Sigma Xi, The Scientific Research Honor Society

The Nature of Emotions: Human emotions have deep evolutionary roots, a fact that may

explain their complexity and provide tools for clinical practice

Author(s): Robert Plutchik

Source: American Scientist, Vol. 89, No. 4 (JULY-AUGUST 2001), pp. 344-350

Published by: Sigma Xi, The Scientific Research Honor Society

Stable URL: https://www.jstor.org/stable/27857503

Accessed: 01-04-2020 18:12 UTC

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at https://about.jstor.org/terms



 $Sigma~Xi,~The~Scientific~Research~Honor~Society~{\it is~collaborating~with~JSTOR~to~digitize},~preserve~{\it and~extend~access~to~American~Scientist}$

The Nature of Emotions

Human emotions have deep evolutionary roots, a fact that may explain their complexity and provide tools for clinical practice

Robert Plutchik

Almost everyone agrees that the study of emotion is one of the most confused (and still open) chapters in the history of psychology. By one estimate, more than 90 definitions of "emotion" were proposed over the course of the 20th century. If there is little consensus on the meaning of the term, it is no wonder that there is much disagreement among contemporary theoreticians concerning the best way to conceptualize emotion and interpret its role in life.

In everyday human existence we conceive of an emotion—anger, despair, joy, grief—as a feeling, an inner state. The internal experience of emotion is highly personal and often confusing, particularly because several emotions may be experienced at the same time. Imagine, then, how difficult the objective study of emotion must be. Most of us often censor our own thoughts and feelings, and we have learned to be cautious about accepting other people's comments about their feelings. The empirical study of a psychological phenomenon so complex and so elaborately cloaked cannot help but present a special challenge.

Compounding the distrust of verbal reports of emotion are the influences of behaviorism and psychoanalysis on psychological research. The behaviorists of the 20th century believed that the only truly reliable, objective information obtainable from living creatures was information about their behavior. A classical

Robert Plutchik is professor emeritus at the Albert Einstein College of Medicine and adjunct professor at the University of South Florida. He received his Ph.D. from Columbia University. He has authored or coauthored more than 260 articles, 45 chapters and eight books and has edited seven books. His research interests include the study of emotions, the study of suicide and violence and the study of the psychotherapy process. Address for Plutchik: 4505 Deer Creek Boulevard, Sarasota, FL 34238. Internet: proban@home.com

behaviorist would hold that emotion is an inner state and thus simply outside the realm of science. For their part, psychoanalysts have made us aware that emotions may be repressed, inhibited or unconscious, and thus unavailable to introspection. Finally, language itself introduces ambiguity and does not make it easy to describe mixed emotions in an unequivocal way. The meaning of emotion terms is often obscure. For example, many people are not sure about the differences between fear and anxiety, guilt and shame, or envy and jealousy. As a result, we often resort to metaphor to attempt to describe emotion. Think, for example, of such expressions as "blowing off steam," "hating someone's guts," "pain in the neck," "lump in the throat" and "a broken heart."

How, then, can emotion be studied and understood? The challenge of developing a theoretical approach is important, because emotions are an essential part of who we are and how we survive; emotional distress impels people to seek help, and indeed the primary concern of psychotherapy is the repair of emotional disorders. To simply declare emotion outside the bounds of scientific study would be irresponsible.

I believe that a scientific and therapeutically useful understanding of emotions is possible. In fact, there are several scientific intellectual traditions that have dealt with this issue. There are an evolutionary (launched by Charles Darwin), a psychophysiological (William James), a neurological (Walter Cannon) and a psychodynamic tradition (Sigmund Freud), in addition to the cognitive perspective that began emerging in the 1950s. More recently neurobiological evidence has begun to inform the discussion; however, identifying the structures of the brain related to emotion is not a theory of emotion, nor can such a theory be built from a knowledge of the chemicals involved in mood states, just as an adequate theory of depression cannot be constructed simply from a knowledge of the availability of serotonin. As the University of Iowa neuroscientist Antonio Damasio has pointed out, when the amassing of data does not resolve a complex issue, it may be necessary to find new ways to conceptualize the problem.

In my view evolutionary theory provides a way to unify a number of theoretical perspectives. Using the tools and methods of evolutionary biology, and pulling together information from other species, we can put emotions in a functional framework—define them in terms of what their adaptive function might be, and thus understand better their biological basis and the apparent connections between them.

