

The Biological Affects: A Typology

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This typology of biological affects is based on developmental–interactionist theory of motivation, emotion, and cognition. *Affects*—subjectively experienced feelings and desires—involve interoceptive perceptual systems based on primordial molecules that characterize neurochemicals. Biological affects involve primary motivational–emotional systems (primes) associated with hierarchically organized neurochemical systems in the brain, including subcortical (reptilian) and paleocortical (limbic) brain structures. Affects fulfill individualistic (selfish) functions (arousal, approach–avoidance, agonistic) and prosocial (cooperative) functions. Selfish and cooperative functions are associated respectively with the right and left hemispheres. Biological affects constitute the physiological bases for higher level affects: social affects (e.g., pride, guilt, shame, pity, jealousy), cognitive affects (e.g., curiosity, surprise), and moral affects.

The study of emotion is flourishing in the social and behavioral sciences, due in part to new capabilities to observe and measure emotion in its myriad manifestations. The resulting work has demonstrated that emotion is relevant to an extraordinary range of disciplines and levels of analysis, from the most basic genetic and neurochemical level to the cultural and historical level. However, it is sometimes unclear how what is labeled *emotion* at one level is related to what is termed emotion at another. How, for example, are basic emotions such as happiness, sadness, fear, and anger related to more primal emotions—drives of sex and power; or to such higher level emotions as pride, jealousy, shame, and remorse? Are curiosity, interest, and boredom emotions? If so, how do they relate conceptually to other emotional phenomena? What about strong feelings associated with moral judgments: admiration and veneration, scorn, and contempt? What are the emotional bases of sympathy and compassion, or cruelty and savagery?

The goal of this article is to approach these and related questions from a developmental–interactionist conceptualization that offers a unified view of motivation, emotion, and cognition (Buck, 1985). Motivation and emotion are considered to be aspects of a common core phenomenon, the motivational–emotional system. Phylogenetically structured (innate) primary motivational–emotional systems or *primes* are special-purpose processing systems that interact with general-purpose processing systems of conditioning, learning, higher order cognition—and in human beings, language—over the course of development. The article uses this general orientation to describe a hierarchy of biologically structured motivational–emotional systems. These are seen to serve as the physiological

basis for higher level social, cognitive, and moral affects. The developmental–interactionist conceptualization of motivation, emotion, and cognition does not seek to debate or refute rival conceptualizations, but rather assumes that most other views are accurate as far as they go but are incomplete. Rather than oppose other positions, the present conceptualization aims to assemble them together in a “metatheory, an integrative mechanism to show the relation between theories that are designed to handle more specific ranges of phenomena” (Buck, 1985, p. 390).

Emotion is defined in terms of readouts of primes (Buck, 1994b).¹ Subjectively experienced feelings and desires or affects are termed Emotion III, one of three sorts of readout of motivational potential that collectively constitute emotion. The other readouts are expressive displays (Emotion II) and adaptive–homeostatic arousal responses (Emotion I). This article focuses on subjectively experienced affect; it summarizes developmental–interactionist theory with appropriate references, extends it in a comprehensive typology of biological affects, and considers how biological affects relate to higher level social, cognitive, and moral affects.

Developmental–Interactionist Theory

Rationale for the Typology

Developmental–interactionist theory argues that neuroscience and evolutionary theory can provide a secure empirical and theoretical foundation for the conceptualization of emotion in general

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¹ The readout conception was presented in an oversimplified way by Fridlund (1991), who likened it to the vague, hydraulic notion of a “spillover,” as in “automatic readouts or spillovers of drive states” (p. 23). This prompted a formal response, as the concept of readout is quite different from the notion of a spillover (Buck, 1994b). A spillover suggests a process that does not occur until a certain point—the container’s edge—is reached, and then becomes uncontrolled. In contrast, the readout is conceived as a process that is constantly occurring: Motivational–emotional systems are always turned on and functioning, albeit at a level that may not be noticed. Also, although individuals may at times lose reasoned voluntary control of their behavior during strong emotion, the motivational–emotional readout does not itself become uncontrolled at a certain point.

and for subjectively experienced affect in particular. At the same time, the importance of the influence of higher level cognitive processes and, in human beings, language must be recognized. To these ends, the theory posits an interaction between physiological processes and higher order cognitive processes analogous in many respects to that proposed by Schachter (1964). He suggested on the basis of the results of the well-known study by Schachter and Singer (1962) that emotions arise from cognitive attributions about one's state of physiological arousal. In this self-attribution theory, arousal contributes the quantitative aspect of emotion, and cognitive appraisal the qualitative aspect. However, this analysis occurred before the complexity of the biological systems underlying emotion was fully appreciated. It is now clear that neurochemical systems structured by evolution can account for much of the qualitative aspect of emotion. The present article examines these neurochemical systems and proposes them as the empirical foundation for the present typology. This biologically based bottom-up approach to defining and differentiating emotions is different from most current typologies of emotion, but is similar to approaches in the tradition of Silvan Tomkins, as noted later.

Notwithstanding this emphasis on biology as the foundation of the typology, the developmental-interactionist view emphasizes the importance as well of higher order cognition and language in interaction with biological factors. In this regard, the Schachter (1964) analysis neglected the developmental aspect of emotion. If making attributions about one's state of arousal is important in emotion, it follows that *learning* how to make such attributions—how to label and respond to an arousal state in a given context—would be critical. The present approach emphasizes that the interaction between complex biological factors and higher order cognitive (and in human beings, linguistic) factors occurs in a developmental context, hence the label *developmental-interactionist*.

Top-down views of emotion. Most current typologies of emotion are based on top-down approaches that define and differentiate emotion based on higher order cognitive processes and rarely mention neurological or physiological mechanisms. Many emotion theories concentrate on how different aspects of the appraisal of environmental events give rise to specific emotions such as anger, fear, or joy (e.g., Frijda, 1994; Lazarus, 1994; Scherer, 1993). Different appraisal theorists have made predictions about how specific dimensions of appraisal, such as the controllability of the event, are associated with specific emotions (Frijda, 1986; Roseman, 1984; Scherer, 1994). Other top-down approaches view emotion in terms of cognitive science, suggesting that emotions originate as disturbances that occur when cognitive processing involving goal-directed plans is interrupted (Mandler, 1975; G. A. Miller, Galanter, & Pribram, 1960; Oatley, 1992; Oatley & Johnson-Laird, 1987; Simon, 1967).

The top-down theories—even those appraisal theories that share many fundamental assumptions—rarely agree about the number or precise nature of specific emotions. As a result, this literature is arguably somewhat fragmented and confused. Indeed, it is often difficult to specify what is and what is not an emotion.

Bottom-up approaches to emotion. Central to the theorizing of Silvan Tomkins (1962–1963, 1982a) is the notion that emotions are based on biological systems structured by evolution. Rather than stemming from higher order cognitive-appraisal processes, emotions are seen to be based on biologically structured systems

that are phylogenetic adaptations, that is, are innate. Such an approach avoids the confusion arising from top-down theories and puts the notion of emotion on a secure conceptual and empirical foundation. Indeed, the finding by Ekman, Sorenson, and Friesen (1969) that isolated tribespeople in New Guinea could both recognize and express pancultural facial displays, substantiating Tomkins's theory, perhaps more than any other single study led to the current renaissance in empirical research on emotion.

Tomkins (1982b) discussed two critical aspects of his theory. One is the notion that the affect mechanism is a separate assembly functioning to amplify other mechanisms of behavior. He argued that the affects are the primary innate biological motivating mechanisms that give urgency to the drives. As Tomkins (1982b) put it,

the drive must be assisted by affect as an *amplifier* if it is to work at all. . . . The affect is, therefore, the primary motivational system because without its amplification, nothing else matters, and with its amplification, anything else *can* matter. It thus combines urgency and generality. It lends power to memory, to perception, to thought, and to action no less than to the drives. (pp. 355–356)

The second central aspect of Tomkins's theory was that the "massive total body response" produced by the affect mechanism "center(s) on the face" (Tomkins, 1982b, p. 354) and that specific affects are associated with innate and pancultural patterns of facial responses. Tomkins argued further that the facial affect displays evolved as "sources of motivating feedback . . . the communication of affect is a secondary spin-off function" (p. 387).

Paul Ekman (1994a) and Carroll Izard (1977) each carried out with colleagues a series of studies involving the judgment of facial expressions of emotion, and each developed a conceptualization of emotion based generally on Tomkins's theory. The resulting data demonstrated to the satisfaction of most investigators that facial expressions have an innate basis, but it was also clear that facial expressions are also influenced by display rules, learned rules about what displays are appropriate under what circumstances. Both Ekman and Izard emphasized how innate factors and socio-cultural learning interact in producing the facial display, developing what Ekman and Friesen (1969, 1975) termed a neurocultural model of emotion.

The Present Approach

The approaches of Tomkins, Ekman, and Izard provide a powerful conceptualization of emotion, viewing it as based on biological systems structured by evolution to steer behavior and, at the same time, describing how cultural expectations can alter emotional reactions. However, both of the central aspects of Tomkins's theory—the notion that the affect mechanism is a separate assembly functioning to amplify other mechanisms of behavior and the emphasis on facial expression—while useful in many respects have drawbacks as well. The notion that drives lack their own biologically based motivational mechanisms is doubtful. I will argue that hunger, thirst, sex, and other drive states associated with bodily needs appear to have their own specific motivational mechanisms, and there is no evidence that more general affect systems are necessary for drives to exert powerful motivational force. Indeed, as I will argue, the more general affect systems may have evolved from more specific motivational systems.

On the other hand, the notion that affects can constitute primary innate biological motivating mechanisms that can be engaged by other systems is extremely useful when applied to the analysis of higher level social, cognitive, and moral systems. The joy and frustration that human beings can experience in exploring the environment and learning to use language, mathematics, poetry, and symbolic logic may very well be based on the ability of these high-level cognitive and linguistic systems to turn on biologically based affect systems. Similarly, the pride one feels at an accomplishment, or the shame at failure, or the moral indignation at some transgression, may be biologically based in attachment systems that make it very important to us that we are, and know how to be, accepted and loved. I argue in this article that this first aspect of Tomkins's theory is not needed to explain the power of basic biological motivational-emotional systems. At the same time, the notion that biologically based affect systems can function as general motivational mechanisms engaged by other systems, is both necessary and profoundly useful in explaining the power of higher level social, cognitive, and moral motives.

The second central aspect of Tomkins's theory, the emphasis on facial expression, as noted, contributed greatly to the current renaissance in research and theorizing on emotion, but a drawback has been that facial expression perhaps became overly emphasized in some accounts. The original notion that facial feedback functions to serve emotional experience perhaps for a time turned attention away from the important roles of central neurochemical mechanisms in emotional experience, and of the facial display in emotional communication and resulting social coordination and organization. Also, I argue that there are important biologically based emotional states that are not associated with specific pancultural facial displays, including family-related prosocial affects involved in parental, play, and bonding behaviors, and reptilian emotions involving sex and power. These arguably meet the eight criteria for biologically based human emotions suggested by Ekman (1994a): automatic appraisal, common antecedents, presence in other primates, quick onset, temporary duration, unbidden occurrence, distinctive physiology, and characteristic display. They are not, however, associated with characteristic facial displays.

In conclusion, the most powerful feature of a bottom-up view of emotion is the possibility of defining and differentiating emotions objectively, without depending on verbal labels and descriptions. Studies in the Tomkins tradition allowed the definition of emotion on the basis of objective facial expressions; this put the analysis of emotion on a secure conceptual and empirical foundation and inaugurated a renaissance of emotion research. However, as noted, the Tomkins approach tended to ignore emotions not associated with pancultural facial displays, particularly the reptilian and prosocial emotions. In the present view, emotion and, more specifically, subjectively experienced affect, can be defined and differentiated in terms of the operation of potentially observable neurochemical systems. The burgeoning understanding of these systems allows the inclusion of a wider variety of biological affects than the Tomkins tradition approach by itself encouraged.

Defining Motivation, Emotion, and Cognition

Motivation and emotion. A fundamental proposition of the present conceptualization is that one cannot coherently conceptualize or define *motivation*, *emotion*, or *cognition* without defining

the others. Each is involved in both of the others: Motivation intrinsically involves emotion and cognition, cognition involves motivation and emotion, and emotion involves motivation and cognition. Motivation is defined as the potential for behavior that is built into a system of behavior control, and emotion is defined as the readout of motivational potential when activated by a challenging stimulus (Buck, 1985, 1988b, 1993a, 1994b). Motivation and emotion are thus seen as two sides of the same coin, aspects of a motivational-emotional system (see Figure 1).

The hypothesized relationship of emotion and motivation is analogous to that of matter and energy in physics. Energy is a potential that is not seen in itself, but rather is manifested in matter, heat, light, force, and so forth. The energy potential in a coiled spring is manifested in force when the spring is released, and the energy potential in an explosive is manifested in heat, light, and force. The energy per se is never shown. Similarly, motivation is conceptualized as a potential that is not seen in itself, but rather is manifested in emotion.

Three readouts of emotion. As noted, the manifestations of motivational potential take three forms, or readouts (see Figure 1). Emotion in the ordinary language sense of the term includes all of these readouts. Emotion I (arousal) serves functions of adaptation and homeostasis through the autonomic, endocrine, and immune systems, such as the fight-or-flight response that organizes bodily resources in emergency situations. Emotion II (expression) serves functions of social coordination through expressive displays (pheromones, postures, gestures, facial expressions, and the like), such as those involved in the coordination of sexual behavior and dominance-submission signaling. Emotion III (experience) serves functions of self-regulation through subjectively experienced feelings and desires, or affects. Thus, affect is seen here in terms of the subjective experience of feelings and desires, and as noted, this affective readout is the focus of this article.

The three sorts of readout are assumed to be functionally independent, each fulfilling its own function. That is, Emotion I evolved in response to basic adaptive challenges involving the maintenance of homeostasis. Emotion II evolved in response to communicative challenges associated with social coordination. Emotion III evolved in response to challenges reflecting the organism's need to know certain bodily processes important in self-regulation, or, as we shall see, bodily affordances. This implies that subjectively experienced affect is not an epiphenomenon nor is it based on visceral-autonomic or facial-somatic feedback. Subjectively experienced affect is an independent phenomenon

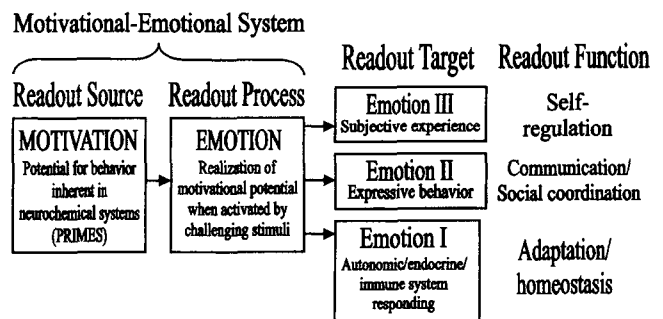


Figure 1. The readout model of motivational emotional systems.

involving an internal perceptual (interoceptive) system serving its own vital functions based ultimately on central neurochemical systems (see Buck, 1980, 1990, 1993b). This point will be expanded later.

Cognition. Cognition is defined generally as knowledge involving raw experience that, driven and guided by motivational-emotional systems, is spontaneously restructured over the course of development (Piaget, 1971). In the present conceptualization, affect constitutes a kind of knowledge: a kind of cognition. Two sorts of cognition are distinguished: *syncretic cognition* is hot, holistic, direct, immediate, and self-evident raw acquaintance; *analytic cognition* is cold, sequential, serial, and linear information processing (see Buck, 1988a, 1990; Buck & Chaudhuri, 1994; Chaudhuri & Buck, 1995; Tucker, 1981). In the next paragraphs I argue that the raw syncretic experience of affect can be conceptualized as a Gibsonian direct awareness of bodily affordances through interoceptive perceptual systems.

Knowledge-by-acquaintance versus knowledge-by-description. The analytic versus syncretic cognition distinction is related to, but not identical to, a distinction between knowledge-by-acquaintance versus knowledge-by-description. Knowledge-by-acquaintance is raw awareness. It was described by Bertrand Russell (1912) as the "presentational immediacy of experience" that is completely self-evident (p. 73). William James (1890) noted,

I know the color blue when I see it, and the flavor of a pear when I taste it . . . but *about* the inner nature of these facts or what makes them what they are I can say nothing at all. I cannot impart acquaintance with them to any one who has not made it himself. (p. 221)

Knowledge-by-acquaintance is always syncretic: direct, immediate, and holistic.

In contrast, knowledge-by-description is constructed from the restructuring or processing of raw perceptual data into an internal representation of reality. Thus, we have direct perceptual acquaintance with events, and knowledge *about* these events based on information processing and inference. Analytic cognition always involves knowledge-by-description, or knowledge *about* knowledge, which is not self-evident but can be false. In analytic cognition information is processed sequentially in a linear fashion, so that discrete pieces of information are serially related to one another. Syncretic cognition may be known by description, as when one element is known spatially relative to another (see Buck, 1990).²

The distinction between knowledge-by-acquaintance and knowledge-by-description has long been made in epistemology. It was made by St. Augustine in *De Magistro* (Marsh, 1956), and it is reflected in many languages, as in the French *connaître* versus *savoir* (James, 1890). The relevance to emotion theory of the distinction between knowledge-by-acquaintance and knowledge-by-description has been increasingly recognized in recent years (Ekman & Davidson, 1994; Epstein, Pacini, Denes-Raj, & Heier, 1996; Laird, 1996; Lazarus, 1991a, 1991b; Strack, 1996).

Gibsonian awareness and affect. Knowledge-by-acquaintance constitutes the raw data of perception, based on perceptual systems evolved to detect information in the form of stimulus energy: in light, vibration, and volatile chemical substances physically present in the environment (Gibson, 1966, 1979). James J. Gibson's theory of ecological realism provides a coherent and detailed account of the evolution of knowledge-by-acquaintance from the

earliest organisms to human perception. Gibson (1979) termed raw perception *awareness*, "To perceive is to be aware of the surfaces of the environment and of oneself in it" (p. 255). According to Gibson (1979), species evolved to be sensitive to those aspects of the environment that afford possibilities or opportunities for behavior, affordances. There are three sorts of raw awareness. First, there is awareness of affordances in the terrestrial environment; this is elementary perception. Second, there is awareness of social affordances provided by other animals; "other animals afford, above all, a rich and complex set of interactions, sexual, predatory, nurturing, fighting, playing, co-operating, and communicating" (Gibson, 1979, p. 128). Emotion II displays are social affordances (Buck, 1984; Buck & Ginsburg, 1997a; McArthur & Baron, 1983). Third, and most relevant to the present article, Gibson (1966) recognized awareness through interoceptors of vague sensations of internal origin—feelings and emotions—the "pangs and pressures of the internal environment" (p. 31). These may be conceptualized as bodily affordances, and in the present view, affects—awareness of the Emotion III readout—constitute awareness of bodily affordances.

