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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.

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).

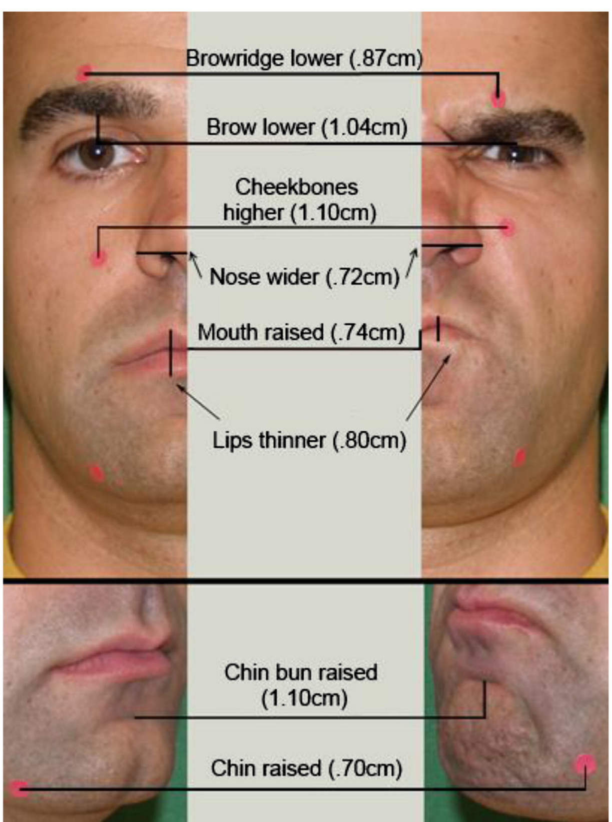

Fig. 1. Effects of the anger face (i.e. action units 4, 5, 7 10, 17, 22, 23, and 24). Note: The right side of the model's face is seen on both the left (as it appeared in the photo) and right (flipped along the y-axis) to control for any fluctuating asymmetry in the face.

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.

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Table 1
Ekman's FACS identifies seven key manipulations in the anger face.

Effect of anger face	Lowers brow-ridge	Raises infraorbital triangle	Widens nose	Raises mouth	Enlarges chin and chin bun	Lips pushed forward	Lips thinned
FACS code	AU 4: Brow lowerer	AU 10: Upper lip raiser	AU 10: Upper lip raiser	AU 10: Upper lip raiser AU 17: Chin raiser	AU 17: Chin raiser	AU 22: Lip funneler	AU 23: Lip tightener AU 24: Lip pressor
FACS manual description of changes (Ekman et al., 2002b)	"Lowers the eyebrow" p. 17	"Pushes the infraorbital triangle up" p. 95	"Widens and raises the nostril wings."	"Raises the upper lip" p. 95 "Pushes the lower lip upward" p. 98	"Pushes the chin boss upward" p. 98	"Lips funnel outward" p. 235	"Tightens and narrows the lips" p. 241
FaceGen feature manipulated	Inner brow ridge—high/low	Cheek bones—low/high	Nose–nostrils wide/thin	Mouth—up/down	Chin—wide/thin	Lips puckered/retracted	Lips thin/thick

2.1.2. Stimuli

The stimuli were created with FaceGen 3.1, a face modeling software package made by Singular Inversions. FaceGen creates three dimensional models of faces that can be morphed by age, race, sex and through direct manipulations of facial features. FaceGen works with a formula that was calibrated with a large number of statistical composites of real faces, enabling average faces to be generated for various age groups and both sexes. We used as our starting point the average European 20 year old male face. Then, for each of the seven constituent features of the anger face this prototype was modified in the direction of anger and in the opposite direction to create two faces: an anger-modified face and a control face. Manipulations were done to approximately the midpoint of the scale (setpoint 4 on a scale from 0 to 10) (see Table 1). Our stimuli consisted of male faces because— in humans—fighting ability is more accurately assessed on male targets than female targets (Sell, Cosmides, et al., 2009; Sell et al., 2010). Indeed, both males and females are more accurate when assessing male targets' fighting ability; a pattern that holds in general and when assessing fighting ability from the face specifically (Sell, 2012).

2.1.3. Procedure

Subjects were presented with each pair of faces side by side (each 9 cm^2, resolution: 150 dpi) in random orders. For each pair of faces (anger modified or its control), subjects were asked to judge which appeared physically stronger. The anger modified face was randomly placed either on the left or right side.

2.2. Results

Fig. 2 shows the percentage of subjects who chose the anger modified face as the more physically strong. As predicted, chi-square tests show that each modification that the anger system makes to the face significantly and independently increases perceived strength.

3. Experiment 2: do the components of the anger face increase perceived maturity?

There is another theory, put forward by Marsh, Adams, and Kleck (2005), that argues that the anger face evolved to enhance the maturity of the face, distinguishing it from immature, neotenous faces, i.e. "the origins of the appearances of anger and fear facial expressions…might lie in the expression's resemblance to, respectively, mature and babyish faces." This position predicts that the constituent parts of the anger face should each—independently—increase the perceived age of the face.

