



Behavioral Ecology (2015), 00(00), 1–6. doi:10.1093/beheco/arv089

Original Article

Human perception of fighting ability: facial cues predict winners and losers in mixed martial arts fights

Anthony C. Little,^a Vít Třebický,^b Jan Havlíček,^c S. Craig Roberts,^a and Karel Kleisner^b

^aDivision of Psychology, School of Natural Sciences, University of Stirling, Stirling FK9 4LA, UK and

^bDepartment of Philosophy and History of Sciences and ^cDepartment of Zoology, Faculty of Sciences, Charles University, Viničná 7, Prague, Czech Republic

Received 18 December 2014; revised 14 May 2015; accepted 22 May 2015.

In antagonistic encounters, the primary decision to be made is to fight or not. Animals may then possess adaptations to assess fighting ability in their opponents. Previous studies suggest that humans can assess strength and fighting ability based on facial appearance. Here we extend these findings to specific contests by examining the perception of male faces from paired winners and losers of individual fights in mixed martial arts sporting competitions. Observers, unfamiliar with the outcome, were presented with image pairs and asked to choose which of the 2 men was more likely to win if they fought while other observers chose between the faces based on masculinity, strength, aggressiveness, and attractiveness. We found that individuals performed at rates above chance in correctly selecting the winner as more likely to win the fight than the loser. We also found that winners were seen to be more masculine, stronger, and more aggressive than losers. Finally, women saw the winners as more attractive than the losers. Together these findings demonstrate that 1) humans can predict the outcome of specific fighting contests based on facial cues, 2) perceived masculinity and strength are putative cues to fighting success available from faces, and 3) facial cues associated with successful male–male competition are attractive to women.

Key words: competition, face appearance, fighting, intrasexual, violence.

INTRODUCTION

Across many animal species, fighting as a form of intrasexual selection (competition between members of the same sex) is common and has led to the evolution of animal weapons, such as horns and antlers, particularly in males (Andersson 1994). Adaptive decisions, or fitness-enhancing decisions, rely on balancing the net benefits against the net costs of particular actions (Krebs and Davies 1998). In antagonistic encounters with other individuals of the same species, the primary decision to be made is to fight or not. The benefits to be gained, such as territory, must be weighed against the costs, the potential for injury or even death.

Although the benefits of fighting will vary across species and environment, the same costs are applicable to many species, and critically, the costs vary greatly depending on whether an animal is likely to be the winner or loser of the fight. We can then expect that animals that engage in intraspecific fighting will possess perceptual/cognitive adaptations to assess the risks involved in this behavior by

assessing fighting ability in their opponents (Parker 1974; Enquist and Leimar 1983) using cues that are potentially related to fighting ability such as body size, strength, and weaponry (Krebs and Davies 1998). Indeed, there is evidence that animals make decisions about fighting based on the assessment of the relative fighting abilities of their opponents (Gosling et al. 1996; Hazlett 1996) and that specific traits in some species can be related to fighting success. For example, in terms of visual perception, variable black facial patterns in paper wasps are related to both body size and social dominance (Tibbetts and Dale 2004) and red chest coloration in gelada baboons is related to troop status, with leader males having the reddest chests (Bergman et al. 2009). Individuals could base their decisions to fight on appearance-linked cues to fighting ability allowing them to compete when likely to win and to avoid costly agonistic interactions when likely to lose.

In humans, there is evidence that male–male competition is important across various different cultures. For example, as noted by Sell et al. (2009), fighting ability is associated with access to resources in the Yanomamo of Venezuela (Chagnon 1983), the Achuar of Ecuador (Patton 2000), and the Tsimane of Bolivia (von

Address correspondence to A.C. Little. E-mail: anthony.little@stir.ac.uk.

Rueden et al. 2008). In other cultures, sports involving ritualized combat between men are common and take many forms, such as Sumo in Japan and stick-fighting in the Suri of Ethiopia. These ritualized forms of combat have a long recorded history, including fencing in the 16th century Germany and gladiatorial combat in Ancient Rome. In line with this evidence for physical combat between men, also noted by Sell et al. (2009, 2012), there are a range of anatomical and physiological sex differences that appear to reflect adaptation to male–male competition in humans, including sex differences in height and upper body strength (Plavcan and Van Schaik 1997; Puts 2010).

