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Mind the Gap

Tracing the Origins of Human Universals

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Chapter 12

From Whence the Captains of Our Lives: Ultimate and Phylogenetic Perspectives on Emotions in Humans and Other Primates

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Let's not forget that the little emotions are the great captains of our lives and we obey them without realizing it.

Vincent van Gogh

Abstract We outline an evolutionary approach to emotions intended to spur further research on the subject in humans and nonhumans alike. Combining adaptationist, comparative, and phylogenetic analyses, we seek to illuminate the functions that emotions fulfill, the reasons why they take the forms that they do, and the extent to which they are shared across species. Using similar logic, we distinguish between emotions and attitudes, cognitive representations of other actors that are both informed by, and potentiate, emotions. Employing select emotions as illustrations, we discuss a taxonomy of emotions. We begin with emotions that address adaptive challenges common across animals, and which require minimal cognitive capacities, features that make it likely that they are widely shared across species. Next, we consider emotions involved in elementary sociality, a category further elaborated in emotions playing a role in parenting and pair-bonding. In light of the importance of dyadic cooperative relationships in primate societies, we describe a set of emotions undergirding such relationships that we expect to be shared by human and nonhuman primates. To a more limited degree, we expect pan-primate similarities with regard to vicarious emotions, those wherein the individual experiencing the emotion is affected only indirectly by the eliciting event. The greater range and complexity of human social relationships, including the human

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propensity to essentialize cultural groups, extend the class of vicarious emotions beyond anything evident in nonhumans. Finally, underscoring the importance of culture in human evolution, we examine moral emotions elicited by norm violations, a pattern unique to humans.

12.1 Introduction

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

Darwin's ([1872] 1955) pioneering work on emotional expressions employed a comparative perspective in order to: (1) substantiate the utility of general explanatory principles by application to all species; (2) demonstrate human descent from nonhuman ancestors; (3) evaluate the innateness of human expressions by showing similarity to other species; and (4) explain some human characters as vestigial traces of ancestral forms. The first two goals have been achieved. Ekman and other modern students of expressions advanced the third goal, and many human facial expressions are now considered pan-cultural. This leaves Darwin's fourth goal. While extreme vestigialism has rightly fallen from favor, many emotions do exhibit evidence of deep histories of successive modification. We will present several examples of emotional systems apparently evolved for one purpose that were subsequently modified to serve a different purpose. In some cases, the properties of an ancestral emotional system appear to have "preadapted" it (Gould and Vrba 1982) to the task demands of a newly arisen adaptive problem (e.g., Rozin et al. 1997; Fessler 2004; Gervais and Wilson 2005). In a number of cases, an extant emotional action tendency has been put to novel use by modifying the eliciting conditions (cf. Tooby and Cosmides 1989; Rozin 1996; Keltner and Anderson 2000). Yet, even with subsequent secondary selection, this process does not necessarily erase the legacy of past selection; substantial

residues of former function sometimes remain, and it is only with reference to ancestral traits that such features become intelligible. Applying this consideration when reverse engineering a trait (“reverse tinkering”; Andrews et al. 2002; Gangestad and Simpson 2007) illuminates the kludge-like structure of emotions that have served multiple functions over evolutionary time.

As the above discussion suggests, phylogenetic and comparative approaches both constrain and inform adaptationist hypotheses (see Maestriperi 2003b; Gangestad and Simpson 2007; Gosling and Graybeal 2007). In addition to controlling for nonindependence of trait correlations in comparative research (Nunn and Barton 2001), “tree thinking” helps to specify the time frame within which the target properties of a trait were selected, while suggesting an ancestral state from which the trait was derived. This refines the task of reverse engineering by rephrasing the ultimate question as: Why did this form emerge given the form from which it emerged? A phylogenetically informed comparative approach can help to parse a trait into aspects that were impacted by selection pressures operating during particular periods in the lineage. This approach highlights the process of secondary selection through which (*contra* Gould and Vrba 1982; Gould 1991) an extant system is not merely exapted (put to new use), but is further subjected to specializing selection for that new function. This process, which we term cooptation, has rarely been foregrounded in the study of the mind.

