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Formidability and the logic of human anger

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Eleven predictions derived from the recalibrational theory of anger were tested. This theory proposes that anger is produced by a neurocognitive program engineered by natural selection to use bargaining tactics to resolve conflicts of interest in favor of the angry individual. The program is designed to orchestrate two interpersonal negotiating tactics (conditionally inflicting costs or conditionally withholding benefits) to incentivize the target of the anger to place greater weight on the welfare of the angry individual. Individuals with enhanced abilities to inflict costs (e.g., stronger individuals) or to confer benefits (e.g., attractive individuals) have a better bargaining position in conflicts; hence, it was predicted that such individuals will be more prone to anger, prevail more in conflicts of interest, and consider themselves entitled to better treatment. These predictions were confirmed. Consistent with an evolutionary analysis, the effect of strength on anger was greater for men and the effect of attractiveness on anger was greater for women. Also as predicted, stronger men had a greater history of fighting than weaker men, and more strongly endorsed the efficacy of force to resolve conflicts—both in interpersonal and international conflicts. The fact that stronger men favored greater use of military force in international conflicts provides evidence that the internal logic of the anger program reflects the ancestral payoffs characteristic of a small-scale social world rather than rational assessments of modern payoffs in large populations.

aggression | evolutionary psychology | recalibrational theory | welfare tradeoff ratio

Anger is part of the basic biology of the human species. It spontaneously appears in infancy (1, 2), is effectively universal in its distribution across cultures and individuals (3, 4), and has a species-typical neural basis (5). To understand the evolutionary biology of anger, however, it is also important to characterize its evolved function—that is, what (if anything) was anger engineered by natural selection to accomplish? A recent model—the recalibrational theory of anger—hypothesizes that the regulatory program governing anger evolved in the service of bargaining, to resolve conflicts of interest in favor of the angry individual (6, 7). More precisely, the function of anger is to orchestrate behavior in the angry individual that creates incentives in the target of the anger to recalibrate upwards the weight he or she puts on the welfare of the angry individual. Here, we report empirical tests of 11 predictions derived from this model.

Engineering Analysis

Anger, Welfare Tradeoff Ratios (WTRs), and Bargaining. In social species, actions undertaken by one individual commonly have impacts on the welfare of others (measured in fitness, or in other currencies). Consequently, neurocognitive programs in social species should have been designed by selection to solve the following computational adaptive problem: For a given choice set involving self and other, how much weight should be placed on the welfare of the other compared with the self? We shall refer to the ratio of these weights as a welfare tradeoff ratio (WRT) between the self (*i*) and individual (*j*): WTR_{ij}.

For example, Hamilton's original model of kin-directed altruism (8) set the ratio of the weights the actor places on self vs. target to r_{ij}, the degree of relatedness between them. Subsequent research in humans confirmed the existence of a neurocognitive specialization that recalibrates altruism in response to cues of genetic relatedness (9). As expected, its circuitry computes an internal regulatory variable, the kinship index, whose magnitude tracks r_{ij}. When the system computes a high kinship index, it up-regulates the weight the individual places on the target's welfare relative to his or her own (that is, it increases WTR_{ij}).

In contrast, the bargaining specialization outlined by the recalibrational model of anger computes the WTR it expects from other to self. Its function is to elicit the maximum WTR from others that it can enforce cost-effectively, given its bargaining position. This bargaining position is set by the individual's relative ability to inflict costs and to confer benefits—external variables that the cognitive architecture must internally register to regulate the individual's negotiative behavior in a fitness promoting way. Hence, instead of a kinship index, the anger system uses two different families of internal variables to regulate behavior: formidability indexes, designed to track the ability of self and others to inflict costs; and conferral indexes, designed to track the ability of self and others to confer benefits.

Biologists have analyzed an array of selection pressures, in addition to kinship, that are relevant to setting WTRs, including reciprocation (10–12), aggression (13, 14), and externalities (15). That is, these models specify strategies that conditionally trade off the welfare of the actor against the welfare of another organism (the target). If they apply to real organisms, these models implicitly require that animals have computational elements capable of implementing such strategies. Circuits are required that (*i*) compute the probable effect of an act on the welfare of the self, (*ii*) compute the probable effect of an act on the welfare of the target, and (*iii*) deploy a weighting function that indexes the degree to which the organism weights the welfare of the target compared with the self (i.e., a welfare tradeoff function).

