



Invited reply

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Accumulating evidence suggests that men do not find body odours of human leucocyte antigen-dissimilar women more attractive

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In our recent study published in *Proceedings of the Royal Society B* [1], we investigated the effects of major histocompatibility complex (MHC; or human leucocyte antigen system, HLA in humans) on men's preferences for women's body odours. Using rigorous methods, we found no evidence that men find body odours of HLA-dissimilar women more attractive than odours of HLA-similar women. In his comment, Wedekind [2] claims that our conclusions were premature, because he found (using our data) a stronger negative relationship between pleasantness and intensity for HLA-dissimilar odours than for similar ones. Although this is an interesting finding, it cannot be considered as a support for HLA-related mate preferences.

Wedekind's comment is rather misleading, for various reasons. First, empirical evidence for HLA-mediated body odour preferences in humans is not nearly as clear as the author would like to assume. In the 20 years since Wedekind *et al.*'s seminal work [3], various studies examining HLA-influences on body odour preferences in humans have been published and the reported findings are mixed. In fact, a recent meta-analysis by Winternitz, Abbate [4] revealed that over all studies with human and non-human primates, results on MHC-mediated body odour preferences are inconsistent and non-significant. It is important to note that Wedekind [2] misinterprets the meta-analysis by Winternitz *et al.* [4]: These authors found preferences for MHC heterozygosity but not for MHC dissimilarity. These are two very different kinds of MHC influences and should not be mixed up. Another recent review outlining disparate and controversial results for human studies is Winternitz & Abbate [5].

Second, Wedekind compares our study with two of his own studies [3,6]. However, our study differs from Wedekind's studies in at least one important aspect: we studied men's preferences for women's body odours while Wedekind *et al.* [3] asked women to evaluate the body odours of men. Wedekind & Furi [6] also included odours of very few women (i.e. two), which may have led to a false positive result. There is reason to believe that males and females might differ regarding the effect of MHC in mate preferences (cf. [6–9]). Because males typically have a higher potential reproductive rate [11] and females often bear greater reproductive costs [12], males might seek females with high perceived fertility to increase the probability for reproduction, while females seek males who are most likely to maximize offspring survival. So, it is conceivable that men rely less on HLA-mediated odour cues when choosing their mates than women. We note that apart from our study [1], only four studies have included men as odour raters. Two of these studies report no preference HLA-dissimilar women [13,14], and two suggest that men show a preference for body odours of HLA-dissimilar women [6,15] (note that Wedekind & Furi included odours of only

two women). These four studies have in common that they did not control for the menstrual cycle phase during which the body odours were collected. Controlling for menstrual cycle phase is important because body odour varies across the cycle. An increasing number of studies report that women's body odour is rated as more attractive if gathered near ovulation compared to odour that was collected in other cycle phases [16–19]. So, if not controlling for menstrual cycle, cyclic effects of odour attractiveness are likely to overwrite any putative HLA-effects. In our recent study [1], we controlled for menstrual cycle phase. We also included a large number of female odour donors ($n = 49$) and collected ratings of 94 men. The results of this study add to the studies suggesting no effect of HLA similarity on women's preferences for men's body odours.

Furthermore, Wedekind mentions in his comment [2] that the female donors in our study were asked to shave their armpits 2–5 days before odour collection, which in his view might reduce the potential link between HLA and body odour attractiveness. However, such a link (if it exists) should still be observable in our study, because only body odours that were perceivable were included in the analyses. We note that only in very few cases (less than 5%) odours were rated as 'non-perceivable'. In addition, it is important to note that the non-perceivable trials were not always from the same pad (i.e. woman). In other words, there was no pad that was not perceivable in all cases: the non-perceivable pads did not come from specific women, but were randomly distributed over different donors. Since men clearly found some odours more attractive than others, it seems unlikely that the odours were too faint to be smelled. It is not surprising that in Wedekind's original study no single odour was rated as 'not perceivable', because in his study, it seems that raters were not given the option to choose 'I cannot perceive the odour'. Wedekind further mentions that the odours that could be perceived were on average rated as less intense in our study [1]

than in Wedekind's study that allowed for axillary hairs [3]. Again, this is not surprising, as Probst *et al.* [1] included only women as odour donors while Wedekind *et al.* [3] included odours of only men, and men's body odours are typically perceived as being more intense than women's (e.g. [20,21]).

The finding that the negative correlation between intensity and pleasantness ratings was stronger for HLA dissimilar than for similar odours is potentially interesting, but the reasons for this interaction is currently unclear. Moreover, the negative relationship between intensity and pleasantness was present in both HLA similar and dissimilar odours and the interaction was only weak. The main interest of Probst *et al.*'s [1] study was to investigate potential HLA-mediated odour preferences in men. We found that none of HLA similarity, HLA heterozygosity, nor rareness of HLA had an effect on how attractive men found women's body odours. The reanalyses by Wedekind do not contradict these findings.

To conclude, we find Wedekind's comment [2] on our recent study [1] is based on many questionable assumptions which, when corrected and put into the right context, do not make a convincing point in challenging our main claims. While the interaction between odour pleasantness and intensity reported in Wedekind's comment might indeed point towards the existence of some form of social signalling, it cannot be considered as a support for HLA-mediated mate preferences.

Data accessibility. The dataset used in our original work is available at Dryad Digital Repository: (<http://dx.doi.org/10.5061/dryad.270h8>).

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