Just as comparative and phylogenetic approaches offer benefits to students of human emotions, so too can adaptationist perspectives enhance the study of nonhuman primate emotions. Because emotion is difficult to quantify, most primatologists have sidestepped the study of emotion, although this is beginning to change (e.g., de Waal 1996; Aureli and Schaffner 2002; Maestriperi 2003a). The conjunction of adaptationist and phylogenetic analyses indicates where one can expect to find homologues of human emotions. It should be possible to predict the taxonomic distribution of emotion traits through a consideration of (1) the phylogenetic relationships among species, (2) the selection pressures thought to produce and maintain a given trait, and (3) the cognitive capacities that constitute prerequisites for the trait. This generates a taxonomy of emotions, ranging from ancient emotions expected to be present in all vertebrates, to conserved pan-primate emotions, to derived emotions expected to be unique to our species. Because explorations of primate emotions are in their infancy, we cannot conduct rigorous tests of our phylogenetic hypotheses. However, there is reason for optimism, as investigators are beginning to employ new methods to probe primate motives (e.g., Silk et al. 2005; Warneken et al. 2007; de Waal 2008; Lakshminarayanan and Santos 2008, Silk and Boyd, this volume), and obstacles to the study of primate emotions are not insurmountable. Below, we sketch a set of phylogenetically informed adaptationist proposals intended to provide starting points for future studies of emotions in both humans and nonhuman primates. This is not an exhaustive description of these species’ emotional repertoires. Rather, our goal is to demonstrate the form that we think such descriptions should take, and to spark further discussion.

A note on terminology: because cultures differentially emphasize or ignore facets of the pan-human spectrum of emotions, any language’s emotion lexicon is

but a crude gloss for the underlying phenomena. Accordingly, the emotion terms used here should be viewed as heuristic labels for adaptations that are not necessarily isomorphic with Anglo-American folk psychology.

12.2 Ancient, Relatively Conserved Emotions

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

Avoiding imminent threats to life and limb is a fundamental determinant of fitness; *fear* marks the presence of such threats, motivating flight as a principal behavioral outcome, with fighting as a secondary outcome when the threat is animate and escape is appraised as impossible. The neural underpinnings of fear appear to be highly conserved, certainly among mammals, and arguably among vertebrates (Panksepp 1998; Braithwaite and Boulcott 2007; Öhman et al. 2007). Fear expressions closely paralleling those present in humans are recognizable in many primates (Parr et al. 2007). This uniformity potentially reflects selection having conserved an adaptive form. Human experimental results support Darwin's ([1872] 1955) supposition that many facial expressions are functional beyond their signal value, as the fear expression enhances perceptual acuity and reaction times to threat (Susskind et al. 2008).

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

that the set of cues that elicits disgust includes representational contamination (Curtis and Biran 2001; Fessler and Haley 2006, Kelly in prep).

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

Ultimately, reproduction, not survival, determines fitness, so we expect all sexually reproducing species to be equipped with an emotion akin to *lust*, the principal motivator of sexual behavior. Although the frequency, form, and elicitors for sexual behavior vary across mammals, the ubiquity of goal-oriented behavior leading to copulation is consistent with such an emotion being widespread. There are several parallels in the task demands associated with mate-seeking and foraging (appetitive cycles; resource-seeking behavior; discrimination among resource options), and, in mammals, there is overlap between the neurophysiological systems regulating proceptive sexual behavior and those regulating ingestive behavior (reviewed in Fessler 2003). This suggests that systems regulating ingestion may have constituted building blocks from which systems regulating sexual reproduction were subsequently constructed. Disgust, antithetical to both hunger and lust, plays a central role in human inbreeding avoidance (Lieberman et al. 2003, 2007; Fessler and Navarrete 2004); likewise, women's sexual disgust sensitivity increases around ovulation, possibly functioning to reduce contact with suboptimal reproductive partners at peak fertility (Fessler and Navarrete 2003). Most primates exhibit marked inbreeding avoidance (Paul and Kuester 2004; Muniz et al. 2006), and it is possible that a similar emotional system is involved. Indeed, we suggest that both the ingestion regulation and sexual regulation facets of disgust are pan-mammalian.

