

Research



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Losing stinks! The effect of competition outcome on body odour quality

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Dominance hierarchy is often established via repeated agonistic encounters where consistent winners are considered dominant. Human body odour contains cues to psychological dominance and competition, but it is not known whether competition outcome (a marker of a change in dominance hierarchy) affects the hedonic quality of human axillary odour. Therefore, we investigated the effect of winning and losing on odour quality. We collected odour samples from Mixed Martial Arts fighters approximately 1 h before and immediately after a match. Raters then assessed samples for pleasantness, attractiveness, masculinity and intensity. We also obtained data on donors' affective state and cortisol and testosterone levels, since these are known to be associated with competition and body odour quality. Perceived body odour pleasantness, attractiveness and intensity significantly decreased while masculinity increased after a match irrespective of the outcome. Nonetheless, losing a match affected the pleasantness of body odour more profoundly, though bordering formal level of significance. Moreover, a path analysis revealed that match loss led to a decrease in odour attractiveness, which was mediated by participants' negative affective states. Our study suggests that physical competition and to some extent also its outcome affect the perceived quality of human body odour in specific real-life settings, thus providing cues to dominance-related characteristics.

This article is part of the Theo Murphy meeting issue 'Olfactory communication in humans'.

1. Introduction

Dominance plays an important role in understanding social behaviour, especially in species with a stable social structure. Different scholars, however, propose various concepts and definitions of dominance. Some are based on theoretical constructs, while others rely on structural or functional empirical observations. A definition with broad applicability, well suited to describing male–male dominance, was proposed by Drews [1, p. 308] who states that 'Dominance is an attribute of the pattern of repeated, agonistic interactions between two individuals, characterized by a consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation'. The consistent winner thus becomes dominant and the consistent loser subordinate.

Drews [1] makes a distinction between dominance status and dominance rank, where the former refers to dyads and depends on individual attributes, while the latter applies to a position within a hierarchy and is affected by group composition. In other words, dominance status refers to an individual's status in a dyad, where the individual is either dominant or subordinate based on the outcome of previous encounters, while dominance rank expresses an individual's position in a dominance hierarchy and can be described either

qualitatively as high or low or, assuming linear hierarchy, by an ordinal number. Dominance rank is thus a relative, not an absolute measure.

(a) Dominance and individual fitness

Dominant status is sometimes linked to higher levels of aggressive behaviour. On the other hand, though, dominance can facilitate conflict avoidance when a non-agonistic assessment results in submissive behaviour on the part of a potential opponent, or when a dominance relationship is already established. One individual can submit to another without a fight because opponents can assess each other based on characteristics closely correlated with competitive ability. This is a way of preventing actual, potentially costly, fights. Such situations do not necessarily require prior interaction between individuals and a decision whether to fight or stand down may be based on an assessment of an opponent's resource holding potential (RHP) relative to one's own. Many characteristics, such as size, strength, weaponry and experience, seem to contribute to the RHP [2]. When such cues are not available or opponents have a similar RHP, the relative fighting ability can be established by actual contest, inferred from an observation of the potential opponent's behaviour towards others, or based on the results of the most recent mutual interaction (since a similar outcome can be expected). The latter, however, requires individual recognition and memory of past encounters [1].

Various animal studies show that dominance status correlates with fitness-related characteristics. Dominance is frequently associated with access to resources, territory range and copulatory behaviour in males. This has been demonstrated by some studies of bird [3] and mammalian species, including rodents [4], carnivores [5], artiodactyls [6] and primates [7]. Where association between dominance status and reproductive success has been tested, a positive relationship was found for instance in white leghorn chickens [8], in mice under caged and seminatural conditions [9,10], in male deer mice (*Peromyscus maniculatus*) [11] and in the golden hamster (*Mesocricetus auratus*) [12]. Nevertheless, not all studies yielded consistent results and some found either no effect or even an inverse one [13,14].

(b) Olfactory assessment of dominance in non-humans

Existing research convincingly demonstrates the importance of olfactory cues in dominance assessments [15]. Even without previous interactions, rodents can differentiate between dominant and subordinate individuals by odour alone [16–18] and in the context of intrasexual competition, lower-ranking males usually avoid the scent of dominant males [19]. Males of a low competitive ability also tend to avoid the odour of males of higher competitive ability [20,21] and are more reluctant to fight with territory owners [22].

Females tend to prefer dominant males [16,18,23–25]. Females are attracted to the scent of dominant males' urine and spend more time in areas associated with the odour of a dominant male [26]. On the day before becoming sexually receptive, females also mark more frequently in a dominant male's area, which usually prompts the male to investigate the space [12] and increases the likelihood of mating with the dominant male. Preference for dominant males would be especially advantageous for females if male dominance rank were heritable. In fact, Drickamer *et al.* [27] showed

that female house mice prefer not only the odour cues of dominant males but also those of their sons. Moreover, oestrous females preferred the odour of males who emerged dominant when encounters were staged [28].

On the other hand, Hurst *et al.* [29] argued that information intrinsically contained in the scent is usually not sufficient for males to decide whether to leave a particular area or not. It seems that individuals need to compare it to their own competitive ability. The males of Algerian mouse (*Mus spretus*) thus learn the association by direct interaction between competitors in the course of which a dominance relationship is established. When deciding whether to opt for fight or flight, individuals can thus use the association between the result of their last interaction and the smell of a mark. Since they can expect a similar outcome in a future interaction, they can predict the cost of such fight and avoid potentially costly consequences. Indeed, subordinate males seem more likely to avoid the scent of a dominant male who had previously defeated them than a control unfamiliar odour [30].