Some work along these lines has been widely popularized in recent years: By now we've all heard authors of best-selling books describe jealousy, love, anxiety and fear in dogs, cats, chimpanzees, baboons, elephants and lions. The bestiaries of the medieval period contained detailed descriptions of emotions in animals. The popular appeal of such explanations may lie in their ability to touch a deep-seated sense of the connectedness of all living things. Although many psychologists have warned of the dangers of anthropomorphism, recent thinking by cognitive scientists and others sees this attitude as an outdated prejudice. The Rockefeller University zoologist Donald Griffin, one of the founders of the field of animal cognition, believes that the "charge of anthropomorphism is a conceited claim that only our species is capable of even the simplest conscious thinking." But there is danger in oversimplifying: A sophisticated understanding is needed to inform clinical practice.

Over the past four decades I have pulled together evidence from various



Carl Sams II/Peter Arnold, Inc.

Figure 1. Great egrets in breeding plumage fight in midair, displaying the agonistic behavior that is the precursor of human emotions such as fear, anger and jealousy. Human emotions, says the author, are best viewed through an evolutionary lens, as adaptations triggered by the challenges of survival and reproduction that are part of every organism's existence. An evolutionary approach, he argues, can sort out the roles of emotion, impulse and action and, in a therapeutic setting, help people understand the circumstances in which emotions can sometimes fail in their adaptive tasks.

studies to form a psychoevolutionary theory of emotion, with the goals of clarifying what emotions are, finding ways to measure them, relating emotions to other psychological disciplines, and informing the practice of psychotherapy. Like many concepts in science, emotions can be best understood by making inferences from certain classes of evidence. Such inferences suggest that emotions or their evolutionary precursors (or prototypes) can be found among lower animals as well as human beings, a fact that can provide fascinating evolutionary insights into our emotions, moods and personality traits. They suggest further that emotion, cognition and action interact in feedback loops and that emotion can be viewed in a structural model tied to adaptation.

Evolution and Emotion

What we call cognition—the activity of knowing, learning and thinking, of which emotion is a part—evolved over millions of years. Charles Darwin recognized that the process of evolution by natural selection applied not only to anatomic structures but also to an animal's "mind" and expressive behavior—a conclusion that led him to write a book on emotional expression. Those who have followed Darwin in studying the evolutionary origins of emotion have sought to understand how emotions increase evolutionary fitness for the individual.

As mentioned above, a few evolutionary origins are easy to postulate. Fear and anxiety in people closely parallel the state of heightened arousal of an animal who senses a predator or a threat to its offspring, a similarity that has been found in neurochemical, anatomical and imaging studies that show these states are mediated by the limbic system, the part of the central nervous system common to lower and higher animals. Love and emotional attachment clearly promote pair bonding, reproduction and parental investment, basic to evolutionary fitness in human beings. But the origins of some other emotions are harder to find. Is there a general principle that can be applied?

The place to start might be with the definition problem. An emotion is not simply a feeling state. Emotion is a complex chain of loosely connected events that begins with a stimulus and includes feelings, psychological changes, impulses to

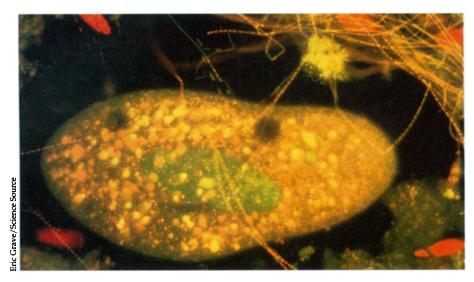


Figure 2. Microorganisms—here a paramecium, mixed algae, diatoms and other plankton—take in food, excrete waste products, avoid predators, reproduce, seek safe environments and explore their world. They must distinguish between predator and prey and, if their mode of reproduction requires it, between a potential mate and a potential enemy. This information-gathering and prediction and other universal adaptations found in all organisms constitute prototype adaptations from which human emotion can be modeled.

action and specific, goal-directed behavior. That is to say, feelings do not happen in isolation. They are responses to significant situations in an individual's life, and often they motivate actions. This definition of emotions allows the concept to be generalized to lower animals without difficulty. From his studies of animals, human infants and human adults, Darwin concluded that expressive be-



Figure 3. Suckling her young, a suricate meerkat mother keeps an eye on her surroundings in a South African nature preserve, ready to protect her offspring from any threat. Psychologists believe cognitive functions evolved to serve emotional and biological needs—in evolutionary terms, in order to predict the future more effectively. In survival situations cognitions and inner states such as arousal tend to be followed by impulses to action—perhaps, in this case, a defensive or protective posture, attack or flight.

haviors communicate information from one animal to another about what is likely to happen; therefore they affect the chances of survival of the individual demonstrating the behavior. "Even insects," he wrote in his 1872 book, "express anger, terror, jealousy, and love by their stridulations."

