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PORTRAIT: Agenesis of the Frontal Lobe

The year was 1912. After a difficult labor of 22 hours, a baby boy was born. J.P. weighed 11.5 pounds, but dropped to 5 pounds after postpartum complications. S. S. Ackerly reports that J.P. appeared to recover from his early trauma and, by age 1, was walking and talking with apparently normal intelligence. But he was a problem child. He was hyperactive and showed no emotion but anger, which he expressed in temper tantrums.

As J.P. grew to school age, he began to wander away. Police would find him miles from home but, evidently, he never showed any fear of being lost. Even severe whippings did not deter him. School was a real problem. Although he was extremely well mannered most of the time, J.P. unexpectedly engaged in inappropriate behaviors such as exposing himself and masturabating in the classroom.

Growing up, he developed no close friendships and was generally disliked. The community blamed his parents for much of the boy’s problems, but nothing they did was helpful. As an adolescent, J.P. pawned his mother’s rings, stole his uncle’s car, and drove to Chicago from Kentucky to spend the money. At 19, when his criminal record for theft began to mount, a psychiatrist began to investigate the nature of his behavioral problems, eventually finding that J.P.’s right frontal lobe was missing and his left was only 50% of normal size. It was the 1930s, and few treatment options existed.

As an adult, J.P. could not hold down a job for more than a few weeks, largely because of his erratic behavior. At one moment, he was charming and, at the next, was reacting out of all proportion to some seemingly trivial matter. Even by age 50, J.P.’s behavior had not changed; he remained hyperactive and alone, largely detached from anything that gives meaning to life, such as love or friendship. He had virtually no social feelings at all and, evidently, was unable to understand what such feelings would be like or to react to emotions in others.

Absent frontal lobes, J.P. had no social skills and showed very little emotion, except in the form of temper tantrums.

Emotion

Emotion, like memory, entails cognitive processes that may either be conscious or lie outside our awareness. We begin this chapter by exploring the nature of emotion and how neuroscientists have studied emotion and developed theories over the past century. Then, we consider contemporary neuropsychological theories of emotion and reported asymmetries in how the brain produces, interprets, and reacts to emotion. Throughout the chapter, we describe how researchers are applying noninvasive imaging techniques to investigate how emotion contributes to social behavior. We end the chapter by detailing how emotion contributes to our sense of self.

The Nature of Emotion

J.P.’s behavior, described in the Portrait, was extreme and certainly not common. More typical is the observation that seemingly minor brain injury can change a person’s personality. To neuropsychologists, impairments of movement,
Historical Views

Interest in the biology of emotion dates to Darwin’s book titled *The Expression of the Emotions in Man and Animals*, published in 1872. Darwin believed that, because emotional behavior is determined by evolution, human emotional expression could be understood only in the context of expression in other animals. Although Darwin’s book was a bestseller in its time, its influence was short-lived and it was temporarily forgotten.

Investigating the Anatomy of Emotion

Psychologists began to speculate about emotions at the turn of the twentieth century, but they had little knowledge about the neural basis of emotional behavior. By the late 1920s, physiologists began to examine the relation between autonomic, endocrine, and neurohumoral factors and inferred emotional states, with particular emphasis on measuring indices such as heart rate, blood pressure, and skin temperature (see reviews by Dunbar and by Brady).

Philip Bard made one of the first major anatomical discoveries about emotion while working in Walter Cannon’s laboratory in the late 1920s. Friedrich Goltz’s studies in the 1890s had shown that decorticated dogs could show strong “rages” responses to seemingly trivial stimuli; the dogs behaved as though a seriously threatening stimulus confronted them (recall J.P.’s behavior). Working with cats, Bard showed that this response depended on the diencephalon, which includes the thalamus and hypothalamus. He found that, if the diencephalon was intact, animals showed strong “emotional” responses, but, if the animals were decerebrate (see Figure 10.2), leaving the diencephalon disconnected from the midbrain, they were unemotional.