12.3 Emotions Associated with Elementary Sociality

As illustrated by disgust at the prospect of sex with individuals identified as close kin, emotion elicitation is contingent on appraisal, the process of construing the nature and meaning of a situation (Scherer 1999). Sociality introduces a complex set of adaptive challenges because there are many ways in which conspecifics can affect fitness, hence many distinct appraisals and consequent emotional responses should attend social interaction. At the most elementary level, because competition for resources is a key determinant of fitness, we expect distinct emotions, with

corresponding appraisals, to address competition. From the perspective of a resource holder, an attempt to displace one from a resource should be appraised as a transgression, the infliction of an unwelcome (i.e., fitness-reducing) cost, or threat thereof. In humans, transgressions elicit *anger*, motivating aggressive retaliation when feasible. While varying in degree across species, many social animals exhibit aggressive responses to actions that investigators plausibly interpret as transgressions. Hence, an elementary anger-like emotion and its eliciting appraisal are probably both ancient and widely shared. This conclusion is supported by the extensive conservation across mammals of the neurophysiological systems underlying aggression (e.g., Dierick and Greenspan 2007).

In humans (particularly young men), anger often motivates disproportionate responses to transgression. Disproportionate responses may be advantageous because they serve as a signal that transgressing is dangerous, generating reputational benefits that deter further transgressions (reviewed in Fessler *in press*). Reputation-based strategies such as this require repeated interactions, the ability to identify and recall individual actors, and the capacity to acquire information as a third-party observer. All of these features are likely present among many social primates (Cheney and Seyfarth 2005), and age-related patterns of impulsive aggression may parallel those found in humans (cf. Fairbanks et al. 2004). Thus, it is likely that the central features of the anger adaptation are a shared ancestral trait among primates.

While the question of applying the appropriate appraisal to a given event is never trivial, this task is particularly complex in the social domain because the range of fitness consequences of social interactions is so large. This complexity is multiplied by the fact that, due to repeat interactions, appraisals of current social actions hinge on past events. We suggest that the substantial informational demands of applying the appropriate appraisal to social events are managed, in part, through *attitudes*, durable, hierarchically organized representations of previously appraised traits and relational outcomes that potentiate differential emotional readiness toward others. Attitudes and emotions are reciprocally related, as attitudes are updated by emotions, and subsequently help to regulate emotions by shaping appraisals. Responsive to the fitness-relevant traits and behaviors of other individuals, attitudes are continuously adjusted over time, thus constituting summary representations that proxy the future fitness implications of all past interactions. Attitudes allow individuals to represent their current relations to others without the need for explicit bookkeeping or recall of all encounters. Via their role in appraisals, these representations adaptively regulate current behavior. Attitudes can thus be conceptualized as “internal regulatory variables,” in the sense that they functionally translate past appraisals into current behavior regulation (see Tooby and Cosmides 2008). This proposal obviates the need to posit complex cognitive operations in some relational domains (the potential complexities of which are discussed in Cords 1997; Silk 2003; see also Aureli and Schaffner 2002; Aureli and Whiten 2003). Likewise, congruent with extensive social psychological findings on implicit attitudes (Greenwald and Banaji 1995), our position does not require positing problematic conscious processes.

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

Competition and hostile intent are also central to *jealousy*. Deriving from a proprietary attitude toward a relationship partner and a corresponding appraisal of potential interlopers as transgressors, this emotion motivates attempts to maintain exclusivity by warding off rivals and restricting the partner's options (reviewed in Smith and Kim 2007). While sociality does not necessitate the formation of discrete relationships, well-differentiated relationships exist in many primate species (see Silk 2007). If such relationships are widespread, jealousy may be widely shared. Elicitors for jealousy will depend on the nature of the threats posed to a relationship. The utility of biparental care in humans leads to sex-specific adaptive challenges, namely the possibility of female extra-pair copulation (leading to misallocation of male parental investment) and male abandonment (leading to reduced female access to resources). A growing literature investigates the corresponding sex-specific relative importance of sexual and emotional infidelity as elicitors of mating jealousy (reviewed in Haselton and Ketelaar 2006). While extensive biparental care is rare among primates, we expect the same logic of an actor-centered appraisal of different threats to a relationship to apply across species.