Extending Darwin's idea a bit, I propose that in general, emotions are activated in an individual when issues of survival are raised in fact or by implication. Such situations include threats, attacks, poisonous substances or the sighting of a potential mate. The effect of the emotional state is to create an interaction between the individual and the event or stimulus that precipitated the emotion. The interaction usually takes the form of an attempt to reduce the disequilibrium and reestablish a state of comparative rest.

Protozoologist Nicola Ricci of the University of Pisa in Italy pointed out in 1990 that every single-celled organism, from the blue-green alga to the eukaryote, is a complete, self-sufficient organism. Single-celled organisms are exposed to daily risks in their environments. They take in food, excrete waste products, avoid predators, reproduce by exchange of genes in many cases, seek safe environments and explore their microbiological world. Thus these simple organisms adapt to many of the same problems as higher, multicellular organisms. Bacteria are capable of very complex metabolic pathways, and, as Ursula Goodenough detailed in these pages in 1991, viruses and bacteria have evolved tactics of camouflage, distraction and mimicry. Even plant cells such as green algae show defensive reactions to touch, and chemical messages signal everything from alarm to sexual attraction in organisms from bacteria to human beings.

As one moves up the evolutionary ladder, it is remarkable to note that a small number of developmental genes can radically alter the behavior of cells and change an amoeba into a multicelled organism. Developmental biologist William Loomis of the University of California, San Diego, estimated in 1988 that "the important evolutionary differences between a guppy and a primate probably lie in only a few hundred genes." Along with the genetic continuum, and evolutionary continuities in structure, function and development, then, it is not surprising that one can discern a behavioral continuum.

Writing in 1980, the late zoologist John Paul Scott of Bowling Green State University pointed out that it is the nature of the environment that creates certain functional requirements for all organisms if they are to survive. Like Ricci's alga, a higher organism must take in nourishment and eliminate waste products. It must distinguish between predator and prey and between a potential mate and a potential enemy. It must explore its environment and orient its sense organs appropriately as it takes in information about the beneficial and harmful aspects of its immediate world. Organisms that are relatively helpless at birth must have ways of indicating the need for care and nurturance.

Only a few classes of adaptive behavior, Scott noted, are found in most species and at most phylogenetic levels. These include eating, the fight-or-flight response, sex, caregiving and investigation. These patterns might be considered prototype adaptations. The connections between behavior and inner states and processes are less obvious. Yet such connections can be made by inference from a variety of evidence. This evidence includes knowledge of stimulating conditions, the effects of behavioral acts, knowledge of typical behavior patterns of the individual and species, choices made when alternatives exist and reactions of other members of one's group or species. A single overt display of emotions can reflect complex states such as approach and avoidance,

attack and flight, sex and aggression, or fear and pleasure. It is not necessarily easy to detect an emotional substrate in the behavior of lower animals, but neither is it necessary to exclude the possibility. Emotion is far more complex than the subjective experience familiar to a human adult, and the concept of emotion can be applied to lower animals as well as human beings. Emotions have an inherent complexity that is in part related to their evolutionary history.

Cognition, Emotion and Evolution

Any organism must determine, on the basis of limited information, whether there is food, a mate or danger in its environment. Depending on the prediction made, the organism makes a decision to escape, to attack, to eat or to mate. The complex processes that go on in the service of biological need include receiving sensory input, evaluating it, capturing the important aspects of the information in symbols and comparing the new information with memory stores. Predicting the characteristics of

environments enables organisms to prepare for those environments.

Psychologist Ulric Neisser of Cornell University compared human beings with computing machines in a seminal article in 1963. He suggested that cognitive functions serve emotions and biological needs. Information from the environment, he says, is evaluated in terms of its ability to satisfy or frustrate needs. What is particularly significant is that each new cognitive experience that is biologically important is connected with an emotional reaction such as fear, pleasure, pain, disgust or depression. From the point of view of evolution, cognition developed in order to predict the future more effectively. The human brain, which has evolved as an adaptation to changing and difficult environments, has now helped create the very environment to which it must continue to adapt.