This notion of a system of internal perception evolved to pick up interoceptive information (affordances) differs from the theories of James (1890), Tomkins (1962–1963), and others who emphasize feedback from peripheral (autonomic, proprioceptive, somatic) systems. The contribution of autonomic (and also expressive) feedback appears to be minimal; on the basis of the lack of sensory as opposed to motor fibers, the viscera and organs of expression (particularly the face) are not optimally organized to pass feedback information to the brain. Indeed, people are relatively insensitive to autonomic cues (Blascovich & Katkin, 1982), and the importance of facial-somatic feedback is also doubtful (Buck, 1980). Moreover, research paradigms such as those involving vocalizations and place preferences in animals (Panksepp, 1989), as well as subjective reports in humans, suggest that organisms are exquisitely sensitive to the actions of certain neurochemical systems.

In the present view, the subjective experience of affects involves the perception of interoceptive stimuli associated with the response of specifiable central neurochemical systems. Ancient informational molecules, particularly peptides, carry out this interoceptive sensory function. In other words, the activity of specific neurochemical systems is associated with interoceptive stimuli affording knowledge-by-acquaintance (awareness) of affects. Affects are

² *Agnosias*, in which elementary perception is intact but "stripped of meaning" (Bauer, 1984, p. 457), may constitute an inability to transfer knowledge-by-acquaintance into knowledge-by-description (Buck, 1990). Agnosias are caused by certain kinds of brain damage, particularly disconnections between sensory and association areas of the cortex. They involve disorders of recognition not caused by sensory dysfunction or unfamiliarity with the stimulus; thus, *prosopagnosia* is the inability to recognize and make discriminations between faces, even the familiar faces of loved ones. The patient may, however, recognize such faces on an unconscious level. Bauer (1984) and Tranel and Damasio (1985) demonstrated that prosopagnosic patients shown pictures of familiar faces have electrodermal responses to the correct name. Agnosias are often strikingly specific to a specific category of stimulus: One patient with long-term bilateral damage to the amygdala could recognize faces and most facial expressions of emotion, but manifested a specific inability to recognize expressions of fear (Adolphs, Tranel, Damasio, & Damasio, 1994; Hamann et al., 1996).

related to universal functional organism–environment contingencies, event clusters that have demanded similar general sorts of adaptation so repeatedly in phylogeny that systems of interoceptive perception have evolved to deal with them, just as systems of exteroceptive perception evolved. The most basic of such contingencies include event clusters involving the basic drives (hunger, thirst, pain avoidance) and biological affects (arousal, approach, avoidance, fighting, and mating).

Special-purpose versus general-purpose processing systems. The perceptual systems that provide knowledge-by-acquaintance are innate; that is, they are phylogenetic adaptations reflecting the operation of genetic systems selected in the process of evolution. These are special-purpose processing systems, in that they have evolved to perform specific functions that in themselves are entirely unlearned (Buck, 1985). In the case of perceptual systems, the function is to provide access to information physically present in the terrestrial environment, that is, information in the light, in vibration, and in volatile chemicals. In the case of the primary motivational–emotional systems or primes, the function is to respond to event clusters that have constituted specific sorts of challenges to individual and species survival over the course of evolution. The responses to such challenges include, as I will show, arousal, approach–avoidance, aggression, sex, and other behaviors supportive of the survival of the individual and the species.

In contrast, knowledge-by-description is a function of general-purpose processing systems that are structured over the course of individual development, that is, by the individual's experience during ontogeny. They reflect the capacity of the species for learning through classical conditioning, instrumental learning, higher order cognitive processing, and language.

Conclusions. To restate the foregoing argument in somewhat different terms, I suggest that the necessary and sufficient conditions for emotion consist of the readout, in response to a challenging stimulus, of potential built into a system of behavior control. This states necessary and sufficient conditions for defining, not only emotion, but also motivation and cognition. The primitive terms of the definition, including challenge, built-in, and behavior control, imply contingencies associated with the natural organism–environment interaction described by Gibson (1966). All organisms have evolved perceptual systems that can be informed by (or can be aware of) certain sorts of events, affordances, in the terrestrial environment. Affordances inform the organism; thus, they constitute information.

Gibson (1966, 1979) argued that the organism, the environment, and information define each other; without an organism (e.g., on a lifeless planet) there is a physical reality but no environment and no information. With the evolution of a self-replicating molecule such as DNA, an organism, environment, and information are simultaneously created, and with the commencement of natural selection, motivation, emotion, and cognition are created as well. Information implies cognition, and motivational–emotional systems sort out the relative importance of information. They evolve to prioritize, to respond to the extent to which events are challenging. Thus, motivational–emotional systems arise by definition with the natural selection of organisms on the basis of their adaptation to challenging environmental events.

It might be noted that, in this definition, motivational–emotional systems, emotional readouts, and raw awareness occur in the

simplest of creatures, but cannot occur in even the most sophisticated of computers. Computers can be very efficient at processing information but they are never actually informed. They respond only to what they are told; they lack the independent knowledge or awareness of affordances in the environment and the capacity independently to adapt that is demonstrated by the most elementary of life forms.

Primary Motivational–Emotional Systems (Primes)

Basic to developmental–interactionist theory is the notion of an interaction between special-purpose systems and general-purpose systems that takes place in a developmental context. More specifically, biologically based primes are considered to be special-purpose systems arranged in a hierarchy, in which the interaction with general-purpose systems becomes more important as one goes up the hierarchy (Buck, 1985). As noted, the readouts of special-purpose systems are in themselves entirely unlearned, but as one goes up the hierarchy, special-purpose systems interact progressively more extensively with general-purpose systems, so that their functioning becomes progressively more flexible and open to learning, cognitive processing, and language. The progressive evolution of learning and cognitive abilities that confer increased behavioral plasticity has been termed *anagenesis* (Gottlieb, 1984).

The simplest sorts of primes are reflexes, such as the knee-jerk reaction. Here, the response of the reflex per se is wholly hard-wired and innate with virtually no flexibility, although reflexes may be combined into relatively complex self-organizing systems: taxes and tropisms (Cofer & Appley, 1964). At the next point on the hierarchy are fixed action patterns or instincts, such as those that motivate the homing and migration migrations of birds and fish. These can involve complex patterns of behavior, which are quite inflexible when examined closely; one cannot teach salmon to change their migratory behavior. The next level of the primes does, however, involve flexibility. Drives involve bodily needs that are signaled to the organism by subjectively experienced affects: feelings and desires (Buck, 1993b). The organism that is hungry, or thirsty, or cold, or in pain is signaled by specific bodily messages. These serve to activate and direct behavior so that the organism has the capacity to explore its surroundings in search of the relevant resources. If the organism is successful in finding food, water, or other resources that satisfy its needs, satiation occurs and the behavior leading to the reward is reinforced. Stimuli associated with reward become positive incentives that can serve as cues in the future when similar needs arise, so that the organism is steered efficiently to the goal. Contrariwise, punishment produces negative incentives that are avoided.

The drives involve specific bodily needs and consummatory behaviors that function to satisfy those needs. The next level of the hierarchy does not involve specific needs or consummatory behaviors. This is the level of the primary affects of Tomkins (1962–1963), Ekman (1994b; Ekman & Friesen, 1969), and Izard (1992, 1994): happiness, sadness, fear, anger, and disgust. These signal the bodily state but do not directly influence behavior. The individual knows that he or she is happy, or angry, and may or may not know why; however, unlike some theorists I do not believe that any specific behavior tendencies are activated. Indeed, the affects function to facilitate flexibility and choice among alternative be-

haviors. The individual has a choice about what to do, and if, for example, anger is felt toward a large person or a small person, the behavior will be different.

As one proceeds up the hierarchy from reflexes to instincts, to drives, to affects, the interaction between special-purpose systems and general-purpose systems has increasingly favored the latter. Arguably, the resulting affect-reason dimension presented in Figure 2 more accurately reflects the relationship between innate factors and learning than does the more usual categorical distinction between emotion and cognition. Also, other phenomena may be meaningfully placed on this dimension. For example, the dimension mirrors the phylogenetic scale, with simple creatures' behavior being mostly a matter of reflex systems (e.g., ants and bees) and creatures with significant analytic-cognitive capacities being at the other extreme. Also, the developmental scale may be represented with the more hard-wired infant at the left and the adult at the right. Similarly, this dimension represents the evolution of the nervous system, with functions served by more primitive structures to the left and increasingly complex functions based on brainstem, hypothalamic, reptilian, paleocortical and neocortical processing to the right.

Affects

Definition. Emotion II involves displays and preattunements affording a direct knowledge-by-acquaintance of others' displays—social affordances in the Gibsonian sense—serving functions of social coordination and, ultimately, social organization (Buck & Ginsburg, 1997a). Analogously, Emotion III is a direct knowledge-by-acquaintance of one's own feelings and desires—in Gibsonian terms a direct interoceptive awareness of bodily affordances serving functions of self-regulation. To repeat, bodily af-

fordances in this context do not involve feedback from autonomic responses or expressive behaviors, rather, Emotion III involves systems of internal perception, or interoceptive perceptual systems, that have evolved to inform the organism of specific events in the bodily milieu.³ The experiential aspects or qualia associated with these interoceptive perceptual systems are feelings and desires, or affects. The event clusters of which they inform include the organism's needs for food (hunger), for water (thirst), for warmth or cold, for sex, and so forth; these are drives involving specific bodily needs. We are also informed of more general need states involving the primary affects of happiness, sadness, fear, anger, and so forth.

More specifically, affect is defined formally as the direct knowledge-by-acquaintance of feelings and desires, based on readouts of specifiable neurochemical systems evolved by natural selection as phylogenetic adaptations functioning to inform the organism of certain bodily events important in self-regulation (Buck, 1985, 1993b, 1994b). Affects are special-purpose, gene-based, neurochemical readouts. Human beings experience affects immediately and directly; the phenomenological subjective reality of affect is self-evident.

In addition, affects are always present; a constant readout of feelings and desires is available to the organism at all times. Information concerning these bodily events is always with us; we can always turn our attention to pick up how hungry, or thirsty, or warm we are, and also how happy, sad, or angry. We tend spontaneously to notice this information only when it is strong or sudden, but like the feel of our shoes on our feet, it is always with us. Relatively strong affects associated with specific elicitors are termed in ordinary language *emotions* as compared with *moods*, which are longer lasting and are not so associated with specific elicitors (see Ekman & Davidson, 1994). Unlike theories that regard emotions as temporary phenomena, the present approach argues that all affects are always turned on, albeit generally at low levels so they are not consciously noticed.

The aspect of affects that makes them problematic for objective science is that they are essentially subjective private events. B. F. Skinner (1953) described the realm of "the world within one's skin" in terms of private events that "may be distinguished by (their) limited accessibility but not, so far as we know, by any special structure or nature" (p. 257). He emphasized that what is different and unique about such events is their "degree of accessibility to the community" (p. 262), which makes it difficult to establish a reliable vocabulary to describe such events. It also makes them singular from a social learning point of view.

Learning about affects: Accessibility and emotional education. Although functioning independently, the Emotion I, II, and III readouts are all reflections of the same motivational-emotional state, so that early in life they are closely correlated to one another. Expression and feeling, for example, are often shown together in young children (Izard, 1978). However, the three readouts are differentially accessible in the process of social learning, so that

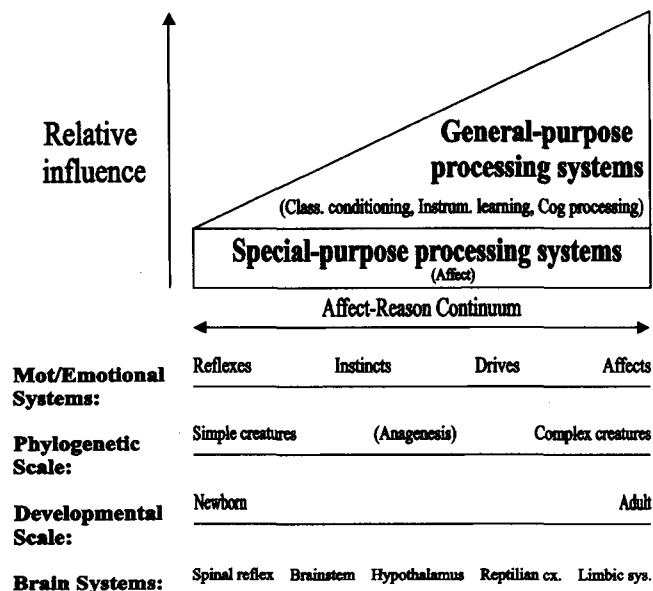


Figure 2. Interaction of special-purpose processing systems (biogenetic factors) and general-purpose processing systems (psychosocial factors) in behavior. Class. = classical; instrum. = instrumental; cog = cognitive; mot = motivational; cx = complex; sys = system.

³ There is a classic question regarding whether autonomic or somatic/facial feedback, or both, affect subjective experience. The position here is that neither is necessary or sufficient for affective experience, but that both may influence neurochemical systems and thereby subjective experience through interoceptive conditioning (Buck, 1980).

they become related to one another in increasingly complex ways over the course of development. Emotion III (experience) is accessible only to the responder, Emotion II (expression) is accessible more to the other than to the responder, and Emotion I (arousal) is normally not accessible without special physiological recording equipment (see Figure 3). Thus, affects are not accessible to others; they are accessible directly only to the responder. The parent does not have direct access to the child's affect or the child to the parent's affect. Therefore, affects must undergo a different sort of social learning than openly accessible events.

Because directly experienced affects are not accessible to others, we learn about affects indirectly, through *emotional education* involving emotional communication (Buck, 1983). Knowing affects by description—that is, being able to respond appropriately and to linguistically label and understand them—requires the same kind of learning and information processing that is required for learning about events in the external environment. Indeed, there is an intrinsic interest and curiosity about the experience of affects just as there is about understanding other aspects of experience. This explains the natural fascination with both positive and negative affects that is reflected in humans' attraction to emotionally arousing media: literature, drama, music, and film.

However, because affects are not accessible to others, the social learning process by which emotions are educated is different from other sorts of social learning, and accurate emotional communication between parent and child is particularly important. Children learn about their subjectively experienced feelings and desires largely through the feedback from others responding to their expressive behaviors. This is termed *social biofeedback* because the behavior of the other provides the child with feedback about a bodily process that is otherwise inaccessible to the child (Buck,

1988b). Also, children imitate and model the emotional behaviors of others; they are strongly drawn to media depictions particularly of affects (such as sex and aggression) that are difficult to deal with interpersonally (Buck, 1988a). The result of social biofeedback and imitation/modeling is emotional education. Children learn labels and expectations concerning their subjectively experienced feelings and desires. The outcome of emotional education is a greater or lesser degree of *emotional competence*. Children learn, or fail to learn, to label their feelings and desires appropriately and to know what to do when these affects occur. Thus, a fundamental proposition of readout theory is that successful emotional education leads to emotional competence, the ability to follow cultural display rules to label, understand, and appropriately express feelings and desires. Contrariwise, deficits in emotional education lead to a kind of emotional helplessness that may contribute significantly to psychopathology (Buck, Easton, & Goldman, 1995; Buck, Goldman, Easton, & Norelli Smith, 1998).

The remainder of this article uses the foregoing conceptualization as a basis for a typology of affects. First, it examines an anatomically based hierarchy of biological affects, beginning with those associated with the more primitive neurochemical systems in the brainstem and midbrain, proceeding to the hypothalamus, to those associated with reptilian and paleocortical or limbic system structures.⁴ It then examines neurochemical networks that cross levels of this anatomical hierarchy. In each case, I review briefly the relevant literature. I then consider how the biological affects serve as the physiological bases of higher level social, cognitive, and moral affects.

Biological Affects I: The Anatomical Hierarchy

Biological affects are readouts of phylogenetically structured primary motivational-emotional systems (primes) associated with specific neurochemical systems. I suggest that the relationship of biological factors to higher level social, cognitive, and moral affects, albeit real, is indirect. With the biological affects, it is possible in principle, and increasingly in practice, to define them operationally in terms of activities of specific neurochemical systems, the presence of neurotransmitters with their agonists and antagonists acting on receptor sites of a specifiable number, anatomical location, and degree of sensitivity.

Using evidence from stimulation and lesioning techniques, many brain functions historically have been associated with specific anatomical locations (the brainstem, the hypothalamus), but newer evidence has made it clear that most brain functions cross hierarchical levels. Therefore, the consideration of the biological affects is organized into two sections. This first section is organized by general brain anatomy proceeding up the hierarchy of brain systems from the brainstem to the limbic system. The second section is organized by individualistic (selfish) and prosocial (cooperative) functions that cross the anatomical hierarchy and are associated with specific neurochemical systems.

What follows is a necessarily brief review of a vast, highly technical, and rapidly growing area of research (see Buck, 1988b;

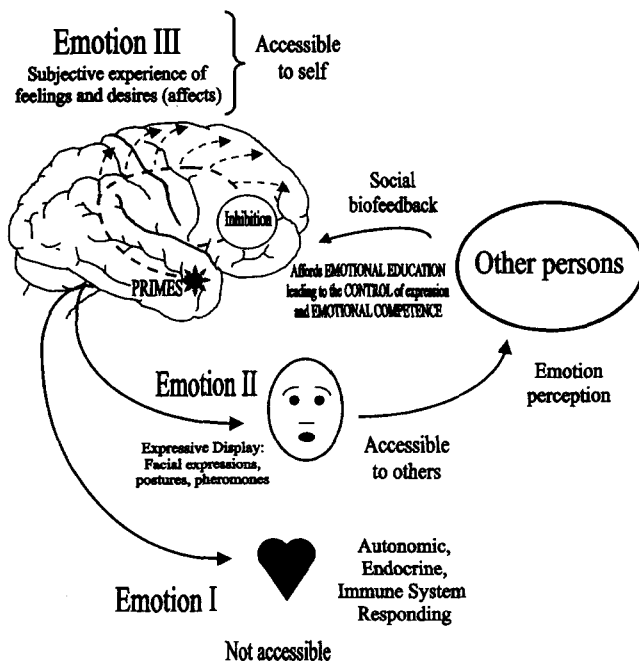


Figure 3. Emotional expression, emotional communication, and social biofeedback.

⁴ The limbic system is defined here as including all paleocortical structures plus the amygdala (Grossman, 1967). Paleocortical or old-layered neural tissue has three to five layers and includes the cingulate and hippocampal gyri; neocortical new-layered tissue has six layers.

Carter, Lederhendler, & Kirkpatrick, 1997; Le Doux 1986, 1993, 1996; Panksepp, 1989, 1993). Findings are presented in historical context, summarizing classic positions that, although often elaborated and complicated by recent findings, nevertheless reveal the basic functions and modes of responding of different brain areas.