Although researchers often analyze kinship, aggressive formidability, reciprocity, and other such variables as single factors considered in theoretical isolation, organisms facing real choices cannot. Each act or choice is an expression of the weight the actor places on the target's welfare, and so a single act cannot express inconsistent weights at the same time. Yet diverse factors will rarely converge on the same weighting function for a specific target: a target may be a sibling, for example, yet have cheated recently in a dyadic reciprocation. To solve this adaptive problem, the brain needs machinery that registers the diverse factors that, taken individually, might call for different weightings, and integrates them into a single weighting function. That is, for those social species like humans whose members are commonly enmeshed in many divergent biological games simultaneously, the evolved neurocognitive architecture needs to be designed to integrate the welfare-relevant inputs (e.g., cues of kinship, formidability) and then generate a welfare tradeoff ratio ($WTR_{actor,\ j}$) as an internal regulatory variable (6, 7). This regulatory variable sets the weight the actor places on the target *j*'s welfare relative to the actor's own welfare in its decision-making. This is necessary for the architecture to decide

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which self-favoring or other-favoring acts to execute.* The higher the WTR is set inside the motivational architecture, the more the actor places weight on the other's welfare compared with the self. Obviously, an organism *i* benefits when another organism *j* increases its WTR toward *i*. It is treated better.

Multiple converging lines of evidence support the hypothesis that WTRs are not just post hoc theoretical constructs, but exist as real neurocognitive elements within the human motivational architecture, playing a role in decision-making† (6, 7). If WTRs are real computational elements in the brains of humans (and other social animals), then their existence could have selected for adaptations whose function is to reach out into the brain of a target, so to speak, and adjust upwards that target's WTR toward oneself. We propose that the emotion of anger is just such a neurocognitive adaptation, and that the conditions that activate it reveal this functional design.

On this theory, when the anger program detects that the other party is not placing "sufficient" weight on the welfare of the actor, anger is triggered. Indeed, experimental evidence supports this view that it is a low WTR, and not just harm per se, that triggers anger (6). When activated, the anger program then deploys the two interpersonal negotiating tactics available to organisms: inflicting costs (aggression); or withdrawing or downregulating expected benefits. The function of these tactics is to recalibrate the target of the anger by showing the target that it will be worse off by continuing to behave in ways that place too little weight on the actor's interests. The preparation for such acts is typically signaled, to allow concessions from the target without proceeding to the costlier acts of infliction or deprivation. Acts or signals of anger communicate that, unless the target increases the weight it places on the angry individual's welfare sufficiently, the actor will inflict costs on, or withdraw benefits from, the target.‡ When these anticipated or experienced fitness costs are greater for the target than the cost of placing more weight on the actor's welfare, then the target's motivational system should increase its WTR toward the actor. In this view, the naturally selected function of anger is to recalibrate the WTR_{ji} in the target's brain, increasing its magnitude so that the target subsequently places more weight on the welfare of the angry individual.

It will be advantageous for the target of the anger to recalibrate its WTR_{ji} upward only when the inflicted costs or withdrawn benefits would be greater than the costs of placing more weight on the welfare on the angry individual. This threshold, therefore, defines the conditions in which anger will be effective in recalibrating the target. Because organisms are selected to pursue strategies when they are effective, this threshold also defines the conditions in which anger should be triggered in the actor. Thus, anger is more likely to be triggered when an actor is positioned to make the price of resisting recalibration high. This price is higher when the actor's formidability (ability to inflict costs on the target) or the actor's ability to confer/withhold benefits is greater. Because these factors give the actor greater leverage over the target, individuals who are more formidable and individuals who are better able to confer benefits should feel "entitled to" a higher WTR from others (that is, they should expect better treatment), should get angry when they do not receive it, and should (other things being equal) prevail more in conflicts of interest. Just as with other neurocognitive programs, there is no claim that humans are consciously aware of the function of the circuitry underlying anger or its computational architecture—just its outputs in thinking and motivation.

It is worth emphasizing that, for humans at least, anger organizes behavior in both cooperative and zero-sum relationships. Humans differ from most other species in the number, intensity, and duration of close cooperative relationships, so traditional models of animal conflict must be broadened to integrate a parallel cooperative dimension. Indeed, the recalibrational model of anger presented here is based on the recognition that certain decision-making problems derivable from evolutionary theories of cooperation (reciprocation or exchange) (11, 16), bargaining (13), and aggression (the Asymmetric War of Attrition) (14) select for a common negotiating architecture—the functional logic underlying anger. Key predictions derived from this model can be tested by operationalizing the factors that are predicted to modulate anger.

Predictions. The recalibrational model of anger predicts that individuals with enhanced abilities to inflict costs or to confer benefits will anger more easily for two related reasons. First, their greater ability to withdraw benefits or inflict costs translates into greater leverage in bargaining over conflicts of interest—meaning that anger is more likely to be successful for them than for others with less leverage. Second, their greater leverage leads them to expect that others will place greater weight on their welfare. The higher the WTR one expects from others (i.e., the higher the anger system sets the threshold of acceptable WTRs from others), the larger the set of welfare tradeoffs that the anger system will process as unacceptable, and angering—especially in a noisy, uncertain world.§

Many factors contribute to the ability to inflict costs or confer benefits, and so should generate principled individual differences in anger. For simplicity of operationalization, however, we selected two for an empirical test of the model: strength and attractiveness.