If emotion is a chain of events, cognition is generally near the beginning of the chain. This is considered an important point in the psychological community, which has put a good deal of effort

into answering the "what comes first?" question, ever since the American psychologist-philosopher William James in 1884 framed the question this way: Is it the feeling of emotion or the physiological changes that are part of emotion? This is actually a pseudoproblem. Emotions are not simply linear events, but rather are feedback processes. The function of emotion is to restore the individual to a state of equilibrium when unexpected or unusual events create disequilibrium. Even if cognitions are generally at the beginning of the chain of events, they can be influenced by events appearing later in the chainstates of arousal, say, or ego defensesthrough a feedback process. Stimulus events, either external or internal (as in dreams), act as primary triggers that start the emotion process going.

The biological aspects of this process have been the subject of considerable recent study. Animal research by Joseph E. LeDoux of New York University has revealed that the conditioned fear response involves several neural

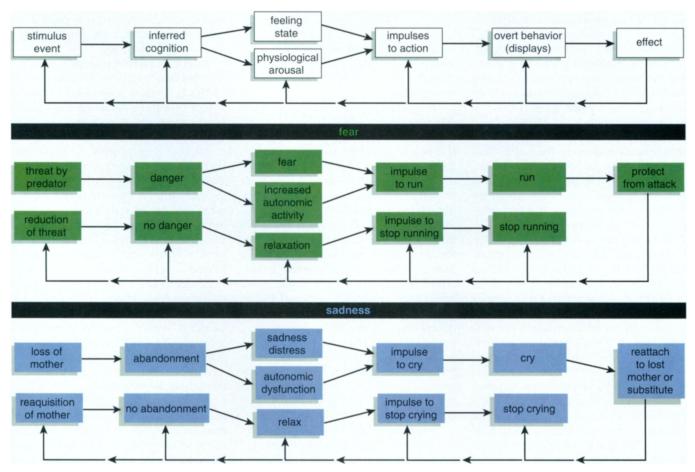


Figure 4. Feedback loops in emotion show how sensory information is evaluated and translated into action or some other outcome that normalizes the relationship between the individual and the triggering event. The inner state perceived as fear may arise from a threat that is perceived as "danger"; the fear triggers an impulse to flee, which results eventually in reduction of the threat. A similar set of homeostatic processes can be seen in the case of sadness in a child experiencing loss of her mother.

stimulus event	cognition	feeling state	overt behavior	effect
threat	"danger"	fear	escape	safety
obstacle	"enemy"	anger	attack	destroy obstacle
gain of valued object	"possess"	joy	retain or repeat	gain resources
loss of valued object	"abandonment"	sadness	cry	reattach to lost object
member of one's group	"friend"	acceptance	groom	mutual support
unpalatable object	"poison"	disgust	vomit	eject poison
new territory	"examine"	expectation	map	knowledge of territory
unexpected event	"what is it?"	surprise	stop	gain time to orient

Figure 5. Although emotional substrates cannot always be discerned in the behavior of non-human animals, many stimuli are experienced by people and animals alike and result in prototypical behavior followed by, generally, the reestablishment of an equilibrium state that might not have been achieved without the impulse precipitated by the inner state. In human experience it is common to use the term "emotion" to describe the feeling state, but in fact emotion is considerably more complex.

pathways with different latencies. Damasio has traced the events in an initial defensive response (fear): The key features of a dangerous animal or event—perhaps color, speed of movement, certain sounds—are detected and signaled to the amygdala, a part of the limbic system deep in the brain. This process is very rapid and is not a conscious one. Signals from the amygdala to prefrontal areas and other locations precipitate the conscious feelings associated with an emotion.

Feeling states tend to be followed by impulses to action. Emotion can cause one's muscles to tense; it can be expressed as a facial gesture, clenched fist or an action such as running, attacking or yelling. Impulses to action are not always followed by action, as clinicians know—often for fear of retaliation or embarrassment. Even when they are, overt behavior is not the end of the emotion process.