Dimensional Versus Typological Views of Affects

There is a long-standing controversy between typological and dimensional classifications of affects. On the one hand, using pan-cultural facial expressions as a major defining feature, Tomkins (1962-1963) used a typological classification of primary affects, distinguishing happiness, sadness, fear, anger, surprise, disgust/contempt, interest, and shame. Ekman and Friesen (1975) and Izard (1971) carried on Tomkins's approach with modifications. On the other hand, studies using the scaling of affective judgments suggest that affects in human beings can be described by dimensions, the most common being arousal and pleasant-unpleasant dimensions (see J. A. Russell & Mehrabian, 1977; Schlosberg, 1952; Tellegen, 1985; Watson & Clark, 1994; Thayer, 1989). The debate between these approaches surfaced anew when J. A. Russell (1994) argued that facial expressions held by Tomkins, Ekman, and Izard to express universal affects might in fact only express degrees of positivity-negativity (see Ekman, 1994b; Izard, 1994).

In the present view, both the dimensional and typological views are correct, but are directed at different levels of the hierarchy of neurochemical systems associated with affects (Buck, 1985). At the base of the hierarchy, arousal and pleasant-unpleasant dimensions are, indeed, fundamental in a sense. The behaviors of even the simplest of creatures vary along arousal and approach-avoidance dimensions, and there are neural systems in the brainstem and hypothalamus associated with these dimensions of behavior located in phylogenetically older parts of the brain.⁵ The influences of these systems persist in specific affects associated with the limbic system. These too can be considered in a general sense to vary along arousal and positive-negative dimensions. But to conclude that arousal and pleasant-unpleasant dimensions are all there is to affect is a mistake, for there is plentiful evidence that different neurochemical systems are associated with happiness, sadness, anger, and fear. Also, we shall see that there is another fundamental dimension of affect that is often overlooked, but that also has its base in the behavior of the simplest of creatures. Some affects are inherently selfish, directed toward the survival of the individual organism, whereas others are inherently social, directed at the survival of the species (MacLean, 1970, 1973, 1993). Of particular interest in this regard are the reptilian affects based on raw and fundamental social and selfish tendencies—sex and aggression—that have been neglected in most current theories of emotion.

Brainstem/Midbrain

The first group of biological primary motivational-emotional systems or primes in the typology involves systems of arousal and approach-avoidance. They are associated with neurochemical systems at the base of the anatomical hierarchy, the brainstem and midbrain. It should be emphasized again that this typology of

biological affects is not logically organized, but rather is biologically organized, following the anatomy of the brain.

Arousal. The reticular formation is a network (reticulum) of fibers and cell bodies in the core of the brainstem extending from the spinal cord to the thalamus. Its importance in the control of arousal and attentional processes was suggested in 1935 by Bremer, who separated the reticular formation from the rest of the brain in cats and demonstrated that coma resulted. Later, Moruzzi and Magoun (1949) found that electrical stimulation of the reticular formation produces electroencephalographic arousal and alerting. Lindsley (1951, 1957) suggested that the ascending reticular activating system (ARAS) is the physiological basis for general arousal. More recent research threw into question this relatively clear and simple picture of the role of the ARAS and the unitary nature of arousal. There appear to be different sorts of arousal: Type I associated with voluntary and purposive behaviors and Type II with automatic behaviors such as startle, vocalization, ejaculation, urination, and defecation (Vanderwolf & Robinson, 1981). The first sort of arousal appears to be cholinergic, with acetylcholine (ACh) as the neurotransmitter (Napier, Kalivas, & Hanin, 1991; Steriade, Gloor, Llinas, Lóse de Silva, & Mesulam, 1990).

The anatomical position of the ARAS in relation to incoming sensory systems suggests how it can function as a filter to produce habituation, blocking incoming stimulation. Much information entering the central nervous system is irrelevant (e.g., the feel of our shoes on our feet). Sensory pathways send fibers into the ARAS so that if the stimulation is weak or repetitive, or both, the ARAS may function to inhibit or fail to excite the brain with regard to that particular stimulation. The ARAS need not know what the stimulus is, only that it is weak or repetitive, or both. Any stimuli that meet these criteria will be, in effect, filtered out.

Approach-avoidance tendencies. Like arousal, approach and avoidance are among the most ancient of functions of systems controlling behavior. Protective reflexes appear in peripheral structures, helping to remove the hand from a hot stove or steel the eardrum against loud noise much more quickly than would be possible were higher centers involved. Pain is one of the most vital of the senses and is associated with neural systems in the spinal cord in which the actions of the neurotransmitter carrying the pain signal, the peptide Substance P, are modulated by important affect-related neuropeptides: endorphins.⁶

The midbrain, specifically the limbic midbrain area, is the origin of systems associated with general approach and avoidance. These systems cross hierarchical levels; reward and punishment effects are associated, respectively, with the medial forebrain bundle (MFB) and the periventricular system (PVS), which course from

⁵ Phylogenetically old structures of the brain are in a sense just as new as the rest of the brain. As evolution proceeds the phylogenetically older structures do change. They are phylogenetically old in the sense that in their general anatomical location they appear earlier in the phylogeny and prenatal ontogeny of the brain and that they are associated with more fundamental functions.

⁶ *Peptides* are generally defined as relatively short chains of fewer than 100 amino acids. Long chains (more than 200) of amino acids are generally considered to be proteins, although some long chains are neurochemically active.

the midbrain through the hypothalamus into the forebrain. The MFB and PVS were distinguished anatomically by Le Gros and Clark in 1932 (Le Gros, Clark, Beattie, Riddoch, & Dott, 1938).

The Hypothalamus

The second group of biological primes in the typology involves systems of reward–punishment or expectancy, defensive and offensive attack, submission, attachment, and sex. They are associated with neurochemical systems in the hypothalamus.

The hypothalamus is well placed to gather evidence of bodily conditions relevant to motivation and emotion. It is liberally supplied with blood vessels that carry chemicals relevant to nutrients, fluid balances, and hormone levels. Also, the hypothalamus plays a major role in the bodily expression of emotion. First, it controls directly the autonomic nervous system. As Hess (1954, 1957) suggested, the anterior hypothalamus is associated with the parasympathetic branch of the autonomic nervous system (source of the relaxation response) and the posterior hypothalamus with the sympathetic branch (source of the fight-or-flight response). The anterior region is also associated with prosocial behaviors involving submission, attachment, and sex, whereas the posterior region is associated with individualistic or selfish behaviors involving aggression, defense, and flight. Second, the hypothalamus controls directly the endocrine system through the pituitary, physically connected to the ventromedial (VM) region of the hypothalamus. However, the hypothalamus does not play an executive role in emotion, typically acting under the influence of higher systems.

Reward–punishment/expectancy systems. As noted, the MFB and PVS course from the midbrain to higher structures through the hypothalamus. James Olds and his colleagues demonstrated that rats would press a bar to stimulate their own brains frequently and untiringly over long periods of time. They would cross a shock grid to get to the bar and ignore food when hungry to press the bar (J. Olds, 1958; J. Olds & Milner, 1954; Routtenberg & Lindy, 1955). J. Olds found these reward effects in much of the limbic system, particularly the septal area, but they were strongest in the MFB coursing through the lateral hypothalamus (M. E. Olds & Fobes, 1981). At about the same time, Delgado and his colleagues found that animals would avoid behavior associated with stimulation in certain areas of the brain (Delgado, Roberts, & Miller, 1954). The strongest of these punishing effects were found in the PVS coursing through the VM hypothalamus, parallel but medial to the MFB (M. E. Olds & Olds, 1963). Routtenberg (1978) concluded that the MFB and PVS are discrete but interacting parallel pathways that, with the reticular formation, mediate motivation. The ARAS mediates general arousal and attention, the reward and punishment systems steer behavior.

A fundamental question about these studies concerns the nature of the motivational state associated with self-stimulation, particularly whether subjective experienced pleasure is involved. J. Olds (1956) assumed that the stimulation was perceived as pleasurable, terming the rewards systems *pleasure centers*. However, if stimulation were withheld for a time, a satiated animal often appeared to lose interest in it, and Deutsch (1963) suggested, on the one hand, that brain stimulation might itself produce the drive for brain stimulation. On the other hand, hungry rats did not lose interest when stimulation was withheld.

Panksepp (1981, 1982) suggested that the MFB reward system

involves a general expectancy that may be associated with the appetitive component of a number of different drives. More specifically, there are centers in the hypothalamus associated with a number of primary drives, including hunger, thirst, sex, and temperature balance (Teitelbaum, 1961). Panksepp (1981, 1982) suggested that these centers contain homeostatic receptors that sense specific imbalances in the internal environment associated with bodily needs. These are capable of influencing activity in the general excitatory (reward) and inhibitory (punishment) pathways coursing through the hypothalamus, so that the animal's behavior is appropriately steered or directed relative to incentives in the environment: food, water, sexual partners, and warmth or coolness. The result is to “elaborate a general capacity of an animal to obtain the fruits of the environment” (Panksepp, 1981, p. 295)—and, one might add, to avoid its pitfalls. The mechanism allowing signals of bodily needs to coordinate with general systems of reward and punishment is a natural extension of the approach and avoidance behaviors of simpler creatures. It made possible a flexible system of instrumental learning, and expectancy system that is responsive to the environment as experienced by the individual organism. This is a general-purpose system.

The organization of drives in the hypothalamus is relevant to Tomkins's (1982b) analysis, noted previously, that the affect mechanism is a separate assembly functioning to amplify other mechanisms of behavior. Specific drive centers in the hypothalamus appear to exert their own independent motivational force, contrary to Tomkins's theory. At the same time, the general expectancy system appears to work much as Tomkins described: to contribute urgency in response to a wide variety of situations and events. I suggest that the specific motivational force exerted by drives in response to stimuli relevant to bodily needs evolved into the more general-purpose affect systems characterized in this case by the expectancy system.

But are these excitatory and inhibitory processes indeed subjectively perceived as affects? One way to investigate this is to determine whether an animal can discriminate between stimulation at different brain sites. Using discrimination learning tasks, Stutz and colleagues suggested that stimulation to different sites within the hypothalamus, and to the hypothalamus and septal area, are perceived as much the same (Stutz, Butcher, & Rossi, 1969; Stutz, Rossi, Hastings, & Brunner, 1974). Discrimination was faster when stimulation was applied to the same structure on the opposite sides of the brain than when stimulation was applied to different structures on the same side of the brain. Panksepp (1981) concluded that anatomically different structures on the same side of the brain produce a “homogenous emotive process” (p. 295).

Another way to investigate the issue of the subjective perception of brain stimulation is to investigate the effects of such stimulation in conscious human beings. The results of self-stimulation studies conducted in the 1950s and 1960s are inconclusive. Bishop, Elder, and Heath (1963) found that overcooperative patients kept pushing a stimulation button regardless of reinforcement schedule, even if the stimulus current were turned off. Sem-Jacobson (1968) suggested that the dominant motivation of patients may often be curiosity, and they may continue to self-stimulate to explore an indefinable sensation even if it is mildly unpleasant. Regarding self-reported emotional experience to brain stimulation, Heath (1963, 1964) reported findings generally consistent with the animal data, with positive responses to stimulation in the lateral

limbic midbrain area and MFB, and stimulation of the medial limbic midbrain area and PVS often eliciting discomfort. The positive responses elicited by septal stimulation often had sexual content, which was absent from the MFB stimulation. J. C. White (1940) reported that electrical stimulation of the hypothalamus did not produce emotional changes in conscious human beings, although strong autonomic responses occurred. Similarly, in his study of 2,651 electrode sites in 82 patients, Sem-Jacobson (1968) found that stimulation of the hypothalamus produced relatively few changes in mood or consciousness.

Still another way to investigate the relationship between the brain and subjective experience is through the subjective responses to manipulations of neurochemical levels. There is much evidence that rewarding and punishing effects are associated with different neurotransmitters, with the most powerful reward effects associated with the catecholaminergic neurotransmitters dopamine (DA) and norepinephrine (NE) and the endogenous morphines or endorphins. Stein (1964, 1968, 1978) suggested that DA is involved in the general activation and initiation of behavior, NE steers or directs the animal to the goal by increasing the signal-to-noise ratio in the brain, and endorphin systems are involved in the relaxed termination of behavior once needs are satisfied (satiated). Recently, Berridge (1996) has made a similar distinction between wanting (associated with DA) and liking (associated with the opioids). These transmitters are associated with drugs of abuse in human beings: Cocaine and amphetamine mimic natural increases in DA and NE levels, and heroin and other opiates mimic increases in endorphin levels (see Koob & Nestler, 1997). As discussed later, drugs that increase levels of the catecholamines tend to have antidepressant, stimulating effects, whereas drugs that reduce or inhibit the catecholamines tend to have sedating or depressing effects, or both (Schildkraut & Kety, 1967).⁷

In summary, activities in reward and punishment systems appear to be accessible to the individual in the form of subjectively experienced affect. Other data on drug discrimination suggest that rats have access to levels of DA (e.g., Barrett, White, & Caul, 1992). However, in the sorts of studies we have considered it is unclear whether this subjectively experienced pleasure and punishment are due to events in the hypothalamus per se or whether the hypothalamic systems are interacting with higher limbic level systems. In any event, the expectancy system indeed appears to function as a general-purpose affective-motivational system along the lines of Tomkins's (1982b) analysis.

Defense, submission, and offensive attack. The hypothalamus is associated with a mechanism by which bodily drives such as hunger, thirst, and sex join together with general reward and punishment systems to obtain the fruits of the environment and avoid its pitfalls, resulting in the capacity for reward-based instrumental learning. Other hypothalamic systems are involved with specific emotions of other sorts, some involving agonistic fight-flight responses, others involving social attachment.

The hypothalamus has been implicated in aggressive behavior since the 1920s. Cannon, Bard and colleagues studied the sham rage response in decorticate cats (Cannon & Britton, 1925). The sham rage response is a ferocious-looking display of hissing, spitting, and clawing, with increased heart rate, blood pressure, sweating, and erection of hair, which was termed *sham* because Cannon assumed that the decorticate animal was incapable of experiencing emotion. Bard (1928) showed that the posterior part

of the hypothalamus was necessary for an integrated sham rage response. When it was removed, only isolated components of the response were observed. In the same year, Hess (1928) reported that electrical stimulation of the perifornical region of the posterior hypothalamus produced well-coordinated rage responses directed against an object of attack. Later studies suggested that rage reactions are channeled from the perifornical region to the central gray of the midbrain (Hunsperger, 1956; MacLean, 1969).

Adams (1979) suggested that the rage reaction is a defensive attack that evolved to protect the organism from attack by predators and that this system was modified in social species to reduce harmful fighting within the group. A submission system evolved in which attack by a dominant and familiar consociate produced, not defensive attack, but submissive behaviors that in turn inhibited the consociate's attack. Some behaviors are common to submissive and defensive attack: a defensive posture, freezing, fleeing, hissing, and squealing. However, whereas defensive attack includes lunging, biting, and striking, submission includes specific postures and vocalizations that appear to constitute appeasement gestures (Lorenz, 1966). Adams suggested that a consociate modulator associated with the VM hypothalamus mediates submission and functions to inhibit the defensive attack.

Another kind of aggressive behavior associated with the hypothalamus is offensive attack, associated with approach and chase and a quiet biting attack. This is associated with the lateral nucleus (LN) of the hypothalamus (Eggar & Flynn, 1963; Hess & Brugger, 1943; Wasman & Flynn, 1962), a region also associated with eating (Brugger, 1943; Teitelbaum, 1961). Offensive attack may correspond with predatory aggression in Moyer's (1968, 1976) typology of aggressive behavior, whereas defensive attack corresponds with fear-induced aggression.

Attachment. Separation from consociates produces distress vocalizations in many species of birds and mammals, particularly in the young. Nestling birds, chicks, kittens, puppies, plus monkey, ape, and human infants show separation induced distress vocalizations (Scott, 1974). Panksepp (1981, 1982) suggested that these calls activate care giving and maternal-parental behaviors. Panksepp studied the brain regions associated with these distress calls, finding them to be rich in the brain's endogenous opiates, the endorphins. In the hypothalamus these regions are found in anterior regions and the preoptic area (POA). Panksepp suggested that the brain opiate systems constitute, in effect, a physiological substrate for attachment and social cohesion (Panksepp, Nelson, & Bekkedal, 1997). It is noteworthy that distress calls do not occur in most reptiles. As noted later, most reptiles are born relatively self-sufficient, without the need for parental care. Correspondingly, parental care is absent in most reptiles, and indeed distress calls might tend to be counterproductive, as some adult reptiles eat their young.

⁷ The rapidly growing current literature on the biological bases of addiction is too large to summarize in detail in this article, but its results are broadly consistent with the present view of the biological bases of affects (see Markou, Kosten, & Koob, 1998; A. J. Roberts & Koob, 1997). For example, Koob and LeMoal (1997) presented drug addiction as a progressively increasing cycle of dysregulation of the brain's reward systems, and Nesse and Berridge (1996) showed how drugs bypass information-processing mechanisms to act on ancient emotional brain mechanisms.

Sex. As noted, the hypothalamus is associated with a variety of primary drives, including needs for food, water, and sex. Although these are usually considered to be drives rather than emotions, they are associated with affective phenomena, subjectively experienced desires of hunger, thirst, and lust. Also as noted, in the present view drives are primary motivational-emotional systems or primes at a lower hierarchical level than primary affects (Buck, 1988b).

The hormonal control of sex is associated with the VM hypothalamus, which is linked physically with the pituitary gland, which releases a variety of hormones, including gonad-stimulating (gonadotropic) hormones, into the bloodstream. Stimulation of the VM nucleus induces estrus in female rats, and VM lesions abolish sexual behavior and lead to gonadal atrophy, which is reversed by hormone treatments (Robertson & Sawyer, 1957; Rogers, 1954).

Manipulations of neural centers controlling sex in the hypothalamus lead to changes that are not associated with gonadal atrophy or reversed by hormonal treatment. Fisher (1956, 1964) demonstrated in male rats that injections of testosterone into lateral POA produced exaggerated male sexual behavior, whereas similar injections into more medial areas produced maternal-like behavior such as nest building. Fisher suggested that the medial preoptic area (MPOA) contains neural circuits for maternal behavior that are normally activated only in female animals. The anterior hypothalamus also appears to contain centers for the neural control of sex. Lesions of this area have permanently abolished sexual behavior in male and female rats, cats, and guinea pigs (Sawyer, 1969). Conversely, electrical stimulation of the anterior hypothalamus leads to increased male-like sexual activity in both males and females. Continuous erection, repeated mounting, and a markedly shorter refractory period following ejaculation were demonstrated by Vaughan and Fisher (1962); similar hypermale behavior has been demonstrated in male and female opossums (Roberts, Steinberg, & Means, 1967) and male monkeys (MacLean & Ploog, 1962) with electrical stimulation of the anterior hypothalamus.

There is evidence that the brain centers associated with sex are turned on or turned off by gonadotropic hormones early in fetal development. Beach, Noble, and Orndorff (1969) demonstrated that a genetic female rat given testosterone at birth shows a masculinized pattern throughout her life. A male rat castrated at birth manifests no male behavior in adulthood, and manifests female behavior when he receives an estrogen injection. In contrast, sexual behaviors of noncastrated male rats are unaffected when they receive estrogen injections in adulthood (Beach et al., 1969).

