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# From Whence The Captains of Our Lives

## Ultimate and Phylogenetic Perspectives on Emotions in Humans and Other Primates

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1           Let's not forget that the little emotions are the great captains of our lives  
2                           and we obey them without realizing it. ~Vincent Van Gogh

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5 *Introduction*

6           It has long been recognized that an evolutionary perspective is useful in investigating  
7 emotions. In this chapter, we employ two complementary applications of evolutionary theory.  
8 One is adaptationism, viewing emotions as discrete adaptations for behavior regulation that  
9 evolved in response to challenges repeatedly confronting organisms over evolutionary time  
10 (Ekman 1992, Frijda 1986, Lazarus 1991, Nesse 1990, Tooby & Cosmides 2008). Each emotion  
11 is elicited by cues to the presence of a recurring fitness-relevant challenge or opportunity, and  
12 each coordinates information-processing, motivational, and physiological systems to respond  
13 adaptively. The second application is phylogenetic and comparative, examining 1) the actual or  
14 expected taxonomic distribution of emotion systems based upon patterns of descent, the  
15 distribution of the relevant adaptive problems, and cognitive capacities, and 2) the logic of each  
16 system's transformation through descent as a result of the interaction of system evolvability,  
17 system affordances, and the structure of adaptive problems. Neither of these applications of  
18 evolutionary theory to the study of emotions has yet been fully realized, and the synergy  
19 resulting from their integration is often overlooked. Our goal is to further develop these  
20 approaches, to demonstrate their complementarity, and to employ them in examining some  
21 aspects of emotions that contribute to the “gap” between humans and other primates.

22           Darwin’s (1872/1955) pioneering work on emotional expressions employed a  
23 comparative perspective in the service of multiple goals: 1) to substantiate the utility of general

1 explanatory principles by application to all species; 2) to demonstrate human descent from non-  
2 human ancestors; 3) to evaluate the innateness of human expressions by showing similarity to  
3 other species; and 4) to explain some human characters as vestigial traces of ancestral forms. The  
4 first two goals have been achieved. Ekman and other modern students of expressions advanced  
5 the third goal, and many human facial expressions are now considered pan-cultural. This leaves  
6 Darwin's fourth goal. While extreme vestigialism has rightly fallen from favor, many emotions  
7 do exhibit evidence of deep histories of successive modification. We will present several  
8 examples of emotional systems apparently evolved for one purpose that were subsequently  
9 modified to serve a different purpose. In some cases the properties of an ancestral emotional  
10 system appear to have "preadapted" it (Gould & Vrba 1982) to the task demands of a newly arisen  
11 adaptive problem (e.g., Fessler 2004, Gervais & Wilson 2005, Rozin et al. 1997). In a number of  
12 cases, an extant emotional action tendency has been put to novel use by modifying the eliciting  
13 conditions (cf. Keltner & Anderson 2000, Rozin 1996, Tooby & Cosmides 1989). Yet, even with  
14 subsequent secondary selection, this process does not necessarily erase the legacy of past  
15 selection; substantial residues of former function sometimes remain, and it is only with reference  
16 to ancestral traits that such features become intelligible. Applying this consideration when  
17 reverse engineering a trait ("reverse tinkering"; Andrews et al. 2002, Gangestad & Simpson  
18 2007) illuminates the kludge-like structure of emotions that have served multiple functions over  
19 evolutionary time.

20         As the above discussion suggests, phylogenetic and comparative approaches both  
21 constrain and inform adaptationist hypotheses (see Gosling & Graybeal 2007, Gangestad &  
22 Simpson 2007, Maestriperi 2003c). In addition to controlling for non-independence of trait  
23 correlations in comparative research (Nunn & Barton 2001), "tree thinking" helps to specify the

1 time frame within which the target properties of a trait were selected, while suggesting an  
2 ancestral state from which the trait was derived. This refines the task of reverse engineering by  
3 rephrasing the ultimate question as: Why did this form emerge given the form from which it  
4 emerged? A phylogenetically-informed comparative approach can help to parse a trait into  
5 aspects that were impacted by selection pressures operating during particular periods in the  
6 lineage. This approach highlights the process of secondary selection through which (*contra*  
7 Gould 1991, Gould & Vrba 1982) an extant system is not merely exapted (put to new use), but is  
8 further subjected to specializing selection for that new function. This process, which we term co-  
9 optation, has rarely been foregrounded in the study of the mind.

10         Just as comparative and phylogenetic approaches offer benefits to students of human  
11 emotions, so too can adaptationist perspectives enhance the study of nonhuman primate  
12 emotions. Because emotion is difficult to quantify, most primatologists have sidestepped the  
13 study of emotion, although this is beginning to change (e.g., Aureli & Schaffner 2002, de Waal  
14 1996, Maestriperi 2003a). The conjunction of adaptationist and phylogenetic analyses indicates  
15 where one can expect to find homologues of human emotions. It should be possible to predict the  
16 taxonomic distribution of emotion traits through a consideration of 1) the phylogenetic  
17 relationships among species, 2) the selection pressures thought to produce and maintain a given  
18 trait, and 3) the cognitive capacities that constitute prerequisites for the trait. This generates a  
19 taxonomy of emotions, ranging from ancient emotions expected to be present in all vertebrates,  
20 to conserved pan-primate emotions, to derived emotions expected to be unique to our species.  
21 Because explorations of primate emotions are in their infancy, we cannot conduct rigorous tests  
22 of our phylogenetic hypotheses. However, there is reason for optimism, as investigators are  
23 beginning to employ new methods to probe primate motives (e.g., de Waal et al. 2008,

1 Lakshminarayanan & Santos 2008, Silk et al. 2005, this volume, Warneken et al. 2007), and  
2 obstacles to the study of primate emotions are not insurmountable. Below we sketch a set of  
3 phylogenetically-informed adaptationist proposals intended to provide starting points for future  
4 studies of emotions in both humans and nonhuman primates. This is not an exhaustive  
5 description of these species' emotional repertoires. Rather, our goal is to demonstrate the form  
6 that we think such descriptions should take, and to spark further discussion.

