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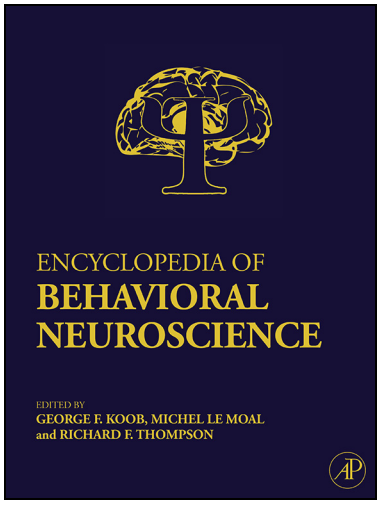

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Evolution of Emotions

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Glossary

Altruism – Behavior in which the actor incurs a cost (up to and including death) in order to benefit another individual.

Emotions – Essentially human constructs used as a shorthand to refer to the range of subjective feelings to which humans are exposed in their conscious actions (to a lesser or a greater degree).

Evolution – The view (usually credited to Charles Darwin) that new species (and their attributes) are derived by the forces of natural selection acting on pre-existing organisms. Essentially more organisms are produced than can flourish, so some of them do better as a consequence of their (often slight) variations. A change in the environment can alter which organisms (or attributes) benefit. It can be contrasted with the view that organisms are separately created.

Kin selection – Occurs when a gene is selected because it increases the reproductive success of relatives of the bearer of the gene. Genes can be selected in such circumstances because genetic relatives are more likely than chance to possess copies of the same gene. Kin selection gives rise to kin-directed altruism. In general, the higher the level of relatedness, the higher the level of altruism.

The Nature of Emotions and Their Evolution

The Oxford English Dictionary defines emotion as "A mental 'feeling' or 'affection' (e.g., of pleasure or pain, desire or aversion, surprise, hope or fear), as distinguished from cognitive or volitional states of consciousness." There has been considerable debate about the actual nature of emotions. They have, at various times, been viewed as feelings accompanying primary instincts (e.g., flight), or even reflections of the internal, physiological changes (e.g., increased heart and respiratory rates) induced by an emotional stimulus (e.g., a predator). At the very least, what we call emotions can be linked to generally reliable patterns of internal changes, relatively precise and recognizable situational contexts, and accumulated experiences.

Starting with Darwin, evolutionary explanations have been proposed for a wide range of emotions. There are at least two ways to situate emotions with respect to evolutionary theory: they may be viewed as adaptations, or they may be viewed as by-products of adaptations. If an emotion is an adaptation, we can immediately say several things about it. To begin with, we can presume that its evolutionary function relates to the voluntary behavior it motivates. Thus, fear motivates avoidance or escape, whereas rage motivates some forms of aggression. In addition, we can say something about the emotion's evolutionary history. For instance, we can presume that, at each stage in its evolution, the resulting successful emotional disposition had behavioral effects that, on average and relative to other existing variants, enhanced its bearers' inclusive fitness (i.e., its ability to make genetic contributions to the next generation).

Probably not all emotions are Darwinian adaptations; some may be better construed as by-products of adaptations. Archer has argued, for example, that grief results from the maladaptive overstimulation of evolved attachment mechanisms, in particular, responses associated with separation from the object of attachment. These reactions usually lead to adaptive patterns of thought and behavior, such as a preoccupation with the lost person and a desire to locate them. However, when the person is deceased, these reactions cease to be adaptive, and constitute the phenomenon of grief. Thus, grief itself is not an adaptation, but can be traced to adaptive aspects of the mind.

It seems worth initially illustrating some of the varied emotions that have been postulated in our species and attempting to link them to physiology and to context.

Anger

Anger or 'rage' is an important emotion that is linked to threat and attack (aggression), both of which are phenomena with wide-ranging and sometimes subtle emotional and biological consequences to our species. Aggression (whether physical or verbal) is actually a highly heterogeneous phenomenon. Attack can, in some cases, be a product of fear (e.g., defense by a cornered subordinate), rather than anger. In such cases of defensive aggression, there is activation of the sympathetic nervous system. Other forms of physical attack (e.g., by a predator on a prey) seem to be accompanied by minimal signs of internal physiological change or arousal (e.g., there is no activation of the sympathetic nervous system). It is also

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clear that angry individuals can be socially inhibited from actually expressing this emotion. Conversely, individuals (e.g., in a military context) can be trained to kill or injure members of their own species without much involvement of anger as an emotion. Having said that, anger is an emotion that is relatively easy to recognize in our species and one with which we are all familiar. Conflict is also a characteristic of virtually every animal species that has been investigated. Indeed, it has been argued that competitive (as opposed to defensive) forms of intra-specific threat and attack, whether directly concerned with the acquisition of food, a mate, a territory, or enhanced social status, are all broadly designed to increase the organism's relative fitness.