Such behavior generally has an effect on the stimulus or condition that started the chain of events in the first place. For example, running from a source of threat reduces the threat and tends to reestablish the condition that existed before the threat. Similarly, if someone loses a parent, crying and grieving tend to elicit supportive and helpful contacts from members of the grieving person's social group and, at least in a symbolic way, provide a sort of reattachment with the lost parent and thus a change in the feeling state.

Overall, emotion is a kind of homeostatic process in which behavior mediates progress toward equilibrium; I call it a behavioral homeostatic, negative-feedback system. Emotion is a chain of events made up of feedback loops. Feelings and behavior can affect cognition, just as cognition can influence feeling.

At the heart of all these descriptions is the idea that emotions have a function in the lives of individuals. This idea arises from an evolutionary perspective, is consistent with psychodynamic thinking and is becoming increasingly accepted in contemporary writings. For example, young organisms require food, protection and transportation. Crying is a major method for getting such care. Fear protects the self, initiates withdrawal and allows general functioning to continue. Shame leads to remorse and a decrease in the probability of repetition of the shameful act.

These examples imply that emotions are part of a social regulation process. Evolutionary theory reminds us that the interests of different individuals are often in conflict: males versus females, parents versus children, brothers versus brothers, group versus group. Genes are

"selfish" and concerned with self-maintenance and self-reproduction. Social interactions and communications reflect this conflict. Listening and speaking are regulated by direct and subtle expressions of emotion—smiles, eye contact or looking away, nods, postural shifts, vocalizations, passive questions and implicit commands ("Why don't you wear a hearing aid?").

Much social interaction involves individuals in different hierarchical positions. In such situations, during conversation there is often a censoring of rebellious thoughts, and a covert competition of ideas. An individual may experience feelings of defiance or may accept a submissive position. Emotions, at both conscious and unconscious levels, regulate such social processes.

Another way to conceptualize emotions as a social-regulation process is in terms of the views of animal communication proposed by Eugene Morton of the Smithsonian Institution and his colleagues. They point out that communication is an assessment/management process aimed at survival. Communication signals are selected in evolution because they substitute for more risky behavior such as fighting.

California ground squirrels stimulate a rattlesnake to rattle by kicking earth at it. This is done because squirrels use the sound of rattling to assess the snake's size and body temperature, two factors that determine how dangerous the snake is to their pups. With many animals, distress calls are adaptive because they may startle a predator into letting go, may attract the attention of other conspecifics to mob the predator, or may attract a larger predator to compete and possibly allow escape. However, it is not always easy to determine the adaptive nature of a given signal.

Emotions are part of the management of the process. Anger, for example, intimidates, influences others to do something you wish them to do, energizes an individual for attack or defense and spaces the participants in a conflict.

Modeling the Emotions

I have used the term "emotion" as a single, general term for a group of phenomena. As complex processes with functional value both in communication and in increasing the individual's chances of survival, emotions represent proximate methods to achieve evolutionary fitness. To integrate many of the things known about emotions, model-making is useful.

In English there are a few hundred emotion words, and they tend to fall into families based on similarity. I have found that the primary emotions can be conceptualized in a fashion analogous to a color wheel-placing similar emotions close together and opposites 180 degrees apart, like complementary colors. Other emotions are mixtures of the primary emotions, just as some colors are primary and others made by mixing the primary colors. Such "circumplex" modeling can be used as an analytical tool in understanding personality as well, and the similarity between the two models is important. I have extended the circumplex model into a third dimension, representing the intensity of emotions, so that the total so-called structural model of emotions is shaped like a cone.

The notion of a circumplex model is not my invention, nor is it new. Social psychologist William McDougall noted the parallel between emotions and colors in 1921, writing that "the color sensations present, like the emotions, an indefinitely great variety of qualities shading into one another by imperceptible gradients...." The first circumplex model was one developed by Brown University psychologist Harold Schlosberg in 1941, after he had asked research participants to judge the emotions posed in a standard set of pictures of facial expression. Schlosberg added the intensity dimension to his model. My own model was proposed in 1958, when I suggested eight basic bipolar emotions: joy versus sorrow, anger versus fear, acceptance versus disgust and surprise versus expectancy.

