The Varieties of Emotional Systems in the Brain

Theories, Taxonomies, and Semantics

Concerning the Number of the Passions, as it hath been variously disputed among Philosophers, so in famous Schools, this Division into Eleven Passions, long since grew of use; to wit, the Sensitive Appetite is distinguished into Concupiscible and Irascible, to the first, are counted commonly six Passions, viz. Pleasure and Grief, Desire and Aversions, Love and Hatred; but to the later five, viz. Anger, Boldness, Fear, Hope and Desperation are wont to be attributed. But this distribution of the Affections is not only incongruous, for that Hope is but ill referred to the Irascible Appetite, and Hatred and Aversion, seem rather to belong to this, than to the Concupiscible: But it is also very insufficient, because some more noted Affections, as Shame, Pity, Emulation, Envy, and many others, are wholly omitted: Wherefore the Ancient Philosophers did determinate the Primary to a certain Number, then they placed under their several Kinds, very many indefinite Species.

Thomas Willis, Two Discourses Concerning the Soul of Brutes (1683)

The delusion is extraordinary by which we thus exalt language above nature:—making language the expositor of nature, instead of making nature the expositor of language.

Alexander Brian Johnson, A Treatise on Language, as quoted by Frank A. Beach, "The Descent of Instinct" (1955)

CENTRAL THEME

Scholars down through the ages have disagreed about the number and nature of basic emotions. Investigators have not even agreed on the criteria to be used in the classification of emotions. A great deal has been written on such matters, but most of it remains controversial. Until recently, this question could not be approached from a neurological perspective. As we will see in this chapter, now it can. First, I will consider how we might define primary emotional systems, or "affect programs," and then summarize the types of basic emotional circuits that exist in the brain. A limited number of powerful primal emotional circuits—those that appear to elaborate fear, anger, seeking, and sorrow—have now been sufficiently well characterized

that they can be addressed cogently through brain research. These universally recognized emotions correspond to the "infantile" feelings that young children exhibit. But this is not a comprehensive list. There are surely others related to sexuality and other more subtle social processes, such as social bonding, separation distress, and play. All emotional taxonomies must remain open-ended until more is known about the brain. I will restrict my discussion here to items for which reasonably coherent evidence exists at the neural level. This does not mean we understand these systems fully, but we do have enough conceptual, neuroanatomical, and neurochemical evidence to make a solid start. In addition, there is probably a much larger number of affective feeling states that arise from the activities of motivational systems, such as those that mediate hunger,

thirst, and sexual urges. Still others may reflect "mixtures," permutations or evolutionary outgrowths of primary systems, that can only be studied coherently once the neurophysiologies and neurochemistries of the basic emotional systems are better understood. Although the primal emotional systems probably arise from genetic dictates, they mold and are molded by experience throughout the life span.

On the Power of Emotions in Human Lives

Imagine an archetypal situation: You are hospitalized in the grip of a serious disease or as a victim of grievous bodily harm. It would not be unusual if you felt insecure and anxious about the future, fearing the worst. You may feel irritated and angry over small insensitivities of staff who seem not to appreciate your plight, but you also experience delight in acts of unexpected attention, kindness, and care. In addition to your physical sufferings, you are distressed to be isolated from your social support system and you experience a persistent sense of loss, loneliness, and general apprehension, broken occasionally by empathetic contacts from old friends and the superficial sympathies of more emotionally distant acquaintances. You feel a bit envious of their good health and a bit jealous when your spouse shows up with a good-looking mutual friend of the opposite sex. You may feel a bit of shame over your dependence and inability to control events. After a few days in bed, you are restless because your body aches, but when you do get up for brief periods, you tire quickly. You feel disgusted by the food you are served, but at least the desserts are moderately pleasant on the tongue. When recovery and release are imminent, hope begins to blossom, and you savor the possibilities of life once more. When you leave the hospital, your joy is magnified by simple everyday pleasures—the warmth of the sunshine, a reassuring caress, and the freedom to experience the world as you choose.

Clearly, the range of our affective feelings is enormous. Most people have little difficulty recognizing and discussing them for what they are-highly influential processes in our personal lives that affect not only the quality of our other mental states but also our sense of bodily well-being. Although we take them for granted, they are intrinsically mysterious forces in our lives, because we have not found a clear scientific way to understand them. Those who are unable to fully experience and express emotions are considered alexithymic, a psychological condition in which individuals rely excessively on their cognitive-rational processes. In their milder forms, such personality styles may be considered sociopathic, while in their most extreme forms they are sometimes deemed psychopathic.1

Although it is self-evident that external events provoke our feelings, emotions actually arise from the ac-

tivities of ancient brain processes that we have inherited from ancestral species. External stimuli only trigger prepared states of the nervous system. The function of ancient emotional systems is to energize and guide organisms in their interactions with the world, but their power arises from their intrinsic nature in the brain. It is useful to document the sundry environmental events and cognitive appraisals that can arouse our emotions, but such peripheral studies can only indirectly inform our scientific understanding of how the brain generates emotions. Accordingly, most of the vast literature that discusses the role of emotions in everyday life will receive little attention here. I will also not cover many subtle human emotions such as jealousy, shame, and vindictiveness, which are discussed in numerous fine monographs and handbooks that have appeared in recent years, some of which are included in the suggested readings at the end of this chapter. It is generally assumed that many of these complex emotions arise from evolutionary elaborations and interactions of the more basic systems with higher brain functions. Here I will focus on those basic emotions that emerge from homologous subcortical brain activities in all mammals.

An Overview of Brain Organization of Emotionality

The organizational principle that has been most commonly used to summarize the neural infrastructure of emotional processes has been Paul MacLean's concept of the triune brain (see Chapter 4 for details). According to the classic version of this view (Figure 3.1), which offers a conceptual cartoon of the major layers of neural development, the functional landscape of the brain is organized in three strata of evolutionary progression. The deepest and most ancient layer is the reptilian brain, also known as the basal ganglia, or extrapyramidal motor system. Here many of our basic motor plans, especially axial or whole-body movements, including primitive behavioral responses related to fear, anger, and sexuality, are elaborated by specific neural circuits. The next layer, known as the limbic system or the visceral brain, contains newer programs related to the various social emotions, including maternal acceptance and care, social bonding, separation distress, and rough-and-tumble play. Finally, surrounding these ancient subcortical regions, which are quite similarly organized in all mammals, we have the neomammalian brain or neocortex, which is rudimentary in other vertebrates and exhibits the greatest diversification among mammalian species. The neocortex can come to be influenced by emotions and influences them through various appraisal processes, but it is not a fundamental neural substrate for the generation of affective experience. Although the cortex can be powerfully moved by emotions and the human cortex can rationally attempt to understand and influence them (sustaining and reduc-



Figure 3.1. Highly schematic representation of MacLean's triune brain concept. The innermost reptilian core of the brain elaborates basic instinctual action plans for primitive emotive processes such as exploration, feeding, aggressive dominance displays, and sexuality. The oldmammalian brain, or the limbic system, adds behavioral and psychological resolution to all of the emotions and specifically mediates the social emotions such as separation distress/social bonding, playfulness, and maternal nurturance. The highly expanded neomammalian cortex generates higher cognitive functions, reasoning, and logical thought. For a more realistic depiction of the same concept, see Figure 4.1. (Adapted from MacLean, 1990; see n. 46.)

ing feelings depending on moment-to-moment appraisals of situations), it apparently cannot generate emotionality without the ancient subcortical functions of the brain. We cannot precipitate emotional feelings by artificially activating the neocortex either electrically or neurochemically, even though, as we will discuss later, emotionality is modified by cortical injury (see Chapters 4 and 16).2

Although the triune brain concept is largely a didactic simplification from a neuroanatomical point of view, it is an informative perspective. There appear to have been relatively long periods of stability in vertebrate brain evolution, followed by bursts of expansion. The three evolutionary strata of the mammalian brain reflect these progressions (Figure 3.1): The basic reptilian core is of similar relative size in all mammals (as long as we account for body size). Other vertebrates also have an abundance of this tissue in their small brains. While the limbic system is comparatively small in reptiles, it is large in all mammals and also of similar relative size across different mammalian species. On the other hand, the degree of mushrooming of neocortex varies widely among mammalian species, being modest in rodents and reaching massive proportion in the cetaceans (whales and porpoises) and great apes (the gibbons, orangutans, gorillas, chimpanzees) and attaining its pinnacle in humans. It is the storehouse of our cognitive skills.