Neural structures associated with mating behavior in the hypothalamus include the MPOA and the bed nucleus of the stria terminalis (BNST). Using c-fos, a marker of neuronal activation, Newman, Parfitt, and Kollak-Walker (1997) reported evidence of mating-induced activation in the MPOA and BNST, as well as medial parts of the medial amygdala. They suggested that these constitute a mating-specific circuit supplying essential signals for mating. The MPOA and BNST are also involved in maternal behavior (including nest building and retrieving pups). Lesions of these areas depress maternal behavior and chemical stimulation, whereas estrogen or prolactin increases maternal behavior, even in male animals (Numan & Sheehan, 1997). The MPOA projects to the ventral tegmental area (VTA) in the midbrain, which gives rise to ascending DA reward systems, which as noted may be important

in the appetitive component of a variety of drives. Moreover, the MPOA has ascending projections to the septal area. Numan (1996) suggested that it is possible that the MPOA constitutes a specifically sexual/maternal motivational/emotional system turning on general appetitive DA systems. This is consistent with Panksepp's (1981) hypothesis noted earlier.

Some species are relatively monogamous. Prairie voles (*Microtus ochrogaster*) show monogamy as evidenced by selective partner preference and selective aggression toward strangers. Life is lived in family groups in a common nest and territory; there is biparental care of the young, incest avoidance, socially regulated reproduction, and less sexual dimorphism. Closely related species, the meadow vole (*M. pennsylvanicus*) and montane vole (*M. montanus*), are nonmonogamous (Carter et al., 1997). Sex differences in brain systems, including a sexually dimorphic nucleus in the MPOA, are generally larger in promiscuous (rat, gerbil, and montane vole) than monogamous (prairie vole) species (De Vries, 1996; De Vries & Villalba, 1997).

The application of these animal data to human beings is controversial. Although it is clear that hormones do not rigidly determine sexual behavior in human beings (Ehrhardt & Meyer-Bahlberg, 1981), there is evidence that hormones play a role, in interaction with other factors, in sex role behavior and possibly sexual orientation. Specifically, there is evidence that the sexually dimorphic nucleus in the MPOA in homosexual men is structurally more similar to women than it is to heterosexual men (LeVay, 1991; LeVay & Hamer, 1994).

Conclusions: The role of the hypothalamus in emotion. The hypothalamus plays a major role in the bodily expression of emotion, but it does not play an executive role, usually acting under the guidance of higher systems. Also, the evidence that the hypothalamus acting alone is associated with the subjective experience of affect is mixed at best. This evidence is consistent with the view of the anatomist James Papez (1937), who noted that whereas the neocortex was reciprocally connected with the thalamus, the paleocortex was connected with the hypothalamus. He suggested that the paleocortex-hypothalamus system represents the anatomical basis for emotion, and that whereas the hypothalamus is responsible for the expression of emotion, it is the paleocortex that is responsible for emotional experience. These paleocortical structures surround the brainstem in a manner suggesting a border and were termed *limbic* structures by Broca (1878) from the Latin *limbus* or border (MacLean, 1970).

Reptilian Emotions: Sex and Aggression

The third group of biological primes in the typology involves systems of reptilian sex and aggression. They are associated with neurochemical systems in the structures of subcortical gray matter comprising the basal ganglia.

In his triune theory of the brain, MacLean (1993) suggested that three kinds of executive systems appeared successively during evolution, the second of which were Papez's paleocortical limbic structures. The first, more primitive, sort of executive system was termed the *reptilian complex*. In MacLean's (1993) words, "the human forebrain has retained the anatomical organization and chemistry of three formations that reflect a respective relationship to reptiles, early mammals, and late mammals" (p. 67). The reptilian brain is illustrated in Figure 4.

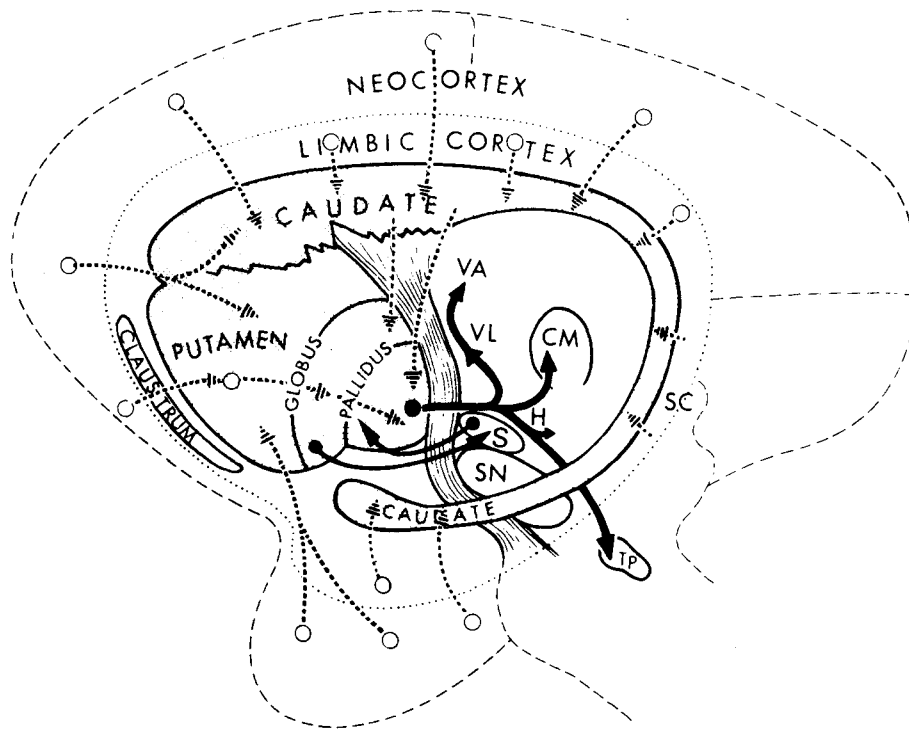


Figure 4. The reptilian brain. A schematic view of the ringlike configuration of the striatal complex in a sagittal section viewed from the left. CM = nucleus centro medianus thalami; H = tegmental area; SC = superior colliculus; SN = substantia nigra; S = corpus subthalamicum; TP = nucleus tegmenti pedunculopontinus; VA = nucleus ventralis anterior thalami; VL = nucleus ventralis lateralis thalami. Note. From *The Triune Brain in Evolution: Role in Paleocerebral Functions* (Figure 4-3, p. 36), by P. D. MacLean, 1990, New York: Kluwer Academic/Plenum Publishers. In the public domain.

Triune theory of cerebral evolution. MacLean (1993) traced the ancestry of vertebrates back to the bony fishes. He pointed out that each of the 28 bones of the human skull "has been inherited in unbroken succession from the air-breathing fishes of pre-Devonian times" (Gregory, 1927/1967, pp. 20–21). Although the forebrain of fish is small compared with its midbrain, removal of the forebrain results in deficits in both mating and aggressive behavior (Noble, 1936). In amphibia, the size of the forebrain becomes comparable with that of the midbrain. With the coming of reptiles, the evolution of the amniote egg made it possible for the first time to adapt to an entirely terrestrial existence. Taking the lizard as a representative of the reptiles, MacLean (1993) outlined its behavioral profile, including its master daily routine and its communicative displays, which include self-assertive signature displays, territorial displays, submissive displays, and courting displays. He summarized this profile as manifesting a basic animality, and inspection of the displays suggests that a kind of raw sex and aggression characterize the comparatively rudimentary social organization of the reptiles.

The reptilian complex. MacLean (1993) argued that the behavioral profile of reptiles is organized by the basal ganglia, including the corpus striatum (caudate nucleus, putamen, and globus pallidus), nucleus accumbens, olfactory tubercle, and satellite aggregations of gray matter. He termed this the reptilian complex or R-complex, and presented evidence in lizards and monkeys that lesions to these structures lead to selective disruption

of communicative displays. Moreover, clinical evidence in diseases in human beings that affect the corpus striatum, including Huntington's disease and Sydenham's chorea, manifest symptoms including deficits in planning and organizing daily activities and ritualistic obsessive-compulsive behaviors. MacLean (1993) noted that in human beings compulsive acts are "notably unaccompanied by emotional feelings" and that the performance of the daily routine "occurs almost automatically, as though propelled by propensities without associated emotion unless the intended acts are thwarted or meet with frustration" (p. 73).

Reptilian aggression? An anecdotal illustration. How does reptilian aggression differ from paleomammalian anger? An anecdotal illustration involves the well-known case of Charles Whitman, the University of Texas graduate student who wrote a letter on the night of July 31, 1966, which stated in part:

I don't understand what it is that compels me to type this letter. . . . I have been a victim of many unusual and irrational thoughts. These thoughts constantly recur, and it requires a tremendous mental effort to concentrate on useful and progressive tasks. . . . After my death I wish that an autopsy would be performed on me to see if there is any visible physical disorder. . . . It was after much thought that I decided to kill my wife, Kathy, tonight after I pick her up from work. . . . I love her dearly, and she has been as fine a wife to me as any man could ever hope to have. I cannot rationally pinpoint any specific reason for doing this. . . . I intend to kill her as painlessly as possible. (Johnson, 1972, p. 78)

Whitman killed his wife and mother later that night and the next morning purchased on credit three rifles, a shotgun, two pistols, and about 600 rounds of ammunition. He then ascended the tower on the University of Texas campus and began to fire, killing 14 more people and wounding 32 before police killed him. An autopsy revealed a malignant, slow-growing tumor in the right hemisphere in the basal ganglia near the amygdala.

In the description of Whitman's actions, there is no evidence of rage, anger, or strong emotion of any kind. Rather, his behavior was methodical, calm, and appropriate enough that he was able after killing his wife and mother to purchase a small arsenal. The letter suggests that Whitman was in the grip of a compulsion that controlled his goals without itself resisting higher level control by rational considerations of his moment-to-moment actions. That compulsion led to ruthless and merciless violence, but not to savage rage, quite the contrary. The nature of violent behavior associated with limbic dysfunction is quite different.

The Limbic System

The fourth group of biological primes in the typology involves systems of activation and inhibition associated with affects of happiness, sadness, and anxiety; agonistic-selfish systems associated with affects of fear, anger, and disgust, and prosocial-cooperative systems associated with affects of submission, lust, attachment, and playful bonding. They are associated with neurochemical systems in the paleomammalian brain, or limbic system.

The limbic system concept. The limbic system concept has three aspects: anatomical, evolutionary, and functional. First, *limbic system* relates to distinct parts of the brain, specifically three to five layered paleocortical or old cortical tissue. Second, as noted, these structures were related to a broader evolutionary context in MacLean's (1993) triune theory. Third, these structures are related functionally to emotion, and specifically the limbic structures are related to Emotion III, affective experience, as are no other parts of the brain.

Some have challenged the limbic system concept, particularly insofar as it seems to imply the embodiment of an emotional brain. Le Doux (1996) pointed out complexities in each aspect of the limbic system concept. He noted that it is sometimes unclear just what brain structures are included in the limbic system, that there are cortical tissues meeting the structural criteria of neocortex in nonmammals, and that parts of the limbic system serve functions not clearly related to emotion. He concluded that the limbic system concept is "imprecise," has "unwarranted functional (emotional) implications," and "should be discarded" (p. 101).

There is indeed some lack of consensus in the definition of what structures are included in the limbic system (and also the reptilian complex), although most definitions specify the former as involving paleocortical and the latter subcortical structures positioned between the hypothalamus and neocortex. Nevertheless, emotional phenomena cannot be confined to the limbic system or to any other part of the brain. Emotional phenomena are intimately integrated into both lower and higher order brain functions. As noted, the function of neurochemical systems that cross hierarchical levels must be examined to give adequate consideration of the biological affects. Furthermore, it is true that, as Le Doux (1996) emphasized, there is not one emotional system in the brain, but many. In this regard, the special position of the amygdala in emotional process-

ing must be recognized. The amygdala is so interconnected with both basal ganglia and paleomammalian structures that it could be arguably included in either the reptilian complex or the limbic system. Indeed, as the work of Le Doux and his colleagues demonstrates, the amygdala itself embodies the functional components of a brain in itself, with sensory, motor, and intervening association areas (Le Doux, 1996; Pitkaenen, Savander, & Le Doux, 1997).

The limbic system and also reptilian complex concepts must be regarded to some degree as metaphorical, useful as shorthand designations characterizing levels of the brain whose functioning relate in general ways to behavioral patterns seen in reptiles and mammals and to different aspects of emotional behavior. As we learn more about these phenomena, our concepts will become both more elaborate and more precise. However, at present there is no effective substitute for the limbic system concept in characterizing a certain level of brain functioning in emotion, one that, apropos to the present article, is intimately involved in affective experience.

Selfish and prosocial affects. As noted, on the one hand, there is little evidence that the hypothalamus is responsible for subjectively experienced affect despite its involvement in basic emotions. Similarly, the reptilian complex does not appear to be associated with affect. There is, on the other hand, considerable evidence that stimulation of the limbic system produces strong emotional experiences. As MacLean (1993) put it, the limbic system is "responsible for the honing of emotional feelings that guide behavior required for self-preservation and the procreation of the species" (p. 67). More specifically, MacLean (1970, 1973, 1981, 1993) distinguished three major circuits in the paleomammalian portion of the triune brain. The first is associated with emotions concerned with self-protection—the selfish demands of feeding, fighting, and fear—and is identified with the amygdala. The other two circuits concern social and sexual matters, the preservation of the species. One of these is identified with the septal area. The septal and amygdala circuits are similar in that both receive much input from the olfactory system, reflecting the importance of the sense of smell in the functions served by these circuits. The olfactory apparatus largely bypasses the third circuit. It is the thalamocingulate circuit and includes the mammillothalamic tract connecting the mammillary bodies with the anterior thalamus and fibers going on the cingulate gyrus. MacLean (1970) noted that this tract is almost absent in reptiles and is greatly elaborated during evolution, reaching its greatest size in human beings. He suggested that this circuit reflects the increasing importance of visual rather than olfactory regulation of social and sexual functions. More specifically, the switch from a reptilian to a mammalian lifestyle was accompanied by the evolution of three patterns of behavior that is typical of mammals but not reptiles: (a) nursing and maternal/parental care, (b) audiovocal communication to maintain contact, and (c) play. The three paleomammalian circuits are illustrated in Figure 5.

In this section I consider the association of limbic mechanisms with the hypothalamic systems and, also, how this relates to the primary affects and other widely recognized emotions, as well as to some not so widely recognized emotions. Specifically, the reward and punishment systems are associated with systems of behavioral activation and inhibition at the limbic system level, which may be associated with some kinds of happy and sad emotions, as well as anxiety. Also, fearful defensive attack may be

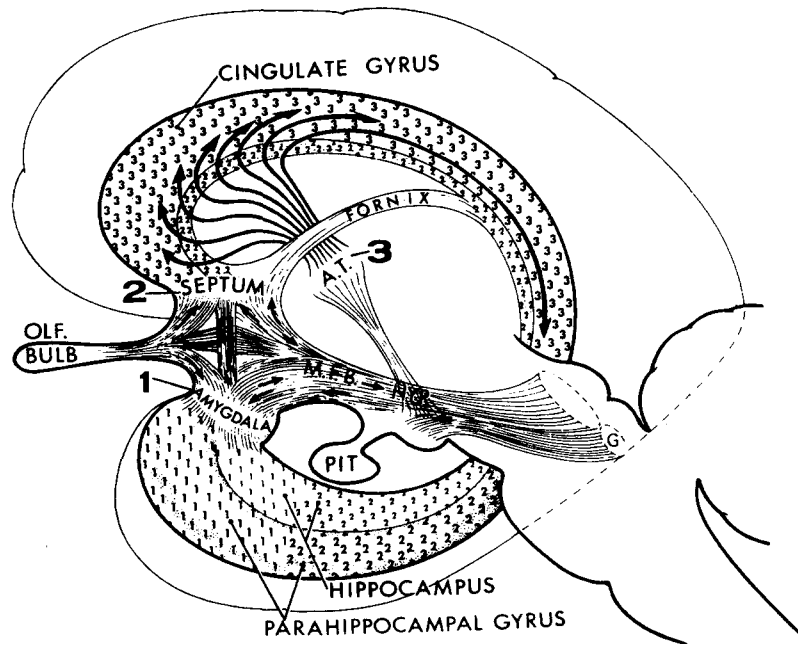


Figure 5. The individualistic and two prosocial systems in the paleomammalian brain (limbic system). Large numerals 1, 2, and 3 identify nuclear groups of the respective amygdalar, septal, and thalamo-cingulate divisions. Small numerals overlie limbic cortical areas predominantly interconnected with these respective nuclear groups. A.T. = anterior thalamic nuclei; G = dorsal and ventral tegmental nuclei of Gudden; HYP = hypothalamus; M.F.B. = medial forebrain bundle; PIT = pituitary gland; OLF. = olfactory bulb. From *Handbook of Emotions* (Figure 6.5, p. 76), by P. D. MacLean, 1993, New York: Guilford Press. In the public domain. Reprinted with permission of the author.

associated with agonistic affects—fear, anger, and disgust—which involve amygdala influences acting through the perifornical and posterior hypothalamus; whereas submission, attachment, playfulness, and lust may be seen as prosocial affects associated with septal and thalamocingulate influences and the anterior hypothalamus.

Happiness-sadness. Like other investigators, including J. Olds (1961), Routtenberg (1978), and Stein (1978), J. A. Gray has emphasized the interaction of the reward and punishment systems that course through the hypothalamus and the arousal functions of the reticular formation, in the determination of behavior. Gray (1977) suggested that the MFB reward system and arousal interact at the level of the septal area, constituting a behavioral activation system (BAS). The organism is motivated to increase activity in this system, and any stimulus associated with reward becomes a positive incentive that serves to increase such activity. As a result, a positive feedback loop is created in which the animal performs behavior that homes in on reward.

The neurochemicals associated with this system, DA and NE, tend to have euphoric effects in moderate amounts, and low levels are associated with depression. Also, electrical stimulation of this system produces positive responses. This suggests that the BAS is important in an elation-depression, or happy-sad, dimension of behavior. However, it should be noted that when neurochemical systems are used to define affect, more than one sort of sadness must be distinguished. In reviewing the catecholamine hypothesis of affective disorders, McNeal and Cimbalic (1986) emphasized

that there are different kinds of major depressive disorders that may be associated with different neurochemical systems. For example, we shall see that NE transmitter systems are implicated in some depressions, but others involve depletions of serotonin (Maas, 1975; McNeal & Cimbalic, 1986).

Anxiety. Whereas the functioning of the reward system seems fairly consistent with the notion of an elation-depression continuum of affects, the functioning of the punishment system has been linked with anxiety. Gray (1982) suggested that punishment is associated with a behavioral inhibition system (BIS) in which the organism is motivated to stop activity. Any stimulus associated with such activity becomes a negative incentive, putting a brake on behavior in a negative feedback loop. Gray (1982) suggested that the operation of the BIS is associated with the occurrence of theta rhythm from the hippocampus, which is driven from the medial septal area under executive control of the frontal cortex. He accordingly termed it the septal-hippocampal-frontal (SHF) system. Lesions in this system produce lasting disinhibitory effects (Gorenstein & Newman, 1980).