Fear

Fear is another important emotion, and is associated with a variety of behavioral responses aimed at protecting the individual from threatening situations. These responses include escape, avoidance, warning displays, defensive aggression, submission, and immobility. In many cases, our fears appear to be tuned to specific threats that our ancestors faced. Research has shown that people are more likely to form some phobias than others (an example of the phenomenon of preparedness). These phobias relate to threats faced by our hunter–gatherer ancestors. Even people living in modern environments are more likely to develop phobias related to ancestral threats, such as snakes and spiders, than they are of developing phobias related to items much more dangerous to them in their modern environments, such as guns, electrical outlets, and fast cars. Similarly, there is ample evidence that laboratory rats and mice retain many of the behavioral responses of their wild progenitors.

Love

Natural selection may also account for the origin of other, more complex emotions. This includes the emotion of love. Like aggression, the word love covers a range of phenomena, including romantic love and the love found among kin (familial love). It is not difficult to imagine the possible significance of romantic love in reproduction. Fisher has suggested that the early stages of romantic love keep couples together for long enough to conceive, whereas attachment or companionate love (which involves deep affection but a lower level of sexual passion) keeps them together until weaning, at around 4 years. Relationships often end after this, as one or both partners may fall passionately in love with someone else. Other forms of love, such as that between parents and their genetic offspring, can be given plausible evolutionary rationales.

Jealousy

Another example of a complex emotion claimed to have an evolutionary origin is jealousy. The suggestion is that, in a monogamous species with high male parental investment, jealousy prompts behavior that lessens the chances that one's mate will engage in extrapair copulatory activity. A large body of research attests to the fact that men are more distressed than women about sexual infidelities. This may be an evolved tendency designed to motivate mate guarding behavior and thereby ensure paternity. Women, on the other hand, appear to be more distressed about emotional than sexual infidelities – that is, about their mate forming a close emotional bond or falling in love with another female. This may be because a male's emotional involvement, more than sex, signals a potential loss of investment in the women and her offspring. A wide variety of evidence demonstrates the sex difference in jealousy. One study, for example, found that men preferentially recall details of sexual infidelity, whereas women preferentially recall details of emotional infidelity. Such findings make good evolutionary sense.

Do Nonhuman Animals Have Emotions?

Some commentators argue that emotions are unique to *Homo sapiens* and that talking about them in other animals is, at best, an expression of anthropocentrism. Others see nothing wrong in assuming that nonhuman animals share many of these characteristics that humans have found generally beneficial to their individual survival and their ability to pass on their genes. Many find it easier to acknowledge emotions in animals with a high degree of resemblance to human beings than they do for species that are more distantly related to us. They often do this on the basis of linking emotions to phenomenological consciousness or sentience (defined as the ability of an entity to recognize something it is like, e.g., what it is like for a bat to be a bat, or for an octopus to be an octopus). The Stanford Encyclopedia of Philosophy notes that "there is broad commonsense agreement that phenomenological consciousness is more likely in mammals and birds than it is in invertebrates. . . while reptiles, amphibians and fish constitute an enormous grey area."

Given the recent flurry of interest in whether fish have sentience and the capacity to suffer (as well as being part of that grey area), it seems instructive to pose the question "do fish show emotions?" The answer has relevance to our position for other vertebrate groups. A number of authorities conclude that the evidence suggests fish do indeed have sentience and the capacity to suffer. Chandroo and co-workers maintain that the "affective states of pain, fear and stress are likely to be experienced by fish in similar ways to tetrapods." Others conclude that fish can

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experience fear-like states and probably have the capacity for suffering.

There are various difficulties associated with this issue. Part of the problem is the word 'sentient'. In some usages, it is simply a synonym for 'animate' or 'responsive to sensory stimuli'. Fish are certainly not inanimate and respond to nociceptive (pain-related) and other stimuli. Others describe sentience as a state of elementary or undifferentiated consciousness. For example, Broom claims "a sentient being is one that has some ability to evaluate the actions of others in relation to itself and third parties, to remember some of its own actions and their consequences, to assess risk, to have some feelings and to have some degree of awareness." This is very much like the definition of phenomenological consciousness.