In short, the size and complexity of the human neocortical toolbox, even when corrected for body size, are much vaster than in all other mammalian species. By comparison, species differences diminish when we focus

on those paleocortical (i.e., ancient limbic cortex) and subcortical systems where the basic emotions are created. Within the cortex, the human brain displays many unique organizational principles, especially among the neural connections that allow us to speak, think, and plan ahead.3 A similar claim cannot be made about subcortical processes, and the conservation of function in lower areas effectively allows us to triangulate fundamental issues across species, using converging evidence from the brain, behavioral, and mental sciences (see Figure 2.4). Although the remarkable cortical development of the human brain has many affective ramifications, including our ability to conceptualize our emotions in a diversity of artistic forms, to the best of our knowledge, the affective power of emotionality arises from subcortical systems that also sway the minds of "lower" animals. Thus, to understand the fundamental nature of emotionality we must decipher the natural order of emotional circuits within the lower reaches of the mammalian brain.

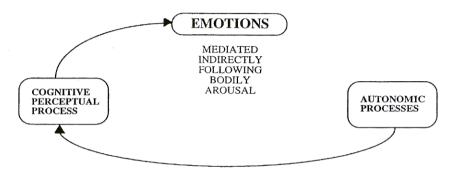
Existing Strategies for the Study of Emotions

Scientists interested in the topic of emotions have yet to agree upon a general research strategy or taxonomy for understanding the basic emotions that can be applied across all mammalian species, and some still reject the notion of "basic emotions" altogether. In experimental psychology, one can presently identify three distinct schools of thought on how we should proceed in our attempts to understand and categorize emotions:

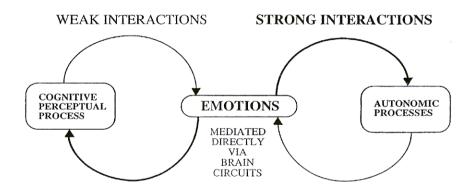
1. The categorical approach: Perhaps the most vocal group consists of investigators who posit the existence of a small set of discrete emotions, or "primes," on the basis of either objective analysis of behavioral expressions, human subjective experiences, established brain systems, or a combination of the above. This categorical approach assumes that certain affective processes—such as fear, anger, sorrow, and joy—ultimately arise from intrinsic systems of the brain/mind

and have a stable and characteristic underlying reality that can be clarified at the biological level. The present analysis is most closely affiliated with this approach, which is contrasted to the next most common approach in Figure 3.2.

2. The social-constructivist approach: Others believe that attempts to pigeonhole certain emotions as basic are fundamentally incorrect and even wrongheaded. They have championed several alternative views. Those who are convinced that humans have no instincts and acquire their various affective proclivities



SOCIAL-CONSTRUCTIVIST VIEW



PSYCHOBIOLOGICAL VIEW

Figure 3.2. Two major current views of how emotions are organized in the brain. The top view represents the essence of the James-Lange perspective (see the "Afterthought" of this chapter), which has guided social-constructivist thinking about emotions to the present day. The bottom view represents a more accurate perspective that is based on existing neuroscience evidence, where centrally situated emotional systems in the brain extensively interact, in strong and weak ways (as highlighted by bolder and lighter lines, respectively), with higher and lower brain functions. A third approach (not shown), the componential one, is really a mixture of the other two. The componential view would be an amalgamation of these views, without the suggestion that there are any coherent emotional systems of the brain. Instead, emotional coordination is achieved by many component responses coming together as a function of learning.

through learning are called social constructivists.5 This approach often focuses its conceptual and experimental inquiries on the way we use words and how we come to label various bodily sensations and patterns of psychic experience. Since all of the words and many cognitive concepts humans apply to affective states must be socially learned, it is assumed that human emotional experience is also constructed by social learning.

Unfortunately, social constructivist frameworks have too commonly disregarded the vast amount of behavioral and physiological evidence for specific emotional response patterns, as well as the wealth of neuroscientific evidence suggesting that there are genetically provided affective infrastructures for different emotions within the brain. The great advantage of constructivist approaches is the full recognition that language is our most important social instrument (see Appendix B). The disadvantage is that this view finds it so easy to overlook the universe of neurobiology that exists independently of our vast, and often deceptive, linguistic abilities.

3. The componential approach: There is also a hybrid position advocated by investigators who focus on the appraisal processes that can trigger emotions. These scholars have emphasized that emotions are accompanied by a variety of bodily changes with many cognitive ramifications. This componential approach generally asserts that emotions are learned states constructed during early social development from more elemental units of visceral-autonomic experiences that accompany certain behavior patterns. In other words, rather than just being a matter of labeling, as some social-constructivists have argued, the componentialists suggest that biologically given subunits are compiled into full-blown emotional systems via cognitive appraisals and learning.6 Although this compromise position is applicable to many aspects of emotions, especially the more complex human social emotions, such as shame, guilt, jealousy, embarrassment, and sympathy, a coherent psychobiological research program based on this viewpoint has yet to emerge.

Clearly, every approach has something to offer, and it seems a bit foolish for theoreticians to battle for primacy in this complex area, where provisional ideas and lack of agreement remain abundant. Emotions can be studied at many different hierarchical levels, and at present there is too little cross talk among the levels. The most important issues can only be resolved with more evidence, and the best biological data presently exist at the categorical level. Although some psychologists consider the creation of basic taxonomies an unrealistic and even useless enterprise, in fact, all three approaches have a role to play in the analysis of the diversity of emotions manifested in actual human experience. As I have argued, "The categorical, componential and social constructivist approaches need not battle over primacy issues. They work best in different domains of inquiry. The categorical approach can iden-

tify basic operating systems that exist in the brain, and the componential and constructivist approaches can provide schemata of how the genetically endowed systems develop their full resolution by interacting with the vast complexity of the real world. It is certain that all of these types of influences contribute to real-life emotional experiences" in humans. However, the psychobiological perspective seems essential for all other levels of analysis. Accordingly, I beseeched, "If we do not fully consider the implications of the neuroscientific evidence (which has largely been obtained through the use of the categorical approach in appropriate animal models), how can the remaining approaches guide us to a rigorous understanding of how emotions are truly constructed in the human brain-mind?"7

The constructivist and componential approaches have yet to provide a powerful strategy for addressing neurological questions, so the existing evidence will be discussed here from the categorical perspective. From my utilitarian vantage, the neural organization of the emotional brain is the single most important question in emotion research today. Its importance lies in its vast potential to lay a lasting foundation for our understanding of human nature, providing a way to objectify subjectivity and to promote breakthroughs in our search for new psychiatric tools to alleviate emotional distress. This approach, because of its mechanistic emphasis, eventually may bring new forms of help to those suffering from despair, anxiety, sorrow, mania, and other disturbances of the inner life. The other approaches, because they do not actively seek to understand the brain substrates, are unlikely to yield such benefits. Without inclusion of a brain analysis, the science of emotions cannot provide answers to the grand and fundamental issues of our lives: What does it mean to be angry? How do we come to feel afraid? Where does sorrow come from? What are joy, happiness, frustration, and the many other passions and hungers that constitute the affective mysteries of our lives?

Taxonomies of Emotions

As highlighted at the beginning of this chapter by Thomas Willis's comments on the passions, there have been many taxonomies of emotions down through the ages and all too many sterile controversies.8 Some scholars, especially those with postmodern deconstructive orientations, believe that psychological processes are intrinsically so complicated by multiple causation that logical analysis through reductionism and manipulation of simple systems (such as those using animal models) will never provide the answers that we need. Diversity of taxonomies and ideas is sustained, and no one's thoughts are excluded. Unfortunately, they cannot all be correct at the biological level.