Given evidence for intrasexual conflict in humans and following theoretical predictions for adaptations to assess fighting ability (Parker 1974; Enquist and Leimar 1983), previous researchers have suggested that humans possess adaptations to infer fighting ability, specifically that fighting ability might be inferred from facial, body, and vocal cues (Sell et al. 2009, 2010). For example, people make relatively accurate inferences about men's physical strength from static facial images (Sell et al. 2009) and voice recordings (Sell et al. 2010), and measurements of physical strength are associated with ratings of fighting ability (Sell et al. 2009). One study has shown that self-rated fighting ability is positively related to acquaintance-rated fighting ability, which in turn is positively related to unfamiliar-person-rated fighting ability based on face photographs (Doll et al. 2014). This work is suggestive of cues to fighting ability being available in faces, but it is important to note that self-ratings and acquaintance ratings are likely to be noisy measures of real fighting ability. Focusing on human facial cues, masculinity in male faces has been associated with perceived dominance (Perrett et al. 1998) and physical strength is positively related to ratings of facial masculinity (Fink et al. 2007). Recent studies have also highlighted that face measurements are associated with aggression in men. For example, facial width scaled for face height is correlated with perceived aggression (Carré et al. 2009), related to self-reported dominance and, relating to real behavior, aggressive behavior in sport (Carre and McCormick 2008; Třebický et al. 2015; Zilioli et al. 2015). Further, one study examining forensic data from skeletons has shown that men with narrow faces are more likely to have died from contact violence than their wider faced peers (Stirrat et al. 2012).

While the accurate assessment of strength and its association with fighting ability (Sell et al. 2009), links between facial measurements and aggression (Carre and McCormick 2008), and that studies have associated fighting success with facial measurements showing that men with wider faces relative to height are more likely to win in mixed martial arts (MMA) competition (Třebický et al. 2015; Zilioli et al. 2015) are all in line with the notion that humans can assess fighting ability from facial cues, they do not provide direct evidence for this notion. One study has, however, examined fighting success based on instances of real fights in MMA sporting contests. Calculating fighting success as the ratio of wins to losses across a fighter's Ultimate Fighting Championship (UFC) fighting career, it was found that the perceived aggressiveness of fighters' faces was linked to their success in actual physical confrontations, although perceived fighting ability and differences in facial shape were only associated with fighting success in heavy-weight fighters (Třebický et al. 2013). This suggests that perceived aggression may be an underlying cue to fighting success rather than the cognitively complex inferred fighting success. However, fighting success across fights is somewhat different to assessing

fighting outcomes from faces in particular contests between pairs of fighters. In other words, only one face is relevant when assessing general fighting ability, whereas, in specific contests, individuals can compare the traits of 2 protagonists. This comparison may enable greater accuracy in judgment. Being able to predict the outcome of contests between 2 individuals may be adaptive because it allows for discrimination between individuals within a group in order to select successful allies or mates. The cue used to discriminate between pairs of others could also be used to assess a person's relative fighting ability. For example, an individual may be able to compare their own estimated ability to a competitor's ability based on appearance to predict their own chances of successfully winning a fight.

In the current study, we examined individual's abilities to directly assess the outcome of particular fights. Although previous results suggest that individuals can assess the fighting ability of particular fighters from their faces based on their overall success across a number of fights (Třebický et al. 2013), here we focused on a more fine-grained analysis in which face images of fighters were presented as pairs such that observers were tasked to judge the difference in perceived traits of the winners and losers of specific fights. We asked observers to judge between the winners and losers of fights for a variety of traits to test ideas relating to intrasexual and intersexual selection. First, we addressed accuracy in judgment by asking observers to choose who they think would win in a fight. Accuracy at this level would indicate that observers are able to assess the relative fighting ability of 2 fighters to correctly predict the outcome. Second, we examined specific cues from faces that may underlie accuracy: perceived masculinity, strength, and aggressiveness. Third, we addressed attractiveness to the opposite-sex because, while perception of fighting ability is often considered the domain of intrasexual selection, it may also be related to intersexual selection. In terms of attractiveness to the opposite-sex, there are benefits that could be associated with preferring better fighters: 1) indirect benefits, genetic benefits that are passed to offspring such as genes associated with health, strength, or high quality immune systems and 2) direct benefits, benefits that are directly passed to mates or offspring such as resources or protection from other males. We then also asked a sample of women who they thought was more attractive out of the pair.

