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Abstract

Accurate assessment of competitive ability is a critical component of contest behavior in animals, and it could be just as important in human competition, particularly in human ancestral populations. Here, we tested the role that facial perception plays in this assessment by investigating the association between both perceived aggressiveness and perceived fighting ability in fighters' faces and their actual fighting success. Perceived aggressiveness was positively associated with the proportion of fights won, after we controlled for the effect of weight, which also independently predicted perceived aggression. In contrast, perception of fighting ability was confounded by weight, and an association between perceived fighting ability and actual fighting success was restricted to heavyweight fighters. Shape regressions revealed that aggressive-looking faces are generally wider and have a broader chin, more prominent eyebrows, and a larger nose than less aggressive-looking faces. Our results indicate that perception of aggressiveness and fighting ability might cue different aspects of success in male-male physical confrontation.

Keywords

fighting ability, aggressiveness, mixed martial arts, geometric morphometrics, competition, face, perception, aggressive behavior, face perception, facial features, evolutionary psychology

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Humans are especially attentive to facial cues and spontaneously attribute age, sex, emotional state, and personality characteristics according to facial traits (Bar, Neta, & Linz, 2006; Willis & Todorov, 2006). A key set of traits affecting facial perception are associated with sexual dimorphism. Individuals with highly developed male-typical facial features are consistently perceived as masculine (Penton-Voak & Chen, 2004), dominant, and aggressive (Perrett et al., 1998; Rhodes, 2006). Consequently, these features may affect experience and attributions in social interactions. For example, ratings of facial dominance in men predict their career progress (Mueller & Mazur, 1996) and age of first sexual intercourse (Mazur, Halpern, & Udry, 1994).

Particular attention has focused on the facial width-to-height ratio (fWHR). Trajectories of bizygomatic width change during pubertal growth independently of the height of the upper face and body height (Weston, Friday,

& Lio, 2007). There is growing evidence linking fWHR to male aggressive and dominant behavior in both controlled conditions and naturalistic settings (Carré & McCormick, 2008; Carré, McCormick, & Mondloch, 2009; but see Deaner, Goetz, Shattuck, & Schnotala, 2012). Furthermore, fWHR predicts cause of death by contact violence: Higher fWHR is less frequently associated with violent death (Stirrat, Stulp, & Pollet, 2012).

Human perception may have evolved through natural selection to be especially sensitive to cues of aggression and competence in fighting (Carré & McCormick, 2008). Anticipation of both cues of aggression in facial expressions (Ekman et al., 1987) or body posture (Duclos

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et al., 1989) and probability of winning seems to be critical for making decisions about whether to flee or fight, influencing risk of injury or death. The perception of aggression cues is especially significant in male-male interactions, in which conflicts are frequently resolved through physical contest. Therefore, men are expected to be more attentive than women to the potential dangerousness of their opponent (Sell et al., 2009).

Previous research has shown that people make relatively accurate inferences about men's physical strength from static images (Sell et al., 2009). In particular, Sell et al. report correlations between measurements of upper-body strength and ratings of fighting ability. Although Sell et al.'s study and the fWHR studies indicate that facial cues may be linked to potential fighting success, there is currently no direct evidence for such a link. Furthermore, participants in previous studies were not facing a real antagonist in an actual direct physical confrontation.

To address the relationship among perception, face shape, and fighting success in the present study, we used data that directly reflected the results of fights among professional fighters. We tested whether the perception of aggressiveness predicts the results of direct physical confrontations because human perception may have evolved to be specifically sensitive to cues of threat and aggression. Fighting ability depends on many factors alongside aggression, so being seen as a powerful fighter does not necessarily equal being seen as aggressive. Therefore, we further collected ratings of perceived fighting ability to test whether people are able to infer actual fighting ability.

To do this, we used the results of past fights among professional mixed-martial-arts (MMA) fighters and their facial photos, which were rated in an online survey. In addition, by use of geometric morphometric (GMM) techniques, we searched for the specific facial traits associated with actual fighting ability and compared them with traits responsible for perceived aggressiveness.