One response to a proliferation of taxonomies is a movement in the opposite direction—toward a minimal-

ist view of emotions. For instance, it is obvious that emotionality is accompanied by bodily and physiological arousal, and some have claimed that is all there is to emotions. Taking a somewhat more complex view are those who recognize that behavioral arousal can take you away from objects or toward objects, so the next simplified level of analysis accepts only the dichotomous distinction of approach versus avoidance. To this day, many are still attracted by the stark simplicity of such dimensional views,9 but a careful reading of the available evidence indicates there is greater complexity to emotional matters in the mammalian brain. Although a simple approach-avoidance dichotomy may be defensible for invertebrate species, in which neural homologies are too obscure to illuminate the human condition, this dichotomy is no longer a tenable conceptualization of mammalian emotions. There are simply too many facts, such as the distinct varieties of emotional behaviors that can be evoked by electrical and chemical brain stimulation, that should dissuade us from making very general behavioral gradients the foundation for our thinking

about emotional matters. By arguing that an approach-avoidance dimension is not a sufficient taxonomy for a neuroscientific analysis of emotions, I do not mean to claim that it is not useful in many realms. First, it must be reaffirmed that all emotional systems have dimensional attributes. namely, variations in the intensity of approach-avoidance and affective-arousal gradients that they generate. Also, the measurement of such higher-order constructs as positive and negative affect has yielded useful conceptualizations of personality that have important implications for understanding psychiatric disorders. People high in negative affect seem to be more influenced by emotions such as fear, sadness, anger, and disgust, and tend to be more prone to anxiety and depression. People with high positive affect tend to be outgoing, more playful and sensation-seeking, and more prone to manic disorders. 10 Clearly, though, these broad dimensions subsume many distinct emotional processes under a broad conceptual umbrella, such as might be constructed by generalized affective readout and labeling mechanisms of the neocortex. Although it is easy to understand why higher brain areas might tend to cluster and hence categorize events simply in terms of desirable and undesirable outcomes (i.e., the cortex, perhaps by its linguistic function, can as easily homogenize as discriminate categories), the neurological evidence summarized here indicates that mammals possess highly specific emotional and motivational systems in subcortical regions from which such generalized affective features may be created. However, we should remember that it is still possible that the various discrete emotional systems derive their impact by interacting with a smaller number of positive and negative affect systems (see Chapter 9 for a discussion of such issues).11

Here I will seek to restrict our focus to basic emotional systems for which there is a core of agreement

among most taxonomists, especially among those who work directly on the brain. 12 Virtually every list ever generated includes anger, sorrow, fear, and joy. Although theorists may have different reasons for classifying a given process as basic, the existence of such processes can also be supported by neuroscientific evidence. Simple linguistic analyses also support the primacy of a fairly short list of primary emotions. If one simply asks people to list the four or five basic emotions they experience, one consistently finds agreement on a fairly short list of items. Often "love" is at the top of the list, but if one excludes that option, then at least 60% of people routinely mention some variant of anger, fear, sorrow, and joy, after which there is a sudden drop to less than 20% in the remainder of responses, composed of a long list of items such as "jealousy," "depression," "desire," and "compassion." It is noteworthy that several items such as "surprise" and "disgust," which figure prominently in many taxonomies based on facial analysis, are rarely selected by people as basic emotions in their individual lives. 13

In recent human research, several prominent emotional taxonomies have been based on the types of facial expressions that people can generate or recognize across different cultures and stages of development. All of these analyses have yielded the four emotions mentioned previously, as well as items such as surprise and disgust, which can also be clearly expressed facially, even though both can be instinctual as well as socially constructed (i.e., sensory versus social disgusts, and fearful versus happy surprise, respectively). However, the use of facial analysis can be easily criticized. I also believe it is a less important criterion than an overall neurobehavioral analysis of action tendencies, but I will not delve into the controversy surrounding the utility of facial analysis. It has been amply aired recently. 14 The essence of the problem is that the face can easily be used as a social display device, which reduces its utility as a monitor of affective states. Here it is important to note that socially constructed and spontaneous facial displays of affect are probably differentially controlled in the brain (i.e., cortically versus subcortically mediated, respectively).15

Even though the face can be a fuzzy measure of specific affects in a variety of social situations, the fact that the face spontaneously expresses emotionality is not controversial. The controversy is how it can be used unambiguously as a valid measure of emotionality. In this context, I would note that humans have a much richer affective facial/bodily repertoire than is encompassed in most emotion theories, and individuals who know how to ham it up can easily express disappointment, lustiness, ecstasy, suspicion, shame, regret, sympathy, love, and other emotions, but in doing so they often follow stereotyped culturally based display rules.

Although in humans and some related primates the face is an exquisitely flexible communicative device, that is not the case for most other mammals, which

exhibit clear emotional behaviors but less impressive facial dynamics. Although most animals exhibit openmouthed, hissing-growling expressions of rage, and some show an openmouthed play/laughter display, they tend to show little else on their faces. 16 Thus, aside from a few studies in primates, facial analysis provides little evidence for cross-species taxonomic issues. Analysis of body postures, dynamic behavior patterns, autonomic measures, and the study of emotional sounds may provide better data for cross-species comparisons, but these lines of investigation are still comparatively underdeveloped. It is hoped that investigators will eventually develop brain measures that can index the presence of affect more directly.

Since a definitive analysis of the cross-species generalizability of basic emotions must include an analysis of brain systems, it is compelling that the recurring items from the preceding analyses are most clearly supported by data from brain research. Indeed, a brain-systems analysis is finally providing a "gold standard" for all other levels of theorizing. As I will summarize in this text, at present there is good biological evidence for at least seven innate emotional systems ingrained within the mammalian brain. In the vernacular, they include fear, anger, sorrow, anticipatory eagerness, play, sexual lust, and maternal nurturance. There are many more affective feelings, such as hunger, thirst, tiredness, illness, surprise, disgust, and others, but they may need to be conceptualized in terms other than what we will here call basic emotional systems.17

Accordingly, before any definitive taxonomy of emotions can be established, we must first have a cogent definition of what it means to be a bona fide emotional process. By failing to do so, investigators have "placed under their several Kinds, very many indefinite Species," as Thomas Willis put it. More recently, I added a similar comment: "The existing lists of basic emotions comprise a menagerie of strange and seemingly incompatible species of dubious evolutionary and epigenetic descent."18 Why should we not consider the feelings of hunger, thirst, pain, and tiredness to be emotions? They are certainly strong affective feelings. However, they do not fulfill all the neural criteria for an emotional system outlined below. The more traditional and quite cogent conceptual rationale is that it is desirable to exclude peripherally linked regulatory responses such as hunger and thirst from that category and to instead call them motivations (for more on this issue, see Chapter 9). In any event, to establish better taxonomies, we must have better inclusion and exclusion criteria to delimit our topic. If emotions, feelings, and moods come in several natural types, we must aspire to be explicit about the type of classificatory scheme we are trying to construct.

Here I will develop the premise that discrete emotions emerge from a variety of coherently operating brain systems with specific properties. A panoramic view of neural systems will allow us to see the outlines

of the major emotional neural "thickets" more clearly. Greater agreement on the use of certain psychological terms will surely be achieved if we anchor them credibly in the objective properties of the brain and body. For these reasons, I will attempt to provide a neurally based definition of emotions, one that specifies necessary criteria, even though it falls short on the sufficiency dimension, especially when we start to consider the many reflections of emotions in personality and cultural development. Thus, the definitional focus here will be on the general brain characteristics of emotional systems. In addition, we will be able to distinguish systems at anatomical and neurochemical levels, especially with regard to neuropeptide controls. At the same time, it will become quite evident that many distinct emotions also share generalized components such as acetylcholine, norepinephrine, and serotonin systems for the control of attention and general arousal functions. Likewise, glutamate and gamma-aminobutyrie acid (GABA) control all cognitive, emotional, and motivational functions. In the tangled skein of brain systems, emotional specificity has traditionally been difficult to pin down, but as we will see, a great deal of precision is emerging from recent neuroscience studies.