METHODS

Participants acting as observers

There were 5 different studies in which participants chose between pairs of faces for different traits. Independent groups of participants judged between faces for: who would win in a physical fight ($N = 69$, men = 32, women = 37, mean age = 29.7, standard deviation [SD] = 10.7, 95% confidence interval [CI], lower: 27.1, upper: 32.2), who is more masculine ($N = 33$, men = 11, women = 22, mean age = 25.6, SD = 8.1, 95% CI, lower: 22.7, upper: 28.5), who is stronger ($N = 30$, men = 10, women = 20, mean age = 30.3, SD = 12.7, 95% CI, lower: 25.5, upper: 35.0), who is more aggressive ($N = 30$, men = 12, women = 18, mean age = 27.4, SD = 8.2, 95% CI, lower: 24.3, upper: 30.4), and who is more attractive ($N = 34$, women = 34, mean age = 29.0, SD = 11.3, 95% CI, lower: 25.1, upper: 33.0). Participants were selected for being older than 16 years of age. For attractiveness judgments, only women reporting to be heterosexual were selected for analysis. Participants were recruited for the study online via a research-based website and the study was conducted online.

Stimuli

The original study population consisted of 285 MMA fighters for which facial photographs and details of their previous fight (opponent and win/loss), as well as facial photographs of their opponent, were available from the official Web site of the MMA division of the UFC (www.ufc.com; database accessed in June 2012). Because this represented the total pool of fighters, excepting unselected fighters for which data or photographs were unavailable, it was possible to match the 285 fighters with their opponent in their most recent fight. Out of the 285 fighters, we created 156 pairs of fights based on the most recent matches for the fighters. From these pairs, 42 pairs were excluded from the analyses because they contained a duplicate fighter from one of the preceding fight pairs.

The final set of images used were of 228 fighters which made up 114 unique pairs representing fights between 2 different fighters. Using the available database, for each pair, 1 fighter was classified as the winner and 1 as the loser.

For each pair of fighters, we obtained data on their weight class, which was the same for each fighter making up the pair. To reduce the number of classifications and increase the sample size of final groupings, we averaged the 7 available weight classes into 3 groupings: lightweight (bantam weight, feather weight, light weight, $N = 48$ pairs), middleweight (welter weight, middle weight, $N = 42$ pairs), and heavyweight (light heavy weight, heavy weight, $N = 24$ pairs).

The stimulus set comprised the official front-on photographs available from www.ufc.com. These photographs appear to have approximately similar lighting and background with individuals posing with an approximately neutral expression. To equate size of the face in the image, all images were aligned to standardize the position of the pupils in the image.

Procedure

Participants were administered a short questionnaire assessing age, sex, and sexual orientation (only used for women rating attractiveness), followed by a forced-choice face test. There were 5 different forced-choice face tests for which the stimuli and procedure were identical except that participants in each test were given different instructions on what type of discrimination they were asked to do. Different participants took part in each of the tests based on random allocation to tests.

In the forced-choice tests, the 114 pairs of winners and losers of MMA fights as described above were shown with both order and side of presentation randomized. Participants were asked to choose 1 face from the pair for a particular trait. Clicking a button below the face selected moved participants on to the next face trial. There was no time limit for responses and both faces remained on screen until participants selected a face.

Specific questions for the 5 tests were:

“Which person is more likely to WIN in a physical fight?”

“Which person is more MASCULINE?”

“Which person is PHYSICALLY STRONGER?”

“Which person is more AGGRESSIVE?”

“Which person is more ATTRACTIVE?”

Statistical analyses

The dependent variable was the choice by each participant of the winner or loser for each pair of fighters for 114 pairs. If the participant selected the winner from the pair, this was scored “1” and if the participant selected the loser from the pair, this was scored “0”.

First, general linear mixed model (GLMM), or multilevel modeling, analyses were conducted using R (R Core Team 2013); specifically, we used the “glmer” function available in the “lme4” package (Bates et al. 2014). Such models allow simultaneous analysis of participant and stimulus effects negating the need to collapse across either. Participant (1|subject) and face pair (1|fight) were specified as random factors in the model. The nature of data entered here was binary (0/1), and so a binomial model was specified using the “glmer” function which fitted the model using maximum likelihood with Laplace approximation. The model as specified in R was as follows:

$$\left(\text{modelA} = \text{glmer} \left(\begin{array}{l} \text{pickwinner} \sim (1|\text{subject}) + (1|\text{fight}), \\ \text{data} = \text{fight}, \text{family} = \text{binomial} \end{array} \right) \right)$$

In this model, where “pickwinner” was whether the subject correctly chose the winner, we tested for a significant effect of the intercept which would indicate a difference from chance (0).