The results of later studies by many investigators (especially Eckhard Hess in the 1940s and John Flynn in the 1960s) show that stimulating different regions of the hypothalamus elicits different “affective responses” in cats. Behaviors associated with attacking another cat (piloerection, hissing, baring of teeth) or attacking a prey animal (crouching, whiskers and ears forward, pouncing) including eating the animal—can result.

The lesion and stimulation studies on the diencephalon were important, because they led to the idea that the thalamus and hypothalamus contain the neural circuits for the overt expression of emotion and for autonomic responses such as changes in blood pressure, heart rate, and respiration. The cortex was envisioned as inhibiting the thalamus and hypothalamus. Conversely, the thalamus was seen as activating the cortex during autonomic arousal, presumably to help direct the emotion to the appropriate stimulus.

The Emotional Brain

James Papez proposed the first major theory in the neurology of emotion in 1937. The structure of the “limbic lobe” (see Figure 3.20) forms the anatomical basis of emotion, Papez reasoned, and the limbic structures act on the hypothalamus to produce emotional states. Although, for Papez, the neocortex played no part in producing emotional behavior, he did believe the cortex to be necessary for transforming events produced by limbic structures into our experience of emotion.
The Papez theory had appeal; it combined behavioral phenomena having no known neurological substrates with anatomical structures having no known function. The idea of an emotional brain gained instant broad approval because Freudian thinking predominated in the 1930s. That an ancient, deep part of the central nervous system controls emotions and instincts in Freud’s unconscious, with the neocortex producing consciousness, was a concept with natural appeal for the psychology of the time.

Cortical Connections of Emotion

Two contributions in the 1930s shed light on the nature of the cortical structures and connections implicated in emotion. In both cases, investigators were studying something other than emotion and made serendipitous findings that fundamentally changed our thinking about the emotional brain.

Klüver–Bucy Syndrome

A major finding came in 1939, when Heinrich Klüver and Paul Bucy announced the rediscovery of an extraordinary behavioral syndrome that had first been noted by Sanger Brown and Edward Schacter in 1888. The Klüver–Bucy syndrome has been subsequently observed in people with a variety of neurological diseases. An obvious aspect of this extraordinary set of behaviors is lack of affect. For example, animals displaying Klüver–Bucy syndrome show no fear whatsoever to threatening stimuli such as snakes or to “threat” signals from humans or other animals, situations in which normal animals show strong aversion.

The behavioral syndrome, resulting experimentally from bilateral anterior temporal lobectomy in monkeys, includes

- tameness and a loss of fear;
- indiscriminate dietary behavior, the monkeys being willing to eat many types of previously rejected foods;
- greatly increased autoerotic, homosexual, and heterosexual activity, with inappropriate object choice (for example, sexual mounting of chairs);
- hypermetamorphosis, a tendency to attend and react to every visual stimulus;
- a tendency to examine all objects by mouth; and
- visual agnosia.

Wendy Marlowe and colleagues reported on a patient with Klüver–Bucy symptoms that resulted from meningoencephalitis (inflammation of the brain and the meninges):

Behavioral patterns were distinctly abnormal. He exhibited a flat affect, and, although originally restless, ultimately became remarkably placid. He appeared indifferent to people or situations. He spent much time gazing at the television, but never learned to turn it on; when the set was off, he tended to watch reflections of others in the room on the glass screen. On occasion he became facetious, smiling inappropriately and mimicking the gestures and actions of others. Once initiating an
perception, language, or memory affect not only how a person expresses and reacts to emotion but also how others perceive that person's emotions. Not so evident to observers, however, is a subject's or patient's feeling of emotion.

Indeed, some view emotion as an inconvenient remnant of our evolutionary past, a nonconscious time when humans literally were driven by "instincts" such as emotion. They believe that humans are fundamentally rational creatures, but emotion is older than thought. People such as J.P., with blunted or lost emotions, may behave in a completely rational manner most of the time but, when making personal and social decisions, they act irrationally.