In most social animals, conflicts establish and maintain dominance rank, which then determines priority of access to resources. As Darwin ([1872] 1955) suggested, ethology provides clues to both the phylogeny and ultimate function of emotions, and this is particularly evident in the case of dominance interactions. Displays often precede, and sometimes obviate, conflict, and threat displays that reduce the costs of conflict are a pervasive aspect of social behavior in primate groups. In most species, body size is a key determinant of success in combat, and, correspondingly, threat displays generally involve an exaggeration of body size. Direct attention (staring) is often a feature of such displays (reviewed in Fessler 2004). In some cases, it is beneficial to acknowledge subordinate status, and appeasement displays are counterpoints to threat displays. Appeasement displays generally involve an attempt to minimize apparent body size and direct attention away from the aggressor. In humans, threat displays are associated with an emotion we term *proto-pride*, and appeasement displays are associated with *proto-shame* (see Fessler 2007;

see also Tracy and Matsumoto 2008). Proto-pride is elicited when an actor appraises herself as occupying a superior position in a social hierarchy and interacting with a subordinate in a context in which the disparity in status is relevant; conversely, when the complementary appraisal occurs, the subordinate feels proto-shame. In each case, the emotion enhances a corresponding attitude that represents in enduring fashion the disparities in status. For the dominant, this attitude includes a sense of entitlement relative to the other, while the converse is true for the subordinate. In keeping with their opposite hedonic valences, this pair of emotions motivates striving for power and social position (Fessler 2007). Given the clear homologies with display behaviors in other primates, and the ubiquity of the relevant adaptive problem across social animals, it is likely that proto-pride and proto-shame are pan-primate; indeed, the core features of these emotions and related appraisals and attitudes may be shared by all mammals, and possibly by most vertebrates.

12.4 Emotions Associated with Parenting and Pair-Bonding

Parental behavior is a defining feature of mammals, although the patterns and extent of parental care vary greatly across species. Parental behavior must be underlain by a discrete motivational system on the part of the parent, complemented by a corresponding system in the offspring (Maestriperi 2003a). We expect these motivations to be modulated by complementary attitudes, what we term *parental attachment* and *offspring attachment*, that represent the fitness value of offspring and parent to one another. These attitudes shape appraisals of actions, determining the circumstances that elicit the corresponding emotions of *parental love* and *offspring love*. For example, positive parental attachment leads a mother to appraise her infant's midnight rooting as affiliation, eliciting parental love, rather than as a transgression that would elicit anger. Offspring develop positive attachment as a result of the experience of receiving succor. In contrast, because offspring impose costs on parents without immediate compensation, the building of positive parental attachment is achieved in part through the pump-priming effects of an emotion (*natal attraction*) that makes interaction with infants intrinsically rewarding, a phenomenon well-documented in primates (e.g., Silk 1999). It appears that, in humans, natal attraction transforms into parental love in part as a result of positive infant responses to parental overtures. Given the general primate trend of reductions in the importance of olfactory cues for parent-offspring bonding, and increases in the importance of behavioral cues (Broad et al. 2006), similar patterns may obtain across primates.

Two different systems appear to underlie human mate selection, courtship, and long-term pair-bonding. *Limerance* (Tennov 1979) is an emotion characterized by intrusive ideation concerning a prospective mate, attention to indications of reciprocation, and a motivation to be near and make a positive impression on the target individual. Both E. Pillsworth and R. Kurzban (pers. comm.) propose

that the intrusive and obsessive nature of limerance are explicable in terms of the need to signal commitment to the target party, given the risk of defection. The most persuasive signals are costly, taking the form of resource provisioning, time allocation, and the public spurning of alternate potential mates. Once a stable mateship has formed, the benefits of signaling are reduced: once both parties have a concrete interest (e.g., offspring) in extended cooperation, it is adaptive to value the other party's welfare, and provide benefits noncontingently. Although investigators (e.g., Hatfield 1988) claim that an emotion, *companionate love*, replaces limerance in pair-bonded couples, much of the phenomenon thus labeled is an attitude rather than an emotion—the actual emotion is only present during punctuated events in which displays of affection reaffirm mutual valuation, reinforcing this attitude. Pair-bonding and biparental investment occur in a variety of mammals, and there is some commonality in the neurophysiological systems that underlie these behaviors (Curley and Keverne 2005; Broad et al. 2006). Thus, it is possible that human limerance and companionate love are complex manifestations of a basic mammalian potential that has been further developed in pair-bonded species.