A second model was specified in which sex of participant and weight category were added as fixed effects to the above model:

$$\left(\text{modelB} = \text{glmer} \left(\begin{array}{l} \text{pickwinner} \sim (1|\text{subject}) + (1|\text{fight}) + \\ \text{sexparticipant} + \text{weightcategory}, \\ \text{data} = \text{fight}, \text{family} = \text{binomial} \end{array} \right) \right)$$

Models were compared using the “Anova” function. A nonsignificant difference between models would indicate that adding sex of participant and weight category did not impact significantly on the original model.

To follow-up these analyses, we additionally included a by-participant and by-face analysis using 1-sample *t*-tests to test if choice of winner over loser was significantly different from chance. Impact of weight category was tested in the by-face analysis using Anova and impact of sex of participant was tested in the by-participant analysis using independent samples *t*-tests.

RESULTS

General linear mixed models

Separate models were computed for: who would win in a physical fight, who is more masculine, who is stronger, who is more aggressive, and who is more attractive.

The first model indicated that choice of “Which person is more likely to WIN in a physical fight” was a significant predictor of winning a match ($\chi^2 = 2.35, P = 0.019$). Adding sex and weight category to the model created a model that was not significantly different from the original model (chi square = 1.66, $df = 3, P = 0.645$).

The second model indicated that choice of “Which person is more MASCULINE?” was a significant predictor of winning a match ($\chi^2 = 2.00, P = 0.038$). Adding sex and weight category to the model created a model that was not significantly different from the original (chi square = 2.54, $df = 3, P = 0.469$).

The third model indicated that choice of “Which person is PHYSICALLY STRONGER?” was a significant predictor of winning a match ($\chi^2 = 2.00, P = 0.045$). Adding sex and weight category to the model created a model that was not significantly different from the original for strength (chi square = 2.27, $df = 3, P = 0.518$).

The fourth model indicated that choice of “Which person is more AGGRESSIVE?” was a significant predictor of winning a match ($\chi^2 = 2.57, P = 0.010$). Adding sex and weight category to the

model created a model that was not significantly different from the original for aggressiveness (chi square = 6.17, $df = 3$, $P = 0.104$).

The last model indicated that choice of “Which person is more ATTRACTIVE?” was a nonsignificant predictor of winning a match ($\chi^2 = 1.76$, $P = 0.079$), although the P value was close to 0.05. Adding weight category to the model created a model that was not significantly different from the original for attractiveness (chi square = 0.43, $df = 2$, $P = 0.808$).

In all of the above models, winners were selected more often than losers. A summary of model statistics for each question is presented in Table 1.

To examine the equivalence of the GLMM analysis with methods involving calculation of means, because these types of analysis are common in the literature, we carried out further analyses in which mean choice was calculated for each face pair and for each participant. We note that variance across fighters is most important to the question of whether individual fighter's faces contain cues to fighting success and so the GLMM above and the by-face pair analyses are more appropriate to answer this question.

By face pair

Mean choice of winner versus loser was calculated for each face pair and face pair was used as the unit of analysis and compared with chance with 1-sample t -tests. This was done separately for: who would win in a fight, who is more masculine, who is stronger, and who is more attractive. We additionally tested for effects of weight category using 1-way Anovas.

One-sample t -tests indicated that winners were chosen significantly more often than losers for winning in a physical fight ($t_{113} = 2.36$, $P = 0.020$, $D = 0.44$), being more masculine ($t_{113} = 2.17$, $P = 0.032$, $D = 0.41$), and being more aggressive ($t_{113} = 2.74$, $P = 0.007$, $D = 0.52$). Although winners were chosen more often than losers, this was not significantly different from chance for being stronger ($t_{113} = 1.97$, $P = 0.052$, $D = 0.37$) and being more attractive ($t_{113} = 1.71$, $P = 0.091$, $D = 0.32$).