Antonio Damasio emphasizes that emotion is a cognitive process that actually contributes to logical thinking. He argues that the mechanisms of reasoning are influenced significantly by both unconscious and conscious signals that come from the neural machinery underlying emotion. Note the contrast between neuropsychologists' use of the word "unconscious" as a synonym for nonconscious brain activity and Freud's use as a hidden or repressed component of the mind. Neuropsychologists use unconscious as shorthand for Hermann von Helmholtz's notion of unconscious inference, processes outside of awareness and learned by experience, whereby observers use knowledge to perceive.

**Feeling Emotion**

What is the last strong emotion you felt? Perhaps you had a serious disagreement with a close friend or received some unexpected, wonderful news. An emotion cannot be described as a unitary event, because emotional processes differ in multiple ways from one another and from other cognitive processes.

An emotional experience may include all sorts of thoughts or plans about who said or did what or what will be done in the future. Your heart may pound, your throat tighten; you may sweat, tremble, or flush. Strong emotional feelings (rage or elation) are not always verbalized. Marked changes in facial expression, tone of voice, or body posture—even tears of sadness or joy—are sufficient to convey emotion to others.

These emotional signals are very powerful and little influenced by experience. Paul Ekman, for example, has documented that basic emotional expressions of anger, fear, disgust, surprise, happiness, and sadness are universally recognized by people throughout the world (Figure 20.1). In this context, that J.P. did not recognize such expressions is all the more curious.
What Is Emotion?

Neuropsychologists view emotion not as a thing but rather as an inferred behavioral state called affect, a conscious, subjective feeling about a stimulus independent of where or what it is. Affective behavior is internal and subjective. As observers, we can infer emotion in others only from their behavior (what they say and do) and by measuring physiological changes associated with emotional processes.

Emotion has many components, and each, in principle, can be quantified as well as observed. A contemporary theory of emotion must include at least four principal behavioral components:

1. **Physiology.** Physiological components include central and autonomic nervous system activity and the resulting changes in neurohormonal and visceral activity. Emotion produces changes in heart rate, blood pressure, the distribution of blood flow, perspiration, and the digestive system, among others, as well as the release of hormones that may affect the brain or the ANS. Although the topic of some debate, at least some emotional states (for example, happiness versus sadness) can likely be differentiated by their associated physiological changes.

2. **Distinctive motor behavior.** Facial expression, tone of voice, and posture express emotional states. These motor behaviors are especially important to observing emotions, because they convey overt action that can differ from observed verbal behavior. Our perception of a person who says that she is fine but is sobbing uncontrollably is different from our perception of the same person when smiling.

3. **Self-reported cognition.** Cognitive processes are inferred from self-reported rankings. Cognition operates in the realm of both subjective emotional feelings (feeling love or hate, feeling loved or hated) and other cognitive processes (plans, memories, or ideas).

4. **Unconscious behavior.** This component incorporates unconscious inference—cognitive processes that influence behavior of which we are not aware. We may make decisions on the basis of "intuition" or a hunch or on other apparently unfounded bases. Recall from Chapter 16, for example, the gambling task in which normal subjects gradually changed their behavior to optimize the outcome but seemed unconscious of why they had chosen to play certain decks of cards over others to win the game. (In contrast, frontal-lobe patients behaved irrationally: they failed to choose these decks, lost all their play money, and had to "borrow" more to continue the experiment.)

The theoretical distinction among physiology, movement, self-reports, and unconscious action as component behaviors of emotional experience is significant, because researchers detect little correlation among the physical states of emotion when all of them are measured in the same subjects. A brief review of a century's research on emotion will set the stage for exploring the anatomy of emotion and discussing contemporary theories in depth.
imitative series, he would perseverate copying all movements made by another for extended periods of time. In addition, he commonly generated a series of idiosyncratic, stereotyped gestures employing primarily his two little fingers which he would raise and tuck end-to-end in repetitive fashion.