In relation to fish (or any other nonhuman animal), one could adopt one of two positions. First, one could regard emotions as being conscious states. This would imply that animals lacking phenomenological consciousness could not have emotions. Conversely, if a particular animal possesses phenomenological consciousness, it could have emotions and the question then becomes, are the emotions experienced by the animal the same as ours? Second, one could take the view that emotions do not necessarily have to be conscious states, but can be defined purely in functional, behavioral, and/or physiological terms. This would imply that, whether or not an animal has phenomenological consciousness, it could still have emotions. The only question is, does it have the same emotions we have or a different set?

The question of consciousness in other animals is thorny, especially when it comes to animals very different than ourselves. For this reason and others, it is probably best to take the second approach. There are then two ways to tackle the question of emotions in other animals. One is to think: "Fear is what I feel in situation X and what I assume other humans feel in situation X. In comparable situations, do other animals experience the same thing as us?" But this is a very anthropocentric approach, and is thus not perhaps the best way to proceed. A second way to approach the question would be to take a comparative perspective maintaining that, in certain situations, humans and other animals act in a comparable manner in response to threatening stimuli. Their senses become fully engaged, they retreat and adopt a defensive posture and their autonomic nervous systems are activated. Although there are differences among species in the details of these actions, they are all clearly evolved solutions to the same general selective pressure, that is, dealing with certain kinds of threats to life and bodily integrity. Furthermore, with some animals (e.g., humans and chimpanzees), the behavioral elements are very similar, presumably because they result from the activation of modified versions of mechanisms inherited from a recent common ancestor. Thus, they have a shared evolutionary function and, in some cases, a high level of shared evolutionary history. These are important commonalities, and therefore we should gather these behaviors under the same heading: fear. Certainly, there are differences in these behaviors across species. But what they have in common is more important. This way of looking at things treats human fear not as the prototypical case which other animals have or do not have, but rather as just one example of a more general phenomenon in nature.

Some Animal Models of Emotions

Clearly many scientists, who use laboratory species in areas such as psychopharmacology, do so because they regard the animals as having emotional experiences that are not too different from those found in human beings. Naturally, if emotions are, in any sense, evolved, this is a wholly appropriate way to screen potentially psychoactive drugs. Willner has proposed a useful list of features diagnostic of properly validated animal models of psychiatric disorders. In addition to predictive validity (the action of the drug in the model should generally correspond to that seen clinically), the model should have face validity (the diagnostic characteristics of the model and the psychiatric disorder should be similar) and construct validity (the theoretical rationale should be convincing). It should be noted (perhaps in support of the evolutionary emphasis) that there has been a recent move from traditional psychological to ethological models rooted in the animal's naturalistic behavior.

Anger or Hostility

A rather heterogeneous battery of tests with rats and mice has been used in the laboratory to tap into the emotion of anger. Some tests assess competitive motivations, others defensive or even predatory motivations. Although this makes it difficult to clearly relate the threat and attack recorded to anger, it has been pointed out that some forms of clinically relevant human aggression are expressions of hyper-fearful emotion and psychopaths may show behavior with parallels to predation.

Anxiety

Rats and mice have traditionally been used in tests to assess potential anxiogenic and anxiolytic drugs using the open field, social interaction, two-chambered light–dark transition, and elevated plus-maze tests that all utilize these rodent's apparent fears of novelty, strangers, bright lights, open spaces, and heights. More ethological tests have utilized the ultrasonic distress calls of mouse neonates and the mouse defense test battery where mice respond to cues from predatory rats.

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Depression

Human depression is described as "a debilitating phenomenon with major depressive episodes lasting at least 2 weeks and with core symptoms of depressed mood and markedly suppressed interest and lack of reactivity to pleasurable stimuli." Rats and mice have been used in a behavioral despair model where they are forced to swim in a confined space. Rodent models have also been developed where animals are subject to chronic unpredictable substantive (e.g., electric shocks, cold water immersion, and light-dark rhythm reversal) or chronic mild (e.g., cage tilt, wetting of cage bedding, and changes to lighting) stressors. Finally (and more ethologically), others have explored loss of social status in the rat as inducing depression-like symptoms. In some cases, the effects of depression-inducing models on anhedonia (a condition where rewards are ineffective), noted above as a symptom of human depression, are studied by looking at reductions in the rate of intracranial self-stimulation of reward centers in the animal's brain.