7         A note on terminology: because cultures differentially emphasize or ignore facets of the  
8 panhuman spectrum of emotions, any language's emotion lexicon is but a crude gloss for the  
9 underlying phenomena. Accordingly, the emotion terms used here should be viewed as heuristic  
10 labels for adaptations that are not necessarily isomorphic with Anglo-American folk psychology.

11

### 12 *Ancient, relatively conserved emotions*

13         All vertebrates confront a common set of elementary adaptive challenges, including  
14 avoiding injury and disease, and finding mates. The core motivational systems that evolved in  
15 ancestral vertebrates in response to these selective pressures have likely been largely conserved  
16 in descendant taxa. Because of their ancient origins, the cognitive prerequisites for these  
17 adaptations are relatively limited. In general, attention to simple exogenous or endogenous cues  
18 suffices to identify the eliciting conditions. Many of these eliciting cues are sufficiently uniform  
19 across circumstances to allow canalization, obviating learning. Below we sketch some of the  
20 relevant adaptive challenges and corresponding emotions. Then, we consider how natural  
21 selection refined these basic building blocks

22         Avoiding imminent threats to life and limb is a fundamental determinant of fitness; *fear*  
23 marks the presence of such threats, motivating flight as a principal behavioral outcome, with

1 fighting as a secondary outcome when the threat is animate and escape is appraised as  
2 impossible. The neural underpinnings of fear appear to be highly conserved, certainly among  
3 mammals, and arguably among vertebrates (Braithwaite & Boulcott 2007, Ohman et al. 2007,  
4 Panksepp 1998). Fear expressions closely paralleling those present in humans are recognizable  
5 in many primates (Parr et al. 2007). This uniformity is potentially explicable in terms of selection  
6 conserving adaptive form. Human experimental results support Darwin's (1872/1955)  
7 supposition that many facial expressions are functional beyond their signal value, as the fear  
8 expression enhances perceptual acuity and reaction times to threat (Susskind et al. 2008).

9       The avoidance of toxins and pathogens is another elementary adaptive challenge. In  
10 humans, *disgust* is involved in the rejection of ingestible contaminants and avoidance of cues  
11 reliably associated with pathogen risk (e.g., rotting flesh or feces). Oral contact is a powerful  
12 disgust elicitor (see Fessler & Haley 2006), and disgust reactions involve gastrointestinal  
13 rejection, suggesting that preventing intoxication was the original function of this emotion.  
14 Disgust was likely subsequently co-opted for prophylaxis by extending elicitors to include  
15 contact with cues of disease (see Kelly in prep.). Human disgust can also be elicited by  
16 representational contamination (transfer of disgust-eliciting status through contact with an  
17 elicitor absent perceptible changes) and a variety of symbolically-mediated events. The  
18 extension of disgust to such cues leads some to argue that disgust is a culturally-constructed  
19 defense against existential anxiety (Rozin et al. 2000). However, this position overlooks design  
20 features evident in the avoidance of contact with stimuli ecologically associated with disease  
21 transmission. Because microbes cannot be detected by the human eye, yet spread through  
22 physical proximity, it is beneficial that the set of cues that elicit disgust include representational  
23 contamination (Curtis & Biran 2001, Fessler & Haley 2006, Kelly in prep.).

1           An ingestion rejection system is found in all mammals. Across primates, we predict that  
2 the degree of elaboration of this system (i.e., number of eliciting cues; flexibility of response)  
3 will vary as a function of carnivory, as meat is a potent source of disease. Similarly, we expect  
4 some form of pathogen-avoidance mechanism to be found in all mammals; because sociality is a  
5 determinant of disease risk, these mechanisms should vary as a function of sociality. In contrast,  
6 because it requires abstract conceptual abilities, we expect representational contamination to be  
7 quite rare. In a number of species, investigators have documented behaviors possibly explicable  
8 as prophylaxis, including avoidance of parasitized conspecifics, and grooming and feces  
9 avoidance (see Nunn & Altizer 2006:159-170 for review on primates). However, it is not known  
10 whether such behavior is motivated by a disgust-like emotion, as it is in humans.