He engaged in oral exploration of all objects within his grasp, appearing unable to gain information via tactile or visual means alone. All objects that he could lift were placed in his mouth and sucked or chewed. He was commonly observed to place his fingers in his mouth and suck them. He did not attempt to pick up objects directly with his mouth, using his hands for that purpose, but was observed to engage in much olfactory behavior. When dining he would eat with his fingers until reprimanded and a fork placed in his hand; he was thereafter able to imitate use of a fork, but failed to remember the task of eating with utensils spontaneously. He would eat one food item on his plate completely before turning to the next. Hyperbulimia [excessive, insatiable appetite] was prominent; he ingested virtually everything within reach, including the plastic wrapper from bread, cleaning pastes, ink, dog food, and feces. Although his tastes were clearly indiscriminate, he seemed to prefer liquids or soft solids.

The patient's sexual behavior was a particular source of concern while in hospital. Although vigorously heterosexual prior to his illness, he was observed in hospital to make advances toward other male patients by stroking their legs and inviting fellatio by gesture; at times he attempted to kiss them. Although on a sexually mixed floor during a portion of his recovery, he never made advances toward women, and, in fact, his apparent reversal of sexual polarity prompted his fiancée to sever their relationship. (Marlowe et al., 1975, pp. 55–56)

The appearance of the Klüver-Bucy syndrome in humans and monkeys apparently requires that the amygdala and inferior temporal cortex be removed bilaterally. H.M., the amnesic patient featured in Chapter 18, does not exhibit the syndrome, despite bilateral removal of the medial temporal structures. Furthermore, monkeys with bilateral amygdalecтомies do not show the Klüver-Bucy syndrome unless the temporal cortex also is removed. Finally, the single case of a man with a bilateral temporal lobectomy identical with the Klüver-Bucy removal showed all the Klüver-Bucy symptoms, with the exception of orality. Instead of placing novel objects in his mouth, he repeatedly inspected them visually.

**Psychosurgery**

At about the time of Klüver and Bucy's discovery, a less dramatic, but in many ways more important, discovery was made. Carlyle Jacobsen studied the behavior of chimpanzees in a variety of learning tasks subsequent to frontal-lobe removals. In 1935, he reported his findings on the effects of the lesions at the Second International Neurology Congress in London. He casually noted that one particularly neurotic
chimp appeared more relaxed after the surgery, leading a Portuguese neurologist, Egas Moniz, to propose that similar lesions in people might relieve various behavioral problems. Thus was born psychosurgery and the frontal lobotomy.

Unbelievably, frontal lobotomies were performed on humans without an empirical basis. Not until the late 1960s was any systematic research done on the effects of frontal-lobe lesions on the affective behavior of nonhuman animals. Experimental findings by several laboratories clearly confirm the results of frontal lobotomies on humans: frontal-lobe lesions in rats, cats, and monkeys have severe effects on social and affective behavior across the board.

Studies in Normal Subjects

Historically, studies in normal subjects have investigated laterality differences but, more recently, there has been an expansion to consider neural aspects of personality and related individual differences. This latter development has led to an emerging field of social cognitive neuroscience, which we shall return to at the end of the chapter.

Laterality studies look not only at the cognitive processes summarized in Chapter 11 but also at the lateralization of affective processes in normal subjects. The basic approach in these studies is to present stimuli to one hemisphere, by using dichotic (or tachistoscopic) techniques, to demonstrate a difference in the performance of the two hemispheres.

If one hemisphere were superior to the other at recognizing tone of voice or facial expression, for example, the superior hemisphere could be inferred to have a dominant role in emotion. We now survey laterality studies briefly, dividing them according to whether they investigate the production of affective behavior or its perception, and conclude by considering how personality differences might relate to brain structure.