Over the centuries, from Descartes to the present, philosophers and psychologists have proposed anywhere from 3 to 11 emotions as primary or basic. All the lists include fear, anger and sadness; most include joy, love and surprise. There is no unequivocal way to settle on a precise number, although factor-analytic studies, similarity-scaling studies, child-development studies and cross-cultural studies are useful. But in the final analysis, this is a theoretical decision to be

Figure 7. To help psychologists understand the relations among emotions, raters were asked to estimate the degree of similarity between certain pairs of emotions. The use of a similarity scaling method produced the empirical angular locations shown in the figure (where opposites have a similarity ranking of -1.0 and identical concepts have a similarity ranking of 1.0). The concepts shown are a selection from a larger population of words.

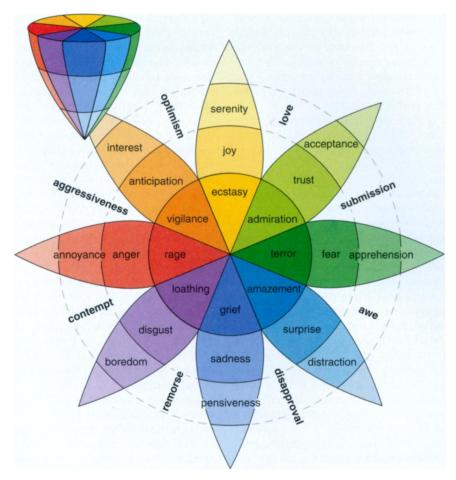
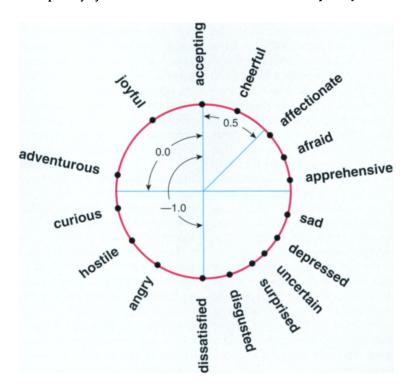


Figure 6. Author's three-dimensional circumplex model describes the relations among emotion concepts, which are analogous to the colors on a color wheel. The cone's vertical dimension represents intensity, and the circle represents degrees of similarity among the emotions. The eight sectors are designed to indicate that there are eight primary emotion dimensions defined by the theory arranged as four pairs of opposites. In the exploded model the emotions in the blank spaces are the primary dyads—emotions that are mixtures of two of the primary emotions.



evaluated in terms of the inferences and insights to which it leads, the research it suggests and the extent to which empirical data are consistent with it. The psychoevolutionary theory assumes there are eight basic emotion dimensions arranged in four pairs.

If there are eight basic emotion dimensions (each with a number of synonyms or related terms), how can we account for the total language of emotions? Various published studies imply that the few hundred emotion words tend to fall into families based on similarity. If we follow the pattern used in color theory and research, we can obtain judgments about combinations—the emotions that result when two or more fundamental emotions are combined, in the same way that red and blue make purple. Judges in these studies have agreed that mixing joy and acceptance produces the mixed emotion of love; disgust plus anger produces hatred or hostility. Such mixtures have been called *primary dyads* in the theory. One can continue on this way and account for hundreds of emotion terms by mixing two or more emotions at different levels of intensity.

As noted above, it is interesting and perhaps important that one of the hypotheses generated from this structural model is that personality traits should have a similar structure. Again we can take cues from language. Although personality is usually taught in universities as if it had little or nothing to do with emotions, words such as gloomy, resentful, anxious and calm can describe personality traits as well as emotional states. An individual can feel depressed, or be a depressed person, feel nervous or be a nervous person. Often people are able to measure both emotional states and personality traits using the same checklist of adjectives, with a simple change in instructions. When research participants are asked how they feel now, or within the past few days, the instruction asks for a self-report of an emotional state or a mood. But they can be asked how they usually feel, a question that yields information about personality traits. At the extremes are pathological states such as mania and paranoia—but even these can be conceived as extreme expressions of such basic emotions as sadness, joy and disgust. Thus personality traits may be conceptualized as being derived from mixtures of emotions. With my colleague Hope Conte, I have been able to find a circumplex structure for certain classes of personality traits.

Furthermore, in recent years there have been more than 100 published studies concerned with identifying personality characteristics in lower animals. Of course lower animals probably should be said to have temperament rather than "personality," but extraversion, emotional stability and agreeableness have shown considerable generality across species. Samuel Gosling of the University of Texas at Austin and Oliver John of the University of California, Berkeley, have identified extraversion and emotional stability as characteristics of animals as low on the phylogenetic scale as guppies and octopuses.