12.5 Emotions Regulating Dyadic Cooperative Relationships

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

Whether by mistake or due to the temptations of short-term rewards for defection, individuals can also inflict costs on their valued partners. If individuals who commit such acts perceive that they have damaged their partners' attitude toward themselves and this is disadvantageous given the utility of the relationship, ameliorative action is called for. *Guilt* is the prototypical emotion elicited when harm is done to an ally (Baumeister et al. 1994; Tangney 1998). Guilt motivates apologies

and, importantly, reparations, compensating the partner for damages and signaling the individual's commitment to the relationship (Trivers 1971). Humans employ theory-of-mind reasoning in contemplating harm done to another; although other primates may not do likewise, this aspect of human guilt may be an extension of the basic phenomenon rather than an intrinsic feature, as many animals appear to calibrate costs inflicted on others. We therefore expect a guilt-like mechanism to be present in many primates, consistent with the observation that conflict among allies is sometimes followed by reconciliatory behavior (reviewed in Flack and de Waal 2000). Lastly, in humans, if reparations are not possible, guilt motivates penance, infliction of self-imposed costs that signal that the individual does not pursue self-interest at the expense of partners. Consistent with the symbolic framing upon which such behavior rests, we expect penance to be absent among nonhumans.

Selection of prospective partners often precedes the exchange of benefits. Several emotions mark the positive evaluation of an individual as a prospective cooperative partner; paralleling pair bonding, an attitude summarizing the value of the relationship is informed by these emotions. *Affiliative liking* is a response to individuals who simultaneously possess valuable attributes and share with the evaluator sufficient commonalities as to constitute useful partners (commonalities are important because they facilitate coordination and enhance the likelihood of shared objectives; Tooby and Cosmides 1996; McElreath et al. 2003). This emotion builds *amicability*, an attitude summarizing the potential utility of the target as a cooperative partner. *Admiration* resembles affiliative liking, and similarly enhances amicability, but is elicited by individuals who possess a greater preponderance of valuable attributes relative to commonalities, an asymmetry that forces the evaluator to invest relatively more in the relationship. *Pity* may be elicited by potential allies who are currently incapacitated and cannot contribute to a cooperative relationship. Pity motivates the actor to provide aid, eliciting gratitude from the incapacitated individual (Cottrell and Neuberg 2005; cf. Trivers 1971 on sympathy).

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

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

Not all incapable individuals evoke pity, as not all constitute potential allies worth rehabilitating (Kurzban and Leary 2001). Additionally, previously beneficial relationships can later prove unprofitable. Such individuals are excluded from future alliances and the benefits thus produced, and are often exploited. Although a considerable literature explores *contempt* as an emotion, findings are inconsistent. We suggest this is because contempt is an attitude, not an emotion (Gervais 2009) it is a representation of the evaluation of an individual as having no value as a current or future ally. As such, it plays a central role in social event appraisal and mediates emotion systems. Without any interest in the welfare of another, any cost imposed by that party is appraised as a transgression, evoking anger. Likewise, any risk of actual or symbolic contagion stemming from association elicits disgust. A lack of interest in the welfare of another also undermines guilt, as damage done does not warrant demonstration of positive valuation; in turn, this mutes anticipatory inhibitions that prevent doing harm. The lack of motivation not to hurt another is compounded by a lack of empathy (where empathy can be viewed as a trans-emotional mechanism for assessing the needs of others), as the needs of the condemned are of no interest to the contemnor. Finally, the contemnor experiences no grief at the death of the condemned, as this event does not reduce the contemnor's fitness.