On the Problem of Defining Emotions

As summarized elsewhere,19 there have been many attempts to define emotions. If we distill them, we might come up with something like this: When powerful waves of affect overwhelm our sense of ourselves in the world, we say that we are experiencing an emotion. When similar feelings are more tidal-weak but persistent-we say we are experiencing a mood. These feelings come in various dynamic forms and are accompanied by many changes in behavior and action readiness, as well as the activities of our visceral organs. Emotions are typically triggered by world events; they arise from experiences that thwart or stimulate our desires, and they establish coherent action plans for the organism that are supported by adaptive physiological changes. These coordinated brain and bodily states fluctuate markedly as a function of time, as a function of minor changes in events, and especially as a function of our changing appraisal of these events. To be overwhelmed by an emotional experience means the intensity is such that other brain mechanisms, such as higher rational processes, are disrupted because of the spontaneous behavioral and affective dictates of the more primitive brain control systems. Although this definition may be adequate for everyday purposes, it does not cover some important aspects of emotional systems, such as how they control personality dimensions, or how emotions really operate to create feelings within the internal psychological landscape of the individuals who experience them.

In any event, the position taken here is that a useful

approach to defining emotions is to focus on their adaptive, central integrative functions as opposed to general input and output characteristics. From this vantage, emotions are the psychoneural processes that are especially influential in controlling the vigor and patterning of actions in the dynamic flow of intense behavioral interchanges between animals, as well as with certain objects during circumstances that are especially important for survival. Each emotion has a characteristic "feeling tone" that is especially important in encoding the intrinsic values of these interactions, depending on whether they are likely to promote or hinder survival (in both the immediate personal and the longer-term reproductive sense). These affective functions are especially important in encoding new information, retrieving information on subsequent occasions, and perhaps also in allowing animals to generalize about new events rapidly and efficiently (i.e., allowing animals to jump to potentially adaptive "snap decisions"). The underlying neural systems may also compute levels of psychological homeostasis or equilibrium by evaluating an organism's adaptation or success in the environment.

In more simple subjective terms, we might say that these systems generate an animal's egocentric sense of well-being with regard to the most important natural dimensions of life. They offer solutions to such survival problems as: How do I obtain goods? How do I keep goods? How do I remain intact? How do I make sure I have social contacts and supports? Such major survival

questions, which all mammals face, have been answered during the long course of neural evolution by the emergence of intrinsic emotional tendencies within the brain. Each emotional system interacts with many others at both higher and lower levels of the neuroaxis, and most of the scientific literature on the topic within psychology deals with the indirect psychological, behavioral, and physiological reflections of these interactions. Once we begin to conceptualize the central source processes, we can begin to craft new definitions of emotions on the basis of neural attributes rather than simply on descriptions of external manifestations.

Thus, from the perspective of affective neuroscience, it is essential to have neurally based definitions that can be used equally well in brain research and in the psychological and behavioral studies we conduct on mature humans, infants, and other animals. I have proposed the following: In addition to the basic psychological criterion that emotional systems should be capable of elaborating subjective feeling states that are affectively valenced (a criterion that has so far defied neural specification), there are six other objective neural criteria that provisionally define emotional systems in the brain. ²⁰ They are depicted schematically in Figure 3.3.

 The underlying circuits are genetically predetermined and designed to respond unconditionally to stimuli arising from major life-challenging circumstances.

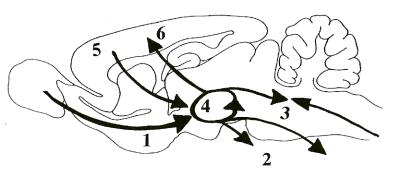


Figure 3.3. The various neural interactions that characterize all major emotional systems of the brain: (1) Various sensory stimuli can unconditionally access emotional systems; (2) emotional systems can generate instinctual motor outputs, as well as (3) modulate sensory inputs. (4) Emotional systems have positive feedback components that can sustain emotional arousal after precipitating events have passed. (5) These systems can be modulated by cognitive inputs and (6) can modify and channel cognitive activities. Also, the important criterion that emotional systems create affective states is not depicted, but it is assumed that arousal of the executive circuit for each emotion is a necessary condition for getting feeling states activated within the brain, perhaps by interacting with other brain circuits for self-representation, such as those that appear to exist in the midbrain periaqueductal and deep tectal circuits that interact with frontal cortical systems (see Chapter 16).

- 2. These circuits organize diverse behaviors by activating or inhibiting motor subroutines and concurrent autonomic-hormonal changes that have proved adaptive in the face of such life-challenging circumstances during the evolutionary history of the species.
- 3. Emotive circuits change the sensitivities of sensory systems that are relevant for the behavioral sequences that have been aroused.
- 4. Neural activity of emotive systems outlasts the precipitating circumstances.
- 5. Emotive circuits can come under the conditional control of emotionally neutral environmental stimuli.
- 6. Emotive circuits have reciprocal interactions with the brain mechanisms that elaborate higher decision-making processes and consciousness.

Of course, as mentioned, there is a seventh psychological criterion: The emotional circuits must be able to generate affective feelings, but this is hard to incorporate into the conceptual diagram. I will eventually develop the idea that affect emerges from the many interactions of emotional systems depicted in Figure 3.3 with primal neural mechanisms that represent "the self" (see Chapter 16), but let us first deal with the available facts concerning the various systems.

In addition to being the deep neural sources of psychic life, emotional circuits achieve their profound influence over the behavior and mental activity of an organism through the widespread effects on the rest of the nervous system. Emotive circuits change sensory, perceptual, and cognitive processing, and initiate a host of physiological changes that are naturally synchronized with the aroused behavioral tendencies characteristic of emotional experience. I will speak of these emotional systems in a variety of ways, using designations such as executive, command, and operating systems, to provide nuances of meaning that may be needed to conceptualize their overall functions. The use of the term executive implies that a neural system has a superordinate role in a cascade of hierarchical controls (i.e., the central "node" in Figure 2.2); command implies that a circuit can instigate a full-blown emotional process; operating implies that it can coordinate and synchronize the operation of several subsystems. Taken together, all of these components yield coherent psychobehavioral and physiological responses that constitute an emotional "organ system." This final term conceptualizes the fact that each system is composed of an anatomical network of interconnected neurons and endocrine, paracrine, and immune influences. As mentioned, certain components are shared by many emotional systems—for instance, a general cortical arousal function (which is partly based on brain norepinephrine and acetylcholine circuits, as described in Chapters 6 and 7) and general inhibitory functions that may help channel information (which are partly based on

brain serotonin and GABA systems). The multiplicity of terminologies is not meant to imply that there are three different types of emotional organ systems; instead, each complex system, like the proverbial elephant being groped by the blind, can be "viewed" from different perspectives.

Even though psychologists have traditionally made a distinction between external (objective, third-person) events and internal (subjective, first-person) events, in functional brain research, especially with regard to processes that have ramifications in conscious awareness, this distinction must be questioned. To make progress in understanding how psychological processes emerge from brain functions, we will eventually have to judiciously combine first-person and third-person views of brain functions.

Indeed, we should always recognize that as far as psychological processes of the brain are concerned, everything after initial sensory integration is internal, while often seeming to remain external. As William James²¹ put it,

Subjectivity and objectivity are affairs not what experience is aboriginally made of, but of its classification. Classifications depend on our temporary purposes. For certain purposes it is convenient to take things in one set of relations, for other purposes in another set. In the two cases their contexts are apt to be different. In the case of our affectional experiences we have no permanent and steadfast purpose that obliges us to be consistent, so we find it easy to let them float ambiguously, sometimes classing them with our feelings, sometimes with more physical realities, according to caprice or to the convenience of the moment.

James went on to point out that it is quite natural for us to attribute feelings to external objects and events, even though they may in fact be part of our bodies: "Language would lose most of its esthetic and rhetorical value were we forbidden to project words primarily connoting our affections upon the objects by which the affections are aroused. The man is really hateful; the action really mean; the situation really tragic-all in themselves and quite apart from our opinion." Thus, from a cognitive perspective our feelings are deeply felt "opinions" and "attributions," but from the affective perspective they truly amount to distinct types of neural activities in the brain. This duality of viewpoints resembles some of the other famous dualities that other sciences have had to accept gracefully, for instance, the particulate and wave characteristics of electrons.²²

In the present analysis, I will de-emphasize the obvious fact that emotions are aroused in us by various external events and instead will focus on the sources of feelings within intrinsic brain functions. Although the emotional tendencies of the brain were designed to respond to various types of real-world events, we must remember that they are not constructed from those

events. Their essential and archaic nature was cobbled together during the long course of brain evolution so as to provide organisms ready solutions to the major survival problems confronting them. Figure 3.4 highlights the adaptive functions of the four most ancient emotional systems that have thus far been reasonably well characterized in neural terms.