11           Ultimately, reproduction, not survival, determines fitness, so we expect all sexually-  
12 reproducing species to be equipped with an emotion akin to *lust*, the principal motivator of  
13 sexual behavior. Although the frequency, form, and elicitors for sexual behavior vary across  
14 mammals, the ubiquity of goal-oriented behavior leading to copulation is consistent with this  
15 emotion being widespread. There are several parallels in the task demands associated with mate-  
16 seeking and foraging (appetitive cycles; resource-seeking behavior; discrimination among  
17 resource options), and, in mammals, there is overlap between the neurophysiological systems  
18 regulating proceptive sexual behavior and those regulating ingestive behavior (reviewed in  
19 Fessler 2003). This suggests that systems regulating ingestion may have constituted building  
20 blocks from which systems regulating sexual reproduction were subsequently constructed.  
21 Disgust, antithetical to both hunger and lust, plays a central role in human inbreeding avoidance  
22 (Fessler & Navarrete 2004, Lieberman et al. 2003, 2007); likewise, women's sexual disgust  
23 sensitivity increases around ovulation, possibly functioning to reduce contact with suboptimal

1 reproductive partners at peak fertility (Fessler & Navarrete 2003). Most primates exhibit marked  
2 inbreeding avoidance (Muniz et al. 2006, Paul & Kuester 2004), and it is possible that a similar  
3 emotional system is involved. Indeed, we suggest that both the ingestion regulation and sexual  
4 regulation facets of disgust are pan-mammalian.

5  
6 *Emotions associated with elementary sociality*

7         As illustrated by disgust at the prospect of sex with individuals identified as close kin,  
8 emotion elicitation is contingent on appraisal, the process of construing the nature and meaning  
9 of a situation (Scherer 1999). Sociality introduces a complex set of adaptive challenges because  
10 there are many ways in which conspecifics can affect fitness, hence many distinct appraisals and  
11 consequent emotional responses should attend social interaction. At the most elementary level,  
12 because competition for resources is a key determinant of fitness, we expect distinct emotions  
13 with corresponding appraisals to address competition. From the perspective of a resource holder,  
14 an attempt to displace one from a resource should be appraised as a transgression, the infliction  
15 of an unwelcome (i.e., fitness-reducing) cost, or threat thereof. In humans, transgressions elicit  
16 *anger*, motivating aggressive retaliation when feasible. While varying in degree across species,  
17 many social animals exhibit aggressive responses to actions that investigators plausibly interpret  
18 as transgressions. Hence, an elementary anger-like emotion and its eliciting appraisal are  
19 probably both ancient and widely shared. This conclusion is supported by the extensive  
20 conservation across mammals of the neurophysiological systems underlying aggression (e.g.,  
21 Dierick & Greenspan 2007).

22         In humans (particularly young men), anger often motivates disproportionate responses to  
23 transgression. Disproportionate responses may be advantageous because they serve as a signal

1 that transgressing is dangerous, generating reputational benefits that deter further transgressions  
2 (reviewed in Fessler in press). Reputation-based strategies such as this require repeated  
3 interactions, the ability to identify and recall individual actors, and the capacity to acquire  
4 information as a third-party observer. All of these features are likely present among most social  
5 primates (Cheney & Seyfarth 2005), and age-related patterns of impulsive aggression may  
6 parallel those found in humans (cf. Fairbanks et al. 2004). Thus, it is likely that the central  
7 features of the anger adaptation are a shared ancestral trait among primates.

8         While the question of applying the appropriate appraisal to a given event is never trivial,  
9 this task is particularly complex in the social domain because the range of fitness consequences  
10 of social interactions is so large. This complexity is multiplied by the fact that, due to repeat  
11 interactions, appraisals of current social actions hinge on past events. We suggest that the  
12 substantial informational demands of applying the appropriate appraisal to social events are  
13 managed in part through *attitudes*, durable, hierarchically organized representations of  
14 previously appraised traits and relational outcomes that potentiate differential emotional  
15 readiness toward others. Attitudes and emotions are reciprocally related, as attitudes are updated  
16 by emotions, and subsequently help to regulate emotions by shaping appraisals. Responsive to  
17 the fitness-relevant traits and behaviors of other individuals, attitudes are continuously adjusted  
18 over time, thus constituting summary representations that proxy the future fitness implications of  
19 all past interactions. Attitudes allow individuals to represent their current relations to others  
20 without the need for explicit bookkeeping or recall of all encounters, and via their role in  
21 appraisals, these representations adaptively regulate current behavior. Attitudes can thus be  
22 conceptualized as “internal regulatory variables,” in the sense that they functionally translate past  
23 appraisals into current behavior regulation (see Tooby & Cosmides 2008). This proposal

1 obviates the need to posit complex cognitive operations in some relational domains (the potential  
2 complexities of which are discussed in Cords 1997, Silk 2003; see Aureli & Schaffner 2002,  
3 Aureli & Whiten 2003). Congruent with extensive social psychological findings on implicit  
4 attitudes (Greenwald & Banaji 1995), our position does not require positing problematic  
5 conscious processes.

6         The interaction of appraisals, attitudes, and emotions is evident in the case of *envy*, the  
7 emotion associated with the goal of displacing a resource holder. In humans, envy is elicited by  
8 the appraisal that, in a zero-sum situation, the target possesses an advantage to which the actor is  
9 entitled. The target is therefore represented as a rival, and there is an enduring attitude of  
10 hostility toward the target (see Smith & Kim 2007) such that the actor is willing to inflict costs  
11 on the target. Likewise, potentiated by this attitude, attempts by the target to retain or increase  
12 control of the resource elicit anger from the actor. Envy is thus usefully contrasted with  
13 *admiration*, in which pursuit of non-zero-sum advantages enjoyed by another does not involve an  
14 appraisal of entitlement, an attitude of hostility, or anger in response to the target's attempts to  
15 control the resource (more on admiration later). Conflict over zero-sum resources is central to  
16 much social behavior, hence we suggest that the core components of the envy system are both  
17 ancient and widely shared. Observations in multiple species of distress at inequitable  
18 distributions (reviewed in Brosnan 2006) are congruent with this suggestion.