(c) Olfactory assessment of dominance in humans

It has been shown that odour cues play a role in dominance assessments in humans as well, whereby for instance, psychological dominance was found to be associated with odour attractiveness. More specifically, women in committed relationships preferred the odour of dominant men when in the fertile phase of their menstrual cycle, while single women and women in non-fertile phases showed no such preference [31]. Similarly, another study found a correlation between self-rated dominance and dominance judged from axillary odour. Interestingly, the correlation was significant only for participants' rating of opposite-sex scent donors. It was therefore argued that dominance judgements are especially important in the mating context [32]. In a subsequent study, significant effects were observed when male raters assessed male and female body odours: a positive correlation was found between dominance and attractiveness ratings of body odour [33]. When raters included both adults and children, only adults were successful in recognizing dominance from adult body odour. It thus seems that the ability to congruently assess dominance may become significant after puberty, possibly owing to mate choice [34]. Interestingly, dominance ratings remain congruent with self-reported dominance even when individuals use fragranced cosmetics [35]. The link between dominance and body odour seems to be related to certain hormones and neurotransmitters, whereby dominant behaviour tends to correlate positively with the level of testosterone (T) and its metabolites [36].

(d) Human olfactory cues to competition and aggression

Relative dominance and rank in a dominance hierarchy are established via repeated agonistic interactions between individuals, which are often accompanied by aggression. Consistent winners of such competitive encounters are considered dominant and losers subordinate. Olfactory cues to competition or aggressive state were also found in humans. The ability to recognize aggressive states by olfaction, among other cues, would help humans to detect individuals

who may pose a threat and avoid potential harm by reacting before such an individual starts behaving aggressively.

Axillary samples collected during a competition (badminton match) elicited a larger skin conductance response (SCR; a marker of sympathetic autonomic activity associated with arousal and orienting towards a meaningful stimulus, whereby emotionally significant stimuli usually elicit a larger SCR) in raters than samples taken during a non-competitive control sport condition (running). When competing, athletes experienced angry and positive feelings, higher T levels, and they felt more dominant after winning a match. SCR response was higher in raters who scored higher on the social anxiety trait, which suggests that socially anxious individuals process threatening social information preferentially [37]. Similarly, aggression-related odours collected during a boxing session induced in raters an impairment of higher-order processing of social information, i.e. a state compatible with an anxiety stress reaction. This effect was observed only in tasks involving a high cognitive load (emotional Stroop word task versus emotional face recognition task), which the authors of the study interpret as reflecting the stress linked to a need to gather further information about potentially dangerous individuals [38]. Still, the results of this experimental study should be further tested in ecologically valid settings to assess their generalizability potential. Neural correlates for the perception of aggression-related odour cues have also been described. They indicate activation in parts of thalamus, hypothalamus, other limbic brain areas and the cingulum. These findings suggest that parts of the brain linked to alarm processing and preferential processing of threat stimuli are involved. When aggression odours were presented as a novel stimulus, they were processed more slowly and with a higher level of attentional disengagement, which may suggest a freeze-like response. At the same time, reaction times were shorter for aggression odours presented after samples from a control condition (non-competitive exercise) [39].

(e) Hormonal mechanisms of olfactory dominance and competition assessments

A positive correlation between dominance rank and T levels has been reported in many animal species [40–42], whereby medium or higher T levels are associated with higher odour attractiveness [43]. The urine of mandrills (*Mandrillus sphinx*) [44] contains chemical cues characteristic of individual rank, while in bank voles (*Myodes glareolus*) the concentration of chemicals released by males correlates with their social status [25]. In territorial scent-marking animals, scent-marking and the products of specialized glands are androgen-dependent [19,45]. In dominant males, these glands are larger and their products have stronger aversive properties [46]. It seems that these properties are owing to various androgen-dependent volatile compounds and lipocalins, such as terpenes, thiazole and brevicomin in mice [47,48], while in rabbits dominance is related to the presence of 2-phenoxyethanol [49].

Evidence indicates that there also exist correlations between hormone levels, aggressive and dominant behaviour, and the outcome of competitive encounters [50]. Aggression and T levels are usually highest during periods of social instability, for instance during the formation of a dominance hierarchy and during the establishment of and

challenges for territory. This effect is described by the ‘challenge hypothesis’, which was first proposed by Wingfield *et al.* [51] and further applied to human behaviour by Mazur and colleagues [52,53 but see 54]. According to this hypothesis, T rises shortly before a contest in anticipation of and as part of preparation for the challenge. Victory then leads to an increase in T and decrease in cortisol (C) levels, while in losers, the effect is opposite [55,56]. For instance, in chacma baboons (*Papio hamadryas ursinus*), T levels increase during periods of rank instability [42], whereby males rising in rank had higher T levels than those whose rank fell [57]. This phenomenon is usually explained by reference to the need, in winners, to prepare for new challenges, whereby elevated T levels can help them prepare for anticipated contests. In losers, a decrease in T levels can help them withdraw from future challenges and prevent possible injuries. Changes in C levels are usually associated with currently experienced stress [52].