Verbal Labels and a **Neurologically Based Taxonomy** of Emotional Processes

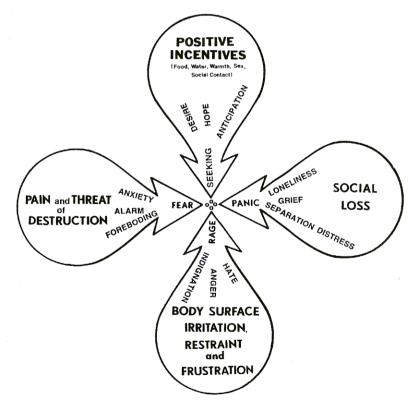
How did emotional organ systems emerge in the mammalian brain? As highlighted by the discussion of Aplysia behavior in the previous chapter, they probably arose from earlier reflexive-instinctual abilities possessed by simpler ancestral creatures in our evolutionary lineage. Gradually, through evolutionary modification and coordination of preexisting capabilities, executive systems emerged that were capable of providing an animal with greater behavioral coherence and flexibility in a variety of primal situations: (1) the search for food, water, and warmth; (2) the search for sex and companionship; (3) the need to care for offspring; (4) the urge to be reunited with companions after separation; (5) the urge to avoid pain and destruction; (6) the urge to express oneself vigorously with decisive actions

if one's self-interests are compromised; (7) the urge to exhibit vigorous social interaction, and perhaps several others. It is reasonable to provisionally call the psychic states corresponding to these emotional urges seeking, lust, nurturance, panic, fear, rage, and play, respectively. Although these are not good scientific labels (because of the excess and often vague meanings of such vernacular terms), most alternatives are not much better (and, I believe, arguably worse). All the options we have are mere words with no intrinsic significance. The best labels should suggest that something very important, of a certain general type, is transpiring in the nervous system, and I will continue to utilize common vernacular labels since they are such a great aid to understandable communication that can help fertilize our search for further clarity. However, as explained in the next section, I will use such terms with a new twist.

Many animal behaviorists have asserted that subjective terms such as anger and fear are bad because they reek of anthropomorphism—the attribution of human mental qualities to animals. My previous analysis of such concerns asserted that

it should be self-evident that the use of anthropomorphism in the study of mammalian emotions cannot be arbitrarily ruled out. Although its application may be risky under the best of circumstances, its validity depends on the degree of evolutionary con-

Figure 3.4. Various environmental challenges were so persistent during brain evolution that psychobehavioral tendencies to respond to such challenges have been encoded as emotional neural circuits within the mammalian brain. Hence, various external stimuli have the capacity to arouse specific emotional tendencies, but these emotional potentials exist within the neural circuits of the brain independently of external influences. Unregulated and excessive activities within these systems probably contribute to major psychiatric disorders. (Adapted from Panksepp, 1982; see n. 26.)



tinuity among brain mechanisms that elaborate emotions in humans and animals. Hence, the degree of anthropomorphism that can have scientific utility in mammalian brain research should be directly related to the extent that emotions reflect class-typical mechanisms as opposed to species-typical ones.23

The available evidence now overwhelmingly supports the conclusion that basic emotional processes emerge from homologous brain mechanisms in all mammals. Of course, emotional systems do not remain static during the life span of an organism-their infrastructures probably change as a function of development and individual experience—but we presently know regrettably little at that level of analysis, at least in the realm of brain research.24

Obviously, the ability of the human cortex to think and to fantasize, and thereby to pursue many unique paths of human cultural evolution, can dilute, mold, modify, and focus the dictates of these systems, but it cannot eliminate them. Since those wonderful human abilities are of secondary importance for understanding the deep nature of emotions, I have decided to use simple vernacular terms to discuss the affective lives of all mammals. However, it is important to be clear that the present aim is not to use such affective labels for emotional systems in explanatory ways but to use them merely as designators for coherently operating brain systems, having important internal and external consequences, that need to be clarified in order for us to understand emotions.

A Proposed Terminological Convention for Discussing Brain Emotional Systems

Short of holding an international convention to resolve terminological issues, the best solution may be to generate a chain of words that reflects the diversity of manifestations in which a specific brain system is involved. Thus, for the first system mentioned earlier, the "appetitive motivational system" that encourages animals to search for all resources, including food, water, and warmth, I once used the designator curiosity/interest/foraging/anticipation/craving/expectancy system.25 This usage reflected my frustration with existing terminologies, but it would be cumbersome to formalize such chains of words as standard usage. Perhaps a good compromise would be to always use two descriptors, one behavioral and one psychological (e.g., foraging/ expectancy system and separation-distress/panic system), to acknowledge that those two sources of information (i.e., first- and third-person perspectives) should always be used conjointly in the study of any basic emotional operating system of the brain.

However, I will utilize a new and simpler convention. Rather than chaining descriptors together, I will select a single affective designator written in UPPER-

CASE letters when it refers to one of the genetically ingrained brain emotional operating systems. This is used to alert the reader to the fact that I am using the term in a scientific rather than simply a vernacular way: I am talking about a specific neural system of the brain that is assumed to be a major source process for the emergence of the related vernacular terminologies but which in the present context has a more clearly restricted neuro-functional referent. In general, I will continue to use the labels I originally employed in the first formal neurotaxonomy of emotional processes,26 but I have decided to relabel one, namely, "the expectancy system," even though the essential meaning of the concept remains unchanged. I do this because the original term I selected was deemed to be vague with respect to positive and negative expectancies. Thus, this "appetitive motivational system" will no longer be called the EX-PECTANCY system but rather the SEEKING system (in Chapter 9, I will further discuss this change and contrast it with alternative terminologies for the underlying system that have been more recently employed by other investigators). The remaining systems will retain the original labels, but again the use of capitalization is designed to convey the fact that these are scientific terms and not just a loose form of folk psychologizing. Also, I will discuss several additional social-emotional systems that have been alluded to earlier (e.g., those related to sexual, maternal, and playful feelings and behavior processes), and here I will raise them to formal status within the emerging neuropsychological taxonomy of emotions. Thus, seven specific emotional systems will be fully discussed in separate chapters of this text.

A major opponent emotional process to SEEKING impulses arising from a brain system that energizes the body to angrily defend its territory and resources will be called the RAGE system. The brain system that appears to be central for generating a major form of trepidation that commonly leads to freezing and flight will be called the FEAR system. The one that generates feelings of loneliness and separation distress will still be called the PANIC system, even though this choice has caused a degree of critical concern since the term panic is also commonly used to designate intense states of fear. Unfortunately, SORROW or DISTRESS would have been just as debatable. My original reason for selecting the term PANIC was the supposition that an understanding of this neural circuit would provide important insights into the neural sources of the clinical disorder known as panic attacks. This position continues to be supported by existing evidence.27 The additional systems for sexual, maternal, and playful feelings will be called LUST, CARE, and rough-and-tumble PLAY systems.

The preceding is not intended as a complete or exclusive list. Perhaps a social DOMINANCE system also exists in the brain, and as has been emphasized several times, surely there are intrinsic neural substrates for

many other basic affective "motivational" feelings such as hunger, thirst, frustration, disgust, pain, and so on. For the time being, I will not capitalize these designators of affective feelings, since we do not know whether they are mediated by distinct types of brain organization, and since they are not the main focus of the text. There are also many higher human sentiments, from feelings of shame to those of sympathy, that are linked via social learning to the basic emotional systems. However, within the conceptual constraints that I have imposed on the present analysis (Figure 3.3), they will not be considered as major subcortical emotional operating systems.

Obviously, there are other ways to feel "good" and "bad" within the brain, and there are many specific types of "pleasures" and "aversions." Many of those that will not be presented as primary emotions here will be discussed in the context of various regulatory interactions in Chapters 8, 11, and 13. For instance, hunger interacts with the SEEKING system. Frustration is one way to activate the RAGE system, and LUST is obviously a multifaceted category.