19         Competition and hostile intent are also central to *jealousy*. Deriving from a proprietary  
20 attitude toward a relationship partner and a corresponding appraisal of potential interlopers as  
21 transgressors, this emotion motivates attempts to maintain exclusivity by warding off rivals and  
22 restricting the partner's options (reviewed in Smith & Kim 2007). While sociality does not  
23 necessitate the formation of discrete relationships, well-differentiated relationships exist in many

1 primate species (see Silk 2007). If such relationships are widespread, jealousy may be widely  
2 shared. Elicitors for jealousy will depend on the nature of the threats posed to a relationship. The  
3 utility of biparental care in humans leads to sex-specific adaptive challenges, namely the  
4 possibility of female extra-pair copulation (leading to misallocation of male parental investment)  
5 and male abandonment (leading to reduced female access to resources). A growing literature  
6 investigates the corresponding sex-specific relative importance of sexual and emotional infidelity  
7 as elicitors of mating jealousy (reviewed in Haselton & Ketelaar 2006). While extensive  
8 biparental care is rare among primates, we expect the same logic of an actor-centered appraisal  
9 of different threats to a relationship to apply across species.

10         In most social animals, conflicts establish and maintain dominance rank, which then  
11 determines priority of access to resources. As Darwin (1872/1955) suggested, ethology provides  
12 clues to both the phylogeny and ultimate function of emotions, and this is particularly evident in  
13 the case of dominance interactions. Displays often precede, and sometimes obviate, conflict, and  
14 threat displays that reduce the costs of conflict are a pervasive aspect of social behavior in  
15 primate groups. In most species, body size is a key determinant of success in combat, and,  
16 correspondingly, threat displays generally involve an exaggeration of body size. Direct attention  
17 (staring) is often a feature of such displays (reviewed in Fessler 2004). In some cases, it is  
18 beneficial to acknowledge subordinate status, and appeasement displays are counterpoints to  
19 threat displays. Appeasement displays generally involve an attempt to minimize apparent body  
20 size and direct attention away from the aggressor. In humans, threat displays are associated with  
21 an emotion we term *proto-pride*, and appeasement displays are associated with *proto-shame* (see  
22 Fessler 2007; see also Tracy & Matsumoto 2008). Proto-pride is elicited when an actor appraises  
23 herself as occupying a superior position in a social hierarchy and interacting with a subordinate

1 in a context in which the disparity in status is relevant; conversely, when the complementary  
2 appraisal occurs, the subordinate feels proto-shame. In each case, the emotion enhances a  
3 corresponding attitude that represents in enduring fashion the disparities in status. For the  
4 dominant, this attitude includes a sense of entitlement relative to the other, while the converse is  
5 true for the subordinate. In keeping with their opposite hedonic valences, this pair of emotions  
6 motivates striving for power and social position (Fessler 2007). Given the clear homologies with  
7 display behaviors in other primates, and the ubiquity of the relevant adaptive problem across  
8 social animals, it is likely that proto-pride and proto-shame are pan-primate; indeed, the core  
9 features of these emotions and related appraisals and attitudes may be shared by all mammals,  
10 and possibly by most vertebrates.

11

### 12 *Emotions associated with parenting and pair-bonding*

13 Parental behavior is a defining feature of mammals, although the patterns and extent of  
14 parental care vary greatly across species. Parental behavior must be underlain by a discrete  
15 motivational system on the part of the parent, complemented by a corresponding system in the  
16 offspring (Maestri 2003a). We expect these motivations to be modulated by complementary  
17 attitudes, what we term *parental attachment* and *offspring attachment*, that represent the fitness  
18 value of offspring and parents to one another. These attitudes shape appraisals of actions,  
19 determining the circumstances that elicit the corresponding emotions of *parental love* and  
20 *offspring love*. For example, positive parental attachment leads a mother to appraise her infant's  
21 midnight rooting as affiliation, eliciting parental love, rather than as a transgression that would  
22 elicit anger. Offspring develop positive attachment as a result of the experience of receiving  
23 succor. In contrast, because offspring impose costs on parents without immediate compensation,

1 the building of positive parental attachment is achieved in part through the pump-priming effects  
2 of an emotion (*natal attraction*) that makes interaction with infants intrinsically rewarding, a  
3 phenomenon well-documented in primates (e.g., Silk 1999). It appears that, in humans, natal  
4 attraction transforms into parental love in part as a result of positive infant responses to parental  
5 overtures. Given the general primate trend of reductions in the importance for parent-offspring  
6 bonding of olfactory cues, and increases in the importance of behavioral cues (Broad et al. 2006),  
7 similar patterns may obtain across primates.