Gray (1982) suggested that the BIS operates in concert with the reticular formation in producing anxiety. He suggested that the BIS acts as a comparator, continually comparing actual with expected stimuli. As long as the expected and the actual match, the BIS remains in a checking mode and the control of behavior resides elsewhere. The checking mode is associated with the Type I arousal that, as noted, Vanderwolf and Robinson (1981) associated with voluntary behavior. If the match does not occur, or if a

stimulus associated with punishment (negative incentive) is encountered, the BIS takes on a control mode. Any motor behavior being executed is immediately inhibited and is furthermore identified as faulty so that it will be performed with more caution in the future. Also, the organism scans the environment to identify stimuli associated with punishment, failure, or nonreward. The control mode is associated with cholinergic Type II arousal and a low frequency theta rhythm in the hippocampus.

Gray (1982) suggested that NE and serotonin are both involved in increasing the range of environmental stimuli that need checking, with NE particularly seeking out important stimuli and serotonin specifying aversive stimuli. High levels of response inhibition are associated with anxiety, and excessively high levels with phobias and obsessive-compulsive neuroses. Gray (1982) suggested further that introverts have high levels of BIS activity relative to extroverts, so that those introverts are more prone to anxiety and inhibition and more susceptible to punishment.

It seems paradoxical at first glance that NE and serotonin are associated with anxiety, as at some levels increases in these neurochemicals is rewarding, having antidepressant effects. One answer is that there is an optimum level of functioning associated with these neurochemicals, so that consistent with the inverted U of classic arousal theory, increases are rewarding to a point, after which they decrease behavioral efficiency and increase anxiety (Hebb, 1955). Another answer is that different receptor systems may be involved in anxiety and antidepressant effects. As we shall see, there are at least 14 different serotonin receptors (Roth, 1994).

Agonistic affects: Fear, anger, and disgust. Gray (1977) stated that the BIS accounts for passive avoidance, where the animal responds to threat with a tense, silent immobility but that it does not account for active fight-or-flight responses. Like MacLean, Gray (1977) associates the latter with the amygdala. They are termed *agonistic* because they involve conflict, competition, or fighting.

Interest in the amygdala can be traced to the Kluver-Bucy syndrome, in which the amygdala is removed bilaterally (Kluver & Bucy, 1937, 1938, 1939). Animals so affected demonstrate a striking lack of evidence of anger, fear, and disgust. Defensive aggressive responses disappear, even in untamable animals such as the lynx; flight responses vanish even to stimuli such as snakes and fire, which are innately feared in monkeys; and the affected animal mouths even such distasteful and painful stimuli as dirt, feces, rocks, and burning matches. Amygdalectomized human beings show analogous patterns of response (Terzian & Dalle Ore, 1955). Stimulation of the amygdala produces effects generally opposite to those of lesions, producing rage-like attack and fear-like defensive behaviors in a variety of species including human beings.

Le Doux and his colleagues have demonstrated direct sensory input to the amygdala that is necessary for the learning of conditioned fear responses (Le Doux, 1993). In the auditory system, the classic auditory pathway proceeds to the ventral part of the medial geniculate body (MGB) and from there to the auditory neocortex. Another pathway terminates in more medial parts of the MGB and proceeds to the amygdala (Le Doux, Sakaguchi, & Reis, 1984). There is evidence of such direct pathways in the visual system as well (Le Doux, Romanski, & Xagoraris, 1989). Le Doux (1993) suggested that these subcortical sensory inputs to the amygdala may constitute an evolutionarily primitive early warning system that triggers fast emotional responses to threatening stimuli: "The

thalamo-amygdala system is several synapses shorter (than the neocortical system) and therefore offers this temporal processing advantage at the expense of perceptual completeness" (p. 112). Microseconds later, more completely processed input enters the amygdala from the neocortex and hippocampus. Le Doux (1993) concluded that the amygdala is essential in the "assignment of affective significance to sensory events" (p. 110). This seems clearly the case in regard to selfish affective significance, although prosocial affects may involve other structures.

Some of the most persuasive evidence that the limbic system is associated with subjectively experienced affect comes both from observations in human beings of the effects of electrical stimulation and brain disease in the amygdala. In psychomotor epilepsy, the patient may experience a variety of emotional feelings. The medial temporal lobe containing the amygdala is particularly susceptible to such attacks. Typical feelings include those that "come into play in the struggle for survival . . . hunger, thirst, nausea, suffocation, choking . . . which may be conjoined with a variety of intense emotional feelings such as terror, fear, anger, sadness, foreboding, strangeness, and paranoid feelings" (MacLean, 1973, pp. 14-15). Mark and Ervin (1970) described a number of cases in which such limbic epilepsy led to violent attacks.

The behavior of persons stimulated in the amygdala contrasts with the behavior exhibited by Charles Whitman, described previously. Here there is evidence of an uncontrollable rage reaction without the behavioral compulsion. Although the feeling is uncontrolled, persons seem to maintain considerable control of their goal-directed behavior. This is illustrated in an interview conducted by King (1961), during which the amygdala of a woman with epilepsy was stimulated. The woman was sitting with the interviewer, and the amygdala was stimulated through telemetry from another location. When stimulated, the woman's voice rose and she apparently experienced strong anger, but maintained control of her behavior, saying "Don't do this to me. I don't want to be mean . . . I just want to hit something." The stimulation was then reduced and she smiled widely and said, "I know its silly, what I'm doing . . . I had no control of myself." The current was then turned up again and she said loudly, "Don't let me hit you. . . . Quit holding me! I'm getting up! You'd better get someone else if you want to hold me! I'm going to hit you!" As she raised her arm as if to strike, the current was reduced and she changed to a wide smile and laugh, "Why does it make me do this? I couldn't help it. I didn't have any control" (King, 1961, pp. 484-485). This pattern of strong and uncontrollable affective experience, combined with some ability to control and choose how one responds to this experience, is the hallmark of the hierarchical level of primes associated with subjectively experienced affects.

Prosocial affects: Submission, lust, attachment, play. Recently, biological processes that regulate social organization and social bonds have received increased attention (Carter et al., 1997). Social groups and pair bonds formed by animals are the context for activities such as mating, parenting, play, nurturance, and dominance-submission. Different species have evolved a wide variety of biological mechanisms serving such social functions (Nicoli & Nicoli, 1995).

As noted, stimulation of the septal area in human beings is associated with positive affect, often with a sexual tinge (Heath, 1964), and septal lesions are associated with disinhibitory effects and an increase in impulsiveness (Gorenstein & Newman, 1980).

MacLean (1973) reported that following septal stimulation a patient reported, "I have a glowing feeling. I feel good" (p. 16), and that stimulation in the septal region produces penile erection in the squirrel monkey (MacLean & Ploog, 1962). He suggested that the septal area is concerned with "primal sexual functions and behavior conducive to procreation" (MacLean, 1993, p. 77).

Stimulation in the anterior thalamic region also produces penile erection (MacLean & Ploog, 1962). As noted, MacLean (1993) suggested that the thalamocingulate circuit functions in a "family-related triad that distinguishes the transition from reptiles to mammals" (p. 77): nursing and maternal care, audiovocal communication, and play. Cingulate lesions have been found to interfere with maternal behavior (Slotnick, 1967; Stamm, 1995), play (M. R. Murphy, MacLean, & Hamilton, 1981), and the separation cry in squirrel monkeys (MacLean & Newman, 1988). MacLean (1993) noted that the cortical area associated with the separation cry receives innervation from areas of the thalamus associated with pain perception, and that the cingulate cortex has a high concentration of opiate receptors. I consider the emotional functions of the opiates in more detail later.

Play is a fundamental process—a vehicle for the development of complex social abilities—that occurs even in the absence of the neocortex (Panksepp, 1996). There is evidence that deprivation of play produces significant social deficits that may be secondary to communicative deficits (Harlow & Mears, 1983; R. E. Miller, Caul, & Mirsky, 1967). Birds and mammals including dolphins, monkeys, and humans change vocal communication in response to group influences, with both aggression and affiliation being important in the process. Snowdon (1997) noted that affiliative vocalizations include separation and reunion calls, mating call songs, and localization calls. In goldfinches, calls characterizing individuals can be influenced by call songs of the mate to produce calls characterizing the dyad, "our song." Babbling in the young pygmy marmoset contains elements of adult affiliative, threat, alarm, and fear sounds. In the cottontail tamarind, chirps occur in feeding contexts, with one chirp associated with approaching food and another with eating. The approach chirp varies in rate with food preferences.

Sociality versus selfishness: Stress alleviation and conflict resolution. The basic physiological facts of the fight-or-flight response are well-established, but much less is known about the physiological effects of positive social contact. There is, however, considerable evidence that social stimuli have the potential to buffer or reduce stress in some animal species and in human beings (Bovard, 1959). Hofer (1984) has argued that social relationships constitute complex and multifaceted regulatory systems in animals and human beings, exerting their effects by communicative non-verbal signals outside the direct awareness of participants: odors, tones of voice, facial expressions, touches, and the precise timing of behaviors. Such signals allow the infant to participate in the regulation of mother-infant interaction (Trevathan, 1984). As noted later, communication takes emotion outside the individual into the regulation and organization of the social milieu (Buck, 1984; Buck & Ginsburg, 1997a).

Dyadic emotion communication is, however, related to concrete, potentially observable events within the organism. For example, attachment is associated with high endorphin levels, and the susceptibility to disease seen by Hofer (1984) in bereavement may be associated with low levels. Also, Uvnas-Moberg (1996) noted that

a pinch increases cortisol levels, but a brush can decrease them, possibly through antistress effects associated with increases in the peptide neurohormone oxytocin (OXY). OXY increases are associated with lowered anxiety, and OXY peaks with socialization; prolactin increases are associated with lower muscle tension; and breast feeding has antistress effects, lowering blood pressure and cortisol levels. OXY increases insulin, possibly by activating the vagus. Massaging male and female rats produces increases in all of the effects produced by OXY, and these effects are blocked by OXY antagonists (Uvnas-Moberg, 1997). I consider the endorphins and OXY further below.

Emotional communication may thus serve critical bioregulatory functions in addition to social regulation. In human beings, a variety of conditions associated with physical illness, including the Type A and Type C personality patterns and alexithymia, may be related to disruptions in emotional communication (Buck, 1988b, 1993a). Kraemer (1996) suggested that the Bowlby-Ainsworth model of the caregiving relationship has evolved into a model of the caregiver as regulatory system, a Gibsonian model emphasizing what the attachment affords the infant. The infant is intrinsically open to entraining patterns of external regulatory stimuli, normally provided by a caregiver. Stimuli control-regulate the infant's behavior; the infant is set to behave toward external stimuli. Thus, a baby can imitate facial expression without seeing itself. Innate behavior matures into goal corrected behavior. Kraemer (1996, 1997) noted that NE, DA, and serotonin levels intercorrelate more strongly in mother-reared than in peer-reared infants; the mother provides an organization to the infant. He suggested that intercorrelation of function reflects organization of function and is arguably more important than level of function.

Socially mediated stress buffering may occur particularly in species characterized by attachment systems, social systems characterized by recognition, preference, and negative responses to separation. Mendoza and Mason (1997) noted that the titi monkey (*Callicebus moloch*) is monogamous, with female-male pairs and offspring living together, whereas the squirrel monkey (*Saimiri sciureus*) is nonmonogamous, with most adult social interaction being with like-sex individuals. Stress-buffering effects of social relationships have been demonstrated in both species, but they show different patterns suggesting qualitative differences in their attachment systems. For example, the separation of mother and infant increase maternal cortisol levels more in the squirrel monkey than the titi, but disturbances and separation from the mate increase cortisol levels more in the titi than in the squirrel monkey.

In addition to social relationships having stress-alleviating effects, there is also evidence that disruptive conflicts may be actively resisted in social species. Aggression is usually considered to be a dispersive, distributive force, but fighting also occurs within groups among animals with close relationships. De Waal and Aureli (1997) suggested that the active social repairing of relationships allows aggression to be a part of primate society. Chimpanzees often reconcile after intracommunity fights, hugging, kissing and grooming each other. Consolation, friendly reassurance contact by a bystander following a fight, is also seen. Often males are reconciled after a fight by a female bystander. There appears to be groupwide interest in conflict resolution. Rhesus monkeys show selective attraction between excombatants, with approximately 30% grooming within 20 min of a conflict compared with 20% among matched controls, but they do not

show consolation as chimpanzees do. The stump-tail macaque has a specific reconciliation gesture, holding the rear end of the other. More reconciliation occurs if the social relationship is important, and self-grooming indicative of tension decreases after reconciliation.

Summary and conclusions. The paleocortical limbic system is associated with a variety of affects involved in self- and species preservation. These include neurochemical systems involving selfish reward and punishment, arousal, anxiety, fear, anger, and disgust; and a variety of prosocial affects. The selfish affects function to promote the survival of the individual, whereas the prosocial affects function at a group level to preserve the species through preserving the interactive, communicative social relationship (Buck & Ginsburg, 1997a).

Cerebral Hemispheres

Cerebral lateralization and selfish versus prosocial emotion. The distinction between selfish and prosocial affects allows a new approach to the question of the relationship of right-hemisphere (RH) and left-hemisphere (LH) responding in emotion. The subcortical and paleocortical systems associated with emotion are lateralized, even in lower animals. NE systems are right-lateralized (Oke, Keller, Medford, & Adams, 1978); systems associated with DA and ACh are left-lateralized (Gainotti, Sorbi, Miceli, & Amaducci, 1982; Laurien, Gallard, Le, & Schopf, 1983), and there is evidence of asymmetry in serotonin systems as well (Mandell & Knapp, 1979). Aggressive behavior is right-lateralized in the brain of the lizard (*Anolis*; Deckel, 1995). In rats, RH damage decreases emotionality (Denenberg, 1981, 1984) and mouse-killing tendencies (Denenberg & Yutzey, 1985).

We noted that the work of Le Doux and his colleagues showed the amygdala to be necessary in the conditioned fear response. Recent studies have suggested that the right and left amygdalae are differentially involved in some kinds of fear responses; specifically, the right amygdala may make a greater contribution than the left to the retention of aversively motivated training. Coleman-Meschers and McGaugh (1995a, 1995b, 1995c) found that the temporary inactivation of the right, but not the left, amygdala by microinjection of drugs disrupted the retention of passive avoidance responding in rats. Consistent with the notion that the right amygdala is involved in the memory for aversive experience, inactivation of the right, but not the left, amygdala attenuated the response to a reduction in reward (Coleman-Meschers, Salinas, & McGaugh, 1996). However, this differential involvement of the right and left amygdala in fear responding may be limited to certain treatment, training, and/or testing conditions, as other studies have not found left-right amygdala differences (Coleman-Meschers, West, & McGaugh, 1997; LaBar & Le Doux, 1996; LaBar, Le Doux, Spencer, & Phelps, 1995).

In human beings, hemispheric dysfunction has been implicated in the major psychoses (Cutting, 1990; Flor-Henry, 1983), and differences in emotional functioning have been associated with RH versus LH epileptic seizure activity (Bear & Fedio, 1977; Flor-Henry, 1984; Kyle, 1988) and brain damage (Folstein, Maiberger, & McHugh, 1977).

The LH is associated with language in most right-handed persons. In contrast, a variety of evidence suggests that the RH plays a special role in both the expression and recognition of emotion

(Borod & Koff, 1990; Borod, Koff, & Buck, 1986; Buck & Duffy, 1980; Etcoff, 1989; Ross, 1981, 1992; Silberman & Weingartner, 1986; Strauss, 1986; Wechsler, 1973). Anatomical differences between the hemispheres in humans may be related to this general language versus emotion distinction. Larger brain areas are generally associated with more refined functions, and in most right-handed persons the LH is longer than the RH and wider in the posterior portion associated with Wernicke's area, reflecting the association of these parts of the brain with language. In contrast, the RH is wider in the front, perhaps reflecting an association with emotion (Geschwind, 1979).

A number of investigators favor the valence hypothesis, that the LH is associated with positive emotion and the RH with negative emotions (see Davidson & Hugdahl, 1995; Flor-Henry, 1979; Gainotti, 1972). For example, Davidson and Fox (1982) demonstrated that social smiling is associated with LH activation in human infants. However, there is evidence inconsistent with the valence hypothesis; for example, the fact that NE and the MFB reward system are right-lateralized does not fit the notion that the RH is associated with only negative affects. Others have suggested instead a right-hemisphere hypothesis, that the RH is particularly associated with the experience, expression, and communication of all emotions (Diamond, Farrington, & Johnson, 1976; Ley & Bryden, 1981; Wexler, 1980).

If the positive-negative distinction is replaced by a prosocial-selfish distinction, so that the LH is prosocial and the RH is selfish, a number of the inconsistent findings fall into place. First, most of the selfish emotions (fear, anger, disgust) are considered to be negative, whereas display rules associated with social emotion often (but not always) encourage the expression of cheerful, positive displays that may be at variance with the true feelings of the responder. Second, it can be argued that language is not in itself unemotional; in fact, human beings derive great satisfaction when language is used successfully (and frustration when it is misused), and it makes sense that such linguistic emotions are associated with sociality (Buck, 1988b, 1994a). Indeed, the social smile of the infant studied by Davidson and Fox (1982) might reflect prosocial attachment emotions as opposed to selfish pleasure.

There is some evidence for the selfish-prosocial hypothesis of brain asymmetry in emotion. Buck and Duffy (1980) found that LH-damaged patients were quite good on a measure of nonverbal sending accuracy involving facial-gestural expressiveness to emotionally loaded slides, significantly better than RH-damaged and Parkinson's disease patients. However, the latter groups and non-brain-damaged patients showed evidence of responding to display rules; they were more communicative in responding to slides of familiar persons and not at all communicative on unpleasant slides. LH-damaged patients did not show this effect; they were relatively less communicative than non-brain-damaged patients on the familiar slides and were quite communicative on unpleasant slides. This result suggested that the RH might be associated with the spontaneous expression of emotion, whereas the LH is associated with learned rules and expectations about how and when emotions should be expressed.

Furthermore, a study of emotional responding during the Wada test, in which the hemispheres are temporarily inactivated by sodium amobarbital prior to a brain operation, suggested that RH inactivation produces changes consistent with a change from selfish to social emotions. A woman who had described herself as

"mad and angry" at being teased for her epilepsy as a child, when the RH was inactivated stated that she was "embarrassed" at the abuse. A man who said he was "angry and frustrated" at the inability of physicians to diagnose his condition when the RH was inactivated described himself as "sorry for people that they had so much trouble finding out what was wrong." Of 10 patients, 8 showed evidence of minimizing or denying primary emotions with RH inactivation (Ross, Homan, & Buck, 1994).