Clearly, we cannot use most emotional words totally unambiguously, no matter how hard we try, which is probably the major reason modern neuroscience continues to avoid the issue of how feelings are organized in the brain. It is truly regrettable that both neuroscience and psychology have cultivated such neglect because of the pervasive semantic ambiguities that, until the neuroscience revolution, prevented us from forming adequate neurally based definitions for such concepts. However, when we begin to discuss the major emotional systems in brain terms, we should gradually be able to tackle the remaining ambiguities ever more empirically.

More important than quarreling about intrinsically ambiguous semantic distinctions (such as, is EX-PECTANCY or SEEKING better? is PANIC or DIS-TRESS better?) is the recognition and study of the varieties of primitive emotional operating systems that exist in limbic and reptilian areas of the brain. And let me reemphasize: The most compelling evidence for the existence of such systems is our ability to evoke discrete emotional behaviors and states using localized electrical and chemical stimulation of the brain. For brain stimulation to activate coordinated impassioned behavior patterns (accompanied by affective states as indicated by behavioral approach and withdrawal tests), electrodes have to be situated in very specific subcortical (i.e., visceral/limbic) areas of the brain. But once an electrode is in the correct neuroanatomical location, essentially identical emotional tendencies can be evoked in all mammals, including humans.²⁸ For instance, we can energize SEEKING by stimulating very specific two-way circuits that course between specific midbrain and frontal cortical areas. We can evoke a similar form of exploratory behavioral arousal by activating the confluent dopamine system chemically with psychostimulant drugs such as amphetamines and cocaine in both animals and humans, as well as with various neuropeptides and glutamate in

Although all emotional systems are strongly linked to behavior patterning circuits, it is important to emphasize that they do many other things, from controlling and coordinating the autonomic (i.e., automatic) functions of visceral organs to energizing the cortex to selectively process incoming information. Obviously, to be effective, emotional behaviors need to be backed up by various bodily and psychological adjustments. Sufficient evidence now indicate's that the executive systems for emotions are also highly influential in generating subjective states in humans and comparable behavioral indices of affect in animals. Unfortunately, I will not yet be able to address this last issue for all of the emotional systems. The evidence is still quite modest for some systems, largely because few investigators are presently working on such important psychological questions.

The Blue-Ribbon, Grade A **Emotional Systems**

And how many basic command systems for emotionality have in fact been reasonably well identified? At least four primal emotional circuits mature soon after birth, as indexed by the ability of localized brain stimulation to evoke coherent emotional displays in experimental animals (Figure 3.5), and these systems appear to be remarkably similarly organized in humans. The four most well studied systems are (1) an appetitive motivation SEEKING system, which helps elaborate energetic search and goal-directed behaviors in behalf of any of a variety of distinct goal objects; (2) a RAGE system, which is especially easily aroused by thwarting and frustrations; (3) a FEAR system, which is designed to minimize the probability of bodily destruction; and (4) a separation distress PANIC system, which is especially important in the elaboration of social emotional processes related to attachment. Although I will focus on each of these systems in separate chapters, as an appetizer, let me briefly highlight these major "Blue-Ribbon, Grade A" emotional systems of the mammalian brain.

1. The SEEKING system (see Chapter 8): This emotional system is a coherently operating neuronal network that promotes a certain class of survival abilities. This system makes animals intensely interested in exploring their world and leads them to become excited when they are about to get what they desire. It eventually allows animals to find and eagerly anticipate the things they need for survival, including, of course, food, water, warmth, and their ultimate evolutionary survival need, sex. In other words, when fully aroused, it helps fill the mind with interest and motivates organisms to

FORWARD LOCOMOTION, SNIFFING, INVESTIGATION STIMULUS-BOUND APPETITIVE BEHAVIOR AGITATION, DISTRESS VOCALIZATION, SOCIAL CONTACT AND SELF-STIMULATION FREEZING, FLIGHT, ESCAPE SOCIAL BONDING IMULUS-BOUND STIMULUS-BOUND FLIGHT DISTRESS VOCALIZATION AND CAPE BEHAVIORS SOCIAL ATTACHMENT RAGE STIMULUS-BOUND AND ATTACK, BITING, FIGHTING

Figure 3.5. The major emotional operating systems are defined primarily by genetically coded neural circuits that generate well-organized behavior sequences that can be evoked by localized electrical stimulation of the brain. Representative behaviors generated by the various systems are indicated, and the approximate locations of the SEEKING, FEAR, and RAGE systems are depicted on a small frontal section through one side of the hypothalamus. As is evident, there is considerable overlap and hence neural interaction among systems. Some of the possible major interactions are indicated by the various interconnecting lines that suggest various excitatory and inhibitory influences among systems. (Adapted from Panksepp, 1982; see n. 26).

move their bodies effortlessly in search of the things they need, crave, and desire. In humans, this may be one of the main brain systems that generate and sustain curiosity, even for intellectual pursuits. This system is obviously quite efficient at facilitating learning, especially mastering information about where material resources are situated and the best way to obtain them. It also helps assure that our bodies will work in smoothly patterned and effective ways in such quests.

When this brain system becomes underactive, as is common with aging, a form of depression results. When the system becomes spontaneously overactive, which

can happen as a result of various kinds of stress, an animal's behavior becomes excessive and schizophrenic or manic symptoms may follow-especially the "functional" forms of psychosis that can be treated with traditional antipsychotic medications (which all reduce dopamine activity in the brain), as opposed to the more chronic forms arising from brain degeneration (as indexed by ventricular enlargement).29

Neuroanatomically, the SEEKING system corresponds to the major self-stimulation system that courses from the midbrain up to the cortex, which has long been misconceptualized as a "reward or reinforcement sys-

tem." In fact, as already mentioned, it appears to be a general-purpose neuronal system that helps coax animals and humans to move energetically from where they are presently situated to the places where they can find and consume the fruits of this world. A very important neurochemical in this system is dopamine, especially the dopaminergic mesolimbic and mesocortical dopamine circuits, which emanate from the ventral tegmental area (VTA) situated at the very back of the hypothalamus (Figure 3.6). These dopamine circuits tend to energize and coordinate the functions of many higher brain areas that mediate planning and foresight (such as the amygdala, nucleus accumbens, and frontal cortex-see next chapter) and promote states of eagerness and directed purpose in both humans and animals. It is no wonder that animals are eager to self-stimulate this system via indwelling electrodes. It now seems clear that many psychostimulant drugs commonly abused by humans, especially the amphetamines and cocaine, produce their psychic appeal by temporarily overarousing this emotional system. To some extent, other drugs such as opiates, nicotine, and alcohol also derive their hedonic appeal by interacting with this system (see "Afterthought," Chapter 6).

2. The RAGE system (see Chapter 10): Working in opposition to SEEKING is a system that mediates anger. RAGE is aroused by frustration and attempts to curtail an animal's freedom of action. It has long been known that one can enrage both animals and humans by stimulating very specific parts of the brain, which parallel the trajectory of the FEAR system. This system not only helps animals defend themselves by arousing fear in their opponents but also energizes behavior when an animal is irritated or restrained. Human anger may get much of its psychic "energy" from this brain system. Brain tumors that irritate the circuit can cause pathological rage, while damage to the system can promote serenity.

3. The FEAR system (see Chapter 11): A FEAR circuit was probably designed during evolution to help animals reduce pain and the possibility of destruction. When stimulated intensely, this circuit leads animals to run away as if they are extremely scared. With very weak stimulation, animals exhibit just the opposite motor tendency—a freezing response, common when

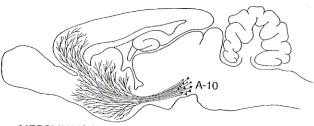
animals are placed in circumstances where they have previously been hurt or frightened. Humans stimulated in these same brain areas report being engulfed by intense anxiety.

4. The PANIC system (see Chapter 14): To be a mammal is to be born socially dependent. Brain evolution has provided safeguards to assure that parents (usually the mother) take care of the offspring, and the offspring have powerful emotional systems to indicate that they are in need of care (as reflected in *crying* or, as scientists prefer to say, *separation calls*). The nature of these distress systems in the brains of caretakers and those they care for has only recently been clarified; they provide a neural substrate for understanding many other social emotional processes.