Strength and Cost Infliction. Ancestrally, a man's upper body strength was a major component of his ability to inflict costs on others by injuring or killing them. Hence, greater strength should set the individual's formidability index higher. Even now, people can accurately assess men's strength from visual cues, and spontaneously base their assessment of others' fighting ability on it [the correlation between subjects' estimates of fighting ability and their assessments of strength in our study population was $r = 0.96$; (17)]; men are also accurate assessors of their own strength (see below). This means people have the information needed to assign higher WTRs toward men they perceive as stronger than themselves without having been explicitly threatened. The WTR that stronger men implicitly expect should, therefore, be higher than that expected by weaker men (all else equal).

Attractiveness and Benefit Conferral. Attractiveness reflects health in both sexes and fertility in women (18), making more attractive people more valuable as sexual partners, mates, and allies (all else equal). Indeed, it is widely documented that more weight is placed on the welfare of attractive people: They are paid more (19), are more likely to be hired for managerial positions (20), are more likely to be elected to public office (21), are given lighter sentences (22, 23), and are viewed more favorably (24). Attractive people should, therefore, register a higher conferral index, and implicitly expect a

*The welfare weighting function should generate a relationship-specific vector—the WTR function—that, for each absolute magnitude of sacrifice potentially made by the actor, produces a WTR—a variable that defines the ratio of the weights placed on the welfare of the actor versus the target, in determining as a decision-making threshold the maximum sacrifice the actor will make for the target.

†Functionally, a given WTR_{ij} in actor *i* toward target *j* should be quasi-stable—that is, it should be constant until the actor is exposed to new information indicating that recalibrating the WTR would increase fitness (e.g., the cheater detection circuit detects *j* cheating *i* in social exchange).

‡Indeed, a theory of the grammar of arguments can be derived from the recalibrational theory of anger (6, 7). The angry individual and the target of anger each communicate their formidabilities, their histories of reciprocity and grievance, and especially their respective views of the costs and benefits involved in the triggering act.

§Of course, those with less leverage will defer more often to those with more leverage. Still, in a noisy social world in which individuals are designed to press in a self-interested direction, even after adjusting for greater deference, a greater proportion of acts should still be unacceptable to those with more leverage. For example, individuals with less bargaining power may probe to see for which cases those with more bargaining power will act to enforce their bargaining power.

higher WTR from others. This should be particularly true for women (see below).

Sex differences in human sociality predict that the effects of these two variables on anger should differ markedly between the two sexes. The distribution of male compared to female upper body strength is such that 99.9% of women are weaker than the average male (25). To the extent that the sexes in a culture are not stably segregated, males will tend to preempt and hence monopolize the use of force as an avenue of negotiation in social groups—an enduring feature of human sociality that should have shaped our species. Cross-culturally, the low deployment of force by women compared to men is well-documented (26–28). Consistent with this view, both men and women are better at assessing strength in men than in women (17). In contrast, in mammals such as humans, access to female sexuality was a far greater limiting factor for male fitness than access to male sexuality was for females (29–31). Insofar as attractiveness reflects fertility and offspring fitness, even small changes in the probability of a woman's granting sexual access constitute a powerful benefit.

Therefore, the recalibrational theory of anger predicts that strength should lead to (*i*) greater success in resolving conflicts in one's favor, (*ii*) greater sense of entitlement (i.e., expectation of better treatment), and (*iii*) greater anger-proneness. The relationship between strength and anger should be specific and functional, not indiscriminate: Strength should predict how easily or frequently one angers, but not necessarily other aspects of anger, such as rumination (how long one remains angry). For example, if the function of anger is to renegotiate a WTR, then it should dissipate once the anger has been expressed and a successful renegotiation has been achieved. Holding on to anger—rumination—should occur when prudential concerns lead one to defer acting on anger while considering when and how to act on it. There are many prudential reasons for deferring action that apply to everyone, weak or strong, attractive or unattractive (e.g., police, reputation, allies, cooperative networks, civil suits).

Attractiveness should also lead to (*iv*) greater success in resolving conflicts in one's favor, (*v*) greater entitlement, and (*vi*) greater anger-proneness. Strength should have a markedly greater effect on these variables for men (*vii*), and attractiveness should have a markedly greater effect for women (*viii*). Ancestrally, stronger males had more to gain and less to lose by fighting than weaker males did. So stronger men should not only be more anger-prone, but also (*ix*) have a greater history of actually using physical intimidation and fighting. Aggression was more efficacious the stronger one was; this should have selected for a decision system that judged aggressive responses as more likely to be successful the stronger one is. Therefore, (*x*) stronger men were predicted to more strongly endorse the view that personal aggression is sometimes a useful or necessary method for dealing with interpersonal conflicts.

