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Around the world, people recognize that humans experience transient alterations of subjective state in response to information; people also agree that these alterations are often (with varying degrees of voluntary control) outwardly expressed, that they motivate action, and that they involve a change in one's perception of oneself, one's surroundings, and one's goals. English speakers label these experiences 'emotions,' and similar terms occur in many languages. Because the constituents of this category vary across languages, some anthropologists argue that emotions are primarily cultural in nature, and are incommensurate across cultures. However, critics of this position note that, while labels and connotations differ across cultures, many emotional expressions (particularly those involving the face) are easily recognized by outsiders, and outsiders learn to map local labels onto their own emotion lexicon. This suggests that, while cultures may determine the meaning of events that elicit emotions, and while cultures may glorify, disparage, ignore, or combine particular aspects of the emotion repertoire, the core aspects of human emotions are species-typical, and hence are likely to be the products of selection.

In *The Expression of the Emotions in Man and Animals* (London, J. Murray, 1872), Darwin presented evidence that some emotional expressions are recognizable across cultures and appear spontaneously in children. Darwin used the similarities between these expressions and those seen in animals to argue for common descent. While this perspective defied the Western anthropocentric tradition, Darwin conformed to that tradition in viewing emotions' effects on reasoning as detrimental, describing human emotions as vestiges of earlier evolutionary stages in

which the intellect was of less importance. While the argument for phylogenetic continuity plays a role in modern explanations of emotions, Darwin's vestigialism has largely been replaced by adaptationism.

Contemporary investigations of emotion relevant to an evolutionary perspective take one of three forms. First, psychologists focus on documenting and categorizing the proximate components of emotion, emotional expression, and emotions' influence on cognition; while questions of adaptive utility motivate these investigations in a broad sense, these issues often do not directly shape hypotheses tested. Second, employing perspectives taken from game theory, scholars explore the utility of particular emotions with regard to strategic dilemmas. Third, evolutionary psychologists seek to explain the influences of emotions on attention, memory, motivation, and other functions in terms of the recurrent challenges that have confronted humans.

As suggested by cross-cultural variation in the nuances of emotion terms, this domain is subject to considerable elaboration. However, despite such elaboration, even unschooled observers intuit that emotion terms are often thematically linked, i.e., terms such as 'terror,' 'fear,' and 'anxiety' all revolve around a single core experience. Furthermore, these core experiences are often associated with readily recognizable facial expressions. This has led many psychologists to propose the existence of discrete 'basic' emotions; it is thought that the full panoply of emotions is generated from these unitary, elementary constituents through processes of combination and/or fine cultural discrimination. Although there is no consensus as to the number of basic emotions, commonly proposed members include happiness, surprise, fear, sadness, anger, disgust, contempt, shame, and guilt.

In contrast to the above perspective, a minority of psychologists argue that unified basic emotions are illusory; rather, any given emotional experience is described as occupying a position

along such spectra as hedonic valence, degree of arousal, and tendency to approach-vs.-avoid. Similarly, facial expressions are thought to rarely involve the full complements of muscular activation claimed to be indexical of particular basic emotions, and are instead composed of a variety of component expressive elements that vary depending upon the details of context, arousal, approach-vs.-avoid, etc.

Proponents of both the discrete and the dimensional views make reference to the adaptive utility of the proposed psychological features. For example, both schools recognize the benefits of coping with imminent threats. However, while discrete emotion theorists argue that a unitary psychological mechanism, *fear*, directs attention to the threat, motivates the avoidance of harm, and focuses memory and problem-solving abilities on the task of coping with the threat, dimensional theorists point out that both the behavioral and the physiological responses to threat, including signaling of intention, depend on the costs and benefits of different courses of action, suggesting the existence of a complex and flexible problem-solving system rather than a distinct psychological mechanism that is activated only in response to threats. The divide between discrete and dimensional emotion theorists thus partially mirrors the debate between evolutionary psychologists and sociobiologists/behavioral ecologists.

Most game theoretic investigations of emotion assume that distinct emotions exist. In a seminal formulation Robert Trivers argues that iterated exchanges create selective pressure for psychological mechanisms that lead the individual to avoid imperiling long-term benefits in favor of smaller short-term gains. Aggression in response to having been cheated is adaptive because it decreases the likelihood of future defections against one, particularly if it is disproportionate relative to the transgression. Because disproportionate response is costly, an auxiliary mechanism is necessary to impel aggression, and outrage serves this purpose. Similarly, because

gratitude in response to generosity motivates reciprocation, actors who feel gratitude avoid the short-term gain to be reaped by defection and obtain the long-term gain provided by cooperation. Using more detailed models, Jack Hirschleifer demonstrates that the advantages of anger and gratitude are not limited to reciprocally altruistic exchanges, but pertain in any situation of potential cooperation.