Analogously to animal studies, links between hormone levels, aggression and competition outcome have also been investigated in humans. The results of some studies seem to support the challenge hypothesis and show T increase and C decrease in winners and the opposite pattern in losers [58–61]. On the whole, however, the results are mixed [62–65]. The hormonal response to competition and its outcome thus seems to be mediated by complex psychological processes, such as mood [66], perceived importance of the competition [67], self-appraisal of performance [62], anxiety and coping styles [68,69].

(f) The current study

Available evidence indicates that in humans, olfactory cues to psychological dominance, competition and aggressiveness not only exist but also that they have particular neurological correlates. However, no research so far has tested the effect of winning and losing a match—which could be viewed as a marker of change in the dominance hierarchy (i.e. victory in successive agonistic interactions leads to a dominant position)—on the hedonic valence of body odour. It seems, however, that an ability to recognize aggressive, dominant, or successful individuals without direct contact in order to adapt future behaviour in terms of either fight or flight or coalition forming would be advantageous. In our study, we chose Mixed Martial Arts (MMA) as a model of real-life physical confrontations, because it is a complex combat sport that employs fighting styles and techniques used both in stance and on the ground. Here, dominance status relates to the dyadic relationship between two fighters established after one or several matches. The fighter who wins more fights than his opponent becomes dominant within a specific dyad. Furthermore, the MMA league has a ranking system that reflects victories of individual fighters in the course of a year. Fighters thus compete to occupy as high (dominance) rank as possible by winning matches. We collected body odour samples during Czech MMA amateur league before and after matches. We also obtained data regarding fighters’ hormone levels (T and C) and affective states (for a review, see [70,71]), because it had been shown that they are associated with both body odour quality and with the competition outcome (e.g. [60,62,72]). We assumed that both victory and defeat in a match will change the quality of axillary secretion. While winning would affect perceived pleasantness and attractiveness of the axillary odour

positively, losing would have a negative effect that will be mediated by T and C hormone levels and/or positive and negative affective states. Moreover, we expected that winning would be accompanied by more positive affective states and increase of T and decrease of C, and vice versa.

2. Methods

All procedures employed in this study conform to the ethical standards of the responsible committee on human experimentation and with the Helsinki Declaration. The study was approved by the IRB at the Charles University, Faculty of Science (approval number 2013/14). All participants were informed about the goals of the study and indicated their willingness to participate by signing informed consent. The study is part of a larger project that included the collection of standardized photographs, basic anthropometric measurements, demographic data and questionnaires on MMA training history.

3. Participants

(a) Body odour donors

We collected samples from 40 amateur male MMA fighters during four rounds of the Czech amateur MMA league held by the local MMA organisation at different locations in the Czech Republic. Only 38 participants, however, provided body odour samples both before and after the match, whereby four of these fought matches in two rounds of the league, which is why we included only samples from their first match. And finally, two matches resulted in a draw and we had to exclude the fighters involved. This left us with a final sample of 32 participants (17 winners and 15 losers, each participated in the study once), mean age 23.79 years (s.d. = 4.74; range 18–37), mean body weight 77.19 kg (s.d. = 9.66; range 60.8–99.5), mean body height 179.34 cm (s.d. = 6.96; range 164–195). Participants were recruited with the help of the league organizer, the Mixed Martial Arts Association Czech Republic (MMAA), via social media (Facebook), posters, oral invitations at gyms, and during individual rounds of the amateur MMA league. Athletes received a compensation of 400 CZK (app. 15 EUR) for their time and potential inconvenience caused by participation in our study.

(b) Body odour raters

In total, 138 raters (31 males), mean age 23.11 years (s.d. = 3.56; range 18–35), assessed the set of odour samples. They were mainly Charles University students who were recruited via e-mails, advertisement on social media (Facebook) and posters in university halls. To avoid possible changes in olfactory perception during the menstrual cycle [73,74], all participating female raters were hormonal contraception users. The raters received 100 CZK (app. 4 EUR) as a reward for participation and compensation for their time.

(c) Body odour sampling

We collected the first body odour sample approximately 1 h before the match and the second sample immediately after the match. To reduce possible inter-individual variation in the use of cosmetics and in hygienic practices, a researcher first wiped participants' armpits with an unperfumed moistened napkin (DM Ebelin Ultra Sensitive, <https://www.dm.cz/>).

As a medium for body odour sampling, we asked participants to wear provided 100% cotton T-shirts (previously washed without washing powder) for 30 min. After sampling, the T-shirts were placed in zip-lock plastic bags. Samples were stored in a cooling box (temperature range 7–12°C) at the match and during transport, and subsequently in a freezer at –21°C (time between collection and freezing was at most 12 h) until taken out for rating. This was done to prevent any further metabolic bacterial action [75,76]. We also collected capillary blood samples from fighters and while their body odour was collected, participants completed a standardized questionnaire regarding their mood.

(d) Hormone samples collection and analysis

Capillary blood samples, which were used to determine T and C levels, were collected by a trained phlebotomist approximately 1 h before and 15 min after a match [77,78]. We opted for capillary blood because after a match, saliva samples would be likely contaminated by blood. The presence of blood components in saliva, even when too small to be visually detected, can affect the values of salivary analytes [79]. Blood samples were taken from the fingertip and the serum portion separated by centrifugation. Samples were analysed at the Institute of Medical Biochemistry and Laboratory Diagnostics of the General University Hospital and the First Faculty of Medicine of Charles University. Serum C was analysed by a chemiluminescent immunoassay (CLIA) Centaur XP Siemens method with a sensitivity of 5.5 nmol l⁻¹. Serum T was analysed by CLIA Architect i2000 Abbott method with a sensitivity of 0.5 nmol l⁻¹ [80].