Although rational deliberative processes cannot by their nature explain the characteristics of emotions, they could in principle be applied to judgments of one's success at fighting. Thus, predictions (*ix*) and (*x*) could also follow from rational choice operating on expected payoffs in modern environments. By selecting an area where internal regulatory variables reflecting ancestral payoffs—if they existed—would produce different patterns of decision-making than reliance on modern payoffs, it is possible to construct a clear test between the recalibrational model and a rational choice explanation for (*ix*) and (*x*).

One such area is decisions involving coalitional violence and war. Humans use force not just as individuals, but also as coalitions. Evidence from hunter-gatherers, small-scale societies, archaeology, and primatology indicates that this has been a pervasive and evolutionarily long-enduring part of human sociality, plausibly at least as far back as the human-chimpanzee common ancestor (32–35). Modern nation-states are examples of coalitions that use force to resolve conflicts in their interest, both domestically and internationally (through the military). What is evolutionarily unprecedented is their vast size, not their status as coalitions (36).

Decisions about initiating coalitional violence should be based, in part, on cues of the relative formidabilities of the contending coalitions, just as decisions about initiating dyadic conflict should be based on cues of the relative formidabilities of contending individuals. In the modern world of vast armies, a man's own formidability or personal strength has no relationship whatsoever to how effective the use of force by his nation-state will be—and so should be disregarded by any rational assessment process. But ancestrally, in small scale coalitions of two or more individuals, a man's own formidability was a significant component of his coalition's formidability. In this context, a man's individual strength should function as one valid input regulating decisions about whether to initiate coalitional aggression. If decisions about when to use coalitional force in the modern world are being produced, in part, by neurocognitive programs that evolved to regulate aggressive decision-making in a small-scale ancestral world, then (*xi*) a man's individual strength should predict his judgments about the effectiveness of the use of state force against adversaries, foreign and domestic. More specifically, stronger men should be more likely to endorse beliefs that the use of military force in international relations and other state conflicts will be more successful and carry lower risk of retaliation. This prediction is contrary to existing political and rational choice theories about decision-making in international affairs. In sum, judgments about the efficacy of state force should parallel judgments about the efficacy of individual force—but more weakly, since the individual constitutes a greater share of his own armed forces, so to speak, but a smaller share of his coalition's.

Present Studies. Studies 1 and 2 tested whether stronger men anger more easily, are more likely to use aggression, and are more likely to endorse physical aggression as a means of settling personal conflicts and conflicts between nations. Study 2 also tested whether stronger men experience more success in conflict and feel entitled to better treatment. Effects of men's attractiveness were assessed in both studies as well. In Study 2, women were tested as well as men, to determine the role of strength and, more importantly, to determine whether women who view themselves as more attractive experience more success in conflicts, feel entitled to better treatment, and anger more easily. The contrasting predictions about the relative importance of strength and attractiveness for men vs. women were also tested.

Study 1 used what can be considered a gold standard for measuring upper body strength—lifting strength as measured on standardized weight lifting machines. Therefore, the men assessed in Study 1 were recruited from a gym. Men who work out at a gym could turn out to be a special population, however; if so, their behavior and assessments might be atypical of men in general. Hence, Study 2 was designed to test whether the results of Study 1 replicate in a sample of men recruited from the college population more generally—men who have no special interest in strength or weight training. For this reason, it used portable measures of strength that had been validated using weight lifting machines.

Results

Strength in Men. Table 1 shows the correlations between physical strength and the seven anger-relevant instruments. The pattern of results was the same regardless of how strength was measured, across both studies.

If perceptions of strength play a role in setting the WTR a man expects from others, then these should be accurate and produce the same pattern of results as objective strength measures. That was the case: In Study 1, measure b, based solely on perceptions of strength by self and others was highly correlated ($r = 0.73$, $P = 10^{-12}$) with our gold standard for assessing upper body strength, men's ability to lift weights as measured by four machines at the gym. Both measures produced the same pattern of results in Study 1, which

Table 1. Correlations between strength and measures (Pearson *r*)