The absence of a prosocial attitude toward some individuals will occur in any species capable of discriminative affiliation. However, while contempt exists whenever valuation of another's welfare has not been raised above zero (what we term *minimal contempt*), contempt can also arise through active diminution of valuation. This occurs when established relationships break down (a possibility in even minimally cooperative species), or upon unfavorable social appraisal in species in which baseline conspecific valuation is greater than zero. A positive default valuation should scale with the possibility of cooperation. For example, we expect an elevated baseline in male chimpanzees owing to the importance of alliances and intergroup defense (Watts 2006). Note that evidence of prosocial behavior in non-human primates (e.g., de Waal 2008; Lakshminarayanan and Santos 2008; but see also Vonk et al. 2008) does not speak to the question of baseline valuations, as subjects in such experiments have histories of prior interaction during which valuations may have been raised. In contrast, evidence that captive chimpanzees spontaneously help unfamiliar humans (Warneken et al. 2007) provides indirect evidence of a positive baseline valuation, at least in this particular interspecific context. Positive default valuation likely reaches its extreme in humans, owing to a history of intergroup competition and dependence on transmitted culture and cooperation (Brewer and Campbell 1976; Richerson and Boyd 2005). In humans, welfare valuation can be readily downregulated in

response to derived cues of low value such as cultural difference (see McElreath et al. 2003) or nonconformity (see Rozin et al. 1999). The combination of the readiness with which this occurs, the subjectively negative affect that marks such attitude change, and the role of contempt in potentiating anger and disgust likely explains why contempt is often miscategorized as an emotion.

12.6 Linked Fate and Vicarious Emotions

Lickel et al. (2005) use the term *vicarious* to describe emotions elicited when events that befall another are treated as if they befell the self (see also Rydell et al. 2008). While possibly phylogenetically linked to emotional contagion, elicitation of vicarious emotions hinges on knowledge of the involvement of others in events, rather than exposure to others' emotion displays. Lickel et al. identify two axes, interdependence and shared identity, that determine vicarious elicitation. We suggest that Lickel et al.'s criteria for interdependence—interaction, joint goals, and shared norms—are constituents of human cooperation. Cooperation links the fates of the participants: the greater the investment in, and payoffs from, cooperative ventures, the more the events that affect one member of the venture also impact other members. Hence, calibrated for degree of cooperative interdependence, it is adaptive to respond to such events vicariously. This process is likely undergirded by attitudes that capture the degree of alignment of interests entailed in cooperation; in turn, these attitudes generate appraisals of events befalling others that parallel appraisals of events befalling the self.

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

Shared identity, Lickel et al.'s (2005) second axis whereby vicarious emotions are elicited, can also be understood as a manifestation of an underlying process whereby the fates of individuals become linked. Humans attribute a shared essence to members of groups, such as ethnies, that exhibit distinctive cultural markers. This essence constitutes grounds for inductive reasoning regarding the actions and attributes of group members, a process thought to occur due to the utility of such markers in predicting behavior (Gil-White 2001). Because essentializing supports

inductive generalization, the fates of members of an essentialized group can become intertwined, as actions by one group member can be taken as indicative of the character of all group members, influencing outsiders' attitudes. Essentializing and inductive generalization are likely matters of degree—some categories of individuals are seen as sharing a great deal of essence, while others less so. Like kinship and degree of cooperation, social identity is thus a variable property that influences vicarious emotion elicitation.

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

12.7 Norm-Based Emotions

Humans differ from other primates in the extent and importance of cooperation, a feature tightly linked to the degree to which norms regulate behavior, as socially transmitted standards define goals, actions, and social relations that promote prosociality and enhance coordination (McElreath et al. 2003). Both our species' exploitation of cooperation and our reliance on norms are likely undergirded by a set of uniquely human emotion systems.