(e) Affective states and pain assessment

A standardized questionnaire (Positive and Negative Affect Schedule, PANAS) [81] was used to assess participants' affective state. The PANAS questionnaire consists of 20 adjectives that describe various positive (e.g. interested, strong and attentive) and negative (e.g. distressed, ashamed and afraid) affective states. Each participant was asked to indicate to what extent he felt a certain way at that moment on a 5-point, verbally anchored scale (1—very slightly or not at all; 5—extremely). PANAS scores were calculated by summing the scores of positive and negative items [81]. Scores can range from 10 to 50, with higher scores representing higher levels of positive and negative affect, respectively.

After a match, contestants were asked to indicate whether they felt any pain on a 7-point scale ('How much physical pain do you feel right now?'; 1—no pain at all, 7—very strong pain).

(f) The odour rating procedure

For rating, we cut a circle from each T-shirt's armpit area (approx. 17 cm in diameter) [82]. Odour samples were removed from the freezer approximately 1 h before the start of a rating session. They were enclosed in opaque 250 ml glass jars labelled with a code. The rating took place over 3 days (each day, one-third of the samples were used) to accommodate a large number of raters and to avoid possible effects of olfactory adaptation in raters. The rating took place in a quiet, ventilated room. The experimenters were present in the room throughout the rating session but the study design was double-blinded.

Each rater received a rating sheet with instructions to judge each sample for (1) pleasantness, (2) attractiveness, (3) masculinity and (4) intensity on a 7-point, verbally anchored scale (e.g. 1—very unpleasant, 7—very pleasant). The instructions read: 'Rate each of the following samples for their pleasantness, attractiveness, masculinity/femininity and intensity on a scale from 1 to 7, using 4 as a neutral answer.' We further verbally described that 'pleasantness' refers to the rater's liking of the sample, 'attractiveness' to attraction, 'masculinity' to perceived manliness and 'intensity' to strength of the sample. Each rater first indicated the code of the rated sample and then marked a number on each scale (the scales were presented in the same order as reported above). Raters were instructed to select the option 'I cannot smell the sample' and refrain from rating if they found the sample's odour too weak to be detected. Those ratings were excluded from the analysis together with the matching ratings for before/after the match. The time spent sniffing was not restricted, and ratings were recorded on a rating sheet immediately after sniffing each sample. The same procedure has been employed in earlier studies (e.g. [83]).

(g) Statistical analysis

Statistical tests were performed using R x64 3.5.3 via RStudio 1.2.1335, jamovi 1.1.2.0 and Mplus x64 8.3.

To assess whether the collected ratings were accurate and stable estimates, we calculated the point of stability (POS, a point at which averages do not meaningfully change with incorporation of additional observations) within a corridor of stability of a mean (COS) [84,85] for each scale and rater's sex. We used the default setting as per Hehman *et al.* [84] and the POS was specified as 95% of observed values falling within ± 0.5 COS of the 7-point scale we used. The number of raters met calculated POS values for all scales except for masculinity (POS=37) and intensity (POS=34) where samples collected before the match were assessed by 31 male raters (electronic supplementary material, table S1).

For exploratory purposes, we ran a bivariate correlation (Pearson's r correlation coefficient reported with 95% confidence intervals [lower level (LL), upper level (UL)]) using individual odour rating as a unit of analysis separately for losers and winners.

To assess perceived differences in body odour samples taken before and after a match in winners and losers, we employed a linear mixed effects models (LMMs) using GAMLj (v. 1.6) jamovi module. In total, we ran four separate models (one model for each rated characteristic) using REML fit. In all models, the rated characteristic (e.g. pleasantness) was a dependent variable, while time (before or after a match), match result (winning or losing) and rater's sex (male or female) were fixed effects factors (with *Simple* contrasts). Rater ID was set as a random-effects factor and interactions between all fixed effects factors were specified, e.g. `model_pleasantness <- lmer(pleasantness rating ~ 1 + time + result + rater sex result:time + result:rater sex + time:rater sex + result:time:rater sex + (1 | ID_rater))`.

The proportions of reduced error (pseudo R^2) for LMMs are reported in R^2 marginal (R^2_M) and R^2 conditional (R^2_C). Effect estimates of LMMs are stated with 95% confidence intervals [LL, UL]. All post hoc comparison p -values are reported with Bonferroni correction.

We performed a general linear model analysis (GLM), again using the GAMLj (v. 1.6) jamovi module to test the

differences between T and C levels collected before and after a match. We ran GLM models for T and C separately, hormone levels were set as a dependent variable, time (before or after a match) and match result (win or lose) as independent factors, while further interaction between time and result was added into the model (e.g. following model syntax `T levels ~ time + result + time : result`). Variability explained by each model is reported as R^2 , effects size as η_p^2 , and Bonferroni correction was used for subsequent post hoc pairwise comparisons. Furthermore, we used the independent samples t -test to explore possible differences in self-assessed pain between winners and losers after a match.

To explore the potential mediating effects of affective states and hormonal levels on perceived odour qualities after a match, we ran a path analysis. All input variables were standardized (STDYX method), we used the full information maximum-likelihood method (FIML, as default in Mplus) to handle missing values, and applied the maximum-likelihood (ML) estimator. Odour ratings were set as dependent variables, emotional states and hormonal levels as mediators, and the match result (win/loss) as a factor.

