Franklin M. Major histocompatibility complex genes, symmetry and body scent attractiveness in men and women. *Behav Ecol* 2003;**14**:668–78
18 Alberts S, Ober C. Genetic variability in the major histocompatibility complex: a review of non-pathogen-mediated selective mechanism. *Yearb Phys Anthropol* 1993;**36**:71–89
19 Rao CV. *An Introduction to Immunology*. Pangbourne: Alpha Science International, 2002
20 Van Valen L. A new evolutionary law. *Evol Theory* 1973;**3**:1–30
21 Milinski M. The major histocompatibility complex, sexual selection and mate choice. *Annu Rev Ecol Evol Syst* 2006;**37**:159–86
22 Wedekind C, Seebeck T, Bettens F, Paepke AJ. MHC-dependent mate preferences in humans. *Proc Biol Sci* 1995;**260**:245–9
23 Wedekind C, Penn D. MHC genes, body odours and odour preferences. *Nephrol Dial Transplant* 2000;**15**:1269–71
24 Brown The new theory of mate choice and the MHC. *Genetica* 1999;**104**:215–21
25 Allendorf FW, Leary RF. Heterozygosity and fitness in natural populations of animals. In: Soule ME, ed. *Conservation Biology: The Science of Scarcity and Diversity*. Sunderland, MA: Sinauer, 1986:57–76
26 Ilmonen P, Penn DJ, Damjanovich K, Morrison L, Ghotbi L, Potts W. MHC heterozygosity reduces fitness in experimentally infected mice. *Genetics* 2007;**176**:2501–8
27 Weatherhead PJ, Dufour KW, Loughheed SC, Eckert CG. A test of the good-genes-as-heterozygosity hypothesis using red-winged blackbirds. *Behav Ecol* 1999;**10**:619–25
28 Potts WK, Wakeland EK. Evolution of diversity at the major histocompatilibility complex. *Trends Ecol Evol* 1990;**5**:181–7
29 Potts WK, Slev PR. Pathogen-based models favoring MHC genetic diversity. *Immunol Rev* 1995;**143**:181–97
30 Stoddart DM. *The Scented Ape: The Biology and Culture of Human Odour*. Cambridge; New York: Cambridge University Press, 1990
31 Van Toller S, Dodd GH. *Fragrance: The Psychology and Biology of Perfume*. Cambridge: Elsevier Science Press, 1992
32 Yamazaki K, Boyse EA, Mike V, Thaler HT, Mathieson BJ, Abbott J, Boyse J, Zayas ZA. Control of mating preferences in mice by genes in the major histocompatibility complex. *J Exp Med* 1976;**150**:755–60
33 Potts WK, Wakeland EK. Evolution of MHC genetic diversity: a tale of incest, pestilence and sexual preference. *Trends Genet* 1993;**9**:408–12
34 Jordan WC, Bruford MW. New perspectives on mate choice and the MHC. *Heredity* 1998;**81**:127–33
35 Rantala MJ, Jokinen I, Kortet R, Vainikka A, Suhonen J. Do pheromones reveal male immunocompetence? *Proc Biol Sci* 2002;**269**:1681–5
36 Roberts SC, Gosling LM, Spector TD, Miller P, Penn DJ, Petrie M. Body odour similarity in non-cohabiting twins. *Chem Senses* 2005;**30**:651–6
37 Penn D, Potts W. How do major histocompatibility complex genes influence odor and mating preferences? *Adv Immunol* 1998;**69**:411–36
38 Ferstl R, Eggert F, Westphal E, Zavazava N, Mullerruchholtz W. MHC-related odors in humans. In: Doty RL, Müller-Schwarze D, eds. *Chemical Signals in Vertebrates 6*. New York: Plenum Press, 1992:205–11
39 Grammer K, Fink B, Neave N. Review: human pheromones and sexual attraction. *Eur J Obstet Gynecol Reprod Biol* 2005;**118**:135–42
40 Gilbert AN, Yamazaki K, Beauchamp GK, Thomas L. Olfactory discrimination of mouse strains (*Mus musculus*) and major histocompatibility types by humans (*Homo sapiens*). *J Comp Psychol* 1986;**100**:262–5
41 Hedrick PW, Loeschke V. MHC and mate selection in humans? *Trends Ecol Evol* 1996;**11**:24
42 McClintock MK. Menstrual synchrony and suppression. *Nature* 1971;**229**:244–5
43 Roberts CS, Little AC. Good genes, complementary genes and human mate preferences. *Genetica* 2008;**134**:31–43
44 Santos PSC, Schinemann JA, Garbardo J, Bicalho MD. New evidence that the MHC influences odor perception in humans: a study with 58 Southern Brazilian students. *Horm Behav* 2005;**47**:384–8
45 Thornhill R, Gangestad SW, Miller R, Scheyd G, McCollough JK, Franklin M. Major histocompatibility complex genes, symmetry and body scent attractiveness in men and women. *Behav Ecol* 2003;**14**:668–78
46 Rikowski A, Grammer K. Human body odour, symmetry and attractiveness. *Proc Biol Sci* 1999;**266**:869–74
47 Garver-Apgar CE, Gangestad SW, Thornhill R, Olp JJ. Major histocompatibility complex alleles, sexual responsivity and unfaithfulness in romantic couples. *Psychol Sci* 2006;**17**:830–5
48 Gangestad SW, Thornhill R. Menstrual cycle variation in women's preferences for the scent of symmetrical men. *Proc Biol Sci* 1998;**265**:927–33
49 Grafen A. Biological signals as handicaps. *J Theoret Biol* 1990;**144**:517–44
50 Wedekind C, Folstad I. Adaptive or nonadaptive immunosuppression by sex hormones? *Am Nat* 1994;**143**:936–8
51 Rodriguez I, Greer CA, Mok MY. A putative pheromone receptor gene expressed in human olfactory mucosa. *Nat Genet* 2000;**26**:18–19
52 Preti G, Cutler WB, Garcia CR, Huggins GR, Lawley HJ. Human axillary secretions influnce women's menstrual cycles – the role of donor extract of females. *Horm Behav* 1986;**20**:474–82
53 Cutler WB, Preti G, Krieger A, Garcia CR, Huggins GR, Lawley HJ. Human axillary secretions influence women's menstrual cycles – the role of donor extract of females. *Horm Behav* 1986;**20**:463–73
54 Kirksmith M, Booth DA, Carroll D, Davies P. Human social attitudes affected by androstenol. *Res Commun Psychol Psychiatr Behav* 1978;**3**:379–84
55 Thorne F, Neave N, Scholey A, Moss M, Fink B. Effects of putative male pheromones on female ratings of male attractiveness: influence of oral contraceptives and the menstrual cycle. *Neuroendocrinol Lett* 2002;**23**:291–7

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