	Men: Study 1, $n = 62$			Men: Study 2, $n = 125$	Women: Study 2, $n = 156$
Strength measures	a	b	c	d	d
Proneness to anger	0.38 ($P = 0.001$)	0.42 ($P = 0.0004$)	0.47 ($P = 0.0001$)	0.32 ($P = 0.0001$)	0.07 ($P = 0.18$)
History of fighting	0.47 ($P = 0.0001$)	0.43 ($P = 0.0002$)	0.47 ($P = 0.0001$)	0.37 ($P = 0.00001$)	0.07 ($P = 0.19$)
Utility of personal aggression	0.34 ($P = 0.003$)	0.30 ($P = 0.009$)	0.35 ($P = 0.003$)	0.33 ($P = 0.0001$)	0.06 ($P = 0.23$)
Utility of political aggression	0.28 ($P = 0.014$)	0.27 ($P = 0.016$)	0.31 ($P = 0.007$)	0.15 ($P = 0.05$)	0.06 ($P = 0.23$)
Entitlement	—	—	—	0.31 ($P = 0.0003$)	0.10 ($P = 0.12$)
Success in conflict	—	—	—	0.23 ($P = 0.005$)	0.13 ($P = 0.06$)
Rumination	0.02 ($P = 0.45$)	0.15 ($P = 0.12$)	0.14 ($P = 0.14$)	0.06 ($P = 0.25$)	0.03 ($P = 0.36$)

Strength measures: a, lifting strength; b, self and other perceptions only; c, flexed bicep circumference + b; d, direct measure of chest/arm strength + c. In Study 1, strength measure c is included because it is the most comparable to the measure d used in Study 2. *P* values one-tailed (all were directional predictions except for rumination).

tested men who work out at a gym; importantly, this pattern replicated in Study 2, which tested a more general population of men.

As the recalibrational theory of anger predicts, stronger men reported having more success resolving interpersonal conflicts in their favor than weaker men did (*Success in Conflict*, Study 2) and felt entitled to better treatment (*Entitlement*, Study 2; see *SI Text*). That is, they expected others to place greater weight on their welfare. Given that stronger men expected a higher WTR from others, there is a larger set of actions by others that would indicate a WTR that is "too low," so they should be more prone to anger. This was true: men's strength was positively correlated with how easily or frequently they anger (*Proneness to Anger*, Studies 1 and 2). As predicted, the relationship between strength and anger was well-circumscribed: Stronger men were more prone to anger but, as expected, there was no significant correlation between men's strength and how long they stay angry (*Rumination*, Studies 1 and 2). Consistent with the hypothesis that stronger men can more cost effectively deploy aggression to resolve conflicts in their favor, strength was positively correlated with having actually used aggression (*History of Fighting*, Studies 1 and 2) and with more strongly endorsing the efficacy of personal aggression (*Utility of Personal Aggression*, Studies 1 and 2).

Importantly, men's strength positively correlated with the *Utility of Political Aggression* scale (Studies 1 and 2), which measured judgments about the efficacy of military force in international affairs and against internal transgressors. The recalibrational theory of anger's analysis of ancestral payoffs predicts this finding, but not rational choice models operating on modern payoffs. There is, after all, no rational basis for an individual thinking the use of force by the state will be more effective when that individual is stronger than when he is weaker.

Strength in Women. As predicted, the effects of women's strength on all measures were much lower than for men and, although in the right direction, in most cases they were not distinguishable from null effects (Table 1). Women cluster at the low end of the population strength distribution. A possible exception was the relationship between women's strength and their *Success in Conflicts* that, while lower than the male relationship, was marginally significant. The statistical power to find effect sizes in the male range was 99% for $r = 0.3$ and 81% for $r = 0.2$, so the null findings for strength in women are probably real (i.e., not Type II errors).

Attractiveness in Women. As predicted, a woman's perception of her own attractiveness was correlated with her proneness to anger, feelings of entitlement, and success in conflict, in a way parallel to that found for strength in men. It was even correlated with her views on the efficacy of personal and political aggression. When strength is controlled for in a regression, the effect sizes for women's attractiveness are virtually unchanged (Table 2). In short, in their pattern of responses, attractive women look like strong men on all measures except (as expected) their history of fighting (see Table S2).

Attractiveness in Men. What about men's attractiveness? The sharp distinction in women between strength as the ability to inflict costs and attractiveness as the ability to confer benefits is blurred in men, both theoretically and empirically. Ancestrally a man's ability to inflict costs on others contributed to his ability to confer benefits on a mate, so indicators of a man's strength should contribute to his attractiveness. Indeed, research has shown that an important component of a man's attractiveness to women is his musculature (37)—an indicator of his strength—and our own data show that strength and attractiveness were more highly correlated for men than for women [Study 1 measure a: $r = 0.23$ ($P = 0.034$), measure b: $r = 0.47$ ($P = 0.00005$), measure c: $r = 0.38$ ($P = 0.001$); Study 2: $r = 0.33$ ($P = 0.0001$)]. For this reason, Table 2 reports zero-order correlations alongside effects of attractiveness in a regression controlling for strength.