8 Two different systems appear to underlie human mate selection, courtship, and long-term  
9 pair bonding. *Limerance* (Tennov 1979) is an emotion characterized by intrusive ideation  
10 concerning a prospective mate, attention to indications of reciprocation, and a motivation to be  
11 near and make a positive impression on the target individual. Both E. Pillsworth and R. Kurzban  
12 (personal communications) propose that the intrusive and obsessive nature of limerance are  
13 explicable in terms of the need to signal commitment to the target party given the risk of  
14 defection. The most persuasive signals are costly, taking the form of resource provisioning, time  
15 allocation, and the public spurning of alternate potential mates. Once a stable mateship has  
16 formed, the benefits of signaling are reduced: once both parties have a concrete interest (e.g.,  
17 offspring) in extended cooperation, it is adaptive to value the other party's welfare, and provide  
18 benefits noncontingently. Although investigators (e.g., Hatfield 1988) claim that an emotion,  
19 *companionate love*, replaces limerance in pair-bonded couples, much of the phenomenon thus  
20 labeled is an attitude rather than an emotion -- the actual emotion is only present during  
21 punctuated events in which displays of affection reaffirm mutual valuation, reinforcing this  
22 attitude. Pair-bonding and biparental investment occur in a variety of mammals, and there is  
23 some commonality in the neurophysiological systems that underlie these behaviors (Broad et al.

1 2006, Curley & Keverne 2005). Thus, it is possible that human limerance and companionate love  
2 are complex manifestations of a basic mammalian potential that has been further developed in  
3 pair-bonded species.

4

#### 5 *Emotions regulating dyadic cooperative relationships*

6 Companionate love and the attitude with which it is intertwined motivate altruistic  
7 behavior toward committed partners. Although pair bonds exist in a limited number of primate  
8 species, long-term affiliative relationships are more common (Silk 2007). In humans, a number  
9 of emotions play key roles in motivating behavior in affiliative and cooperative relationships.  
10 *Gratitude* follows the receipt of a welcome benefit provided by another party, motivating  
11 reciprocation (Trivers 1971), and enhancing the attitude toward the other. Gratitude thus  
12 facilitates the initiation and maintenance of cooperative relationships (McCullough et al. 2008).  
13 Gratitude is subjectively and behaviorally differentiated from a sense of indebtedness  
14 (McCullough et al. 2008). This is understandable in functional terms, as gratitude marks an  
15 increased estimation (summarized in the attendant positive attitude) of the potential long-term  
16 utility of the relationship, while indebtedness stresses the short-term burden of repayment,  
17 indexing a different type of relationship. Many primates differentiate among individuals and act  
18 in light of past interactions, exhibiting durable alliances and affiliative behaviors (van Schaik &  
19 Aureli 2000). This suggests that a gratitude-like mechanism may be both widely shared and of  
20 considerable antiquity (Bonnie & de Waal 2004).

21 Whether by mistake or due to the temptations of short-term rewards for defection,  
22 individuals can also inflict costs on their valued partners. If individuals who commit such acts  
23 perceive that they have damaged their partners' attitude toward themselves and this is

1 disadvantageous given the utility of the relationship, ameliorative action is called for. *Guilt* is  
2 the prototypical emotion elicited when harm is done to an ally (Baumeister et al. 1994, Tangney  
3 1998). Guilt motivates apologies and, importantly, reparations, compensating the partner for  
4 damages and signaling the individual's commitment to the relationship (Trivers 1971). Humans  
5 employ theory-of-mind reasoning in contemplating harm done to another; although other  
6 primates may not do likewise, this aspect of human guilt may be an extension of the basic  
7 phenomenon rather than an intrinsic feature, as many animals calibrate costs inflicted on others.  
8 We therefore expect a guilt-like mechanism to be present in many primates, consistent with the  
9 observation that conflict among allies is sometimes followed by reconciliatory behavior  
10 (reviewed in Flack & de Waal 2000). Lastly, in humans, if reparations are not possible, guilt  
11 motivates penance, infliction of self-imposed costs that signal that the individual does not pursue  
12 self-interest at the expense of partners. Consistent with the symbolic framing upon which such  
13 behavior rests, we expect penance to be absent among nonhumans.

14        Selection of prospective partners often precedes the exchange of benefits. Several  
15 emotions mark the positive evaluation of an individual as a prospective cooperative partner;  
16 paralleling pair bonding, an attitude summarizing the value of the relationship is informed by  
17 these emotions. *Affiliative liking* is a response to individuals who simultaneously possess  
18 valuable attributes and share with the evaluator sufficient commonalities as to constitute useful  
19 partners (commonalities are important because they facilitate coordination and enhance the  
20 likelihood of shared objectives; McElreath et al. 2003, Tooby & Cosmides 1996). This emotion  
21 builds *amicability*, an attitude summarizing the potential utility of the target as a cooperative  
22 partner. *Admiration* resembles affiliative liking, and similarly enhances amicability, but is  
23 elicited by individuals who possess a greater preponderance of valuable attributes relative to

1 commonalities, an asymmetry that forces the evaluator to invest relatively more in the  
2 relationship. *Pity* may be elicited by potential allies who are currently incapacitated and cannot  
3 contribute to a cooperative relationship. Pity motivates the actor to provide aid, eliciting  
4 gratitude from the incapacitated individual (Cottrell & Neuberg 2005; cf. Trivers 1971 on  
5 sympathy).