3.1. Methods

To test this hypothesis against our prediction that the anger face makes the individual appear physically strong, we had each of the seven face pairs that were previously rated for strength rated for age.

3.1.1. Subjects

Thirty-one subjects from the psychology subject pool at UC Santa Barbara (mean age = 19, SD = 1.4) participated for partial course credit.

3.1.2. Procedure

The methods and stimuli for experiment 2 were identical to experiment 1, except subjects were asked to pick which face appeared "older."

3.2. Results

For four of the seven major features modified by the anger expression, the manipulation did significantly increase perceived age (see Fig. 2). This can be contrasted with results from experiment 1 showing that all seven of the features increased the perceived strength of the target. The evidence is entirely consistent with the view that the features of the anger face evolved to enhance cues of strength, but only partly consistent with the view that the anger face enhances cues of maturity.

4. Experiment 3: do the components of the anger face increase perceived maturity or strength in older faces?

The fact that four out of seven of the constituent features of the anger face increased perceived age could be due to the positive relationship that exists between fighting ability and age at young ages. In other words, because male strength peaks in the 20s (Walker, Hill, Kaplan, & McMillan, 2002) and fighting ability near 30 (von Rueden, Gurven, & Kaplan, 2008), making a young face look stronger may lead to the inference that the target is older. In order to decouple increasing age from increasing strength, we repeated our tests with faces of older men. For older men, increasing age would no longer predict increases in strength. Again, we generated seven pairs of faces, each of which contrasted a constituent feature of anger with its opposite (see Fig. 2) and had the faces rated for both strength and age.

4.1. Method and stimuli

The design of experiment 1 was replicated exactly, but with new stimuli of older faces. The faces were generated following the same procedure as experiment 1, but instead of the prototype

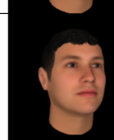
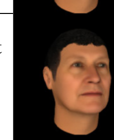
Effect of anger	FACS code	Muscles used	Experiments 1 & 2: Young Faces				Experiment 3: Older Faces			
			Anger	Control	Anger makes the face:		Anger	Control	Anger makes the face:	
Lowers brow-ridge	AU 4: Brow Lowerer	Depressor Glabellae; Depressor supercilii; Corrugator			**Stronger 94% X^2=111.8 p=10^{-25}**	**Older 84% X^2=14.2 p=.0002**			**Stronger 89% X^2=41.0, p=10^{-9}**	No effect 50% X^2=0.0 p=1.0
Raises infraorbital triangle	AU 10: Upper Lip Raiser	Levator Labii Superioris; Caput Infraorbitalis			**Stronger 86% X^2=73.3 p=10^{-16}**	**Older 94% X^2=23.5 p=10^{-6}**			**Stronger 65% X^2=6.1 p=.014**	**Younger 38% X^2=3.9 p=.049**
Widens nose	AU 10: Upper Lip Raiser				**Stronger 85% X^2=70.4 p=10^{-16}**	**Older 68% X^2=3.9 p=.05**			**Stronger 68% X^2=8.7 p=.003**	**Older 65% X^2=6.1 p=.014**
Raises mouth	AU 10: Upper Lip Raiser AU 17: Chin Raiser	Levator Labii Superioris; Caput Infraorbitalis, Mentalis			**Stronger 75% X^2=36.5 p=10^{-8}**	No effect 48% X^2=0.03 p=.86			**Stronger 73% X^2=13.6 p=.0002**	**Younger 35% X^2=6.1 p=.014**
Enlarges chin and chin bun	AU 17: Chin Raiser	Mentalis			**Stronger 78% X^2=45.1 p=10^{-10}**	No effect 61% X^2=1.6 p=.21			**Stronger 73% X^2=13.6 p=.0002**	No effect 53% X^2=2.4 p=.62
Lips pushed forward	AU 22: Lip Funneler	Orbicularis Oris			**Stronger 80% X^2=52.1 p=10^{-12}**	No effect 58% X^2=0.8 p=.37			**Stronger 70% X^2=10.2 p=.001**	**Younger 24% X^2=17.5 p=.00003**
Lips thinned	AU 23: Lip Tightener AU 24: Lip Pressor				**Stronger 71% X^2=25.4 p=10^{-6}**	**Older 81% X^2=11.6 p=.001**			No effect 52% X^2=.06 p=.81	**Older 76% X^2=17.5 p=.00003**

Fig. 2. Effect of each feature of the anger expression on perceived strength and age, tested on both young and old faces.

being set for a 20 year old European male it was set to a 60 year old European male.

4.1.1. Subjects

Each pair was presented to 132 (88 female) students from the psychology subject pool at UCSB, (mean age = 21.09; SD =5.09) who participated for partial fulfillment of course credit.