Method

Participants

In total, 618 individuals from the Czech Republic (216 men, mean age = 26.98 years, $SD = 6.35$; 402 women, mean age = 26.18 years, $SD = 6.22$) rated photographs of fighters for perceived aggressiveness, and a further 278 (98 men, mean age = 28.31 years, $SD = 9.99$; 180 women, mean age = 27.1 years, $SD = 7.52$) rated the same photos for perceived fighting ability. All participants gave informed consent to participate in the study.

The stimulus set consisted of 146 photographs selected from 336 portraits of MMA fighters that are freely accessible on the official Web site of MMA division Ultimate Fighting Championship (UFC; www.ufc.com; photos

downloaded in July 2011). To avoid potential confounding effects on raters' perceptions, we selected only images fulfilling the following criteria: (a) apparent non-African or non-Asian origin, (b) facing directly into the camera, (c) absence of beard or moustache, and (d) hair not obscuring the face. The images were subsequently standardized regarding the position of the face in the image (e.g., same position in vertical axis), and the background color was changed to gray (hex #808080 in red, green, blue color space).

For each fighter, we obtained data on his age ($M = 29.77$ years, $SD = 4.6$), weight class (bantamweight, up to 61.2 kg; $n = 14$; featherweight, up to 66 kg; $n = 14$; lightweight, up to 70.3 kg; $n = 34$; welterweight, up to 77.1 kg; $n = 32$; middleweight, up to 83.9 kg; $n = 19$; light-heavyweight, up to 93.0 kg; $n = 19$; heavyweight, up to 120.2 kg; $n = 14$), number of fights in the UFC (range = 1–38, $M = 8.78$, $SD = 7.02$), and number of wins in the UFC (range = 0–27, $M = 5.86$, $SD = 5.19$). To assess whether the tested effect varied across the weight classes, we merged the seven weight classes into three: lightweight (up to 70.3 kg), middleweight (70.4–83.9 kg), and heavyweight (over 83.9 kg).

To account for varying numbers of fights among fighters, we computed fighting success as the proportion of wins relative to the total number of fights. There are no official rules for selection of a particular individual for a fight in the UFC, and the fights are arranged by managers of the individual fighters (R. Andrš, personal communication). It seems unlikely that such a selection process might systematically bias the effect under investigation. To estimate the possible effect of facial damage on judgment of photos, one of the authors (V. T.) assessed each photo for marks of apparent damage using binary coding (0 = damage absent, $n = 34$; 1 = damage present, $n = 112$).

Procedure

Each participant reported his or her sex and age and then rated either aggressiveness or fighting ability of a set of 50 randomly selected photographs, presented in random order. Aggressiveness ratings were done using a 7-point scale (from 1, *not aggressive at all*, to 7, *very aggressive*). For fighting ability, participants judged whether the depicted person was a good fighter (from 1, *not at all*, to 7, *excellent*). Each participant's ratings were converted to z scores to account for differences in scale use, and a mean standardized score was calculated for each photograph.

GMM analyses

We used a GMM approach to investigate which facial features of the 146 MMA fighters are responsible for the

perception of aggressiveness and fighting success. The GMM technique is a set of analytical procedures for multivariate statistical analysis of shape. Its mathematical and theoretical background is well understood, and it has been widely used in biological applications (for a recent review, see Baab, McNulty, & Rohlf, 2012). GMM's main strength is that it takes into account information about the spatial relationships among the measured variables that is preserved during analysis, and this information can be later visualized in the form of thin-spline deformation grids.

The 71 landmarks (including 36 semilandmarks) were digitized in tpsDig2 software (Version 2.14; Rohlf, 2009a). Landmarks are anatomically (or at least geometrically) corresponding points that can be delineated in different individuals, whereas semilandmarks denote curves and outlines. The definitions of landmarks and semilandmarks were adopted from previous studies (Kleisner, Kocnar, Rubesova, & Flegr, 2010; Kleisner, Priplatova, Frost, & Flegr 2013; Schaefer, Lauc, Mitteroecker, Gunz, & Bookstein, 2006).