Sex differences in selfish versus prosocial emotion. Gur and his colleagues reported sex differences in resting metabolism in the brain areas associated with emotion. Right-handed participants were given an injection of isotope-labeled glucose and then lay in a dimly lit, quiet room with their eyes open with instructions to remain "quiet and relaxed without either exerting mental effort or falling asleep" (Gur et al., 1995, p. 528). Positron-emitting tomography (PET) scan images of their brains were crossregistered with corresponding magnetic resonance images (MRI) to assure alignment with individual brain anatomy. The test lasted at least 90 min. Results indicated that, for both women and men, metabolic activity was highest in the basal ganglia and lowest in the corpus callosum. The groups also showed similar metabolism in nonlimbic frontal, parietal, and occipital regions. However, men showed higher relative metabolism in temporal-limbic regions (the lateral and ventromedial aspects of the temporal lobes). More specifically, the raw absolute metabolic rates were higher in men than in women in the occipital temporal region, temporal pole, hippocampus, amygdala, and orbital frontal cortex. In contrast, women had higher relative metabolism in the middle and posterior cingulate gyrus. To assess individual differences, female-typical and male-typical scores were obtained by subtracting standardized metabolic rates in the temporal-limbic region from those in the cingulate. Results indicated that only 17 of the 61 participants (4 women and 13 men) had gender-atypical scores.

As noted, the amygdala in the temporal-limbic region is concerned with selfish emotions associated with self-preservation, whereas the cingulate is concerned with prosocial emotions associated with species preservation. The implication of the Gur et al. (1995) study is that men have more relative activity in brain areas associated with selfish emotions and women in brain areas associated with prosocial emotions. It should be noted that such patterns of brain activity could be a result of sex-role-related social learning.

Another interesting aspect of the Gur et al. (1995) study was that it examined the right versus left lateralization of brain activity in different brain regions. Consistent with the right-handedness of these participants, metabolism was found to be higher in the left in regions that control contralateral motor functions (premotor, motor, and sensorimotor cortex, midbrain, and pons) and higher in the right for the cerebellum, which influences motor functions ipsilaterally. There was also higher metabolism in LH regions involved in verbal-analytic cognitive functions (the medial and inferior frontal, parietal, superior, and inferior temporal cortices). Important for the present analysis, activity in the prosocial cingulate gyrus was also left lateralized. In contrast, and consistent with theories of RH dominance in selfish emotional processing, metabolism was higher in the RH in most ventro-medial temporal lobe regions of the limbic system and their projections in lenticular regions of the basal ganglia. The greater relative left-sided metabolism in the cingulate gyrus and greater relative right-sided me-

tabolism in the temporal limbic system accords well with the suggestion considered earlier that selfish emotions are right-lateralized and prosocial emotions left-lateralized (Ross et al., 1994).

Biological Affects II: Neurochemical Systems

We have proceeded up the hierarchy of neurochemical systems from the brainstem to the cerebral hemispheres to examine the sorts of control associated with the functioning at various anatomical levels. Another way to organize the exploration of the biological bases of emotion is by their functions: arousal, approach-avoidance, agonistic, and prosocial. As noted, the biological systems underlying these functions cross anatomical levels, appearing in all four levels of biological primes outlined in the previous section. These systems can often be associated with specific neurochemical systems, that is, synaptic transmitters, their agonists and antagonists, and the receptor sites on which they operate.

Neurochemical systems involve functionally arranged sets of neurons and receptor sites, essentially an expansion of Hebb's (1949) classic notion of cell assemblies. Neurotransmitters and hormones, or neurochemicals, act by altering the response properties of these systems (Kravitz, 1988). Neurohormones may be released by exteroceptive sensory input (day-night cycles, displays of other creatures, presence of food) or interoceptive input, or both, reflecting bodily needs and desires (hunger, thirst, sex). They act to sensitize "receptor-enriched territories within the nervous system that function together either to read out a new patterns of behavior or to enhance or diminish the effectiveness of an existing pattern" (Kravitz, 1988, p. 1775). This sensitization acts as a gain-setting mechanism that biases output systems, resulting in displays, fight-or-flight reactions, exploratory tendencies, and food search. "What is changed is that the organism now responds to particular sensory stimuli with an altered output appropriate to the new situation" (Kravitz, 1988, p. 1776). Genetic-environmental influences can produce wide individual variation in the effectiveness of any given neurochemical as a gain-setting mechanism. For this reason, any given neurochemical may have different effects in different individuals.

The fundamental chemical units of neural transmission evolved long before the appearance, within the phylum Chordata, of the vertebrate brain and spinal cord. The earliest traces of the latter appear in fossils from the Cambrian period, beginning 570 million years ago (W. F. Walker, 1987). In contrast, the classical transmitter molecules evolved at least 1,000 million years ago, and they are found in virtually all phyla. These transmitters evolved the ability to activate a range of ion channels in membranes, resulting in excitation or inhibition, acting through receptor sites. Homologies between invertebrate and vertebrate receptors suggest that the basic receptor subunits evolved at least 800 million years ago (R. J. Walker, Brooks, & Holden-Dye, 1996).

Emotion has been termed a fuzzy concept in a fuzzy hierarchy (J. A. Russell & Fehr, 1994), but arguably biological affects can be conceptualized and defined quite concretely in terms of neurochemical systems whose functioning is, in principle, observable (Buck, 1985). Defining affects in this way enables us to be specific, avoiding the definitional problems often associated with emotional labels, and at the least, a consideration of neurochemical

systems can provide "biological constraints . . . useful in the generation of theories of emotion" (Le Doux, 1993, p. 115).

Amine Neurotransmitters

The first kind of neurochemical system to be examined involves amine neurotransmitters, with particular attention to dopamine, norepinephrine, and serotonin.

The amines. The amines are divided into two broad categories: the catecholamines DA, NE, and epinephrine (EPI), and the indole amines including serotonin (also known as 5-hydroxytryptamine or 5-HT) and histamine. The amines function as neurotransmitters, that is, chemical substances released into the synaptic space that separates cells, carrying excitatory or inhibitory influences from the presynaptic cell to the postsynaptic cell. The amine neurotransmitters are manufactured in the presynaptic cell, within which they are broken down by the enzyme monoamine oxidase (MAO). Once released into the synaptic space, they are taken back into the presynaptic cell in a reuptake process, and they are broken down by the enzyme catechol-O-methyl-transferase (COMT).

The physical arrangement of the synapse provides several ways to intervene in aminergic functioning. The neurotransmitters may be manipulated directly by injection or restriction of critical dietary elements such as tyrosine, from which DA and NE are produced. Alternatively, the neurotransmitter may be manipulated indirectly by manipulating the enzymes that break it down either inside or outside the cell, or by manipulating the reuptake process. These three indirect routes are taken respectively by MAO inhibitors, iproniazid, and imipramine. All of these have been used as antidepressants, apparently functioning by increasing amine levels.

The catecholamines. As noted, the catecholamine neurotransmitters DA and NE are associated with reward; the most powerful self-stimulation effects come from neural systems rich in these substances. Also, drugs that increase catecholaminergic activity, such as cocaine and amphetamine, tend to have antidepressant effects and to increase attention, awareness, and the speed of mental activity: "The mind is filled with energy and a sense of purpose and power" (Panksepp, 1981, p. 360). On the other hand, drugs that reduce catecholaminergic activity, such as reserpine, induce sedation, feelings of fatigue, and in some persons, depression.

These findings contributed to the catecholamine hypothesis of affective disorder (Schildkraut, 1969). That hypothesis states that "some, if not all, depressions may be associated with a relative deficiency of NE at functionally important adrenergic receptor sites in the brain, whereas elations may be associated with an excess of such amines" (Schildkraut & Kety, 1967, p. 28). Indeed, Kety (1970) stated that

practically every drug which has been found effective in altering affective states in man has also been found to exert effects on catecholamines in the brain in a way which would be compatible with the possibility that these amines are involved in the mediation of these states and in the actions of the drugs which affect them. (p. 65)

However, there is evidence that the catecholamine hypothesis is both limited and incomplete. First, as we have seen, the effects of DA and NE are not uniformly positive. Panksepp (1986) noted that DA activity promotes response initiation to both positive and negative incentives. Also, NE can increase sensitivity to both

positive and negative stimuli. At low levels of challenge, an increase in NE may be rewarding, but at high levels of challenge an increase may cause anxiety (Gray, Owen, Davis, & Tsaltas, 1983; Zuckerman, 1984). As noted previously, NE may be associated with an inverted U effect in which increases from relatively low levels are positively associated with behavioral efficiency, whereas increases from high levels produce lower behavioral efficiency.

In reviewing evidence relevant to the catecholamine hypothesis, McNeal and Cimbalic (1986) concluded that, although there is much evidence that deficits in NE transmitter systems are involved in some major depressive disorders, depression is not a single disorder but a class of disorders, some of which involve other neurotransmitter systems. As noted, depletions of 5-HT are involved in some depressions (Glassman, 1969; Kramer, 1993). Maas (1975) suggested that there are two sorts of depression: Type A involves a disorder of NE systems, whereas Type B involves 5-HT.

Monoamine oxidase. As noted, MAO is the enzyme that breaks down the amines—DA, NE, and also 5-HT—in the central nervous system. Lower levels of MAO translate into higher levels of the amines, and as noted, higher levels of amines have antidepressant–euphoriant effects. Drugs that inhibit MAO (MAO inhibitors or MAOIs) are therefore used as antidepressants. It is uncertain whether their antidepressant effects are related to their effects on the catecholamines, their effects on 5-HT, or both (Kramer, 1993).

Natural MAO concentrations may be assayed in humans from blood platelets (D. L. Murphy, 1973). These concentrations show wide individual variations, which have been related to behaviors in both animals and human beings that appear to reflect a general introversion–extraversion dimension of personality (see Buck, 1988b). For example, in rhesus monkeys high MAO levels have been associated with passivity, inactivity, and a lack of social responsiveness, whereas low levels are associated with high play behavior, activity, and social contact (Redmond & Murphy, 1975; Redmond, Murphy, & Baulu, 1979). In humans, MAO levels tend to be negatively related with sensation seeking and impulsiveness, and positively related to inhibition (Castrogiovanni, Maremmani, Bongioanni, & Marazziti, 1990–1991; Zuckerman, 1993; Zuckerman, Buchsbaum, & Murphy, 1980). For example, Sher et al. (1994) assessed MAO activity in 557 men (ages 21–26). They found low MAO levels to be associated with an undercontrolled behavioral style, cigarette use, and illicit drug use. Also, when exposed to an anxiety provoking stressor, low MAO participants showed stronger stress-dampening responses on heart rate measures compared with high MAO participants, although general reactivity to the stressor did not differ in the two groups. High and low levels of MAO have been linked with inhibitory and disinhibitory psychopathology, respectively (Bongioanni, 1991).

Serotonin. 5-HT is an indole amine neurotransmitter involved in a wide variety of psychophysiological functions that often appear to have antagonistic or counterbalancing influences vis-à-vis catecholaminergic (DA and NE) systems. Thus, 5-HT promotes sleep, parasympathetic activation, and the antistress relaxation response (see Buck, 1988b). There are at least 14 separate 5-HT receptors divided into 7 main families. Alterations in these receptors occur in a variety of psychological disturbances, includ-

ing personality disorders, anxiety, depression, eating disorders, schizophrenia, and drug-induced psychotic states (Roth, 1994).

Sjoerdsma and Palfreyman (1990) distinguished periods in the history of understanding of 5-HT, beginning with its isolation and identification in 1953. A Drought Era (1970–1979) corresponded to the period when American scientists emphasized the catecholamine hypothesis of depression, whereas European scientists emphasized 5-HT. This was succeeded by a New Era after 1979, when 5-HT receptor subtypes were distinguished and new drugs with receptor selectivity were developed. Drugs that bind to specific 5-HT receptor subtypes include the selective serotonin reuptake inhibitors (SSRIs) that are used in the treatment of major depression. One of these, fluoxetine, is widely known by its brand name Prozac (Kramer, 1993). There is evidence of the usefulness of specific SSRIs in the treatment of personality disorders with aggressive and impulsive features, obsessive-compulsive disorders, panic disorders, eating disorders, and premenstrual tension, among other conditions (Boyer, 1992). Recently introduced antidepressants block the reuptake of both NE and 5-HT (Richelson, 1996).

Recent reviews have confirmed a link between low levels of 5-HT function and impulsive aggression, particularly in men (Asberg, 1994; Brown, Botsis, & van Praag, 1994; Coccaro, 1993; Tunier, Verhoeven, & van Praag, 1995). As Siever and Trestman (1993) pointed out, symptoms of impulsive aggression seen in antisocial personality disorder in humans may be analogous to the behaviors shown by animals given lesions that interfere with 5-HT function. These include failures to delay gratification or to suppress punished behavior.

It is interesting that there is a relationship between 5-HT levels and dominance; the level of 5-HT in the blood of dominant male vervet monkeys is twice as high as the levels in subordinate males (McGuire, Raleigh, & Brammer, 1984). Similar findings have been observed in lizards (Summers & Greenberg, 1995); rats (Blanchard et al., 1993); and University of California, Los Angeles, fraternity members—fraternity officers have higher 5-HT levels than other members (McGuire et al., 1984). In male vervet monkeys, the leader's high 5-HT level appears to be maintained by the submissive behavior he receives from his followers. If the leader is removed from the group, his 5-HT falls to normal. If the leader is removed and 5-HT functioning is enhanced in one of the subordinate animals by giving the 5-HT precursor tryptophan and the reuptake inhibitor fluoxetine (Prozac), the subordinate tends to acquire high dominance status (Raleigh et al., 1991).

The association between 5-HT and dominance is not limited to higher vertebrates but has also been demonstrated in lobsters (*Homarus americanus*). Livingstone, Harris-Warrick, and Kravitz (1980) found that injections of 5-HT in freely moving lobsters produce a posture similar to the characteristic dominance posture: a rigid flexion of the legs and abdomen so that the animal stands high with tail tucked under, with the claws raised and open. Conversely, injections of octopamine (the phenol analogue of NE; Breen & Atwood, 1983) produce an opposite posture similar to the characteristic subordinate posture. There is a rigid hyperextension of the legs and abdomen so that the animal crouches low, with the claws stretched out in front (Livingstone et al., 1980; Weiger & Ma, 1993). The extremity and duration of these effects were related to dosage. Livingstone et al. (1980) observed similar results in crayfish (*Procambarus clarkii*, *Astacus fluviatilis*, and *A. astacus*). The production of these opposing postures results from the triggering

by 5-HT or octopamine of particular motor programs in the central nervous system (Kravitz, 1988; Ma & Weiger, 1993).

It is noteworthy that McGuire et al. (1984) found dominance to be associated with high levels of 5-HT, whereas other evidence links low levels with impulsive aggression. The crucial difference may be between confident dominance and frustrated hostility. Contrary to conventional wisdom, the most powerful dominant male is often not the strongest and most aggressive. In wolves, the dominant male is often the most effective politician, who builds coalitions that cooperate in driving aggressive males from the pack (Ginsburg, 1991).

As noted, the link between low 5-HT and impulsive aggression is stronger in men than in women. Kramer (1993) suggested that low 5-HT functioning is also associated with rejection sensitivity, a condition in which a person is pathologically vulnerable to rejection and loss. He suggested further that this condition is particularly prevalent in women, and indeed, that it may be at the basis of the symptoms of a once-common neurotic disorder now rarely diagnosed: hysteria. In fact, female hysteria and male antisocial aggression have been related to one another in other accounts; for example, Gray (1971) suggested that psychopathy and hysteria have a common foundation in extreme extraversion. If this is correct, it might be speculated that both conditions are associated with failures by extraverts to establish gender-appropriate social bonds and that it is this failure of bonding rather than the extraversion per se that might be associated with low 5-HT functioning. This speculation assumes that the social environment normally maintains 5-HT levels. If an individual is loved and respected, her or his 5-HT levels will be high. Rejection and social failure is involved with low levels of 5-HT, which is associated with impulsive aggression in men and rejection sensitivity in women.

This speculation relates to a larger point regarding the relationship between social-situational factors versus biological factors in the control of behavior. Conventional wisdom often suggests that behavior is under the control of both innate biological factors and learned factors sensitive to situational demands and expectations, and that the demonstration that a neurochemical system is involved in the control of some behavior is often taken to mean that innate factors predominate. For example, if poor people are found to have low 5-HT levels, some might argue that their poverty is somehow biologically based. However, correlation does not prove causation, and it is just as possible that factors associated with poverty—powerlessness, childhood deprivation, poor diet, social isolation, jobs that impose high demands with low decisions—themselves contribute to low 5-HT functioning (see R. B. Williams, 1995).⁸

⁸ The relative contribution of genetic and environmental factors to behavior is often expressed as heritability, which attempts to express the ratio of variation due to genetic determination to overall variation. Heritability estimates are typically based on twin studies, where monozygotic (MZ) twins are genetically identical, being derived from the same zygote, and dizygotic (DZ) twins shared the same uterine environment but are genetically different. It is often assumed that heredity rather than environment determines the extent that MZ twins are more similar (concordant) than DZ twins. For example, MZ twins have a concordance rate of schizophrenia of 48%, as opposed to 17% for DZ twins. This has been interpreted as indicating that the risk of schizophrenia "varies with the amount of gene sharing and not with the amount of experience sharing" (Gottesman, 1991, p. 97). However, heritability may be overestimated from simple MZ twin concordance rates. Most MZ twins are monozygotic

The Peptide Neurohormones

The second kind of neurochemical system to be examined involves peptide neurohormones, with particular attention to those that seem to have important affective properties: the endorphins, cholecystokinin, oxytocin and vasopressin, gonadotropin-releasing hormone, and corticotropin releasing factor.

The peptides. In recent years there has been increased understanding of perhaps the most fundamental, even primordial, sort of neurochemical: behaviorally active chemicals, which are in fact much older than neurons. There are 16 amino acids that can be strung together like beads on a string; they are the building blocks of protein. Peptides are chains of amino acids, the sequencing of which determines the shape of the molecule and therefore its chemical activity. Neurochemically active peptides have been identified in chains as short as two amino acids and as long as 200 or more (Cordes, 1985). They fit into suitable receptor sites on the cell membrane and other active locations like a key in a lock, altering biological activities at the receiving site in fundamental ways.

Peptides are ancient substances that appear not only in the nervous systems of higher animals but also in insects, segmented worms, plants, and single-celled yeast and bacteria (Loumaye, Thorner, & Catt, 1982; Pert, 1985). For example, single-celled protozoa have peptides similar to adrenocorticotrophic hormone (ACTH), the endogenous opiate beta-endorphin, cholecystokinin, gonadotropin-releasing hormone, and insulin (LeRoith, Shiloach, Roth, & Lesniak, 1980; LeRoith et al., 1981; W. L. Miller, Baxter, & Eberhardt, 1983). This suggests that the peptides are involved in the most fundamental sorts of intracellular and intercellular communication. The evolution of the peptides began early in the unicellular stage of life, and genes specifying these substances "have been conserved virtually unchanged throughout the whole of invertebrate and vertebrate history" (Niall, 1982, p. 617).