4. Results

(a) Associations between rated characteristics

In both winners and losers, we found a strong positive correlation between perceived odour pleasantness and attractiveness (r values range between 0.829 and 0.922) before and after a match (electronic supplementary material, tables S3a,b). In losers, pleasantness and attractiveness correlated positively with intensity before the match ($r=0.683$ and 0.53 , respectively) and negatively with masculinity after a match ($r=-0.528$ and -0.588 , respectively). Intensity, on the other hand, correlated negatively with attractiveness after a lost match ($r=-0.515$). In winners, masculinity correlated negatively with ratings of pleasantness ($r=-0.621$) and attractiveness ($r=-0.733$) after a match and positively with intensity both before ($r=0.625$) and after ($r=0.935$) a match. No significant correlation was found between intensity and both pleasantness and attractiveness (all r values were <0.27).

In losers, we also found that attractiveness ratings before a match had a significant negative correlation with negative affective states ($r=-0.545$), while in winners it correlated significantly negatively with T levels ($r=-0.733$). Also in winners, T levels before a match correlated positively with rated masculinity ($r=0.67$).

For the full results of data exploration, see electronic supplementary material, tables S3a,b.

(b) The effect of match outcome on perceived body odour quality in winners and losers

We found that rater's sex was a significant factor only in the case of masculinity ratings ($\beta=-0.495$ [-0.754 , -0.237], $p<0.001$), whereby female raters tended to give overall higher ratings. Furthermore, in the masculinity rating model, the interaction between time (pre- and post-match) and rater's sex was significant ($\beta=0.371$ [0.102 , 0.639], $p=0.007$). Female raters rated the samples of both winners and losers collected before and after a match as equally masculine.

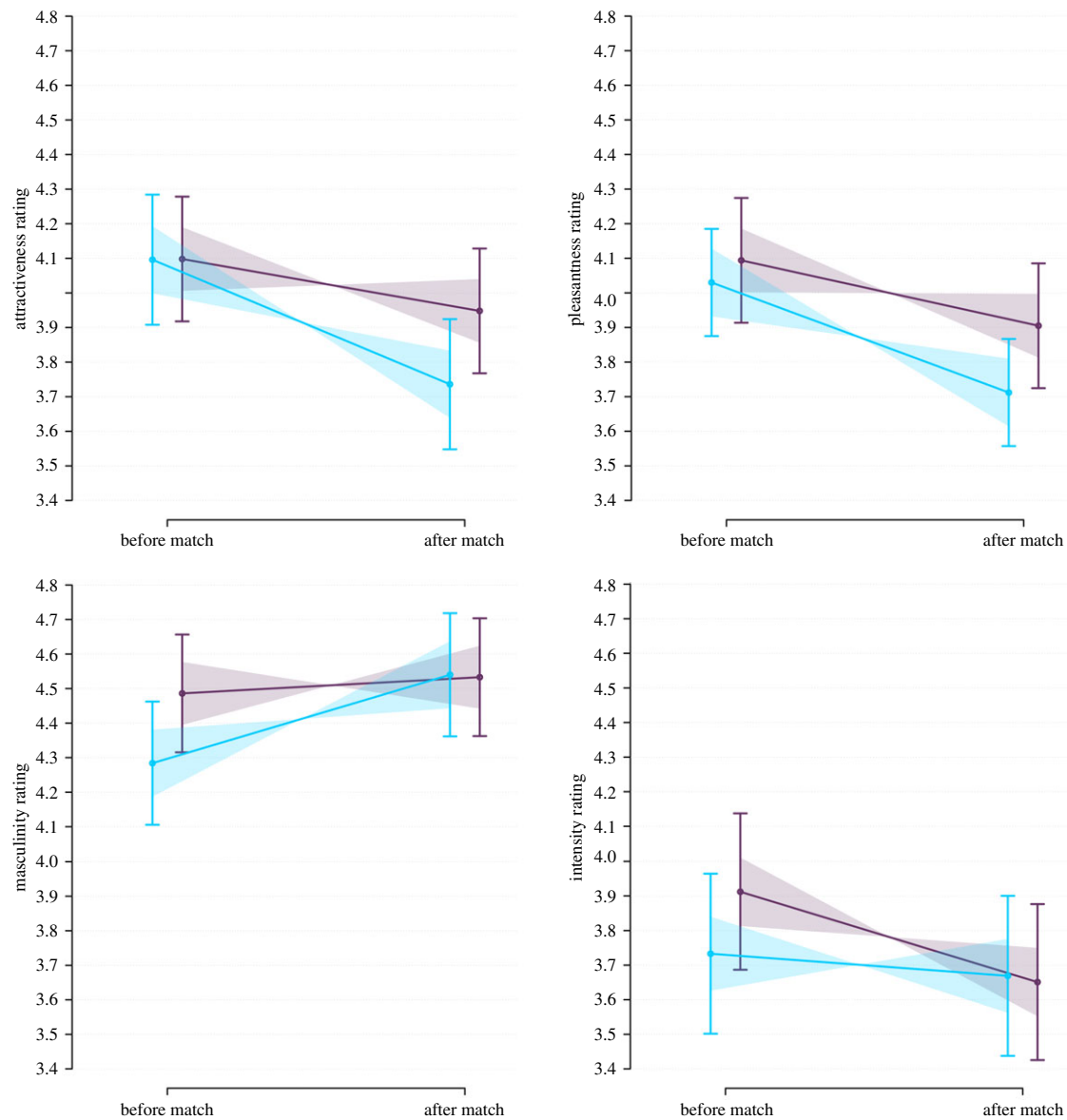


Figure 1. Differences in body odour ratings between winners and losers before and after the match. Dots indicate mean rating and error bars their 95% confidence interval (CI). Semi-transparent bowtie areas indicate 95% CI of the fixed effect of difference between the mean ratings of attractiveness, pleasantness, masculinity and intensity in winners (dark purple, upper traces) and losers (light blue, lower traces) before and after match. (Online version in colour.)