6 Alliances that yield extensive benefits over a long period must begin with a positive  
7 appraisal of the other's value as a cooperative partner, and a motivational stance that entails  
8 willingness to provide benefits. It is therefore likely that affiliative liking and amicability exist  
9 in many social animals, constituting fairly ancient traits. Because dominance hierarchies create  
10 asymmetries in power between potential cooperators, we also expect some version of admiration  
11 to be present in many animals capable of calibrating the provision of benefits in light of relative  
12 status. Primates seem to exhibit this capacity, and observers have reported obsequious affiliation  
13 directed at dominants by young subordinates (A. Pusey personal comm., Walters & Seyfarth  
14 1987). Evidence for pity is considerably weaker, as individuals seem more likely to avoid an  
15 injured or sick group member than to provide aid (e.g., Goodall 1986a; but see also Preston & de  
16 Waal 2002). It is unclear whether this is because other primates lack the requisite theory of mind  
17 capacity, cannot judge the probability of recovery and future usefulness of potential allies, or  
18 other factors.

19 *Grief* is the emotion felt at the death or loss of partners. The magnitude of grief appears  
20 proportional to the impact of the loss on one's fitness, suggesting that grief is adaptive to the  
21 extent that it motivates individuals to seek out replacement partners. Some primates do show  
22 marked physiological responses to losses of preferred companions (Engh et al. 2006), and make  
23 efforts to expand their social networks in the weeks that follow loss.

1 Not all incapable individuals evoke pity, as not all constitute potential allies worth  
2 rehabilitating (Kurzban & Leary 2001). Additionally, previously beneficial relationships can  
3 later prove unprofitable. Such individuals are excluded from future alliances and the benefits  
4 thus produced, and are often exploited. Although considerable literature explores *contempt* as an  
5 emotion, findings are inconsistent. We suggest this is because contempt is an attitude, not an  
6 emotion (Gervais in prep.) – it is a representation of the evaluation of an individual as having no  
7 value as a current or future ally. As such, it plays a central role in social event appraisal and  
8 mediates emotion systems. Without any interest in the welfare of another, any cost imposed by  
9 that party is appraised as a transgression, evoking anger. Likewise, any risk of actual or  
10 symbolic contagion stemming from association elicits disgust. A lack of interest in the welfare of  
11 another also undermines guilt, as damage done does not warrant demonstration of positive  
12 valuation; in turn, this mutes anticipatory inhibitions that prevent doing harm. The lack of  
13 motivation not to hurt another is compounded by a lack of empathy (where empathy can be  
14 viewed as a trans-emotional mechanism for assessing the needs of others), as the needs of the  
15 contemned are of no interest to the contemnor. Finally, the contemnor experiences no grief at the  
16 death of the condemned, as this event does not reduce the contemnor's fitness.

17 The absence of a prosocial attitude toward some individuals will occur in any species  
18 capable of discriminative affiliation. However, while contempt exists whenever valuation of  
19 another's welfare has not been raised above zero (what we term *minimal contempt*), contempt  
20 can also arise through active diminution of valuation. This occurs when established relationships  
21 break down (a possibility in even minimally cooperative species), or upon unfavorable social  
22 appraisal in species in which baseline conspecific valuation is greater than zero. A positive  
23 default valuation should scale with the possibility of cooperation. For example, we expect an

1 elevated baseline in male chimpanzees owing to the importance of alliances and intergroup  
2 defense (Watts 2006). Note that evidence of prosocial behavior in nonhuman primates (e.g., de  
3 Waal et al. 2008, Lakshminarayanan & Santos 2008; but see also Vonk et al. 2008) does not  
4 speak to the question of baseline valuations, as subjects in such experiments have histories of  
5 prior interaction during which valuations may have been raised. In contrast, evidence that  
6 captive chimpanzees spontaneously help unfamiliar humans (Warneken et al. 2007) provides  
7 indirect evidence of a positive baseline valuation, at least in this particular interspecific context.  
8 Positive default valuation likely reaches its extreme in humans, owing to a history of intergroup  
9 competition and dependence on transmitted culture and cooperation (Brewer & Campbell 1976,  
10 Richerson & Boyd 2005). In humans, welfare valuation can be readily downregulated in  
11 response to derived cues of low value such as cultural difference (see McElreath et al. 2003) or  
12 nonconformity (see Rozin et al. 1999). The combination of the readiness with which this occurs,  
13 the subjectively negative affect that marks such attitude change, and the role of contempt in  
14 potentiating anger and disgust, likely explains why contempt is often miscategorized as an  
15 emotion.

16

### 17 *Linked fate and vicarious emotions*

18 Lickel et al. (2005) use the term *vicarious* to describe emotions elicited when events that  
19 befall another are treated as if they befell the self (see also Rydell et al. 2008). While possibly  
20 phylogenetically linked to emotional contagion, elicitation of vicarious emotions hinges on  
21 knowledge of the involvement of others in events, rather than exposure to others' emotion  
22 displays. Lickel et al. identify two axes, interdependence and shared identity, that determine  
23 vicarious elicitation. We suggest that Lickel et al.'s criteria for interdependence -- interaction,

1 joint goals, and shared norms -- are constituents of human cooperation. Cooperation links the  
2 fates of the participants: the greater the investment in, and payoffs from, cooperative ventures,  
3 the more that events that affect one member of the venture also impact other members. Hence,  
4 calibrated for degree of cooperative interdependence, it is adaptive to respond to such events  
5 vicariously. This process is likely undergirded by attitudes that capture the degree of alignment  
6 of interests entailed in cooperation; in turn, these attitudes generate appraisals of events befalling  
7 others that parallel appraisals of events befalling the self.