One-way Anovas (dependent variable = mean choice of winner, fixed factor = weight category) indicated no significant effect of weight category for judgments of winning in a physical fight ($F_{2,111} = 0.72$, $P = 0.491$, $\eta_p^2 = 0.013$), masculinity ($F_{2,111} = 1.15$, $P = 0.319$, $\eta_p^2 = 0.020$), strength ($F_{2,111} = 0.32$, $P = 0.724$, $\eta_p^2 = 0.006$), aggressiveness ($F_{2,111} = 2.37$, $P = 0.099$, $\eta_p^2 = 0.041$), or attractiveness ($F_{2,111} = 0.14$, $P = 0.871$, $\eta_p^2 = 0.002$).

By participant

Mean choice of winner versus loser was calculated for each participant, and participant was used as the unit of analysis and compared with chance with 1-sample t -tests. This was done

separately for: who would win in a fight, who is more masculine, who is stronger, and who is more attractive. We additionally tested for effects of sex of participant using independent samples t -tests.

One-sample t -tests indicated that winners were chosen significantly more often than losers for winning in a physical fight ($t_{68} = 7.86$, $P < 0.001$, $D = 1.91$), being more masculine ($t_{32} = 4.93$, $P < 0.001$, $D = 1.74$), being stronger ($t_{29} = 6.57$, $P < 0.001$, $D = 2.44$), being more aggressive ($t_{29} = 5.34$, $P < 0.001$, $D = 1.98$), and being more attractive ($t_{33} = 6.96$, $P < 0.001$, $D = 2.42$).

Independent samples t -tests indicated no significant effect of sex of participant for judgments of winning in a physical fight ($t_{67} = 0.69$, $P = 0.493$, $D = 0.17$), masculinity ($t_{31} = 0.31$, $P = 0.762$, $D = 0.11$), strength ($t_{28} = 1.46$, $P = 0.156$, $D = 0.55$), or aggressiveness ($t_{28} = 0.97$, $P = 0.342$, $D = 0.37$).

Correlations among judgments

Using data by face pair, we ran Pearson product-moment correlations to examine relationships between the different attributes. Correlations can be seen in Table 2. Significant positive correlations were found among the judgments of winning in a physical fight, masculinity, strength, and aggressiveness (all $r > 0.490$, all $P < 0.001$). None of these variables, however, was significantly related to attractiveness judgments (all $P > 0.05$).

Previous authors have argued that masculinity in male faces may not be attractive because it is associated with negative attributions, such as aggressiveness (Little et al. 2011; Puts et al. 2012). We tested this idea by examining the relationship between choice as more masculine and choice as more attractive while controlling for both choice as more aggressive and stronger. To examine how women's preferences were related to these traits independently, we entered perceived masculinity, strength, and aggression as predictors of women's attraction in a linear regression. This revealed a significant overall model ($F_{3,110} = 6.23$, $P < 0.001$,

Table 2

Intercorrelations among perceived traits based on the choice of a face out of a pair for each question

	Masculine	Strong	Aggressive	Attractive
Win fight	0.783**	0.815**	0.720**	0.150
Masculine		0.743**	0.699**	0.175
Strong			0.490**	0.139
Aggressive				-0.120

**Significant at $P < 0.01$.

Table 1

Model summaries for choice of the winner as more likely to win, more masculine, stronger, more aggressive, and more attractive of 114 pairs of fighters

	Winner	Masculine	Strong	Aggressive	Attractive
Estimate	0.203	0.183	0.238	0.238	0.193
Mean	0.550	0.546	0.559	0.559	0.548
Standard error	0.086	0.088	0.119	0.092	0.110
χ^2/P value	2.35/0.019	2.08/0.038	2.00/0.045	2.57/0.010	1.76/0.079
Participant, N	69	31	30	30	34

Estimate is the probability of picking the winner on the logit scale and the standard error reported is that of the estimate.

$R^2 = 0.145$) in which masculinity was significantly positively ($\beta = 0.514$, $P < 0.001$), aggressiveness was significantly negatively ($\beta = -0.474$, $P < 0.001$), and physical strength was not significantly ($\beta = -0.011$, $P = 0.932$) associated with women's choices for attractiveness.

DISCUSSION

Our data demonstrated that both men and women perceive winners of fights differently from losers. Specifically, from the mixed model analyses, winner's faces were more likely to be seen as able to win the fight, physically stronger, more aggressive, more masculine, more aggressive, and more attractive to women than loser's faces (although this last effect was nonsignificant, $P = 0.079$). We found no significant effects of sex of observer or weight category of fighter for these judgments. Similar effects were seen in by-participant and by-face pair analyses, although effects were strongest in the by-participant analyses. This difference is the result of greater variance between face pairs than between observers in terms of choices. For example, while the mean choice is identical ($M = 0.543$), for choice of winner as winning in a physical fight, the SD was lower across participant ($SD = 0.05$) than across face pair ($SD = 0.20$).