Male raters, on the other hand, found the post-match samples of losers more masculine than their pre-match ones, while no difference between pre- and post-match ratings was found in winners (see electronic supplementary material, figure S1 and tables S4, S5 and S6). With respect to rated pleasantness, attractiveness and intensity, we found no sex differences.

In all four models, we found a significant effect of time (pre- and post-match) on perceived body odour quality. Perceived pleasantness ($\beta = -0.257$ [$-0.392, -0.122$], $p < 0.001$), attractiveness ($\beta = -0.258$ [$-0.392, -0.123$], $p < 0.001$) and intensity ($\beta = -0.161$ [$-0.306, -0.016$], $p = 0.03$) had decreased, while perceived masculinity ($\beta = 0.145$ [$0.02, 0.288$], $p = 0.025$) increased after a match. The effect of match result (winning or losing) was bordering the formal level of statistical significance ($\beta = 0.131$ [$-0.005, 0.268$], $p = 0.059$) only with respect to pleasantness, where it was lower in losers. For the remaining odour qualities, the match result had no significant effect. Furthermore, we found no statistically significant interaction between the time and result in any model of perceived body odour qualities (figure 1; electronic supplementary material, tables S4 and S5).

(c) The effect of match outcome on hormone levels

The overall GLM model for T, which explained only 6.3% of variability, was not statistically significant ($F_{1,36} = 0.806$, $p = 0.499$, $\eta_p^2 = 0.063$) and we found no significant differences in T levels between winners and losers, between before and after a match, or in interaction of these two variables. Analysis showed that the GLM model for C, which explained 56.9% of variability, was significant ($F_{1,28} = 1.341$, $p < 0.001$, $\eta_p^2 = 0.569$). In particular, C levels were higher after a match than before it ($F_{1,28} = 31.129$, $p < 0.001$, $\eta_p^2 = 0.526$, β estimate = 341.241 [215.957, 466.525]). Match outcome and interaction between outcome and time were not, however, significant predictors of C levels (electronic supplementary material, figure S2 and tables S7 and S8).

(d) The mediating effect of affective states and hormone levels on perceived odour quality

Since our sample size was too small for the requirements of path analysis, we reduced the number of variables by

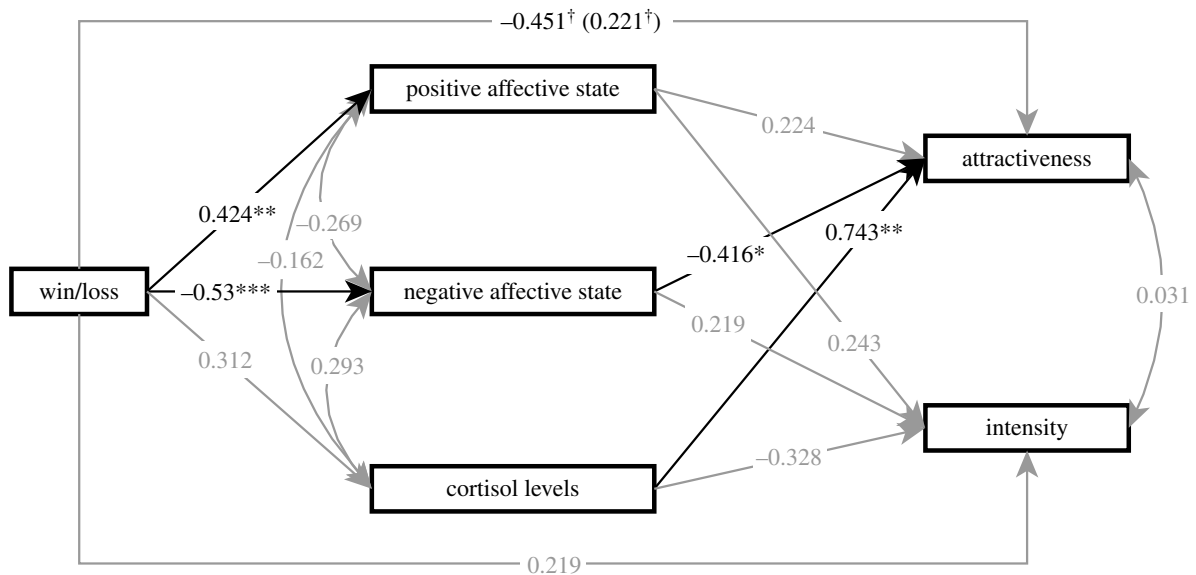


Figure 2. A mediation model of direct and component effects of a match result, affective states and hormone levels on perceived body odour attractiveness and intensity. Black lines represent significant effects, grey lines non-significant effects and the value in brackets represents an indirect effect (win/loss \Rightarrow negative affective state \Rightarrow attractiveness). $^{\dagger}p \leq 0.06$, $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

excluding intercorrelated variables from the model. Pleasantness, attractiveness and masculinity ratings were highly correlated, so we left in the model only attractiveness and intensity as dependent variables. We also excluded T levels because they did not differ between the two conditions. C levels, negative affective state and positive affective state measures were entered as independent variables and match outcome (win/loss) as a factor in the model.

