

Original Article

The human anger face evolved to enhance cues of strength

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ABSTRACT

Animals typically deploy their morphology during conflict to enhance competitors' assessments of their fighting ability (e.g. bared fangs, piloerection, dewlap inflation). Recent research has shown that humans assess others' fighting ability by monitoring cues of strength, and that the face itself contains such cues. We propose that the muscle movements that constitute the human facial expression of anger were selected because they increased others' assessments of the angry individual's strength, thereby increasing bargaining power. This runs contrary to the traditional theory that the anger face is an arbitrary set of features that evolved simply to signal aggressive intent. To test between these theories, the seven key muscle movements constituting the anger face were systematically manipulated one by one and in the absence of the others. Raters assessed faces containing any one of these muscle movements as physically stronger, supporting the hypothesis that the anger face evolved to enhance cues of strength.

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The human anger face is an early (Stenberg, Campos, & Emde, 1983), reliably-developing (Galati, Sini, Schmidt, & Tinti, 2003), species-typical (Ekman, 1973) expression consisting of a stereotyped array of coordinated muscle contractions (Ekman & Friesen, 1978) (see Fig. 1). However, why did evolution give the human facial expression of anger the particular form that it has? The most common position is that the anger face is a universal but arbitrary signal of aggressive intent (Blair, 2003; Matsumoto, Hee Yoo, & Chung, 2010; Schmidt & Cohn, 2001). According to this widespread view, the expression would have evolved to be salient and distinguishable from other emotional expressions (Darwin, 1872), but there need be nothing functional about the particular pattern of muscle movements *per se*. We agree that the anger expression functions as a signal (Reed, DeScioli, & Pinker, 2014), but we propose that the specific array of muscle contractions that constitute the anger face was in fact tailored by selection to be functional rather than arbitrary. Specifically, during conflicts of interest, natural selection favored displaying those configurations of muscle activation that amplified others' assessments of the sender's fighting ability—in the human case, those configurations that amplified cues of strength. This hypothesis is made plausible by recent work showing the existence of cues of strength in the face—cues that are rapidly and spontaneously assessed when estimating another's fighting ability (Sell, Cosmides, et al., 2009; Trebicky, Havlicek, Roberts, Little, & Kleisner, 2013; Zilioli et al., 2014).

1.1. Theoretical background

An animal's fitness is crucially dependent on the outcomes of conflicts of interest. Accordingly, selection should have organized behavioral systems in animals that bargain for improved outcomes in these conflicts. In particular, aggression is a type of bargaining behavior that deploys the threat or actuality of cost-infliction as a tool to incentivize others to reduce their resistance to the aggressor's realization of its interests (Huntingford & Turner, 1987). In humans, these tactics are largely regulated by anger—a neural system that evolved to orchestrate bargaining behavior in order to cost-effectively resolve conflicts of interest in favor of the angry individual (i.e. the recalibrational theory of anger; see Sell, Tooby, & Cosmides, 2009; Sell, 2011b; Tooby, Cosmides, Sell, Lieberman, & Sznycer, 2008). On this view, the triggering of anger signals the expressor's assessment that the existing situation does not sufficiently reflect the angry individual's interests, given its bargaining power. The greater the fighting ability of the individual, the more costs it can inflict, and the better its bargaining position is. This is why selection favored the evolution of aggression and phenotypic traits that enhance the ability to inflict costs on competitors.

As has been documented in hundreds of species, relative fighting ability in animals is a crucial determinant of winning conflicts (Arnott & Elwood, 2009). In consequence, selection generally favors the evolution of neural designs that (a) assess fighting ability in conspecifics and (b) use those assessments to make decisions about whether to cede or contend for a resource (Arnott & Elwood, 2009; Enquist & Leimar, 1983). Mutant designs that enhance the cues of fighting ability used by these assessment mechanisms will spread (e.g., piloerection, dewlap inflation) because such shifts in assessment by rivals will lead to better outcomes for the animal displaying

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enhanced cues. Such enhancement of cues will persist provided that the predictive relationship between the cue and the animal's actual fighting ability is maintained to some degree (Maynard Smith & Harper, 2003). Cues that are constrained by the physical structure of the feature being assessed (i.e. "indices") generally meet this requirement, and thus many species have been selected to configure their morphology in ways that send enhanced signals of size and strength during agonistic bargaining (Darwin, 1872; Huntingford & Turner, 1987; Maynard Smith & Harper, 2003).

This logic applies equally to humans: selection is expected to have favored assessment mechanisms among our ancestors that exploited available indices of fighting ability. Recent evidence demonstrates that humans can and do assess cues of physical strength when evaluating fighting ability, presumably because strength was a substantial component of fighting ability. Indeed, these assessment systems appear well-designed to estimate fighting ability rather than strength *per se*, e.g., assessments of fighting ability privilege cues of muscularity over simple height or weight, upper body strength over lower body strength, and more accurately assess men than women (Sell, Cosmides, et al., 2009; Sell et al., 2010; Sell, 2012). The last datum is relevant because numerous data sets have established that upper body strength in modern males is about 90% greater than in females (Abe, Kearns, & Fukunaga, 2003; Lassek & Gaulin, 2009), with the distributions of the two sexes only minimally overlapping. For this reason and others, aggression will be a more important tool of social negotiation for men than women (Archer, 2004; Campbell, 2002; Daly & Wilson, 1988; Wrangham & Peterson, 1996), and both men and women should be (and are) better calibrated to assess male strength (Sell, 2012). Moreover, as predicted by the model that anger is the expression of a neural bargaining system, physically stronger men get angry more easily, experience more favorable resolutions of conflicts

of interest, and consider aggression a more legitimate way to settle conflicts (Sell, Tooby, et al., 2009).