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

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

There are three basic kinds of explanations for the coevolution of cultural norms and norm based emotions. Boyd and Richerson (2002) contend that punishment can stabilize any behavior, and cultural group selection favors the predominance of group-beneficial norms (see Silk and Boyd, this volume). Norm violators are punished, as are those who fail to punish norm-violators, and this generates selective pressure favoring the propensity to treat norms as extensions of the self, as this reduces the frequency with which the actor is punished. A second view holds that norm-based emotions are a product of natural selection acting directly on individuals (e.g., Haley and Fessler 2005; Kurzban et al. 2007). Here, actors compete in a marketplace of prospective allies; because conformists are predictable, adherence to cultural norms increases an actor's attractiveness in this regard. Actors can advertise their adherence to cultural norms by punishing norm violators and rewarding those who exemplify norms, with the reputational benefits thus gained outweighing the costs of these actions. The fitness advantages of inclusion in cooperative ventures thus favor emotion systems in which norms are treated as extensions of the self. Finally, a third view holds that unique features of human sociality, such as intergroup conflict and reproductive leveling, provided the necessary conditions for biological group selection in humans. Group selection favored the evolution of prosocial motivations, including norm-based emotions that motivate third-party punishing and rewarding behaviors (e.g., Gintis et al. 2003; Bowles 2006).

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

Shame and pride exemplify the evolutionary process of co-optation and modification: despite employing the same display behaviors, qualia, and action tendencies as proto-shame and proto-pride (see above), the key eliciting conditions differ, as proto-shame and proto-pride focus exclusively on relative position in a social hierarchy, do not rely on norms as evaluative criteria for behavior, and do not involve theory-of-mind reasoning (Fessler 2007). The action tendencies associated with shame similarly reveal its kludge-like structure. Although parties offended by norm violations are best mollified by apologies and public commitments to future

conformity, shame paradoxically interferes with these behaviors by motivating flight and hiding, tactics more appropriate to dealing with dominants than to placating judgmental community members. Proto-shame and proto-pride, ancestral pan-primate rank-related emotions, were modified in the hominid line. With the rise in importance of norms, coercive force (dominance) was largely replaced by freely-granted deference (prestige) as a determinant of social position (Henrich and Gil-White 2001). Apparently, because prestige is contingent on the opinions of others, existing emotions that motivated rank-striving behavior were modified by selection so as to include an assessment of others' evaluations of the actor. Whether to avoid punishment, enhance inclusion in cooperative ventures, or generate non-contingent group-beneficial behavior, these emotions were then further refashioned, shifting the focus away from rank, and toward norm adherence. Contemporary humans exhibit all three forms of these emotions – the ancestral forms that focus on dominance-based rank, the intermediate derived forms that focus on prestige, and the final derived forms that focus on norm adherence.

All three forms of shame and pride can be experienced vicariously. As we would expect to also be true among primates that engage in coalitional aggression, vicarious proto-pride or proto-shame should be experienced whenever an ally enjoys victory or suffers defeat relative to a rival. Vicarious prestige-based pride and shame, though limited to humans, should exhibit a similar pattern. Finally, whenever a person linked to the actor via a shared social identity succeeds or fails with regard to normative standards, to the extent that others will engage in inductive generalizing, those successes or failures will influence how others treat the actor, hence the actor should experience vicarious pride or shame (see Lickel et al. 2005). The primary exception to the latter pattern occurs when identity sharing is incomplete, in which case an actor can distance herself from a norm violator in order to manage third parties' assessments; in this case, moral outrage, rather than vicarious shame, may be elicited (cf. Haley 2002).

Shame and pride illustrate the extensive re-working that can be achieved through processes of co-optation and modification. However, as the vicarious versions of these emotions demonstrate, substantial functional changes can also occur merely by extending an emotion's eliciting conditions. We propose that an emotion that we term *normative guilt* is elicited by norm violations absent a harmed relationship partner – within the worldviews in which they are defined, many sins do not harm other people, yet the sinner experiences guilt nonetheless. This extension is made possible by our elaborately developed ability to manipulate representations of social others. In some manifestations of normative guilt, the represented partner is a culturally-constructed nonexistent agent (a deity, ancestor, etc.; cf. Darwin [1871] 1909: 115–116 on remorse); in others, the imagined partner is a representation of the actor's kin network or cooperative group; and, in the most abstract manifestation, the (only dimly imagined) partner is a representation of society as a whole. In each case, violating a norm leads actors to undertake reparations or penance as if, by doing so, they mitigated the harm done, or signaled their future reliability. Normative guilt thus illustrates one of the most profound disjunctions between ourselves and our non-human primate relatives, namely the nature of the

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

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