Some Implications

An evolutionary framework supplies the study of emotions with such concepts as functional thinking, the generality of mechanisms across phyla, developmental theory (to explain, for instance, attachment), and the concepts of inclusive fitness and proximate and ultimate causation.

Happily, in combination with the sequential, structural and derivative systems described above, evolutionary theory can provide not only a way of organizing data in the fields of emotion, personality and psychopathology, but also new tools for clinical practice.

A therapist must uncover and identify emotions. An evolutionary approach suggests that the subjective feeling states of emotion (the labels they are given) are usually more ambiguous and obscure than are the associated impulses to action. We need not insist like the behaviorists that only overt behavior is suitable for study; however, impulses to action may be probed whether or not the action takes place.

In addition, successful adaptation implies the ability to feel and express all emotions in appropriate settings. Applied to emotion, the societal dictate that "there is a time and a place for everything" actually encapsulates the idea that all emotions can be adaptive within human society. It is a matter of sorting out the specific circumstances in which emotions can sometimes fail in their adaptive tasks

The psychoevolutionary theory has guided the development of tests for measuring moods, personality traits, ego defenses and coping styles. It has also proposed a connection between emotions and the existential crises that all human beings are subject to—those involving hierarchy, territoriality, identity and temporality.

Bibliography

- Agosta, W. C. 1992. Chemical Communication: The Language of Pheromones. New York: W. H. Freeman.
- Damasio, A. R. 1994. *Descartes' Error*. New York: G. P. Putnam's Sons.
- Darwin, C. 1965. The Expression of the Emotions in Man and Animals. Chicago: University of Chicago Press. (Original work published 1872.)
- Goodall, J. 1987. The Chimpanzees of Gombe: Patterns of Behavior. Cambridge, Mass.: Belknap.
- Goodenough, U. W. 1991. Deception by pathogens. *American Scientist* 79:344–355.
- Gosling, S. D., and O. P. John. 1999. Personality dimensions in nonhuman animals: A crossspecies review. Current Directions in Psychological Science 8:69–75.
- Griffin, D. R. 1992. Animal Minds. Chicago: University of Chicago Press.
- Kessin, R. H., and M. N. Van Lookeren Campagne. 1992. The development of social amoeba. American Scientist 80:556–565.
- LeDoux, J. E. 1998. *The Emotional Brain*. London: Weidenfeld & Nicolson.
- Loomis, W. F. 1988. Four Billion Years: An Essay on the Evolution of Genes and Organisms. Sunderland, Mass.: Sinauer Associates.
- Neisser, U. 1963. The imitation of man by machines. *Science* 139:193–197.
- Owings, D. H., and E. S. Morton. 1998. Animal Vocal Communication: A New Approach. New York: Cambridge University Press.
- Plutchik, R. 1980. *Emotions: A Psychoevolutionary Synthesis*. New York: Harper & Row.
- Plutchik, R. 1989. Measuring emotions and their derivatives. In *Emotion: Theory, Research, and Experience: Vol. 4. The Measurement of Emotions* (pp. 1–35), ed. R. Plutchik and H. Kellerman. San Diego, Calif.: Academic Press.
- Plutchik, R. 1994. *The Psychology and Biology of Emotion*. New York: HarperCollins.
- Plutchik, R. 1997. The circumplex as a general model of the structure of emotions and personality. In *Circumplex Models of Personality and Emotions* (pp. 17–46), ed. R. Plutchik and H. R. Conte. Washington: American Psychological Association Press.
- Plutchik, R. 2000. Emotions in the Practice of Psychotherapy: Clinical Implications of Affect Theories. Washington: American Psychological Association Press.
- Ricci, N. 1990. The behavior of ciliated protozoa. *Animal Behavior* 40:1048–1069.
- Scott, J. P. 1980. The function of emotions in behavioral systems: A systems theory analysis. In Emotion: Theory, Research, and Experience: Vol. 1. Theories of Emotion (pp. 35–56), ed. R. Plutchik and H. Kellerman. San Diego, Calif.: Academic Press.
- Stossel, T. R. 1990. How cells crawl. *American Scientist* 78:408–423.
- Wayne, R. 1993. Excitability in plant cells. *American Scientist* 81:140-151.

Links to Internet resources for "The Nature of Emotions" are available on the *American Scientist* Web site:

http://www.americanscientist.org/ articles/01articles/plutchik.html