The mediation model significantly explained $\approx 52\%$ of variation in attractiveness ($R^2 = 0.519$, s.e. = 0.25, $p = 0.038$), but only $\approx 16\%$ of variation in intensity ratings ($R^2 = 0.157$, s.e. = 0.138, $p = 0.253$). The path model revealed a direct effect of match result (win/loss) on rated attractiveness, which bordered on the formal level of statistical significance ($\beta = -0.451$, s.e. = 0.238, $p = 0.057$) and a non-significant direct effect of match result on intensity rating ($\beta = 0.219$, s.e. = 0.227, $p = 0.335$). Total indirect effects were significant for win/loss \Rightarrow attractiveness rating ($\beta = 0.547$, s.e. = 0.236, $p = 0.021$). The only indirect effect bordering on significance level was observed for the direction win/loss \Rightarrow negative affective state \Rightarrow attractiveness rating ($\beta = 0.221$, s.e. = 0.117, $p = 0.06$) (figure 2). Furthermore, we found a significant positive relationship between match result and positive affective state ($\beta = 0.424$, s.e. = 0.145, $p = 0.003$) and C levels and attractiveness rating ($\beta = 0.743$, s.e. = 0.229, $p = 0.001$), while a negative association was observed between match result and negative affective state ($\beta = -0.53$, s.e. = 0.127, $p \leq 0.001$) and between negative affective state and attractiveness ($\beta = -0.416$, s.e. = 0.188, $p = 0.026$). For full results, see figure 2 and electronic supplementary material, table S9a,b.

(e) Differences between winners and losers in self-assessed pain

We did not find any statistically significant differences between winners (mean = 2.19, s.e. = 0.41) and losers (mean = 2.33, s.e. = 0.485) in self-assessed pain after a match ($t_{29} = 0.231$, $p = 0.819$, $d = 0.083$) (electronic supplementary material, table S10).

5. Discussion

In this study, we tested the effect of winning and losing a physical confrontation on human body odour quality and investigated factors that may mediate observed changes. We expected that winning would have a positive effect on body odour quality and losing a negative effect on it. We also predicted that winning would be associated with positive affective states, a rise in T levels and decrease in C levels, while losing would be characterized by the opposite pattern. Moreover, we hypothesized that these factors would mediate a change in body odour quality.

We found that after a match, perceived odour pleasantness, attractiveness and intensity significantly decreased, while masculinity increased in both winners and losers. Nevertheless, the decrease in pleasantness was more pronounced in losers, which suggests that losing has a more negative effect on body odour quality. We found no statistically significant differences in body odour ratings between winners and losers either before or after a match. Path analysis showed that a loss led to a decrease in odour attractiveness and this effect was mediated by participants' negative emotions.

Winning a match may entail a rise in the dominance hierarchy, while losing lowers the rank: in our case, the match score was added to a personal profile, which affects the league rank. Both losing and winning have consequences for both competitors. Nonetheless, the relatively more profound odour changes in losers suggest that losing may be perceived as having more serious consequences because it may be linked not only to lower league ranking but also to more or less serious injuries. In ring-tailed lemurs (*Lemur catta*), injury affects the chemical composition of secretion and injury status can be discerned by other individuals [86,87]. Similarly, it could be expected that fighters who lost suffered more injuries during a match and that might be reflected in their body odour. In our study, however, that does not seem to be the case since self-assessed pain did not significantly differ between winners and losers and it was not associated with any of the rated odour characteristics.

Our results thus indicate that competitive situations *per se* can have an effect on body odour, because after a match, while masculinity increased, both pleasantness and attractiveness decreased. The influence of competition on body odour has been demonstrated already by Adolph *et al.* [37], although they found that the tested odour samples affected exposed individuals on a subliminal level without any perceived differences between competition-linked and control odours. In our study, the perceived odour quality changed, which could be linked to increased sweating owing to the physical effort during the match. Thermoregulation involves mainly eccrine glands [88], which during exertion produce more diluted, watery, and less oily secretion consisting mostly of water and electrolytes derived from blood plasma and sodium chloride [89]. The change in odour quality we observed could thus be owing to the different quality of sweat. This finding should raise caution with respect to using sports odours as control stimuli (e.g. [90,91]), because they may have somewhat different properties than for example odours collected during sleep (e.g. [83]).

(a) Link between dominance and body odour

The results of some animal studies suggest dominant individuals may have specific intrinsic odour qualities [27] that are probably androgen-dependent [43]. In our study, however, ratings of pre-match body odour were similar for winners and losers, suggesting no prior differences in fighters' body odour quality. Still, we obtained data on the result of only one match and have no information about the fighters' current rank position. We cannot, therefore, draw stronger conclusions about possible links between various qualities of body odour and rank in the dominance hierarchy. In other words, we do not know whether there exists any connection between dominance rank and specific odour qualities, although previous studies did find some olfactory cues to psychological dominance [31,33].