All configurations of landmarks and semilandmarks were superimposed using a generalized Procrustes analysis (GPA), which standardizes the size of the objects and optimizes their rotation and translation so that distances between corresponding landmarks are minimized. We used principal component analysis (PCA) to translate original data (shape coordinates) into orthonormal principal components; this approach ensures the multivariate normality. The PCA scores matrix represented by all principal components and carrying the information about face shape was saved and used for further analyses. Both GPA and PCA were carried out in tpsRelw (Version 1.46; Rohlf, 2008).

For testing the effects of perceived aggressiveness, fighting success, and weight on shape coordinates, we performed permutational multivariate analysis of variance using distance matrices with 9,999 permutations (the Adonis function in the Vegan package in R; Oksanen et al., 2011); the Euclidean method was used as a distance measure. We ran a multiple multivariate regression with principal component scores as the response variable and with scores of perceived aggressiveness, fighting success, and weight as explanatory variables. The shape changes associated with perceived aggressiveness were visualized by a thin-plate spline interpolation function, available in tpsRegr (Version 1.36; Rohlf, 2009b), as a deviation from the overall mean configuration (the consensus) of landmarks.

Statistical analysis

The effect of fighting success on perceived aggressiveness and perceived fighting ability was tested using

general linear models (the "lm" function in R) using the mean z score of perceived aggressiveness or fighting ability as the response variable, fighting success of the rated fighter as the explanatory variable, and fighter's age, fighter's weight, and rater's sex as confounding variables. The association between bivariate variables was assessed by Pearson's correlation, in which data were normally distributed; otherwise, we used either Pearson's correlation with bootstrapping with 10,000 iterations or Kendall's test for ordinal data. Statistical plausibility of linear models was evaluated by F tests. Effect sizes were expressed by partial R^2 ; we report adjusted R^2 in all results.

Results

Correlational and linear regression analyses

All correlational analysis were performed using the full photo set ($N = 146$). First, we tested the effects of potentially confounding variables, such as fighter's age and rater sex, on perceived aggressiveness and perceived fighting ability. Fighter's age was not significantly correlated with perceived aggressiveness ($r = .13$, $p = .128$). However, there was a significant positive correlation between age and perceived fighting ability ($r = .358$, $p < .001$). Judgments of aggressiveness ($r = .93$, $p < .001$) and fighting ability ($r = .95$, $p < .001$) by male and female raters were highly correlated; therefore, we analyzed the ratings of both sexes together. We also found a significant positive correlation between the ratings of aggressiveness and perceived fighting ability ($r = .483$, $p < .001$).

Subsequently, we found a significant positive association between perceived aggressiveness and fighting success ($r = .203$, $p = .014$). In contrast, there was no significant association between perceived fighting ability and fighting success ($r = .069$, $p = .409$). Linear regression showed a similar result after age was added as a covariate, $F(1, 143) = 0.969$, $p = .326$, $R^2 = .007$; the effect of age was significant ($p < .001$).

However, both perceived aggressiveness ($r = .31$, $p < .001$) and perceived fighting ability ($r = .296$, $p < .001$) were also positively correlated with weight; therefore, we added weight into the linear regression models. In this analysis, perceived aggressiveness was independently predicted by both fighting success, $F(1, 143) = 4.91$, $p = .028$, $R^2 = .033$, and weight, $F(1, 143) = 13.68$, $p < .001$, $R^2 = .089$. To test for the interaction between weight and fighting success, we fitted a model with both the main effects and the interaction of weight and number of wins. Comparing the two models, we found that the more complex model including both main effects and the interaction did not fit the data better than a simple model with

two main effects ($p = .331$). The more parsimonious model with weight and fighting success as main effects was thus preferable.