Crucially, accurate cues of fighting ability have been found to exist in the face alone, and are spontaneously and rapidly assessed when estimating fighting ability (Sell, Cosmides, et al., 2009; Trebicky et al., 2013; Zilioli et al., 2014). If anger functions as a bargaining system in humans, then it follows that humans should have evolved to deploy facial morphology in a way that enhances these cues during aggressive bargaining. We hypothesize that the universal anger expression evolved for that function. Over evolutionary time, selection would build neural circuits that, at the onset of anger, co-activated those discrete muscle movements in the face that increased the appearance of strength. Hence, the signal of the onset of a bout of power-based bargaining (i.e. anger) would be simultaneous to and constituted by facial enhancements of cues of strength. In short, the universal human anger facial expression is an adaptation for enhancing cues of strength.

The accepted method for establishing the evolved function of an adaptation was best articulated by George Williams (1966): researchers must show that features constituting the candidate adaptation are so well-organized to bring about the solution to an identified adaptive problem that the coordination between adaptive problem and phenotypic solution cannot be plausibly explained by chance. Therefore, if the anger face is an evolved adaptation designed for enhancing cues of strength and fighting ability in the face, then each of the seven distinct major modifications that comprise the anger face should, independently, make the face appear physically stronger. The null (and widely accepted) hypothesis is that the features of the anger face are arbitrary, and so should show no particular relationship to judgments of strength.

2. Experiment 1: do the components of the anger face increase perceived strength?

To test whether each feature that constitutes the anger expression increases perceived strength, we used a program calibrated with a large number of statistical composites of real faces to generate seven pairs of faces. Each pair contrasted a single feature of the face as modified by anger (e.g. lowered brow) with the opposite modification (e.g. raised brow). Raters then chose the stronger of the pair to determine the effect of each component of the anger face.

2.1. Methods

The actual facial components that are modified by human anger have been extensively documented by Ekman and colleagues in their Facial Action Coding System (FACS) (Ekman, Friesen, & Hager, 2002a). Ekman et al. identify facial movements as various combinations of "action units" (hereafter AU), which consist of stereotyped contractions of specific facial muscles. In the case of anger, Ekman and his colleagues identified the classic closed-mouth anger expression (as modeled in Fig. 1) as the result of the following action units: AU: 4, 5, 7, 10, 17, 22, 23, and 24 (see Ekman et al., 2002a, Table 10-1). Quotes from the FACS manual (Ekman, Friesen, & Hager, 2002b) documenting the effects of action units 4, 10, 17, 22, 23 and 24 on facial structure are listed in Table 1. Two action units—the glare ("upper lid-raiser"—AU 5) and the squint ("the lid-tightener"—AU 7) were excluded from analyses because they are mutually exclusive, have opposite effects on the face, and naturally occur at different times (see 4.3 for data and discussion on this topic).

2.1.1. Subjects

The raters in our experiment were taken from the psychology and criminology subject pools at the University of California, Santa Barbara (35 subjects [25 female], mean age = 18.9, SD = 1.2) and Griffith University, Mount Gravatt (106 subjects [80 female], mean age = 24.9, SD = 8.3) respectively. Students received partial course credit for participation.

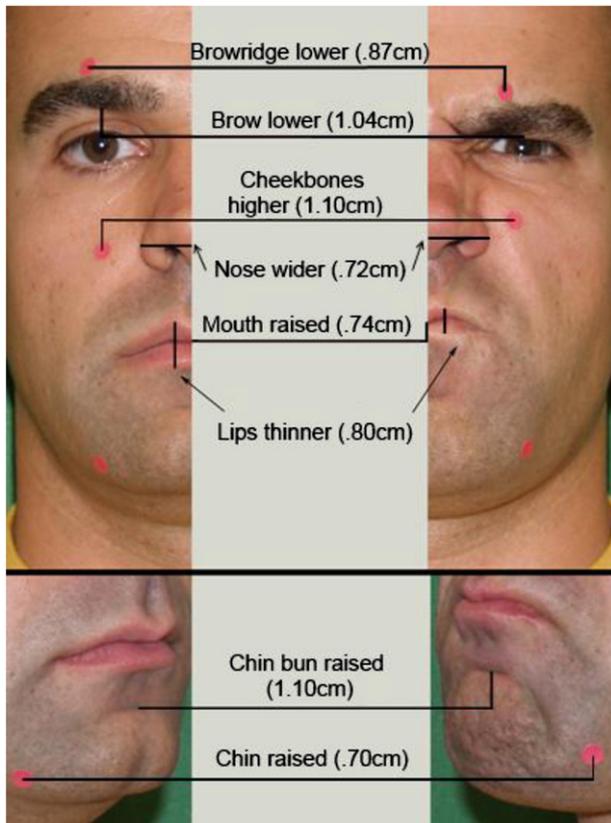


Fig. 1. Effects of the anger face (i.e. action units 4, 5, 7, 10, 17, 22, 23, and 24). Note: The right side of the model's face is seen on both the left (as it appeared in the photo) and right (flipped along the y-axis) to control for any fluctuating asymmetry in the face.

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