Consistent with attractiveness giving leverage in relationships, men's attractiveness predicted their sense of entitlement and success in conflict, and this relationship remained significant even after controlling for differences in their strength. Men who view themselves as more attractive were also more prone to anger in both studies; this

Table 2. Correlations between attractiveness and measures*

	Women: Study 2, $n = 156$		Men: Study 2, $n = 125$		Men: Study 1, $n = 62$		
	Zero order	β (c/str-d)	Zero-order	β (c/str-d)	Zero-order	β (c/lifting-a)	β (c/percep-b)
Proneness to anger	0.23 ($P = 0.002$)	0.22 ($P = 0.003$)	0.14 ($P = 0.06$)	0.04 ($P = 0.34$)	0.39 ($P = 0.001$)	0.32 ($P = 0.004$)	0.25 ($P = 0.028$)
History of fighting	0.03 ($P = 0.34$)	0.03 ($P = 0.37$)	0.08 ($P = 0.17$)	−0.04 ($P = 0.32$)	0.25 ($P = 0.027$)	0.14 ($P = 0.11$)	0.05 ($P = 0.35$)
Utility of personal aggression	0.18 ($P = 0.014$)	0.17 ($P = 0.02$)	0.12 ($P = 0.09$)	0.01 ($P = 0.46$)	0.26 ($P = 0.02$)	0.19 ($P = 0.06$)	0.15 ($P = 0.13$)
Utility of political aggression	0.15 ($P = 0.033$)	0.15 ($P = 0.04$)	−0.03 ($P = 0.37$)	−0.09 ($P = 0.18$)	0.28 ($P = 0.013$)	0.23 ($P = 0.035$)	0.20 ($P = 0.08$)
Entitlement	0.31 ($P = 0.00008$)	0.30 ($P = 0.0001$)	0.26 ($P = 0.002$)	0.18 ($P = 0.025$)	—	—	—
Success in conflict	0.22 ($P = 0.003$)	0.22 ($P = 0.003$)	0.28 ($P = 0.0008$)	0.23 ($P = 0.007$)	—	—	—
Rumination	0.05 ($P = 0.26$)	0.05 ($P = 0.26$)	−0.02 ($P = 0.40$)	−0.04 ($P = 0.33$)	0.09 ($P = 0.25$)	0.09 ($P = 0.25$)	0.02 ($P = 0.44$)

*βs are the effect sizes for attractiveness in a regression controlling for strength measures (indicated by letter, see Table 1). *P* values are one-tailed (all were directional predictions except for rumination).

effect was significant in Study 1, but marginal in Study 2, where it disappeared after controlling for differences in their strength.

Effects that should be driven primarily by the ability to inflict costs—fighting history and judgments about the efficacy of personal and political aggression—were indeed not predicted by men's attractiveness at all in Study 2, and most of the zero-order effects in Study 1 disappeared or became marginal after controlling for strength (Table S1 and Table S2).

As predicted, the effects of men's strength were much more robust. In both studies, when strength and attractiveness were entered into a regression, strength continued to independently predict anger, entitlement, success in conflict, fighting history, and judgments of the efficacy of personal and political aggression. Indeed, there was little or no diminution in the effect sizes for the instruments most related to aggression (Table S1 and Table S2).

Discussion. Eleven predictions were derived from the recalibrational theory of anger, and all of them were empirically supported. No other theory predicts this complex, subtle, and precise pattern of results.

These studies are intended as an initial proof of concept: They tested just two out of a larger potential set of negotiative factors. Theoretically, anything that enhances or diminishes the ability to inflict costs or confer benefits should have parallel effects on anger, entitlement, and success in conflicts, proportionate to their magnitudes. Because strength is only one factor of many contributing to the ability to inflict costs in men, and attractiveness is only one factor of many contributing to the ability to confer benefits in women, it is striking how large their effects were. We expect that as other characteristics determining the ability to inflict costs or to confer benefits are measured, more of the differences between individuals in anger-proneness will be explained.

For example, humans often rely on alliances and coalitions to inflict costs negotiatively, so the explained component of individual anger-proneness, entitlement, and so on, should be even greater when alliances and hierarchical status are taken into account. Familiarity with and access to weapons is another factor that ought to contribute to anger-proneness—one that may even play some role in explaining cases of explosive violence and terrorism. Similarly, the many factors that generate individual differences in the ability to confer benefits—resources, skills, social influence, wealth, status—should also modulate anger. Yet, it is important to note that we do not know whether the anger system is ontogenetically open in its identification and weighting of factors, or whether it is biased toward factors that were operative ancestrally. The striking finding that strength predicts more favorable attitudes toward the use of military force implies that at least some of these relationships are set phylogenetically by ancestral payoffs, rather than through experienced payoffs.