4.1.2. Procedure

Seven pairs of faces were generated, each of which contrasted a constituent feature of anger with its opposite (see Fig. 2). Subjects were then instructed either to pick the "stronger" or "older" of the two photos (*between subjects*).

4.2. Results

The results, shown in Fig. 2, replicate our central hypothesis: for six of the seven pairs the anger face was picked as physically stronger. Again, the constellation of changes that anger makes to the face appear well designed to increase the perceived strength of the target. The effects of the modifications on perceived age were inconsistent, with only two features making the faces appear older and three features actually making the face appear significantly younger.

4.3. Eye manipulations and the anger face

Two action units—the glare ("upper lid-raiser"—AU 5) and the squint ("the lid-tightener"—AU 7) were excluded from our analyses because they are mutually exclusive, have somewhat opposite effects on the face, and naturally occur at different times. AU 5 (upper lid raiser, dependent on the *levator palpebrae superioris*) is known to raise the upper eyelid to produce a glare, thus increasing the visible portion of the eye, but AU 7 (lid tightener, dependent on the *orbicularis oculi* and *pars palebralis*) tightens the eyelids into a squint and thus reduces the visible portion of the eye. Given that these modifications have somewhat opposite effects—one exposing the eyes and the other obscuring them, it was not possible to predict their effect on perceived strength. Nevertheless, because of its empirical interest eye exposure was manipulated and its effect on perceived strength and age documented; the data are presented below with our interpretation.

Pairs of faces were generated with larger and smaller eyes (FaceGen feature: eyes—small/large) and presented to subjects who chose the stronger or older of the pair (*between subjects*). Eye size had no effect on the perceived strength of the face (for young faces, 46% chose the larger eyed man as stronger, $\chi^2 = .70$, $p = .40$; for older faces the large and small eyed faces were each chosen on 50% of the trials). Large eyes reliably made the face look younger however, (young faces: 77%, $\chi^2 = 9.32$, $p = .002$; old faces: 62%, $\chi^2 = 3.88$, $p = .049$).

Although not tested here, we think that the eye manipulations during anger serve two separate functions. The lid-raiser is a surprise cue: "I have detected that your conduct violates my expectations and I am now signaling my entry into the anger state" that triggers the eye-direction detector in the target of anger (Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000). The squint improves visual acuity of the object in the center of the visual field (Sheedy, Truong, & Hayes, 2003)—a useful state for someone considering assault. Thus these modifications are predicted to occur at different stages of anger. These hypotheses have yet to be tested.

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5. General discussion

Taken together, these experiments show that the constellation of features that comprise the anger face was selected for over evolutionary time to enhance cues of physical strength during agonistic bargaining. These results are consistent with previous literature showing that several of the components of the anger face are more prominent in males—the sex that shows evidence of combat design (Becker, Kenrick, Neuberg, Blackwell, & Smith, 2007; see Sell, Hone, & Pound, 2012 for evidence of combat design). Sexually dimorphic features with a male bias include prominent cheekbones, wider noses, lower browridges, and larger chins (Penton-Voak et al., 2001; Lefevre et al., 2012; Trebicky et al., 2013). Similar research shows components of the anger expression positively correlate with judgments of dominance—e.g. low browridge, wide nose (Toscano, Schubert, & Sell, 2014); low browridge, thin lips, wide nose (Windhager, Schaefer, & Fink, 2011). However, the current study is the first systematic test of the individual components of the anger expression, and in doing so it confirms that these features are improbably well-designed to solve the adaptive problem of bargaining with threats of force.

This research leaves an important question unanswered: why do these particular features co-vary with physical strength such that anger can bundle this particular set of muscles into a formidability-enhancement display? We speculate that these features relate to bite strength, rapid oxygenation, blunt force resistance or some combination of these. Future research will need to explore these hypotheses.

Finally, this research exemplifies the ability of a functional theory of anger to make specific predictions about multiple aspects of the complex anger system. The recalibrational theory (Sell, 2011b)—like other functional evolutionary theories—can use the adaptationist program (Williams, 1966) to make concrete predictions about any aspect of the target adaptation that has been subjected to natural selection. On the other hand, traditional, non-evolutionary theories of anger are descriptive in nature and are limited to the variables and relationships specified by their authors. Furthermore, without an evolutionary perspective, such theories cannot explain why the components of anger function the way that they do. In contrast, the recalibrational theory of anger—using basic models of animal conflict—has predicted and explained many diverse features of anger including individual differences in anger thresholds and how they are calibrated differently between men and women (Sell, Tooby, et al., 2009; Lukaszewski, 2013), the triggers that escalate anger-based aggression (Sell, 2011b), the content of anger-based arguments (Tooby et al., 2008; Sell, 2011b), the criteria for forgiveness and the content of apologies (McCullough, Kurzban, & Tabak, 2013; Sell, 2011a), the computational structure of disrespect (Sell, 2011a,b), and now the design of the universal anger expression.

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