Following Trivers, Robert Frank argues that the preference for short-term gains is a consequence of the tendency, common to all vertebrates, to discount the future. To this Alan P. Fiske adds a list of biases in human cognition, including propensities to overestimate one's own abilities, to ignore base rates, to overvalue immediate gains relative to probabilistic costs, and to both overestimate the probabilities of conjunctive events and underestimate the probabilities of disjunctive events. These biases undermine individuals' abilities to establish and maintain advantageous long-term relationships by causing the benefits of defection to loom large relative to the costs. However, because emotions such as love and guilt constitute immediate rewards and punishments, they change the subjective costs and benefits of present action in ways that countermand the temptation for short-term gain, committing an individual to a course of action that yields long-term benefits. In addition, by leading individuals to act in ways that are currently costly, these emotions generate honest advertisements of likely future behavior, thereby shaping the responses of the alter. Furthermore, via two pathways, emotions may shape behavior in an adaptive fashion even when future interactions will not involve the same alter. First, to the extent that an individual's inclination to act in a particular fashion a) is affected by past behavior, habits, etc., and b) is expressed in a manner that others can detect, then it pays to adhere to a pattern consistent with a preference for long term gain (by showing gratitude, reacting aggressively to transgressions, etc.). Second, to the extent that others know of an individual's

past actions, her behavior in one interaction can profitably shape many future interactions with many other alters.

Many authors propose that guilt evolved in order to a) dissuade individuals from harming beneficial relationships and/or b) motivate them to repair damage done to such relationships. One difficulty with these explanations is that, even granted the existence of cognitive biases, selection should favor the ability to surreptitiously cheat, yet guilt motivates reparation even when the transgression is undiscovered. This raises the possibility that guilt, while premised on emotions such as regret and sympathy, may be a product of cultural rather than biological evolution. The latter explanation accounts for the absence of universal facial or postural expressions of guilt, signals which would be expected if the capacity to feel guilt had been selected due to the advantages of reassuring others of one's good intentions.

Evolutionary theorists have noted that romantic love functions to commit individuals to a long-term cooperative mateship and signal that commitment to the partner, two valuable functions given human infant altriciality. Romantic love exhibits a distinct chronology, with an initial period of obsessive ideation eventually giving way to a less intrusive form of attachment. The early phase may both strongly dissuade defection during a period of scrutiny and motivate energetic signaling of commitment; once a cooperative enterprise has been established, sunk costs may reduce the necessary intensity on both counts.

Love is closely tied to jealousy. Evolutionary psychologists examine emotions such as jealousy in light of recurrent adaptive challenges. For example, David Buss notes that a principal hazard for men is misdirected investment due to cuckoldry, while a principal hazard for women is cessation of male provisioning due to abandonment. Consistent with these observations, Buss finds that men are more disturbed by the prospect of a mate's sexual infidelity, while women are

more disturbed by the prospect of a mate's emotional attachment to rival women.

Some evolutionary psychologists argue that emotions may be more diverse than either traditional psychologists or Western folk models suggest. For example, rather than discussing a single emotion, *fear*, that is a response to imminent danger, evolutionary psychologists predict the existence of multiple types of fear, each associated with such distinct classes of threats as predators, rival conspecifics, social exclusion, snakes and spiders, etc.; further subdivisions may occur on the basis of context. In *Evolutionary psychology and the emotions* (In M. Lewis and J.M. Haviland-Jones, eds., Handbook of Emotions (2nd ed.), pp. 91-115), Leda Cosmides and John Tooby argue that each emotion is a superordinate programs that serves to govern the activities of, and interactions between, specialized programs concerning a wide variety of psychological and physiological mechanisms. Activation of a given emotion, say, fear of predators in the twilight, directs attention to relevant information (potential signs of predators), sharpens sensory modalities relevant to that information (visual, auditory, etc.), cues patterns of interpretation (ambiguous shadows look like predators, etc.), readies relevant motor patterns (flight or fight), reassigns priority among goals (escape versus feeding, mating, playing chess, etc.), searches relevant memory categories (information about predators), and so on. This perspective provides a solution to the dimensional theorists' complaint that physiological and behavioral responses to a given stimulus vary with the physical and social context, since 'fear of predators when escape is possible' will be qualitatively different from 'fear of predators when escape is impossible,' etc. Similarly, dimensional theorists' complaints regarding the disjunction between emotions and expressions, and the lack of uniformity of the latter, can be addressed with the observation that, because some adaptive challenges are best met with a communication of intent while others are better served by the absence thereof, only some emotions involve an

expressive component. At the same time, similarities among many of the members of a class of emotions, or among the most memorable or commonly experienced members of that class, can explain the apparent existence of basic emotions.

While human emotions are clearly derived from a psychological foundation shared by social mammals, we likely possess some emotions that are considerably less developed, or wholly absent, in other creatures. Humans are unique in the extent of their reliance on socially transmitted information in coping with physical and social environments. An important class of emotions consists of those which mediate the acquisition, use, and dissemination of cultural information. Admiration of successful persons involves a desire for proximity and a willingness to provide client services to obtain it, as well as a desire for close observation and imitation. These patterns lead individuals to adopt ideas and practices of probable local utility. At a larger scale, conformity to cultural values, beliefs, and practices makes behavior predictable and allows for the advent of complex coordination and cooperation; shame and pride motivate an assessment of prevailing norms, an awareness of the presence of observers, and conformity to pervasive expectations when under observation. Conversely, contempt and moral outrage motivate publicizing the actions of nonconformists, excluding them from cooperative endeavors, and inflicting costs upon them. A richer understanding of the evolution of contempt and moral outrage is needed given that punishment plays a key role in maintaining cooperation. Finally, while considerations of kin selection and reciprocal altruism indicate that many animals should experience emotions in a corporate fashion (i.e., harm to kin or allies is experienced as harm to self, etc.), humans link their identities to group membership at scales not explicable in terms of kin selection or reciprocal altruism, suggesting that the benefits of coordination and cooperation favored the evolution of highly developed human corporate sensibilities.

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