Given the potential importance of male intrasexual selection in human evolution (Chagnon 1983; Plavcan and Van Schaik 1997; Patton 2000; von Rueden et al. 2008), our data are in line with the notion that humans possess perceptual/cognitive adaptations to assess the risks involved fighting by assessing fighting ability in other humans, as expected in a species that engages in such behavior (Parker 1974; Enquist and Leimar 1983). Although previous researchers have suggested that humans possess adaptations to detect fighting ability based on perceptions of strength (Sell et al. 2009, 2010) and correspondence between self-rated and acquaintance-rated fighting ability (Doll et al. 2014), here we show direct evidence that humans can predict the actual outcome of specific fights based on facial information, in line with a previous demonstration that the perceived aggressiveness of fighters' faces was linked to their career fighting success (Třebický et al. 2013). Although humans do not necessarily have obvious evolved phenotypic weaponry, such as horns or antlers seen in nonhuman species (Krebs and Davies 1998), humans may display cues to their fighting abilities and possess adaptations to help guide their choice to fight specific individuals (Parker 1974; Enquist and Leimar 1983).

We tested for sex differences in each judgment but found no significant effects. It might be expected that men would pay more attention to cues to male–male competitive ability because such contests are more relevant to them, but our data suggests that women perform similarly in discriminating winners from losers on the basis of facial appearance (see also Třebický et al. 2015). We note, however, that our sample sizes were relatively small for examining sex differences because this was not the main aim of the study. Sex differences may indeed be found using larger sample sizes or in alternative situations that emphasize the relevance to men over women, such as in real-life competitive situations.

We note that across all types of judgments, the perceptual difference between winners and losers was relatively small. Given the number of other variables that could determine the winner and loser of these fights, we think it would be surprising if facial cues accounted for the majority of the variance, and of course, small advantages can prove important over evolutionary time scales. There are also other reasons why the effects seen here are likely to

be modest. In our study, observers were limited to seeing static 2D face information. Stronger relationships between facial appearance and fight outcome may be possible under different experimental conditions, for example, if participants were given 3D face images or were exposed to the faces for more time. Given our interest was in static facial cues, we excluded lots of potential cues to fighting ability. In real-life fights, body size and dynamic cues are available which may increase accuracy. Additionally, the fighters here belong to a relatively homogenous group of highly trained athletes and are therefore well matched. This is an interesting case in discriminating winners and losers as this is likely to be a harder task than predicting who will win in less balanced fights. Indeed, fighters here were also further matched in terms of weight category specifically designed to create more even odds. In real fighting situations, where weight, as a proxy for muscle mass or strength, is more uneven, we might predict greater success in predicting the outcomes of fights.

In terms of specific cues to fighting success, winner's faces were generally seen as more masculine and stronger than loser's faces. Facial masculinity is then a potential cue to fighting ability and is also positively related to perceived dominance (Perrett et al. 1998), real physical strength (Fink et al. 2007), and testosterone levels, although the relationship with testosterone may be somewhat more complex than a simple linear relationship (Pound et al. 2009). Judgments of perceived physical strength from faces have been previously highlighted as a proxy for judgments of fighting ability (Sell et al. 2009), with perceived strength relating to actual measured strength (Sell et al. 2009). There are also links between facial measurements and aggression (Carre and McCormick 2008) and one previous study has shown that fighters with more aggressive appearing faces are more likely to have higher success in their fights over the careers (Třebický et al. 2013). Given these traits are potentially interlinked, they could all relate to fighting success via the same mechanism. For example, underlying levels of testosterone could underpin facial cues to masculinity, strength and aggression. Of course these traits may be also associated with fighting success for different reasons. For example, strength may be a good predictor of who wins fights because it is linked directly to the outcome of competition, but in more evenly matched fights, cues to behavioral aggression may also be used to predict winners independent of strength (see also Třebický et al. 2013). In fact, there may be shared and unshared factors relating to fighting success for each of these 3 factors.