After weight was added as a covariate in the linear regression, perceived fighting ability was predicted by weight, $F(1, 143) = 13.29$, $p < .001$, $R^2 = .085$, but not by fighting success, $F(1, 143) = 0.242$, $p = .624$, $R^2 = .002$. This might be due to a ceiling effect of attributed weight. In other words, raters might have primarily used cues of weight to attribute fighting ability (Deaner et al., 2012), which in turn obscured the effect of fighting success, as the actual fights take place within defined weight categories. We therefore tested the hypothesis that heavyweight fighters are seen as better fighters than those with lighter weights. We ran a one-way ANOVA with perceived fighting ability as the dependent variable and weight category as a factor. The effect of weight category was significant, $F(2, 143) = 5.97$, $p = .003$, $R^2 = .077$. Pairwise comparisons (tests of least-significant differences) showed that heavyweights were seen as significantly better fighters than lightweights ($p = .001$), but the differences between ratings of middleweight and heavyweight fighters ($p = .074$) and between middleweight and lightweight fighters ($p = .078$) were close to significant.

Subsequently, we tested the correlation between perceived fighting ability and actual fighting success separately for individual weight categories. We found a close-to-significant correlation between perceived fighting ability and fighting success in heavyweights ($n = 33$, $r = .301$, $p = .088$), but there was no significant correlation in middleweight ($n = 51$, $r = -.127$, $p = .375$) and lightweight fighters ($n = 62$, $r = .076$, $p = .558$). Finally, facial damage showed a significant positive correlation with perceived fighting ability ($n = 146$, $\tau = .196$, $p = .004$) but not with perceived aggressiveness ($n = 146$, $\tau = .073$, $p = .28$).

GMM analyses of aggressiveness

We used multivariate regressions to test for possible associations among perceived aggressiveness, fighting success, and facial configuration. The regression of shape data (represented by multiple PCA scores) on perceived aggressiveness showed a significant relationship between perceived aggressiveness and facial shape, $F(1, 144) = 2.42$, $p = .024$, $R^2 = .017$. Controlling for the effect of the weight, we found that the effect of face shape was close to significant, $F(1, 143) = 1.97$, $p = .055$, $R^2 = .013$, whereas weight was significantly related to facial shape, $F(1, 143) = 2.74$, $p = .015$, $R^2 = .019$. To test for the interaction between weight and perceived aggressiveness, we fitted a model with both the main effect and the interaction of weight and aggressiveness. The interaction was significant,

$F(1, 142) = 2.48$, $p = .027$, $R^2 = .017$, which indicates that facial features responsible for attribution of aggressiveness are associated with weight distribution. Therefore, for explorative purposes, we separately tested for the same effect in both extremes of weight distribution. We found a significant effect of perceived aggressiveness in heavyweights, $F(1, 31) = 2.13$, $p = .037$, $R^2 = .064$; the same effect was not significant for lightweights, $F(1, 60) = 1.78$, $p = .071$, $R^2 = .029$.

The regression of shape data on fighting success was not significant, $F(1, 144) = 0.65$, $p = .743$, $R^2 = .004$, but weight had a significant effect on facial morphospace, $F(1, 144) = 2.72$, $p = .013$, $R^2 = .019$. When we ran the same analysis for both extremes of weight distribution, we found a significant effect of fighting success in heavyweights, $F(1, 31) = 2.18$, $p = .033$, $R^2 = .065$; however, no similar effect was found in lightweights, $F(1, 60) = 0.83$, $p = .558$, $R^2 = .014$.

To compare facial traits associated with perceived aggressiveness and fighting success, we used the tps interpolation function to visualize the results of shape regressions. Deviations from the mean facial configuration linked with the perception of aggressiveness included dilations and contractions of the grid in the bizygomatic range and around the eyes and jaw (Fig. 1). The aggressive-looking faces were generally wider and had a broader chin and larger nose than the nonaggressive-looking faces. The grid was markedly contracted around the eyes, showing an effect of deep-set eyes beneath prominent eyebrows. Significant shape differences associated with higher fighting success in heavyweights included a narrower chin, wider bizygomatic range, and a more horizontally depressed grid around the eyes (Fig. 2). The morphology of fighting success was also characterized by a bigger nose and mouth with a distinct philtrum, compared with a typical losing fighter's face.