(b) Sex-related differences in rating

The absence of significant sex-linked differences in raters' assessments in most rated characteristics suggests that these odour cues have no specific role in intra- or intersexual selection. The sole exception was masculinity ratings. Overall, losers' post-match body odour was rated as more masculine than their odour before a match. This effect was driven by male raters who evaluated losers' body odour as more masculine after a match. Females did not perceive any difference between pre- and post-match quality. Comparison between the calculated POS values and the actual number of male raters, however, indicates a lower stability in masculinity rating by men, which is why this result should be interpreted rather cautiously. Future studies should further investigate these findings to assess their robustness.

(c) The mediating effect of affective states and hormone levels on body odour quality

If we view winning and losing a fight as a way of change in an individual's rank in dominance hierarchy, then a change of position can be reflected in body odour and others can use it to assess the result of competition. This effect could be owing to changes in hormone levels (T and/or C) associated with victory or defeat. This effect has been repeatedly shown in

previous studies (e.g. [60,62]). T stimulates the proliferation of sebocytes and affects the function of apocrine sweat glands [92]. Similarly, C has an either direct or indirect link (via adrenaline) with the activity of apocrine glands [93], which can, in turn, affect the quality of body odour. Two studies that investigated the association between T and C levels and body odour quality produced rather contradictory results. Rantala *et al.* [72] found no significant correlation between T levels and either intensity or attractiveness of men's body odour. Interestingly, however, they found that C concentrations were positively associated with odour attractiveness, though not its intensity. Using a larger sample and a slightly different methodology (a longer sampling period and elimination of samples from men who reported violations of instructions on the use of fragranced cosmetics), Thornhill *et al.* [94] observed that women in the fertile phase of their menstrual cycle preferred body odours of men with higher T levels than women in the non-fertile phase. This study did not, however, find any significant relation between odour preferences and C levels.

Our study showed no significant effect of competition outcome on T levels. C levels, however, were higher after a match, which suggests that a match is a stressful event for both winners and losers. The positive relationship between C levels and perceived odour attractiveness, shown by mediation analysis, is in line with a previous study by Rantala *et al.* [72]. Similarly, we found that C levels did not significantly correlate with intensity ratings (a marker of the amount of perspiration), which indicates a qualitative, not quantitative effect. Glucocorticoids possess certain immunosuppressive qualities [95,96] and it has been hypothesized that only immunocompetent individuals can maintain high C levels [97], which is why such preference would be adaptive.

Another set of variables that have previously been linked to both competition outcomes and body odour are affective states. Body odour can contain cues to affective states such as happiness [98], disgust [99], fear [100], anxiety [90], stress [91], but also aggression [38] and contexts such as competition [37]. This is why we investigated possible mediating effects of changes in hormone levels and affective states. A path analysis showed not only a direct effect of competition outcome on perceived odour attractiveness, where a loss led to decrease in odour attractiveness, but also a mediating indirect effect of negative affective state, where the more negative emotions participants experienced, the less attractive was their perceived body odour. Exploratory correlation analysis showed further relationships between some odour characteristics, affective states and hormone levels, which are in line with the evidence summarized above. These findings, however, should be interpreted with caution owing to our relatively small donor sample.

(d) Study limitations

It is a common procedure in body odour studies to ask odour donors to avoid activities that could affect body odour quality, such as eating spicy food, using soaps, deodorants, demanding physical activities, smoking etc. the day before and on the day of sampling (e.g. [83,31]). Owing to logistical reasons, we were able to contact study participants only a few hours before the match. They did not, therefore, receive any such list of restrictions and followed their habitual regime without any standardization as to diet, smoking, shaving,

the use of fragranced cosmetics or dietary supplements. This may have introduced some noise to the data and obscured some effects. Nevertheless, we were still able to detect some significant changes and the use of a within-subject experimental design should diminish inter-individual differences. Such an approach has a higher ecological validity, although future studies should investigate the issue under more standardized settings as well.

We explored the possible effect of injuries on body odour quality using a single question regarding participants' self-perceived pain as a proxy for suffered injuries. Admittedly, a record of actual injuries would be a more objective measure, because participants' answers may be biased by competitiveness and excitement induced by the competition. These data were not, however, available and we did not want to overload participants with additional tasks and screenings.

In the present study, we used hedonic ratings to assess changes in body odour quality induced by winning or losing a match. Apart from explicit subjective ratings, future studies could employ some objective psychophysiological measures such as skin conductance, heart rate, possible activation of different brain areas by fMRI or variance in time activation by EEG.

Finally, future studies should collect data from the same individual both after a victory and a loss in a competition to assess the effect of outcome on body odour directly. In our field study conditions, such balanced design could not be implemented. It therefore remains as a challenge for future research.

6. Conclusion

In our study, we offer the first evidence that not only the context (competition) but also its outcome, viewed as a marker of

change in a dominance hierarchy, affects the hedonic valence of body odour in real-life settings. Losing a match had a negative effect on perceived odour quality and these changes seem to be related to both affective states and hormonal levels. Our findings thus provide new converging evidence to the effect that, similarly to other mammals, human body odour plays a role in olfactory communication and can provide cues to dominance and competition-related characteristics.

Data accessibility. The dataset supporting this article was uploaded as part of the electronic supplementary material.

Authors' contributions. J.F., V.T. and J.H. substantially contributed to study conception and design. J.F., V.T., R.K., D.S. and J.B. performed data collection, V.T. analysed the data, J.F., V.T. and J.H. performed interpretation of data. J.F., V.T. and J.H. drafted the article and R.K., D.S. and J.B. provided critical revisions. All authors approved the final version of the manuscript for submission.

Competing interests. We declare we have no competing interests.

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