Peptide hormones from endocrine glands act through the bloodstream. It was once thought that peptide hormones are produced only in the specialized glands, ACTH from the pituitary, insulin from the pancreas, and so on. Now these substances have been found throughout the body—in the brain, in the placenta, and in the cells of the immune system—and it has been suggested that virtually any bodily cell can produce virtually any peptide in small

amounts (Niall, 1982). It was also once thought that peptide hormones have their effects peripherally on the body. It is now known that they affect the brain as well—peptides act as neurotransmitters, carrying information between cells at synapses, as well as hormones—so the old distinction between hormones and synaptic transmitter substances has been blurred. The term *neurohormone* has been coined to describe the functioning of these substances. Furthermore, the central effects of the peptides on the brain are often related to their peripheral effects. Cholecystokinin (CCK) acts peripherally in digestion and centrally in the regulation of appetite; OXY is involved peripherally in childbirth and the production of milk and centrally in maternal attachment; and corticotropin releasing factor (CRF) is involved peripherally in the production of ACTH and centrally in facilitating avoidance behavior (Panksepp, 1993).

The neuropeptides have been characterized as informational substances that coordinate the internal milieu of the organism. Pert (1985) noted that these substances are distributed in mood-regulating areas of the brain and suggested that each neuropeptide may bias information processing in a unique way when occupying a given receptor site. "Each neuropeptide's 'tone' might produce a typical mood state" (as cited in Cordes, 1985, p. 18).

The endorphins. The term *endorphin* was coined in the early 1970s as a contraction of endogenous morphine, morphine produced by the body. The term was used by Hughes and his colleagues, who were the first to isolate and identify opiatelike substances in the vas deferens and later in the brain (Hughes, Smith, Morgan, & Fothergill, 1975). The brain's opiates were found to be part of a chain of 91 amino acids that makes up a polypeptide called beta lipotropin. The first 41 of these constitute ACTH, 42 through 60 constitute MSH (melanocyte stimulating hormone), which darkens the skin in response to ultraviolet light, and 61 through 91 constitute beta endorphin. Beta endorphin is among the most powerful analgesic (pain killing) substances known. It is 100 times more powerful than morphine and is more addictive to human beings than heroin (Panksepp, 1993). Fragments of beta endorphin—amino acids 61 through 65—are constituents of enkephalins that are found in the brain. These have less profound analgesic properties, and they seem to function as synaptic transmitters in that they have a rapid onset and brief duration of action compared with the more hormonelike beta endorphin (Bolles & Fanselow, 1982).

Pain is regulated by the endorphins in the spinal cord, where interneurons containing enkephalins inhibit the release of the peptide neurotransmitter substance P, which carries the pain message. This phenomenon acts much like the model proposed in Melzack's (1961) gating theory of pain: the enkephalins in effect shut the gate (Iverson, 1979). This and other effects of the endorphins are countered by naloxone, a substance that binds to the same receptor sites used by the endorphin molecules, blocking their effects. Thus, naloxone counters the analgesic effects of morphine and can be used to counter heroin overdoses.

As noted, Panksepp (1981, 1982; Panksepp et al., 1997) suggested that the endorphins are associated with social attachment and that attachment is associated with increased levels of endorphins. In this regard, the endorphins have two other effects in common with opium, morphine, and their powerful cousin, heroin: They are associated with subjectively experienced euphoria, and they inhibit breathing. The functions of these three characteristics are illustrated in the high levels of the endorphins in the unborn

(MC), having shared the same placenta; but some MZ twins are dichorionic (DC), with separate placentas (all DZ twins are DC). Davis, Phelps, and Bracha (1995) found significant differences in concordance between MZ twins estimated to have been MC and those who were DC. Concordances for MZ twins with MC markers averaged 60%; in contrast, concordances for MZ twins without MC markers averaged 10.7%. Thus, a twin who experienced a different intrauterine environment than an identical cotwin who became schizophrenic, developed the disorder only 10.7% of the time, even though the twins were genetically identical. This suggests with other evidence that brain abnormalities caused by second-trimester events are a necessary component in the development of schizophrenia (Bracha, 1991; Bracha & Gilger, 1993). Such events may be associated with the intrauterine hormone environment (Turnquist, 1993), prenatal exposure to alcohol (Lohr & Bracha, 1989), prenatal anoxia, and/or fetal infections (Torrey et al., 1994). This research demonstrates the inadequacy of heritability estimates as indices of pure genetic influence; the variation due to the prenatal environment may be incorrectly attributed to the genes in many heritability estimates.

fetus; it is protected from pain, it is presumably euphoric, and it must not breathe. Mother–infant bonds also depend on opiate systems (Keverne, 1996). At birth, a sudden drop in endorphins occurs that may be traumatic to both the infant and the mother. Higher levels may be regained in the course of mother–infant communication and bonding; this may be a reason that the bonding experience can be highly rewarding to both.

Separation, on the other hand, is highly aversive, and is associated with what Panksepp (1982) termed *panic*. Separation is associated with distress vocalizations, which, as noted, distinguish mammals from reptiles and are associated with septal and cingulate systems rich in the opiates. These vocalizations are reduced by low, nonanalgesic doses of morphine, whereas the opiate antagonist naloxone increases distress calling. In general, naloxone has effects similar to those of separation: Naloxone increases physical contact and nipple contact as well as distress calls (Keverne, Nevison, & Martel, 1997). Grooming increases opiate levels, and naloxone increases grooming, whereas morphine decreases grooming.

Panksepp (1981) suggested that these data “indicate the specificity of endogenous brain opiate systems in organizing social behavior” (p. 300). This suggests, in turn, that opiate addiction may be related to brain mechanisms of social attachment, that strong attachments increase endogenous opiate levels. We literally may be, as the song says, “addicted to love.” In addition, separation may be analogous to morphine withdrawal; the pain prominently described in bereavement may literally be caused by hypersensitivity in pain systems associated with low opiate levels. The importance of the opiate systems in attachment is, unfortunately, mirrored in the indifference to social attachment on the part of opiate addicts. Having satisfied their cravings chemically, such individuals do not need others and are notoriously lacking in the kinds of social emotions that, as I argue later, are based biologically on attachment.

Cholecystokinin. As noted, CCK is a peptide involved in appetite regulation. Peptides similar to CCK have been identified in unicellular organisms (Loumaye et al., 1982). CCK has been found to cause symptoms of fear in rats and monkeys. In human beings, CCK injections induce feelings of anxiety and fear without external cause (Bradwejn, 1993; Harro, Vasar, & Bradwejn, 1993). Patients subject to panic attacks recognize these feelings as being like those associated with their usual attacks. Studies using a combination of PET scanning and MRI show that CCK increases blood flow in limbic areas associated with fear (Reiman, Fusselman, Fox, & Raichle, 1989).

Oxytocin. OXY and vasopressin (VP) are posterior pituitary peptide hormones derived from an evolutionary divergence of an ancestral hormone, vasotocin, that has been identified in unicellular organisms (Loumaye et al., 1982) and facilitates sociosexual responses in reptiles and birds (Moore, 1987). OXY and VP appear to have central functions that are at the same time related and quite opposite to one another. The fact that they share the same ancestral hormone raises questions about how the behaviors that they regulate differ in mammals from those in reptiles and birds. Specifically, OXY and VP may be relevant to the differentiation of female- and male-typical sexual and aggressive behaviors in mammals.

Peripheral effects of OXY include the control of lactation and of uterine contractions. Its central effects are associated with maternal

behavior and nurturance (Insel, 1992; Panksepp, 1992; Pederson, Caldwell, & Brooks, 1990). OXY and maternal behaviors are regulated by sex steroids and offspring stimuli in many species (Bale & Dorsa, 1995; Pederson, 1997). In rats, OXY enhances sexual receptivity in the female, and OXY antagonists decrease receptivity (Benelli et al., 1994; Caldwell, Johns, Fagg, Senger, & Pederson, 1994). Central administration of OXY reduces infanticide in animals (McCarthy, 1990), increases sexual behavior in both males and females (Richard, Moos, & Freund-Mercier, 1991), and decreases separation distress (Panksepp, 1992). Orgasm is characterized by increased OXY release in both females and males (Richard et al., 1991).

In the female prairie vole, OXY has been shown to be both necessary and sufficient for the development of pair bonds (Insel, 1992; J. R. Williams, Insel, Harbaugh, & Carter, 1994). Mating is associated with OXY release and increased social bonding and contact. The OXY may function to cement partner preferences in that the individuals may prefer whom they are with when OXY increase occurred (Carter, 1996). Compared with the more solitary and nonmonogamous montane vole, the prairie vole is characterized by side-by-side social postures, ultrasonic vocalizations by pups to separation, and a high cortisol response to separation. The montane vole shows none of these characteristics and exhibits weaker maternal and paternal behaviors. Brain areas associated with OXY are much larger in the prairie vole (Insel, Young, & Wang, 1997).

Panksepp (1993) has suggested that OXY is “a prime candidate for mediating feelings of acceptance and social bonding” (p. 93). The actual subjective effects of OXY in human beings remain a matter of conjecture, but Panksepp (1993) suggested that the apparent abilities of OXY to modulate sexual and socioaffective moods indicate potential applications both to the reduction of child abuse and certain forms of impotence.

Vasopressin. The peripheral effects of VP, formerly known as antidiuretic hormone, include inhibiting water excretion in the kidney and raising blood pressure. Centrally, VP does not affect separation distress or female sexual behavior, but male sociosexual behaviors, including aggressive behaviors, are promoted (Koolhaas, van den Brink, Roozendaal, & Boorsma, 1990). Conversely, VP antagonists reduce male intraspecies aggression in hamsters (Potegal & Ferris, 1989). In the male prairie vole, it is VP rather than OXY that facilitates partner preferences. VP also induces selective intraspecies aggression (Windslow, Hastings, Carter, Harbaugh, & Insel, 1993), perhaps acting through the central amygdala (Gingrich, Huot, Wang, & Insel, 1997).

VP is associated with both testosterone and estrogen levels. Castration in rats reduces VP neural systems in the brain by approximately one half (De Vries, Buijs, Van Leeuwen, Caffé, & Swabb, 1985), and estrogen stimulates the expression of the VP gene, resulting in a massive increase in VP in the BNST and other brain structures (Fink, Sumner, Rosie, Grace, & Quinn, 1996). Panksepp (1993) suggested that VP may be a “specific carrier for male dominance and persistence urges” (p. 93) and may mediate “heightened tendencies for males to exhibit aggression, and it is possible that the underlying subjective emotional correlate is one of increased irritability and anger” (p. 94).

Gonadotropin-releasing hormone (GnRH). The hypothalamus regulates gonadal function by controlling the secretion of luteinizing hormone and follicle stimulating hormone (FSH) from the

anterior pituitary gland. Luteinizing and FSH releases are regulated by an interaction of GnRH and sex steroids. GnRH (luteinizing hormone-releasing hormone) is secreted from the hypothalamus into the portal system that supplies blood to the anterior pituitary. It enhances the release of both the luteinizing hormone and FSH in mammals and has been found to be active in birds, reptiles, and fish as well (Schally, 1978). Indeed, a peptide mating pheromone of the yeast *Saccharomyces cerevisiae* is similar to GnRH (Loumaye et al., 1982). Loumaye et al. noted, "it is intriguing that a pheromone responsible for mating and zygote formation in a unicellular organism is both structurally and functionally related to the peptide serving a key role in mammalian reproduction" (p. 1324).

The peripheral effects of GnRH include promoting spermatogenesis in males and preparing the female body for ovulation, stimulating the production of estrogen and progesterone in the female and androgens in the male. Centrally, GnRH increases sexual proclivities. In hamsters, chemosensory and other sensory inputs trigger intracerebral GnRH release, which then facilitates mating behavior (Meredeth & Fernandes-Fewell, 1993). GnRH has rewarding effects as demonstrated by their abilities to establish conditioned place preferences in male rats. These preferences, however, are absent in gonadectomized animals (de Beun et al., 1991). Panksepp (1993) suggested that GnRH "may well prove to be a prime mover in human libido" (p. 94).

Corticotropin releasing factor. CRF released from the periventricular hypothalamus causes the release of ACTH from the pituitary, which in turn releases a variety of stress hormones, glucocorticoids including cortisone from the adrenal cortex. Centrally CRF instigates a "coordinated central stress response that has a major impact on the elaboration of both fear/anxiety and separation distress in the brain" (Panksepp, 1993, p. 92). CRF has been implicated in mediating negative affects associated with withdrawal from a variety of drugs of abuse, including alcohol, cocaine, opiates, and cannabis (Rodriguez de Fonesca et al., 1997).

Panksepp (1993) suggested that CRF is associated with a particular kind of stress-induced depression or burnout in human

beings. NE inhibits CRF activity, and CRF excites NE activity, so that normally CRF turns itself off, in a negative feedback loop through increased NE. Chronic CRF activity due to stress can lead to NE overactivation and the eventual depletion of brain NE that is difficult to reverse because there is no longer any way to turn off the CRF (Risch, 1991). In this way, chronic stress can promote "semipermanent brain changes that at the psychological level may be experienced as despair" (Panksepp, 1993, p. 92).

Panksepp (1993) suggested that CRF might play a role in the long-term effects of early social isolation. A pattern of response to isolation in children has been long recognized. Initial distress and active protest gives way to despair, and finally detachment, where permanent damage may be done to the ability to form social attachments (Bowlby, 1969, 1973, 1980). Panksepp (1993) suggested that "early social isolation may facilitate the long term genetic and neurosecretory activity of the CRF system that precipitates a cascade of events leading from protest to despair—from the experience of separation to the experience of depression" (p. 92).

Summary and Discussion

This review of the biological affects demonstrates the complexity of the subject and the multiplicity of neurochemical systems involved. To summarize, Figure 6 organizes the biological affects by levels of the brain crossed with functions, with arousal, approach-avoidance, agonistic-selfish, and prosocial functions represented at various hierarchical levels: protoplasm (prebrain), brainstem, hypothalamus/R complex, and limbic system.

The essence of the difference between selfish and prosocial affects is that the former support self-preservation and the latter support the preservation of the species. As noted previously, affects associated with MacLean's (1993) amygdala circuit of the limbic system—fear, anger, disgust—are identified as agonistic because they involve conflict, competition, or fighting. The approach-avoidance and arousal affects also count as selfish according to MacLean's (1968, 1969, 1970) definition, in that they

System Level	Individualist "selfish" affects/behaviors			Prosocial "cooperative" affects/behavs.
	Arousal	Approach/Avoidance	Agonistic	
Protoplasm (pre-brain)	Basic arousal/activation	Positive-negative taxes and tropisms	Basic territorial and agonistic behaviors	Basic sexual and aggregative behaviors
Brainstem	Reticular activation system	Approach-avoidance systems	Aggressive, defensive reflexes.	Sex reflexes, submission
Hypothalamus/R-complex	Attention	Reward-punishment systems	fight or flight response/Territoriality	Relaxation response/ Sex and courtship
Limbic system (paleocortical)	Advanced attention systems: Type I & II (Hippocampus)	Behavioral Activation and Inhibition systems Happy, sad, anxiety (Prefrontal)	Fear, anger, disgust (Amygdala)	Lust, submission, parenting, attachment, play, panic (Septal; Mamm.-Cing.)

Figure 6. Hierarchy showing hypothesized relationships between biological affects and neurochemical systems. Mamm.-Cing. = Mammillocingulate.

are dedicated to self-preservation. In this view, happiness is a positive selfish affect, sadness and anxiety negative but nonagonistic selfish affects, and arousal a nonvalenced selfish affect.⁹

Selfishness and sociality: The group selection debate. One of the logical consequences of distinguishing selfish and prosocial affects is the implication that the preservation of the individual and the species are not always compatible. More specifically, prosocial affects are not necessarily always conducive to the preservation of the individual, or even the individual's genes, as opposed to the doctrine of the selfish gene (Dawkins, 1976; Dawkins & Krebs, 1978). The present view requires that natural selection take place at the level of the group as well as that of the individual. The notion of group selection has been the subject of recent controversy (see Wilson & Sober, 1995). It is disputed by many evolutionists in part because of the assumption that natural selection works at the level of the gene (G. C. Williams, 1966). In Dawkins's terms, genes are replicators; they are maintained virtually intact from generation to generation, whereas individuals and groups are not. G. C. Williams and Dawkins do not recognize any significant mechanisms by which genes can be selected by group characteristics.

The communicative gene hypothesis. The reply is that group characteristics can and do in fact evolve by the selection of individual characteristics through the evolution of communication. The mechanism of group selection can be explained by the communicative gene hypothesis, which posits that spontaneous emotional communication based on communicative genetic systems form the basis of social behaviors (Buck & Ginsburg, 1991, 1999). Emotional communication is based on innate displays and preattunements, in displays on the part of the sender and preattunements to those displays on the part of the receiver (Buck, 1984). Displays and preattunements are genetically encoded in the individual sender and receiver, respectively. However, although emotional communication is genetically based in individuals it functions on a group level, specifically on the level of the *communicative relationship*. In threatening, submitting, courting, and warning, both sender and receiver benefit from communication; what is selected is communication, which simultaneously involves both sending accuracy and receiving ability. More specifically, when animals threaten, court, or warn, the results are relevant to the survival of the genes of both individuals. *What* is selected are the sending and receiving characteristics of the individuals involved (displays and preattunements, respectively), but the selection occurs at the dyadic-relational level (Buck & Ginsburg, 1999). Note that there is no requirement that the individuals involved be genetically related to mutually benefit from successful dyadic communication.

In this way, group characteristics—communicative relationships between individual senders and receivers—are selected through the selection of individual sending and receiving mechanisms. These relationships, such as dominance and courting relationships, serve roles within the group, which, like genes, are maintained over the generations. Examples include insect societies (ants, bees, termites) where roles within the group have been maintained for tens of millions of years through communicative relationships. Indeed, in the terminology of Dawkins (1976), communicative relationships and roles are in fact replicators, in that they are maintained virtually intact from generation to generation.

Thus, the elements of spontaneous communication are geneti-

cally encoded qualities of the individual sender and receiver, but they function at the relational-dyadic level, and it is at the relational-dyadic level that selection then takes place. When this occurs, the unit of natural selection is not the individual but the communicative relationship, a group-level phenomenon based on the communication, the sending and receiving, of individuals (Buck & Ginsburg, 1991, 1997a, 1999). For example, Rabb, Woolpy, and Ginsburg (1967) described how the wolf pups from separate litters raised together without adult tutors developed the social roles of a natural pack in the wild from their own interactions; the wolf pack is, in effect, a sociogenetic unit organized by communication.

Affects as voices of the genes. A detailed examination of the issue of group selection would take us far afield, but particularly relevant to the present article is the notion that *affects function as voices of the genes*. Affects are ways in which the genes influence, persuade, or cajole the individual to behave in ways conducive to the preservation of the individual or the group/species, or both. The selfish affects, in this view, are readouts of selfish genes in the tradition of Dawkins (1976), and the prosocial affects are readouts of prosocial genetic systems, which are phylogenetic adaptations selected through the survival of critical group/species characteristics expressed through communication (Buck & Ginsburg, 1991, 1997a, 1997b; Ginsburg, 1974, 1976).