8         Reduced by the coefficient of relatedness, it is also adaptive to react to events affecting  
9 kin as if they affected oneself, since one's own fitness is at least partially aligned with one's kin.  
10 Kinship is separate from cooperation, and hence from action interdependence in Lickel et al.'s  
11 (2005) sense – while kin-recognition mechanisms may rely on propinquity and interaction as  
12 cues of relatedness, kin should experience vicarious emotions even when the level of social  
13 interaction and degree of shared goals and norms is low. While some form of cooperation is  
14 found in many mammals, nepotistic behavior predates this, suggesting that kin-based vicarious  
15 reactions were co-opted long ago for use in the cooperative domain. We expect that any primate  
16 emotion experienced in an individual fashion will also be experienced in a vicarious fashion  
17 given the proper elicitors, just as we expect to find attitudinal proxies of fitness alignment  
18 resulting from either cooperative interdependence or kinship.

19         Shared identity, Lickel et al.'s (2005) second axis whereby vicarious emotions are  
20 elicited, can also be understood as a manifestation of an underlying process whereby the fates of  
21 individuals become linked. Humans attribute a shared essence to members of groups, such as  
22 ethnies, that exhibit distinctive cultural markers; this essence constitutes grounds for inductive  
23 reasoning regarding the actions and attributes of group members, a process thought to occur due

1 to the utility of such markers in predicting behavior (Gil-White 2001). Because essentializing  
2 supports inductive generalization, the fates of members of an essentialized group can become  
3 intertwined, as actions by one group member can be taken as indicative of the character of all  
4 group members, influencing outsiders' attitudes. Essentializing and inductive generalization are  
5 likely matters of degree – some categories of individuals are seen as sharing a great deal of  
6 essence, while others less so. Like kinship and degree of cooperation, social identity is thus a  
7 variable property that influences vicarious emotion elicitation.

8         Noting that essentialism is adaptive in interacting with animals, Gil-White (2001)  
9 suggests that essentialist social cognition derives from this ancestral trait. We concur, adding  
10 that the coexistence of multiple hominid species during human evolution may have facilitated a  
11 process of co-optation wherein the phenotypic markers used in essentialist reasoning were  
12 expanded to include culturally-transmitted traits, as interspecific cultural diffusion might have  
13 blurred the line between biological and cultural phenotypes. Given both the utility of inductive  
14 generalizations and evidence of primate anti-predator strategies that involve a degree of learning  
15 and are directed at specific species or genera (e.g., Seyfarth et al. 1980), it is plausible that the  
16 ancestral interspecific form of essentialist reasoning is widely shared. In contrast, the use of  
17 symbols to mark cultural affiliation and reinforce cooperation, the related importance of  
18 essentialist reasoning, and the resulting role of shared identity as an elicitor of vicarious  
19 emotions are all uniquely human.

20

### 21 *Norm-based emotions*

22         Humans differ from other primates in the extent and importance of cooperation, a feature  
23 tightly linked to the degree to which norms regulate behavior, as socially-transmitted standards

1 define goals, actions, and social relations that promote pro-sociality and enhance coordination  
2 (McElreath et al. 2003). Both our species' exploitation of cooperation and our reliance on norms  
3 are likely undergirded by a set of uniquely human emotion systems.

4         Paralleling the extension of eliciting conditions through appraisal modification that  
5 occurs in vicarious emotion systems, in *moral outrage*, *moral disgust*, and *moral approbation*,  
6 events that do not involve the actor elicit emotions as if they did: moral outrage and moral  
7 disgust are, respectively, anger and disgust elicited by others' norm-violating actions; moral  
8 approbation is a gratitude-like emotion elicited by others' exemplary performance of normative  
9 ideals (Fessler & Haley 2003). Moral outrage motivates inflicting costs on the norm violator as  
10 if in retribution; moral disgust motivates avoiding the norm violator as if in contamination  
11 avoidance (Gutierrez & Giner-Sorolla 2007); and moral approbation motivates providing a  
12 benefit to the norm-embodier as if in response to a benefit received. As in vicarious emotions, in  
13 each case, the emotion modifies an attendant attitude toward the target despite no direct  
14 interaction. However, whereas in vicarious emotions a connection to the self is made via another  
15 person, in these emotions, the connection is solely via the norm at issue.

16         Socially-transmitted standards for behavior play a much more restricted role in the lives  
17 of nonhuman primates, and evidence for norm enforcement by disinterested parties is very  
18 limited (see Flack et al. 2005). In contrast, although the proportions in which they occur likely  
19 differ across cultures, moral outrage, moral disgust, and moral approbation are all readily  
20 observable in any human society (for example, see Henrich et al. 2006).

21         There are three basic kinds of explanations for the co-evolution of cultural norms and  
22 norm-based emotions. Boyd and Richerson (2002) contend that punishment can stabilize any  
23 behavior, and cultural group selection favors the predominance of group-beneficial norms (see

1 Silk & Boyd this volume). Norm violators are punished, as are those who fail to punish norm-  
2 violators, and this generates selective pressure favoring the propensity to treat norms as  
3 extensions of the self, as this reduces the frequency with which the actor is punished. A second  
4 view holds that norm-based emotions are a product of natural selection acting directly on  
5 individuals (e.g., Haley & Fessler 2005, Kurzban et al. 2007). Here, actors compete in a  
6 marketplace of prospective allies; because conformists are predictable, adherence to cultural  
7 norms increases an actor's attractiveness in this regard. Actors can advertise their adherence to  
8 cultural norms by punishing norm violators and rewarding those who exemplify norms, with the  
9 reputational benefits thus gained outweighing the costs of these actions. The fitness advantages  
10 of inclusion in cooperative ventures thus favor emotion systems in which norms are treated as  
11 extensions of the self. Finally, a third view holds that unique features of human sociality, such  
12 as intergroup conflict and reproductive leveling, provided the necessary conditions for biological  
13 group selection in humans. Group selection favored the evolution of prosocial motivations,  
14 including norm-based emotions that motivate third-party punishment and rewarding behavior  
15 (e.g., Gintis et al. 2003, Bowles 2006).