Discussion

It has been suggested that fighting ability might be inferred from facial cues (Sell et al., 2009). In this article, we present the first direct evidence that the perceived aggressiveness of fighters' faces is linked to their success in actual physical confrontations. Although perceived aggressiveness was also associated with weight, our results show that the two effects are independent. Perceived fighting ability was predicted only by weight, and its link to fighting success was restricted to heavyweights. We further found systematic differences in structural configurations of faces with high and low perceived aggressiveness. However, the association between facial configuration and fighting success was restricted to heavyweight fighters.

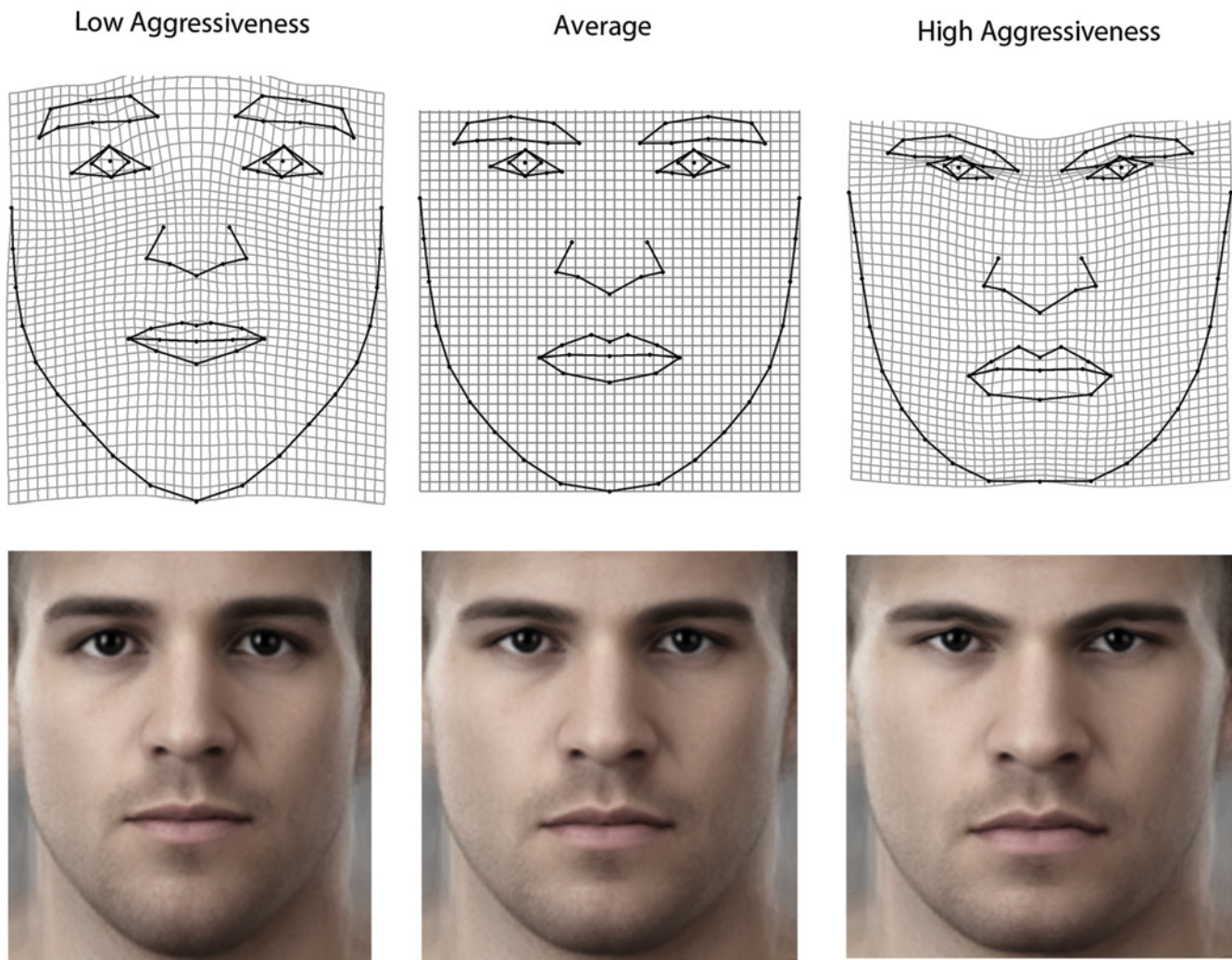


Fig. 1. Visualization of the shape regression on perceived aggressiveness by thin-plate spline-deformation grids (top row) and composite visualizations (bottom row), based on mean results for all fighters. Results are shown separately for low and high perceived aggressiveness, with the average reference shown for comparison; the effects were magnified 3 times for better visibility. The composite visualizations are based on landmark configurations estimated by shape regression; the effects are shown within the observed range.

Although there was a moderate positive correlation between perceived aggressiveness and perceived fighting ability ($r = .48$), our results indicate that the two variables might be underpinned by slightly different cognitive processes. First, judgments of fighting ability seem to focus on general probability of winning a fight, which is substantially related to size and weight (Deaner et al., 2012). This is supported by the fact that heavyweight contestants were seen as better fighters than lightweight contestants. Perhaps this is why we found no association between perceived fighting ability and actual fighting success in the overall sample of fighters who fight within individual weight categories—in combat sports (including MMA), weight categorization avoids large disparities

in weight between contestants. In contrast, ratings of aggressiveness might focus on the probability of winning a fight that would actually take place. More specifically, individuals assessing the chances of winning a fight as low might flee or attempt reconciliation, thus avoiding likely losses. We think it likely, therefore, that most fights occur where competitors are relatively equally matched, and in such contexts, people employ judgments of aggressiveness to predict fight outcomes.

We employed GMM analysis to reveal the facial features linked to perception of aggressiveness. It is apparent that higher aggressiveness corresponds to facial morphology with lower level of fatty deposits, especially in the cheeks and chin area. This is probably