More specifically, the way that genes communicate, both between and within organisms, involves motivational-emotional systems or primes, through social displays and preattunements and subjectively experienced affects, respectively. The behaviors of relatively simple creatures such as ants and termites are more or less controlled by the genes; as organisms become more complex, behaviors are increasingly cajoled—enticed or charmed—by the genes. In this sense, affects are voices of the genes in complex organisms. Behavior is flexible and modifiable by learning, and indeed complex organisms are hard-wired to be flexible; free choice is biologically determined.

Higher Level Affects

Biological Versus Higher Level Affects

Developmental-interactionist theory proposes that the subjective readout of all of the biological affects is always accessible to us, just as is the feel of our shoes on our feet (Buck, 1985, 1994b). In effect, the voices of the genes as subjectively experienced

⁹ Positive and negative valence seems to be an obvious characteristic of affects at first glance, but on reflection valence becomes problematic. Positive affects are generally seen as good, and negative affects as bad. Indeed one of the general conclusions about the nature of emotion voiced by Ekman and Davidson (1994) is that "people seek to maximize the experience of positive emotions and to minimize the experience of negative emotions" (p. 412). This is not, however, consistent with the fact that many people apparently like the negative emotions triggered by horror films, action-adventure films, and tearjerkers. The more effectively fear, anger, sadness, and even disgust are triggered by films, the more popular they seem to be (Buck, 1988a). Also, if positivity and negativity were defined in approach-avoidance terms, anger would be a positive emotion. One of the advantages of defining basic affects by biological criteria is that the adaptive consequences of affects for the individual and the species are emphasized, rather than their valence.

affects are ever present, usually whispering, sometimes shouting and commanding, occasionally screaming. We always have access to how warm and hungry, happy and angry, we are, and these systems are always turned on so that we are always warm, hungry, happy, angry, and so forth, to some extent. However, we tend consciously to notice affects only when they are relatively strong. Then we may call them in ordinary language *moods* or, at higher levels, *emotions*.

The drives and individualistic affects are distinct in that they require no object; they exist independently of any social or situational context. It is always meaningful to ask someone how hungry, or cold, or happy, or aroused, or angry they feel at any given moment, and it is not necessary to specify any object or person in such a question. The individualistic affects exist on their own, an aspect of bodily functioning, always turned on, albeit normally at low levels.

The prosocial affects also always exist, but do so in the context of a particular social relationship; one can always ask how loving, attached, or affiliative one feels but only with regard to someone with whom one has a specific personal or social relationship. All social or personal relationships can be meaningfully characterized by the prosocial affects, and the relevant prosocial affects are accessible whenever a given personal or social relationship is salient.

Higher level affects include social, cognitive, and moral affects. These affects are not always with us in the sense that the biological affects are. I view them as being based on the biological affects, but they respond to challenges in the social and terrestrial environments, and they therefore exist relative to events outside the organism: other persons, external stimuli, or situations including events in memory and imagination. Higher level affects are involved in coping with life challenges (Lazarus, 1966) and concerns (Frijda, 1986) and in responding to the unexpected (Oatley, 1992). Moreover, higher level affects require developmental experience vis-à-vis other organisms or the environment, or both, to become functional, that is, to become effectively and competently experienced and expressed.

We have examined a number of biologically based affects, including affects associated with different sorts of reward, satiation, erotic attraction, maternal/parental love, play, and bonding. I suggest that prosocial affects involving attachment are the biological bases of social affects, including pride, guilt, shame, envy, jealousy, pity, and scorn. Furthermore, I suggest that individualistic affects involving expectancy compose the biological basis of exploratory cognitive affects such as interest, boredom, curiosity, and surprise.

Tomkins's (1982b) theory offers a way to understand how attachment and expectancy can come to underlie higher level affects. Contrary to Tomkins's view, drives such as hunger and thirst are associated with special-purpose motivational systems that can be localized in the hypothalamus. These are special purpose in that they are related directly to bodily needs and specific consummatory stimuli. However, in addition there are general-purpose reward-punishment or expectancy systems coursing through the hypothalamus that allow the association of consummatory stimuli with other events—incentives—which then can take on positive or aversive motivational force of their own. The result is a general-purpose motivational system capable of supporting virtually any sort of exploratory behavior and instrumental

learning. In my view, and consistent with Tomkins's (1982b) analysis, the expectancy system continued in this motivational role as more complex cognitive functions evolved. Therefore, the excitement felt by human beings with successful higher level cognitive and linguistic exploration, as well as the frustration and potential burnout and despair brought on by failure, is based ultimately on the expectancy system.

An analogous argument may be made for the prosocial affects acting as a separate assembly functioning to support the motivation of social behavior, contributing basic feelings of bonding, affection, and love, as well as panic, when those feelings are not reciprocated. The same principles are involved in both expectancy and attachment, deriving directly from evolutionary theory. In the case of prosocial affects, the special-purpose systems seen for example in prairie voles evolved into more general-purpose systems characterized by the prosocial affects.

Attachment: The Biological Basis of Social Affects

The social affects. As noted, the evolution of mammals was associated with a remarkable diversity of attachment mechanisms that tend to moderate selfish tendencies. Collectively, these biologically based attachment mechanisms determine an individual's motivation to bond with others through the prosocial biological affects. In this way attachment constitutes the physiological basis of the higher level social affects, a powerful motivational force amounting to, in effect, a biologically based addiction to love. Social affects are based biologically in the prosocial affects, but they exist with regard to other persons and events. When one feels proud, or ashamed, or jealous, it is with respect to other persons and specific situations. It is only meaningful to inquire about social affects if other persons and situations are specified or implied.

Two fundamental social motives. Attachment involves strong biologically based affects that have intrinsic motivational consequences. This motivation arising from attachment has two aspects: the need to follow/exceed expectations, and the need to be loved. That is, following or exceeding expectations, and being esteemed by others, are associated with strong positive feelings of social acceptance, bonding, and love; whereas failures to meet expectations and to be esteemed are associated with feelings of social rejection, distress, and panic. Therefore, because of attachment a person is strongly motivated to conform, to do that which is expected, and indeed to exceed expectations, and a person is strongly motivated to be esteemed and loved by others. These social motives are among the strongest of human motives and are largely responsible for the great flexibility of human behavior (Buck, 1988b).

Individuals can attain or fail to attain these social goals themselves, and they can compare themselves with other persons who attain or fail to attain these goals. When success and failure at meeting these two goals on the part of the self and the other are combined, the result is an array of eight specific social affects. If one succeeds in meeting/exceeding expectations, one tends to experience *pride*; if one fails, one tends to experience *guilt*; if the comparison other succeeds, one tends to experience *envy*; if the other fails, one tends to experience *pity*. If one succeeds in being loved, one tends to experience *joy/arrogance*; if one fails, one tends to experience *shame*; if the comparison other succeeds, one

tends to experience *jealousy*; if the other fails, one tends to experience *scorn* (Buck, 1988b).

Attachment theory and the social affects. Securely attached persons should be assured of being loved, so that all else being equal their need to follow/exceed the expectations of others should be relatively stronger than their need to be loved. Contrariwise, a person who is insecurely attached should be unsure of being loved, so that their need to be loved should be relatively stronger than their need to follow or exceed expectations. Therefore, a securely attached person should tend to feel pride, guilt, envy, and pity in situations in which an insecurely attached person should tend to feel joy or arrogance, shame, jealousy, and scorn, respectively. Further discussion of the social affects would take us too far afield, but it is clear from the present analysis that attachment theory can be used to aid in the analysis of the nature and dynamics of the social affects.

Expectancy/Effectance: Biological Basis of Cognitive Affects

Just as the prosocial affects furnish the biological basis for the social affects, I suggest that individualistic affects involving reward–punishment and expectancy systems furnish a biological basis for cognitive affects. Also, just as the social affects exist with regard to other persons, the cognitive affects exist with regard to events. When we feel curious, interested, surprised, bored, or burned out, it is with respect to a specific event or circumstance. It is only meaningful to inquire about cognitive affects if some situational circumstances are specified or implied.

Developmental–interactionist theory of cognitive affects. The cognitive affects fit the developmental interactionist theory of motivation and emotion as follows. Again, motivation is defined as potential inherent in a system of behavior control, and emotion as the readout of that motivational potential. In the case of cognitive motivational–emotional systems, the motivational potential includes both tendencies to be rewarded by exploratory behavior mediated for example by the BAS and tendencies to be punished by such behavior mediated by the BIS. Individual differences in these tendencies vary along a dimension related to extroversion–introversion, which expresses the general ease of being rewarded or punished, or both (Gray, 1982). These differences may be both genetically based (i.e., related to temperament) and socially learned (Buck, 1979, 1988b). The cognitive affects involve subjectively accessible readouts of rewarding or punishing expectancies associated with ongoing behavior. Just as with the biological affects, cognitive affects may be with us even though we may not notice them. Unlike the biological affects and like the social affects, they must always relate to something outside the organism. As noted, we are interested *in* something or surprised *at* something, stubborn, confused, or confident *about* something. The ultimate function of the cognitive affects is education, the drive to explore and to learn *about* one's raw experience.

Expectancy and effectance motivation. I suggest that, just as social affects are based biologically in prosocial attachment systems, cognitive affects are based biologically in individualistic reward–punishment/expectancy systems coursing through the hypothalamus into the forebrain. As noted, general-purpose processing systems respond to the fruits and dangers in the environment in such a way that the individual organism becomes through experi-

ence able to obtain the former and avoid the latter. The work of Olds, Milner, and others is reflected in Panksepp's (1982) analysis of the expectancy system, which may provide the motivational component to a number of specific drives. This basic reward–punishment system can also motivate more general exploratory behaviors, resulting in general motives to explore and to understand the unfamiliar.

R. W. White (1959) pointed out that exploratory, stimulus-seeking behaviors have a common property: They have an effect on the environment. He proposed that effective interaction with the environment is intrinsically rewarding, that exploratory behaviors are directed, selective, and persistent, and motivated by an intrinsic need to deal with the environment, which he termed *effectance motivation*. The result is that the child gains *competence* in dealing with the environment. R. W. White's analysis implies that the process of coming to know the environment is in itself not a cold cognitive process but rather is strongly charged affectively, with powerful feelings including expectancy, curiosity, boredom, interest, surprise, and, perhaps, stubbornness. A number of theories have central concepts similar to R. W. White's competence: Rotter's (1966) locus of control, Heider's (1958) and DeCharms's (1968) personal causation, Bandura's (1991) self-efficacy, and Deci and Ryan's (1991) intrinsic motivation are prominent examples. These approaches, however, have not considered in detail the nature of the hot affects that arguably underlie the development and maintenance of cold analytic cognition.

The Social and Cognitive Bases of Moral Affects

I suggest that moral affects are based on social and cognitive affects, requiring both social experience and cognitive development to become maturely expressed. Moral affects are associated with learned expectations about what circumstances *should* result in the social affects of pride, guilt, shame, pity, scorn, and so on. These expectations are expressed in notions of distributive and retributive justice that specify how good and bad outcomes, respectively, should be meted out. In essence, moral affects provide the motivational force, the fire, underlying the sense of justice.

Historically, the study of moral capacities has not typically involved the notion of moral affects. Research has generally focused on either moral judgment, the ability to tell right from wrong, or moral behavior, the tendency to act in accordance with moral prescriptions when confronted by sometimes-complex situational pressures (Buck, 1988b). However, moral judgments and behaviors rarely occur in an affective vacuum, more often, judgments of right and wrong are accompanied by strong affects, both positive (moral rapture) and negative (moral indignation). Indeed, moral feelings are some of the strongest and most persistent motivators of human behavior.

I have argued that there are specific biological bases for both social and cognitive affects, but that both require experience; social experience is necessary for the mature expression of the social affects, and cognitive affects underlie the process of cognitive development by motivating exploration. Both social experience and cognitive development are necessary for the development and mature expression of moral emotions, and the nature of moral judgment, behavior, and feeling does change with the process of moral development. Indeed, with the process of cognitive development, social affects naturally become moral affects, in that they

are aroused by moral judgments. A comparison other's failure might produce either pity or scorn, depending on whether the failure was judged to be deserved.

Social and cognitive development, accompanied and motivated by social and cognitive affects, is both necessary and sufficient for the development of morality. Given that the child cares about others and learns about the workings of the world, moral development accompanied by moral affects is *arguably inevitable*. However, a failure of attachment, caused for example by social isolation or abuse, leads to an uncaring deficiency in the social affects and a consequent deficiency in the moral affects, a sociopathic lack of conscience.

Summary: Biological Bases of Higher Level Affects

The social learning processes connecting biologically based affect systems and higher order affects are summarized in Figure 7. Prosocial affects interact with social challenges to yield social affects; affects associated with reward and punishment interact with environmental challenges to yield cognitive affects. This interaction occurs over the course of development. Failures in attaining social or environmental competence can be associated with depressive disorders. As noted, there are two sorts of major depressive disorders: Type A involves NE systems, whereas Type B involves serotonin (5-HT; Maas, 1975). Stress associated with the failure to meet terrestrial–environmental challenges can cause Type A depression associated with low NE and a consequent inability to be rewarded, and failure to meet social challenges and consequent subordinate status can cause Type B depression by an interaction-mediated lowering of serotonin (5-HT). The attainment of competence in understanding and dealing with the environment is normally accompanied by strong social affects involving attachment. Attachment feelings and understanding combine in the moral affects.

General Conclusions

It is perhaps useful to recall the developmental–interactionist conceptualization that seeks to integrate the disparate phenomena

considered in this article. At base is the notion that all life forms express simultaneously and in parallel selfish tendencies for individual survival and prosocial tendencies for species survival. These tendencies, the yin and yang of mortal existence, inhere in the genes. Selfish and prosocial genes specify selfish and prosocial neurochemical systems, including neural networks, receptor systems, neurotransmitters, enzymes, and relevant molecular agonists and antagonists. The selfish neurochemical systems include reward–punishment systems, arousal systems, and agonistic affect systems. These provide the affective underpinnings of effectance motives and the higher level cognitive affects such as curiosity, expectancy, interest, and surprise. These are involved directly in the motivation of cognitive development. The prosocial neurochemical systems include sex-related affects as well as attachment affects associated with bonding, parental behavior, and play; these provide the affective underpinnings of social motives and the higher level social affects including pride, joy, guilt, shame, envy, jealousy, pity, and scorn. These are involved directly in the motivation of social development. Prosocial affects can contribute to cognitive development and individualistic affects to social development as well; thus social motives can fuel environmental exploration, and the social as well as the terrestrial environment is a subject of exploration. Serious failure in the attainment of competence can lead to burnout, despair, and Type A depression associated with NE depletion, whereas rejection and failure in the social realm can lead to Type B depression associated with depletion of 5-HT. Moral development occurs naturally with cognitive and social development, with moral judgments being invested with strong moral affects reflecting both selfish and prosocial considerations.

The grand aim of the present article, together with previous explications of developmental–interactionist theory, is to elaborate an integrated view of the three classical concepts in psychology: motivation, emotion, and cognition. This is a metatheory, not testable in itself, but rather meant to show the interrelationships of theories designed to handle more specific ranges of phenomena. For example, it suggests how Gibsonian theory and Piagetian

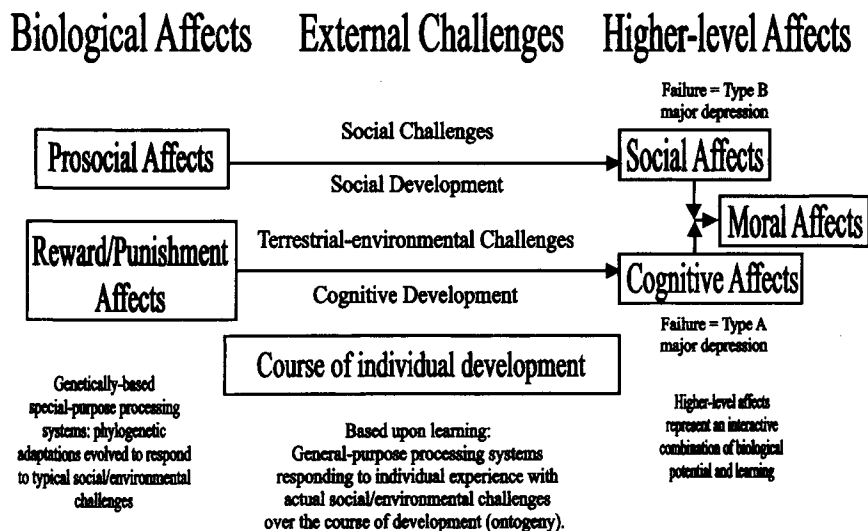


Figure 7. Hypothesized relationships between biological affects and higher level affects.

theory—often considered to be at loggerheads—are in fact compatible: Gibsonian theory is applicable to the understanding of raw knowledge-by-acquaintance and Piagetian theory to the attainment of knowledge-by-description. Several features set the present view apart from other approaches to emotion. For example, it explicitly integrates emotion theory with Gibsonian perceptual theory. It suggests that biological affects constitute voices of the genes that are always present at some level in human experience, if usually at an unnoticed whisper. It suggests that children learn about these affects—emotional education—in a social learning process that differs in specific ways from usual social learning because the affects are private events. It also presents an emotion typology based not on fuzzy logic and slippery language but on the functioning of concrete and potentially observable neurochemical systems.

An additional aim of the theory is to use this integrated view to suggest new areas of research. Examples of this are the notion that Type A and B depression are associated with nonsocial and social failure, respectively, and the notion that the RH and LH are particularly associated with individualistic and prosocial affects, respectively. Also, with attachment as the biological basis of the social affects, secure and insecure attachment styles may be predictably related to the social affects. The latter notion will be explored in a future article focused in detail on the higher level affects.

The typology of affects presented in this article is only a first step; little is known about the dynamic relationships between the affects enumerated here. Is sadness related to anger or to fear? Do feelings of shame or guilt evoke depression? Can they instead evoke anger? Does shame cause depression only when one is also a target of scorn by others? Does remorse reduce depression? Does altruism based on empathy induce feelings of pride? Are there different implications in the pursuit of selfish happiness as opposed to social joy? I suggest that the short answer to each of these questions is yes, but the issues of why and how these effects may occur have barely begun to be understood. Much theorizing and research on affective dynamics and their effects on individual and social functioning remains to be done.

This article has concentrated on affect, the syncretic–cognitive readout of emotion. It has considered the communicative readout of emotion only in passing and the arousal–homeostatic readout hardly at all. The present view of affect is in essence an extension of social learning theory and is in this sense squarely in the mainstream of American psychology. The difference with other social learning theories is that subjective experience is taken to be an authentic source of knowledge in its own right, which interacts with other cognitive processes over the course of development in ways that are just beginning to be understood and appreciated.

In discussing approaches to attacking the problem of private events by objective science, B. F. Skinner (1953) noted that “the line between public and private is not fixed. The boundary shifts with every discovery of a technique for making private events public The problem of privacy may, therefore, eventually be solved by technical advances” (p. 282). Indeed, new advances in biology have begun to allow us to observe subjective events objectively. However imperfectly, we are beginning to enter the realm of private events, to listen to the muffled but discernible voices of the genes.

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