5. In addition to the preceding primitive systems that are evident in all mammals soon after birth, we also have more sophisticated special-purpose socioemotional systems that are engaged at appropriate times in the lives of all mammals-for instance, those that mediate sexual LUST (see Chapter 12), maternal CARE (see Chapter 13), and roughhousing PLAY (see Chapter 15). Each of these is built around neural complexities that are only provisionally understood. Sexual urges are mediated by specific brain circuits and chemistries that are quite distinct for males and females but appear to share some components such as the physiological and psychological effects of oxytocin, which also promotes maternal motivation. We now realize that maternal behavior circuits remain closely intermeshed with those that control sexuality, and this suggests how evolution gradually constructed the basic neural substrates for the social contract (i.e., the possibilities for love and bonding) in the mammalian brain.

As we will see, maternal nurturance probably arose gradually from preexisting circuits that initially mediated sexuality. Likewise, the mechanisms of social bonding and playfulness are closely intermeshed with the circuitries for the other pro-social behaviors. Because of the lack of hard data, I will focus more on the behaviors mediated by these circuits than on the associated subjective feelings. However, the neuroanatomical, neurophysiological, neurochemical, and neurobehavioral clarification of such emotional control systems is a prerequisite to addressing the underlying affective issues substantively.

Figure 3.6. Schematic summary of the mesolimbic and mesocortical dopamine system on a lateral midsaggital view of the rat brain. This system allows the frontal cortex and the ventral striatum of the "reptilian brain" to process appetitive information effectively. The system mediates many forms of drug addiction and is also imbalanced in some forms of schizophrenia.



MESOLIMBIC / MESOCORTICAL DOPAMINE SYSTEM

The Emotional Systems Are Evolutionary Tools to Promote Psychobehavioral Coherence

In sum, these basic emotional systems appear to rapidly instigate and coordinate the dynamic forms of brain organization that, in the course of evolution, proved highly effective in meeting various primal survival needs and thereby helped animals pass on their genes to future generations. Of course, most of animal behavior is directed toward effective survival, but contrary to the beliefs of early behaviorists, learning mechanisms are not the only brain functions that evolved to achieve those ends. While general-purpose learning mechanisms may help animals behave adaptively in future circumstances because of the specific life experiences they have had, emotional circuits help animals behave adaptively because of the major types of life challenges their ancestors faced in the course of evolutionary history. The instinctual dictates of these circuits allow organisms to cope with especially challenging events because of a form of evolutionary "learning"—the emergence of coordinated psychobehavioral potentials that are genetically ingrained in brain development. We might call these behaviors evolutionary operants. The inheritance of emotional command systems is probably polygenic, and the actual neural circuits that constitute each emotional organ system are obviously more complex than we presently understand. What follows in the ensuing chapters is a mere shadow of reality, but we are finally beginning to grasp the nature of these important brain functions that have, for too long, been ignored by psychologists. An understanding of these systems may prepare the way for a deeper understanding of many traditional psychological problems like the nature of learning and memory, as well as the sources of personality and psychopathology.

In addition to activating and coordinating changes in sensory, perceptual, motor, and physiological functions-which all appear to be suffused with poorly understood central neuroaffective states—the executive circuits for the basic emotions probably also help enable and encode new learning. This is accomplished by specialpurpose associative mechanisms that are probably linked to fluctuating activities of each emotive system, and, as has been observed with all other forms of learning, the transmitter glutamate is a major player in all emotional learning that has been studied. As noted in the previous chapters, efficient learning may be conceptually achieved through the generation of subjectively experienced neuroemotional states that provide simple internalized codes of biological values that correspond to major life priorities for the animal. For instance, through classical conditioning (see Figure 1.2) emotionally neutral stimuli in the world can be rapidly imbued with emotional salience. Thus, memory coding and cognitive processes are closely related to emotional arousal, but emotionality is not isomorphic with those processes.

Before we can proceed to a discussion of the details of these emotional systems of the brain, it will first be essential to briefly summarize the successes of the "neuroscience revolution" upon which our future understanding of emotions and motivations must be built-including advances in our understanding of neuroanatomy (see Chapter 4), neurochemistry (see Chapter 5), and neurophysiology (see Chapter 6). Also, since developmental and aging issues are so important in present-day psychology, I would close this chapter by sharing my perspective on these topics. The following short essay will hopefully tie the many threads of thought we have covered in the first three chapters into a compact and coherent viewpoint.

The Ontogeny of Emotional Processes

A common question in developmental psychology is: What develops in emotional development? One approximate pictorial answer to this question was already provided in Figure 2.1. Each emotional system has an ontogenetic life course that we are beginning to understand at a neurobiological level. The answer which I have previously provided to this question went as follows:

Traditional answers to this question will focus on the increasingly sophisticated interactions a child has with its world. From a psychological perspective, I would say that the main thing that develops in emotional development is the linking of internal affective values to new life experiences. However, in addition to the epigenetic processes related to each individual's personal emotional experiences leading to unique emotional habits and traits, there is also a spontaneous neurobiological unfolding of emotional and behavioral systems during childhood and adolescence. Some neuro-emotional processes are strongly influenced by prenatal experiences, for instance the ability of early hormonal tides to control the brain substrates of gender identity.

Modern neuroscience is showing that the brain is not as unchanging a computational space as was commonly assumed. Neurochemical systems develop and remold at both pre- and post-synaptic sites throughout the lifespan of organisms. For instance receptor fields proliferate and shrink during specific phases of ontogenetic development, and they can show permanent changes in response to life events. Indeed, neurons in specific adult motivational systems can expand and shrink depending upon the environmental challenges and the resulting hormonal tides to which an animal is exposed. It is becoming ever increasingly clear that there is a dynamic interaction between environmental events and genetic events in the brain. With such complexities, it is a risky business to suppose that the stages of emotional and moral development that we see in

human children are simply due to the specific life experiences they have acquired. At the same time, it is foolhardy to push the biological view too far. Even with identical genetic backgrounds, there is a great deal of epigenetic diversity in the fine details of the nervous system. Only the general groundplans for brain connectivities are encoded within the genes, and probably quite indirectly at that (e.g., via expressions of various trophic factors). Neural growth is responsive to a large number of internal and external stochastic processes that lead to a diversity of detailed differences in every nook and cranny of the brain. But despite the infinite variety in the details, the overall plan of the mammalian brain has been highly conserved.

After birth, a great deal of neural unfolding remains to be completed in every species, and we can be reasonably confident that the maturation of specific neural systems does establish essential conditions for the unfolding of certain forms of emotionality. A few examples: 1) Social bonding (imprinting) processes are especially sensitive at certain times of life. 2) The separation distress system seems to exhibit increasing sensitivity during the initial phase of postnatal development, a long-plateau period, and a gradual decline during puberty. 3) Rough and tumble play exhibits a similar pattern. 4) Rats exhibit strong tendencies for maternal behavior during early juvenile development, at times comparable to those when human children are especially infatuated by dolls and play-mothering. 5) Parental tendencies are heralded by neurochemical changes, even genetic de-repression within the oxytocin system, which helps promote maternal intent. 6) And, of course, emotional aspects of sexuality mature at puberty under the sway of genetically controlled hormonal progressions, "developing" gender-specific impulses which were "exposed" as neurohormonal engrams during infancy.

Although there are many psychosocial specifics which develop concurrently, depending on the unique life experiences of individuals, the natural unfolding of neurobiological processes underlying emotionality should not be minimized. Indeed, we need to consider how the experiences of important life events feed back onto the structure of the underlying neural systems. For instance, does an enriched environment invigorate the exploratory systems of the brain? Do repeated experiences of social-loss in early childhood change the vigor and configuration of separation-distress systems? Answers to such compelling questions can now be achieved with certain long lasting neuronal markers (such as fluoro-gold) which can be administered at specific times of psychoneurological development, to see whether the morphological patterns in specific neuronal circuits are remodeled under the sway of specific environmental/emotional challenges. When we finally begin to do such experiments, we will truly

be addressing the pervasive nature-nurture interactions that help mold the brain/mind throughout maturation.30

For relevant literature citations please refer to the original of the above, as well as several recent reviews that summarize the development31 and aging32 of emotional systems within the brain. As highlighted at the end of the quoted passage, this area is ripe for powerful new investigations of how the underlying neural substrates change as a function of normal neurobiological development, as well as individual experiences.