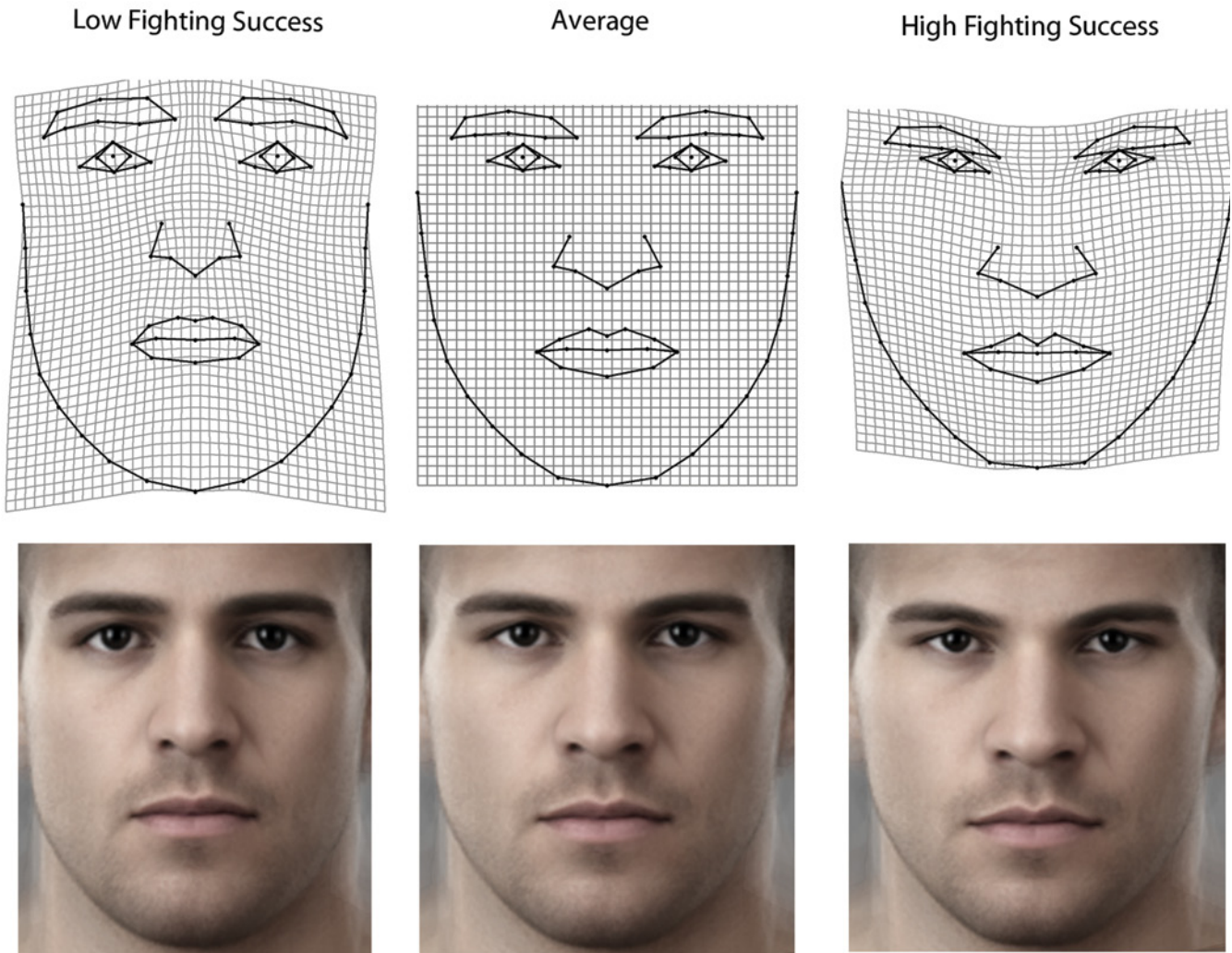


Fig. 2. Visualization of the shape regression on fighting success by thin-plate spline-deformation grids (top row) and composite visualizations (bottom row), based on faces of heavyweight fighters. Results are shown separately for low and high fighting success, with the average reference shown for comparison; the effects were magnified 3 times for better visibility. The composite visualizations are based on landmark configurations estimated by shape regression; the effects are shown within the observed range.

due to successful fighters maximizing overall physical performance, reducing subcutaneous fat. Another possibility is that, by removing body fat, a fighter may not increase his fighting ability per se but can increase his win/loss record by pairing himself with smaller opponents who have less muscle. This may also explain why better fighters had different faces only among heavyweights (the only weight category in which the trade-off is relaxed). Apart from soft tissue, we observed a significant effect of apparent “aggressive gaze,” which is achieved by the horizontally narrowed eye area, probably due to the developed masculine features such as prominent superciliary arches. In certain respects, our results parallel those of Carré et al. (2009), who found

that fWHR is a reliable cue to propensity to aggression. The deformation grids (Fig. 1) modeling the shape changes associated with perceived aggressiveness show proportional increases of bizygomatic width and smaller distance between the eyes and mouth. Nevertheless, the GMM analysis also showed that differences are not restricted to the area captured by fWHR. Other facial traits, including the shape of the nose, mouth, chin, and, especially, eye area all significantly contribute to perceived aggressiveness and potentially reflect the probability of winning. Our results were not entirely explained by cues associated with a history of fighting, such as scars and wounds, as our measure of facial damage was not related to perceived aggression.

To explore the facial features that perceivers use to infer aggressiveness, we compared, again using GMM analyses, similarities in perceptual morphospace and morphospace linked to fighting success for heavyweight classes (Figs. 1 and 2). These comparisons revealed the extent to which the perception of aggressiveness corresponds to the actual success in fights. The shape changes associated with high fighting success strongly resemble transformations predicted along the attribution of aggressiveness. However, estimated configurations of aggressiveness also show certain inconsistencies with prediction of fighting success: For example, the thinner chin and mouth associated with the estimated configuration of high fighting success does not correspond to the prediction of attribution of high aggressiveness associated with a broad chin.