In predicting women's preferences, the zero-order correlations indicated nonsignificant correlations between other judgments and attractiveness judgments. However, when controlling for other judgments in the regression analysis, masculinity was positively related, aggressiveness negatively related, and strength was unrelated to faces being selected as attractive to women. This is suggestive that while women found winner's faces as more attractive than losers, this was due to differences in perceived masculinity. This further highlights that masculinity and aggressiveness, while having similar effects on perceived intrasexual competition abilities (winning fights), have quite different effects in term of intersexual selection (their attractiveness to women). Indeed, the benefits of avoiding aggressive male partners are clear despite the fact that such males may be successful in intrasexual competition. Here, controlling for perceived aggressiveness and strength, the relationship between judgments of masculinity and attractiveness increased from $r = 0.175$ to 0.514 ($Z = 2.92$, $P = 0.004$). Previous studies have shown that women moderate their preferences for masculine facial cues according to their recent experience of visual environmental cues of direct male–male competition and violence. In these previous studies,

women preferred more masculine male faces after exposure to cues of direct male–male competition and violence (Little et al. 2013), which is consistent with idea that women here preferred the faces of men who were most likely to be successful in male–male competition. Perhaps such preferences reflect that ideal men should be able to compete successfully but not actively seek out conflict (indicated by high perceived aggression). In this way, women may select men who can defend themselves, their partner, and their offspring from other men but who do not continually seek conflict. Indeed, it has previously been argued that women may face a trade-off in selecting masculine appearing partners because, while such partners may be more dominant, masculine partners may not possess behavioral traits, such as cooperativeness or faithfulness, that are desirable in a long-term partner (Little et al. 2011; Puts et al. 2012). In such preferences, it is difficult to tease apart the role of indirect from direct benefits. This is because preferences for successful competition can relate to both. For example, preferring men who are likely to win in fights can lead to direct benefits in terms of resources as such men may most successfully defend or acquire resources. However, such preferences can also lead to potential indirect benefits by passing genes for the successful defense or acquisition of resources on to male offspring, if these factors are heritable. In other words, if women prefer traits that are associated with the ability to provide direct benefits and mate with these men, the factors associated with ability to provide direct benefits may also be passed to her offspring thereby providing indirect benefits (see Kokko et al. 2003). It is then likely that both direct and indirect benefits from men play a role in generating preferences for the faces of men likely to win fights.

In summary, we found that individuals performed at rates above chance in correctly selecting the winner as more likely to win the fight than the loser. We also found that winners were seen to be more masculine, more aggressive, and stronger than losers. Finally, women saw the winners as more attractive than the losers. The effect sizes for each of these relationships were generally small but could have potentially important evolutionary consequences. Together these findings demonstrate that 1) humans can correctly predict the outcome of specific fighting contests, 2) perceived masculinity/strength/aggressiveness are all putative cues to fighting ability available from faces, and 3) facial cues associated with successful male–male competition are attractive to women.

FUNDING

A.C.L. was supported by a Royal Society University Research Fellowship. V.T., J.H., and K.K. are supported by a Czech Science Foundation grant (15-05048S).