At a popular level, many attribute the constellation of traits identified here—anger-proneness, strength, and favorable attitudes toward aggression—to the effects of testosterone, hypothesizing that testosterone increases both muscle mass and anger-proneness. Although some component of anger-proneness might be explained in this way, the difficulty with this view is that existing studies of testosterone in humans show that the effects of testosterone on aggression are weaker (typically $r = 0.20$ for aggression) (38) than the effects of strength on aggression and anger reported herein ($r = 0.32$–0.47). This, therefore, raises the reciprocal question: Are effects usually attributed to testosterone better attributed to a computational system that tracks relative strength? It may be that steroid rage (for example) results from the reverse causal arrow: Steroids increase strength, which then lowers anger thresholds. The one unexpected finding in Study 2—that attractiveness in women predicts their attitudes toward personal and political aggression—also undermines the counterhypothesis that the effects reported here are a byproduct of testosterone. This is because testosterone in women is unlikely to be either high enough, or sufficiently associated with attractiveness, to be the causal agent operating here.

Although we do not know why attractive women have favorable attitudes toward aggression, it is logically possible that ancestrally, attractive women drew enough social power to direct others to employ aggression on their behalf. Social influence should have been partially fungible in ancestral social groups, e.g., formidable men would have had access to more resources, enhancing their ability to confer benefits; attractive women would have had access to formidable men, enhancing their ability to inflict costs.

We expect the architecture of anger we outlined to be species-typical and, therefore, cross-culturally universal (e.g., see ref. 39). However, we do expect that in cultures where the sexes are socially sex-segregated, and/or the male-female strength distribution overlaps more, the effects of strength on anger in women may be greater.

It is worth noting that these findings are surprising, in light of existing theories of anger, whether formal or intuitive. For example, the idea that individual differences in anger must be rooted in a past history of negative treatment is undercut by the finding that more attractive people are more anger-prone; attractive people receive better treatment from others, not worse. The results also militate against frustration-based theories because people who experience better treatment anger more easily: Stronger men and more attractive women were more anger-prone, yet their goals were thwarted less often—they reported more success in resolving conflicts in their favor, not less. More broadly, emotion researchers tend to consider anger as involved primarily with aggression, but the association between attractiveness and anger supports the view that anger is also involved in cooperative relationships. Because strength is correlated with height (17), our findings also challenge the existence of the Napoleon complex—the proposal that smaller men overcompensate for their size by exaggerated anger-sensitivity. Our data show that shorter men were not more anger-prone (*SI Text* and Table S3).

Finally, one might hope that the decision to go to war is arrived at rationally, in response to objective conditions. Moreover, it would be delusional in the modern world to think that your personal strength determines—or even influences—how effective your nation's military will be in a war. Yet our subjects' strength predicted their attitudes toward military action. This is exactly what one would expect if assessments about the use of coalitional force by the state—an evolutionary anomaly—are generated, at least in part, by mechanisms that evolved for assessing the success of coalitional force by small groups of which one is a member. If governmental decision-makers are like other humans, then their musculature may be playing a role, unconnected from rational evaluation, in their decisions to go to war.

Conclusions

Humans evolved embedded in small scale social networks and were chronically exposed to both cooperative and conflictual interactions. Over the last several decades, evolutionary biologists have produced a series of elegant theories of the selection pressures that encompass cooperation, aggression, and bargaining—all of which should have applied to humans during our evolution. There is an especially large body of evidence supporting evolutionary theories of aggression in other species, and biologists will find the relationship reported here between strength and history of fighting in humans to be fully consistent with theoretical expectations. Equally significant is the evidence showing that individual differences in the ability to confer benefits—an aspect of cooperation—operates analogously to individual differences in cost infliction (aggressive formidability) in social negotiation. What is particularly satisfying is that (*i*) components of all three theories can be distilled and fit together to produce a theory of what the regulatory architecture that underlies social negotiation should look like, (*ii*) the outputs of this architecture parallel known phenomena associated with anger, and (*iii*) the evidence reported here supports the detailed predictions derived from the recalibrational model of anger. Converging results from other studies support the view that welfare tradeoff ratios are psychologically and computationally real, and that insuf-

ficient welfare tradeoff ratios are the conditions that trigger anger (6). These results show how an evolutionary approach can help to illuminate the computational architecture underlying emotion and motivation.

Methods

Subjects. All subjects were paid $10 for their participation. For Study 1, 62 men (mean age, 21) were recruited from a gym at the University of California, Santa Barbara (UCSB). For Study 2, 125 men (mean age, 20) and 156 women (mean age, 19) were recruited from the UCSB student center. Ninety-six percent of UCSB undergraduates are from California.