One may wonder why the link between facial configuration and fighting success is restricted to heavyweight fighters. However, fighting success is a complex measure, and it is conceivable that proportional significance of aggressiveness varies across weight classes. Testosterone-linked characteristics such as muscle mass, power, and aggression might be relatively more important for successful attack techniques among heavyweights, whereas in lightweights, characteristics that are only loosely linked to testosterone, such as dexterity and speed, might be proportionally more significant (Sterkowicz-Przybycien, 2010). As the level of muscularity and masculinity—and also aggressive behavior—correlates with testosterone levels, specific facial configuration in heavyweights may be due to the effect of testosterone and other hormones affecting growth (Lassek & Gaulin, 2009). Similarly, the negative relationship between the ratio of the second and fourth fingers, thought to be an indicator of prenatal testosterone levels, and the fighting performance of Japanese sumo wrestlers supports this view (Tamiya, Lee, & Ohtake, 2012).

One might also question how far findings based on a specific sample such as MMA fighters can be generalized. Individuals involved in professional MMA adhere to specific daily training and dietary routines, and our findings could reflect these specific conditions. However, as the fighters are rewarded according to fighting success, they are presumably highly motivated to win, and differences in their physical fitness are rather subtle. These facts diminish the chances of finding the predicted effects, and it is conceivable that in real-life settings, the judgments based on appearance might actually be more predictive than reported here. Another defining factor of the fighters in the MMA sample is that their encounters are limited to predefined weight classes. At face value, this seems to be far from ancestral conditions. In contrast, one may argue that real fights occur only rarely between antagonists that are highly unequal in weight and strength. In

most such cases, the weaker side would likely choose a strategy that avoids physical confrontation. In this respect, combats within weight classes may more closely resemble real-life situations.

From an evolutionary perspective, our results indicate selective pressures in ancestors of modern humans to be perceptually sensitive to facial cues associated with aggression and fighting ability. If aggressive-looking people are in fact more likely to be better competitors, and perhaps more likely to engage in aggressive behavior, it would be highly adaptive to recognize such a potentially dangerous antagonist in order to avoid physical confrontation and minimize the risk of injury and possible death. However, our results also show that inferences of fighting success and aggressiveness based on facial shape might hold only within a specific spectrum of individuals. Similarly, Zebrowitz and Rhodes (2004) reported congruent attributions of health and intelligence only in the lower half of the attractiveness distribution; however, raters inappropriately employed similar cues in the other half of the distribution as well. Zebrowitz and Rhodes explain this by an overgeneralization effect. The evolution of such an effect can be subsumed within error-management theory, which predicts that false-positive and false-negative errors might have highly biased consequences in terms of survival or fitness (Haselton & Buss, 2000). Here, the costs of false-positive attributions of aggressiveness to harmless individuals might be disproportionately higher than false-negative attributions to dangerous opponents. However, the degree and direction in disproportion of costs between false-positive and false-negative attributions remains to be empirically tested. Males might be expected to be more sensitive to aggressiveness judgments, as they frequently use force to settle intrasexual conflict. In contrast, for women, it should also be advantageous to assess a potential male aggressor, as such attributions can reflect males' capability to protect themselves and their offspring from other men. This is supported by our results, as we did not report any significant sex difference in perception of aggressiveness or fighting ability, and the ratings of men and women were highly correlated ($r = .93$ and $r = .95$, respectively).

In conclusion, our results support the hypothesis that humans are able to infer aggressiveness from the face of potential opponents. Such an ability exploits the correlates between the facial traits responsible for perception of aggressiveness and those facial features that reflect the actual likelihood to succeed in male-male physical confrontation.

Author Contributions

V. Třebický, J. Havlíček, and K. Kleisner developed the study concept. All authors contributed to the study design. Data

collection was performed by V. Třebický and K. Kleisner; K. Kleisner performed the data analysis. V. Třebický, J. Havlíček, and K. Kleisner drafted the manuscript, and S. C. Roberts and A. C. Little provided critical revisions. All authors approved the final version of the manuscript for submission.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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