Handling editor: Alexei Maklakov

REFERENCES

- Andersson M. 1994. Sexual selection. Princeton (NJ): Princeton University Press.
- Bates D, Maechler M, Bolker B, Walker S. 2014. lme4: linear mixed-effects models using Eigen and S4. R Package Version 1.1-7. <http://CRAN.R-project.org/package=lme4>.
- Bergman TJ, Ho L, Beehner JC. 2009. Chest color and social status in male geladas (*Theropithecus gelada*). *Int J Primatol*. 30:791–806.
- Carré JM, McCormick CM. 2008. In your face: facial metrics predict aggressive behaviour in the laboratory and in varsity and professional hockey players. *Proc Biol Sci*. 275:2651–2656.
- Carré JM, McCormick CM, Mondloch CJ. 2009. Facial structure is a reliable cue of aggressive behavior. *Psychol Sci*. 20:1194–1198.
- Chagnon N. 1983. Yanomamo: the fierce people. 3rd ed. New York: Holt, Rinehart and Winston.
- Doll LM, Hill AK, Rotella MA, Cardenas RA, Welling LLM, Wheatley JR, Puts DA. 2014. How well do men's faces and voices index mate quality and dominance? *Hum Nat*. 25:200–212.
- Enquist M, Leimar O. 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *J Theor Biol*. 102:387–410.
- Fink B, Neave N, Seydel H. 2007. Male facial appearance signals physical strength to women. *Am J Hum Biol*. 19:82–87.
- Gosling LM, Atkinson NW, Dunn S, Collins SA. 1996. The response of subordinate male mice to scent marks varies in relation to their own competitive ability. *Anim Behav*. 52:1185–1191.
- Hazlett BA. 1996. Assessments during shell exchanges by the hermit crab *Clibanarius vittatus*: the complete negotiator. *Anim Behav*. 51:567–573.
- Kokko H, Brooks R, Jennions MD, Morley J. 2003. The evolution of mate choice and mating biases. *Proc Biol Sci*. 270:653–664.
- Krebs JR, Davies NB. 1998. Behavioural ecology: an evolutionary approach. Oxford: Blackwell Science.
- Little AC, DeBruine LM, Jones BC. 2013. Environment contingent preferences: exposure to visual cues of direct male–male competition and wealth increase women's preferences for masculinity in male faces. *Evo Hum Behav*. 34:193–200.
- Little AC, Jones BC, DeBruine LM. 2011. Facial attractiveness: evolutionary based research. *Philos Trans R Soc B Biol Sci*. 366:1638–1659.
- Parker GA. 1974. Assessment strategy and evolution of fighting behavior. *J Theor Biol*. 47:223–243.
- Patton J. 2000. Reciprocal altruism and warfare: a case from the Ecuadorian Amazon. In: Cronk L, Chagnon N, Irons W, editors. Adaptation and human behavior: an anthropological perspective. Hawthorne (NY): Aldine de Gruyter. p. 417–436.
- Perrett DI, Lee KJ, Penton-Voak IS, Rowland DR, Yoshikawa S, Burt DM, Henzi SP, Castles DL, Akamatsu S. 1998. Effects of sexual dimorphism on facial attractiveness. *Nature*. 394:884–887.
- Plavcan M, Van Schaik C. 1997. Interpreting hominid behavior on the basis of sexual dimorphism. *J Hum Evol*. 32:345–374.
- Pound N, Penton-Voak IS, SurrIDGE AK. 2009. Testosterone responses to competition in men are related to facial masculinity. *Proc Biol Sci*. 276:153–159.
- Puts DA. 2010. Beauty and the beast: mechanisms of sexual selection in humans. *Evo Hum Behav*. 31:157–175.
- Puts DA, Jones BC, DeBruine LM. 2012. Sexual selection on human faces and voices. *J Sex Res*. 49:227–243.
- von Rueden C, Gurven M, Kaplan H. 2008. The multiple dimensions of male social status in an Amazonian society. *Evo Hum Behav*. 29:402–415.
- Sell A, Bryant GA, Cosmides L, Tooby J, Sznycer D, von Rueden C, Krauss A, Gurven M. 2010. Adaptations in humans for assessing physical strength from the voice. *Proc Biol Sci*. 277:3509–3518.
- Sell A, Cosmides L, Tooby J, Sznycer D, von Rueden C, Gurven M. 2009. Human adaptations for the visual assessment of strength and fighting ability from the body and face. *Proc Biol Sci*. 276:575–584.
- Sell A, Hone LSE, Pound N. 2012. The importance of physical strength to human males. *Hum Nat*. 23:30–44.
- Stirrat M, Stulp G, Pollet TV. 2012. Male facial width is associated with death by contact violence: narrow-faced males are more likely to die from contact violence. *Evo Hum Behav*. 33:551–556.
- R Core Team. 2013. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. Available from: <http://www.R-project.org/>.
- Tibbetts EA, Dale J. 2004. A socially enforced signal of quality in a paper wasp. *Nature*. 432:218–222.
- Třebický V, Fialová J, Kleisner K, Roberts SC, Little AC, Havlíček J. 2015. Further evidence for links between facial width-to-height ratio and fighting success: commentary on Zilioli et al. *Aggress Behav*. 41:331–334.
- Třebický V, Havlíček J, Roberts SC, Little AC, Kleisner K. 2013. Perceived aggressiveness predicts fighting performance in mixed-martial-arts fighters. *Psychol Sci*. 24:1664–1672.
- Zilioli S, Sell AN, Stirrat M, Jagor J, Vickerman W, Watson NV, Jagore J. 2015. Face of a fighter: bizygomatic width as a cue of formidability. *Aggress Behav*. 41:322–330.