Procedure. Subjects were tested individually, as follows. (*i*) Each completed a questionnaire that included scales designed to measure *Proneness to Anger*, *History of Fighting*, *Tendency to Ruminate*, *Utility of Personal Aggression* and *Utility of Political Aggression*; Study 2 added scales to measure *Success in Conflict* and *Entitlement*. (*ii*) Height, weight, hip circumference, waist circumference, chest circumference, unflexed bicep, flexed bicep, and neck circumference were measured. (*iii*) The subject was photographed. (*iv*) Measures of upper body strength were taken.

Materials. ***Study 1.*** Proneness to anger—how easily or frequently one becomes angry—is conceptually distinct from how long one stays angry (rumination) and from the actual use of aggression. Existing anger instruments conflate these three phenomena, so new instruments were made, incorporating appropriate questions from prior anger instruments and adding new ones when necessary. Subjects indicated their agreement or disagreement with each item on a scale from 1 (strongly disagree) to 7 (strongly agree). See *SI Text* for full list of items. Typical items for each instrument were as follows: (*i*) *Proneness to Anger*: ''It is harder to get me angry than other people'' (reverse coded) 11 items, Cronbach's $\alpha = 0.70$. (*ii*) *Tendency to Ruminate*: ''Sometimes I stay mad for days'' five items, $\alpha = 0.78$. (*iii*) *History of Fighting*: ''I have physically intimidated someone who had it coming'' five items, $\alpha = 0.82$. (*iv*) *Utility of Personal Aggression*: ''If I don't respond to provocations and do something to make the wrong-doers pay, they'll just do more to hurt me in the future'' seven items, $\alpha = 0.63$. (*v*) *Utility of Political Aggression*: ''I think it is a mistake to go after Middle Eastern countries that harbor terrorists. This will just lead to more attacks on America in the future'' (R) six items, $\alpha = 0.85$. Study 1 was conducted in May 2003, just after the initial U.S. invasion of Iraq.

Study 2. *Success in Conflict* and *Entitlement* scales were added to the original five scales. *Success in Conflict*: e.g., ''When there's a dispute, I usually get my way'' seven items, $\alpha = 0.78$. *Entitlement*: e.g., ''I deserve more than the average person'' 15 items, $\alpha = 0.60$. Some new items were added to all scales from Study 1 except history of fighting, increasing their reliability (*Proneness to Anger*: $\alpha = 0.85$; *History of Fighting*: $\alpha = 0.79$; *Rumination*: $\alpha = 0.81$; *Utility of Personal Aggression*: $\alpha = 0.81$; *Utility of Political Aggression*: $\alpha = 0.89$).

Strength Measures. ***Study 1.*** Upper body lifting strength was assessed on four weight-lifting machines at a gym: arm curl, abdominal crunch, chest press, and super long pull. Maximum lifting strength on each machine was converted to a z-score and then averaged. (details in ref. 17).

Although we wanted to obtain an objective measure of strength, the WTR an individual expects from others should be a function of how strong he believes himself to be relative to others and how strong others perceive him to be. For strength self-perception, subjects were asked to fill in the blank in the following statement: ''I am stronger than <blank>% of other men.'' Perception of strength by others was obtained by averaging, for each target, ratings of full body photographs in standard dress with head edited out of the photo (details in *SI Text* and ref. 17). Data from Study 1 show that perceptions track reality. Subjects' actual lifting strength was correlated with their self-perceived strength at $r = 0.66$ ($P = 10^{-8}$) and with others' perceptions of their strength at $r = 0.66$ ($P = 10^{-8}$), with no sex differences in ratings (see also ref. 17).

Study 2. Sell et al. (17) showed that 66% of the variance in upper body lifting strength as assessed on weight-lifting machines can be accounted for by adding together the standard scores for three measures, each of which accounts for unique variance: flexed bicep circumference, others' perceptions of strength based on ratings of photographs, and self-perceived strength (the latter two described above; adding in other morphological measures did not improve prediction). To these scores we added a direct measure of chest/arm strength, taken with a Rolyan hydraulic hand dynamometer with its handles inverted (procedure described in ref. 17). All scores were standardized within-sex. Men in Study 1 were approximately one-half standard deviation stronger than those in Study 2 (*SI Text*).

Attractiveness Measures. The WTR an individual expects from others should be a function of how attractive that individual perceives him- or herself to be relative to others, which is based on frequent comparisons with others of their sex (40) plus their lived experience of how easily they attract members of the opposite sex. For this reason, subjects were asked to fill in the blank in the following statement: ''I am more attractive than <blank>% of other men'' (Study 1), and ''I am more attractive than <blank>% of others of my sex'' (Study 2). These were z-scored within sex.

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