AFTERTHOUGHT: The Classic **Neurological Theories of Emotion**

During the past decade there has been a remarkable resurgence of interest in the psychology of emotions, and the books cited as suggested readings cover that vast cognitive literature. By comparison, neurological approaches to emotions are not well cultivated. This book seeks to correct that neglect, but in doing so it will focus heavily on a new and integrated view of matters at the expense of a great deal of past thinking in the area. Since past historical views will not receive as much emphasis here as they do in more traditional texts, I would at least briefly describe the four classic milestones in historical discussions of emotions from the biological perspective:

1. The James-Lange theory, 33 proposed over a century ago, suggested that emotions arise from our cognitive appraisal of the commotion that occurs in our inner organs during certain vigorous behaviors. This theory had a "gut appeal" for many investigators, since it makes it much easier to study emotional processes by studying peripheral physiological changes that can be easily monitored. And, of course, it is common to experience various forms of visceral commotion during emotions. It was a short step to assume that emotions are the cognitive readout of such visceral processes. This logical coup d'état circumvented critical brain issues (see Figure 3.2) and provided fuel for a great deal of relatively influential, but apparently misleading, research concerning the fundamental nature of emotions.34 Although this "Jamesian" perspective has remained an especially attractive theory for cognitively oriented investigators who do not pursue neuroscience connections, neuroscientists severely criticized most of the major tenets of this peripheral-readout theory many

2. In 1927, Walter Cannon, a physiologist at Harvard, constructed a detailed, empirically based rebuttal to the James-Lange approach.35 His key points were as follows (I will also briefly indicate, in italics, how Cannon's criticisms could be effectively countered using more recent data): (i) Total separation of the viscera from the brain by spinal cord lesions did not im-

pair emotional behavior. However, the intensity of emotions was diminished somewhat by such manipulations, and now we also know that the viscera secrete many chemicals (especially hormones and neuropeptides) that may feed important information back to the brain indirectly.36 (ii) The viscera are relatively insensitive structures, and often very similar visceral changes occur in very distinct emotional states. However, more recent evidence does suggest that the patterning of many visceral changes is modestly different among different emotions.37 (iii) Finally, Cannon noted that visceral changes are typically too slow to generate emotions, and artificial hormonal activation of organ activities (e.g., via injections of adrenalin) is not sufficient to generate specific emotions. However, now we do know that injections of certain gastric peptides can rapidly produce emotional episodes. For instance, intravenous administration of cholecystokinin can provoke panic attacks.38

Cannon proceeded to propose a brain-based theory, whereby specific brain circuits (especially thalamic ones) were deemed to be essential for the generation of emotions. Although we now know that other brain areas are generally more influential in emotionality than thalamic circuits (including the amygdala, hypothalamus, and central gray), Cannon did focus our attention on the psychobiological view. At present, it is undeniable that such a view will have to be a cornerstone for the scientific understanding of emotions, but the bodily processes emphasized by the James-Lange theory cannot be ignored. Indeed, bodily changes during emotions are so complex and extensive that there is plenty of room for many feedback influences onto central control processes from peripheral sources. The recent discovery of powerful interlinkages between the brain and immune processes provides new levels of interaction between peripheral and central functions. For instance, many of the cytokines-molecules that communicate between different immune compartments-have powerful direct effects on affective brain functions, and brain emotional processes modulate the intensity of immune responses.³⁹ Recent work suggests that the feeling of illness that we experience during a bacterial infection arises to a substantial degree from the release of interleukin-1, which activates various sickness behaviors and feelings by interacting with specific receptors within the brain. 40 We will probably discover similar neurochemical vectors for the feelings of tiredness and other forms of malaise, but the study of such linkages is just beginning. They could not have been even vaguely imagined 60 years ago when the classic brain theories of emotions were first being proposed.

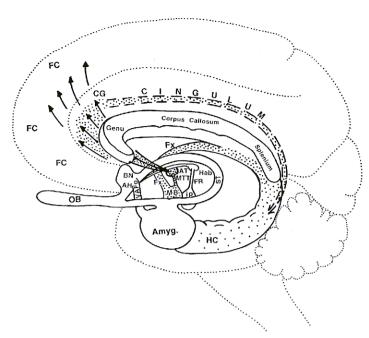
3. In 1937, James Papez, a neuroanatomist at Cornell University, asserted that "emotion is such an important function that its mechanism, whatever it is, should be placed on a structural basis" and proceeded to delineate the central neuronal circuitry that he believed might mediate emotions.41 Even though he did not clearly specify which emotion(s) he was concerned with, ana-

tomically he was quite specific. He based much of his reasoning on early brain ablation experiments and the study of a brain disease that induces rage, namely rabies, which is known to damage the hippocampus. Papez suggested an interconnected series of brain areas that might subserve emotionality in general; this has come to be known as the Papez circuit. He envisioned how sensory input into the thalamus could be transmitted both upstream and downstream. He suggested that the anterior thalamus distributed emotional information to anterior cortices, especially the cingulate area, information from which was transmitted via the cingulum pathway to the hippocampus and then via the fornix to the mamillary bodies, which then distributed emotional signals back to the anterior thalamus (via the mamillothalamic tract), as well as downward to autonomic and motor systems of the brain stem and spinal cord (see Figure 3.7). These higher areas have been the focus of considerable emotional theorizing in recent years.42

The Papez circuit provoked a great deal of experimental work, but ultimately it turned out to be more of a provocative idea than a correct one. Although recent work has affirmed that the cingulate cortex is important for elaborating certain emotions, especially social ones such as feelings arising from separation and bonding,43 the remaining brain areas of the Papez circuit are not essential executive components within emotional systems. Of course, many of these areas do participate in support mechanisms that interact with emotional processes. For instance, both the thalamus and the hippocampus help elaborate sensory and memorial inputs to emotional systems.44 Apparently this hippocampal spatial analysis system helps integrate information about contextual cues that can precipitate fearful responses, such as being scared of environments in which one has received an electric shock.⁴⁵ This just goes to show that ultimately all brain areas participate in emotions to some extent, but here we will consider only those that seem to be central to the integrative-executive emotional processes and feeling states themselves.

4. In 1949, Paul MacLean elaborated upon Papez's theme46 and helped firmly establish the concept of the "limbic system" as the focal brain division that must be investigated in order to understand emotionality. As detailed in the next chapter, he identified the medial surfaces of the telencephalic hemispheres (including cingulate, frontal, and temporal lobe areas—especially the amygdala) and interconnections with septal, hypothalamic, and central-medial brain stem areas as part of the neural landscape that constituted the "emotional brain." Although many modern neuroscientists disagree that the limbic system should be considered an anatomically and functionally distinct entity,47 most agree that the brain areas highlighted by MacLean are essential substrates of emotionality. Moreover, an increasing number of investigators are beginning to appreciate that future progress will depend critically upon our ability

Figure 3.7. Schematic of the limbic system with the Papez circuit highlighted in stippling. FC: frontal cortex; CG: cingulate gyrus; OB: olfactory bulbs; BN: bed nucleus of the stria terminalis; AH: anterior hypothalamus; VAFp: ventral amygdalofugal pathway; Amyg: amygdala; HC: hippocampus; Fx: fornix; AT: anterior thalamus; MB: mamillary bodies; MTT: mamillo-thlamic tract; Hab: habenula; FR: fasciculus retroflexus; ip: interpeduncular nucleus.



to detail the neuroanatomical, neurophysiological, and neurochemical substrates of the psychobehavioral functions. 48 For this reason, the next three chapters will provide broad overviews of the foundation disciplines that are essential for making progress in the field. In the next chapter we will discuss neuroanatomy with a focus on the reptilian brain and visceral-emotional brain commonly known as the limbic system.

Suggested Readings

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