Although some human emotions such as social phobia do not appear amenable to developing meaningful animal models, the above items suggest that some emotional constructs have utility, at least across the class *Mammalia*.

Relating Emotions to Evolution

It seems appropriate to consider the lines of evidence and debate that have led people to conclude that emotions are subject to evolutionary pressures. These are largely focused on the human species, and can be divided into a number of broad categories.

Sociobiological Theories

One line of evidence concerns the fact that certain aspects of emotional behavior are predictable from sociobiological theories.

Kin selection theory

Hamilton's kin selection theory (KST) assumes that individuals will tend to favor others with whom they share a higher than average proportion of genes (i.e., relatives). KST helps to predict emotional responses to individuals of differing degrees of genetic relatedness. For example, greater relatedness is associated with greater emotional closeness. Similarly, it has been found that grief following the death of a loved one increases as a function of relatedness.

Parental investment theory

A number of sex differences in emotional expression make good sense in light of Trivers's parental investment theory. Littlefield and Rushton suggested that grief would be positively correlated with average levels of parental investment for a sex. Consistent with this prediction, they found that, on average, mothers grieved the death of a child more than fathers. Based on this work, Archer made the interesting observation that, in species with a low male parental investment, such as polygynous elephant seals, males would not be expected to grieve the death of offspring at all, whereas in monogamous species, males would be expected to grieve.

There are other examples. Campbell has argued that, due to differences in parental investment, females are more valuable to offspring than males, and this is one reason they have evolved greater restraint in regard to risk taking. Consistent with this view, she has found that, though females are just as susceptible to anger as males, they are less likely to engage in direct aggression. This appears to be because they are more fearful than males about the potential consequences of aggression.

Reciprocal altruism theory

Another theory that helps make sense of the suite of human emotions is Trivers's reciprocal altruism theory (RAT). RAT suggests that people have evolved to engage in patterns of reciprocal exchange, and to avoid the problem of being cheated (i.e., helping someone who does not return the favor). Trivers suggests that, to enact this behavioral strategy, we are equipped with a set of emotional response patterns. Anger and dislike motivate us to withdraw help to cheaters, or to punish them. Gratitude and a sense of obligation motivate us to reciprocate help received from others. Guilt occurs when we fail to reciprocate help, and may be a way of avoiding reprisals. These and other emotion reactions make good sense in light of RAT, which helps bolster the case that they have an evolutionary origin.

Direct Evidence for Evolutionary Origin

There is also more direct evidence that emotions have an evolutionary origin. This includes Ekman's research showing the apparent cross-cultural universality of many of the basic emotions. Many emotions are associated with facial expressions and displays that appear to be universal among human beings. These include happiness, anger, sadness, fear, disgust, and surprise. The case for the evolutionary origin of emotions is further bolstered by the fact that analogs of several facial emotional expressions are found in nonhuman animals, and are elicited by similar situations. There is therefore strong evidence that at least the basic repertoire of emotions has an evolutionary origin.

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General Conclusions

Although behavior is not directly subjected to evolutionary forces, it seems likely that there is some commonality in the emotions displayed by a range of animal species. The commonalities suggest that nonhuman animal models of human emotions are relatively meaningful and that one should take into account these phenomena when considering animal welfare.

See also: Animal Tests for Anxiety; Animal Models of Sexual Function; Cooperation; Comorbidity – Depression; Communication of Emotions in Animals; Depression; Emotions; Evolutionary and Developmental Issues in Cognitive Neuroscience; Emotion–Cognition Interactions; Fear, Anxiety, and Defensive Behaviors in Animals; Fear Conditioning; Fear: Potentiation and Startle; Genes and Behavior: Animal Models; Human Evolutionary Genetics; Human Fear and Anxiety; Infant Bonding and Attachment; Motivation; Neural and Pharmacological Substrates of Aggression; Neuropsychological Aspects of Anxiety Disorders; Neural Bases of Defensive Aggression; Neurobiology of Offensive Aggression; Neural Substrates of Conditioned Fear and Anxiety; Neural Substrates of Unconditioned Fear, Defense, and Anxiety; Offensive and Defensive Aggression; Psychiatric and Substance Use Disorder Comorbidity; Physical and Emotional Pain; Subjective Experience and the Expression of Emotion in Man; Sex Hormones, Mood, and Cognition; Social Bonding and Attachment; Stress and Emotionality.

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