16         Although at present it is difficult to determine which of the above accounts accurately  
17 describes hominid evolution, or whether some additional account is needed, it is nonetheless  
18 clear that humans possess the motivational architecture upon which these perspectives converge.  
19 The aversive emotion *shame* is elicited by the appraisal that others are aware of one's failure to  
20 conform to important norms, while the rewarding emotion *pride* is elicited by the appraisal that  
21 others are aware of one's success in exemplifying important norms (reviewed in Fessler 2007).  
22 Even holding aside the limited role of norms among nonhuman primates, we expect shame and  
23 pride to be uniquely human, as they are contingent on sophisticated theory-of-mind reasoning.

1 Shame and pride exemplify the evolutionary process of co-optation and modification:  
2 despite employing the same display behaviors, qualia, and action tendencies as proto-shame and  
3 proto-pride (see above), the key eliciting conditions differ, as proto-shame and proto-pride focus  
4 exclusively on relative position in a social hierarchy, do not rely on norms as evaluative criteria  
5 for behavior, and do not involve theory-of-mind reasoning (Fessler 2007). The action tendencies  
6 associated with shame similarly reveal its kludge-like structure. Although parties offended by  
7 norm violations are best mollified by apologies and public commitments to future conformity,  
8 shame paradoxically interferes with these behaviors by motivating flight and hiding, tactics more  
9 appropriate to dealing with dominants than to placating judgmental community members. Proto-  
10 shame and proto-pride, ancestral pan-primate rank-related emotions, were modified in the  
11 hominid line. With the rise in importance of norms, coercive force (dominance) was largely  
12 replaced by freely-granted deference (prestige) as a determinant of social position (Henrich &  
13 Gil-White 2001). Apparently, because prestige is contingent on the opinions of others, existing  
14 emotions that motivated rank-striving behavior were modified by selection so as to include an  
15 assessment of others' evaluations of the actor. Whether to avoid punishment, enhance inclusion  
16 in cooperative ventures, or generate non-contingent group-beneficial behavior, these emotions  
17 were then further refashioned, shifting the focus away from rank, and toward norm adherence.  
18 Contemporary humans exhibit all three forms of these emotions – the ancestral forms that focus  
19 on dominance-based rank, the intermediate derived forms that focus on prestige, and the final  
20 derived forms that focus on norm adherence.

21 All three forms of shame and pride can be experienced vicariously. As we would expect  
22 to also be true among primates that engage in coalitional aggression, vicarious proto-pride or  
23 proto-shame should be experienced whenever an ally enjoys victory or suffers defeat relative to a

1 rival. Vicarious prestige-based pride and shame, though limited to humans, should exhibit a  
2 similar pattern. Finally, whenever a person linked to the actor via a shared social identity  
3 succeeds or fails with regard to normative standards, to the extent that others will engage in  
4 inductive generalizing, those successes or failures will influence how others treat the actor, hence  
5 the actor should experience vicarious pride or shame (see Lickel et al. 2005). The primary  
6 exception to the latter pattern occurs when identity sharing is incomplete, in which case an actor  
7 can distance herself from a norm violator in order to manage third parties' assessments; in this  
8 case, moral outrage, rather than vicarious shame, may be elicited (cf. Haley 2003).

9 Shame and pride illustrate the extensive re-working that can be achieved through  
10 processes of co-optation and modification. However, as the vicarious versions of these emotions  
11 demonstrate, substantial functional changes can also occur merely by extending an emotion's  
12 eliciting conditions. We propose that an emotion that we term *normative guilt* is elicited by  
13 norm violations absent a harmed relationship partner – within the worldviews in which they are  
14 defined, many sins do not harm other people, yet the sinner experiences guilt nonetheless. This  
15 extension is made possible by our elaborately developed ability to manipulate representations of  
16 social others. In some manifestations of normative guilt, the represented partner is a culturally-  
17 constructed nonexistent agent (a deity, ancestor, etc.; cf. Darwin 1909:115-116 on remorse); in  
18 others, the imagined partner is a representation of the actor's kin network or cooperative group;  
19 and, in the most abstract manifestation, the (only dimly imagined) partner is a representation of  
20 society as a whole. In each case, violating a norm leads actors to undertake reparations or  
21 penance as if, by doing so, they mitigated the harm done, or signaled their future reliability.  
22 Normative guilt thus illustrates one of the most profound disjunctions between ourselves and our  
23 nonhuman primate relatives, namely the nature of the internal representations that constitute the

1 informational environment in which emotions operate. Despite our common origins, the  
2 complexity of humans' internal representations, and the fundamentally cultural nature of those  
3 representations, create a gap between our emotions and those of other primates, a gap that bears  
4 minding indeed.

5

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