The Production of Affective Behavior

The results of a series of studies by Ruth Campbell demonstrate that facial expressions are not always symmetrical but rather tend predominantly to the left side of the face. Asymmetries may range from the hardly noticeable—such as the flicker of a smile on the left side of Mona Lisa’s face (on the right in the painting)—to the pronounced—such as a raised eyebrow, wink, or lopsided smile on the left side of the face. In one study, Morris Moscovitch and Janet Olds surreptitiously recorded the facial expressions of people in restaurants, finding a left-side preponderance. They confirmed this observation by carefully analyzing video recordings of people recounting sad and humorous stories, again finding a left-side bias in facial expressions.

Asymmetrical facial expressions show right-hemisphere specialization in producing emotion consistent with its presumed specialization in perceiving facial expressions (see Figure 11.8). It is tempting to speculate that right-hemisphere specialization in producing and interpreting nonverbal behavior is analogous to left-hemisphere specialization in producing and interpreting language, but it has yet to be proved. We caution that the apparent specialization of the
right hemisphere in the perception of faces could easily be interpreted as a specialization for the perception of complex visual stimuli, of which faces are an example.

The Perception of Relevant Stimuli

To date, studies of the perception of emotionally loaded stimuli by normal subjects have examined only vision and audition. For both modalities, the stimulus is usually presented to one hemisphere selectively, either alone or in competition with information presented simultaneously to the opposite hemisphere.

Vision

Two procedures are used for the visual presentation. In one of them, faces with different expressions (for example, sad and happy) are presented tachistoscopically to the left or right visual field, and the subject is asked to identify the facial expression. The results show the left visual field to be superior at correct identification, which can be interpreted as demonstrating a right-hemisphere specialization for perceiving facial expression, an important aspect of nonverbal communication.

The second procedure employs an ingenious technique devised by Smart Dimond (see also a more recent study by Wittling and Roschmann). By using special contact lenses, Dimond and his colleagues were able to project several types of films selectively to the left or right hemisphere. Subjects rated each film on a scale of 1 to 9 on four emotional dimensions—humorous, pleasant, horrific, or unpleasant.

Films presented to the right hemisphere were judged more unpleasant and horrific and produced greater ANS activation (as measured by heart rate) than did these same films presented to the left hemispheres of other subjects. Dimond and his colleagues concluded that the two hemispheres hold an essentially different emotional view of the world. Curiously, if the films were shown to both hemispheres simultaneously, the ratings closely resembled those of the right visual field (the left hemisphere), suggesting that left-hemisphere perception is dominant.

Audition

Studies of asymmetries in the auditory perception of emotions generally employ a dichotic-listening technique, which generally shows a left-ear superiority for emotion-laden sounds such as laughing or crying. A compelling experiment employed as stimuli a number of short sentences spoken in happy, sad, angry, and neutral voices (Ley and Bryden, 1982). These sentences were dichotically paired with neutral sentences of similar semantic content.

Subjects were instructed to attend to one ear and to report the emotional tone of the target sentence and indicate its content by checking off items on a multiple-choice recognition sheet. Virtually every subject showed a left-ear advantage for identifying the emotional tone of the voice and, at the same time, a right-ear advantage for identifying content. This result is analogous to that obtained by Dimond and his colleagues, who found that the two hemispheres deal with visual material in a similar manner: left eye for emotional tone and right eye for content.
Personality Differences and Brain Structure

Many personality traits or emotional behaviors characteristic of brain-damaged patients can be observed in people without known brain injury. This observation leads us to speculate that differences in cerebral organization, whether genetically or environmentally derived, form the basis of different human personalities. For example, one could hypothesize that people who are hypercritical may have relatively smaller or less-active temporal lobes than those who are not hypercritical. Or that people without much facial expression have smaller or less-active frontal lobes than normal.

Studies using noninvasive imaging have begun to show that individual differences in personality traits are correlated with individual differences in brain activation in specific brain regions. One of the best examples comes from a series of studies by Turhan Canli and his colleagues examining the neural basis of extraversion and neuroticism, two personality traits linked to both emotion and health. Personality tests can be used to identify the degree of extraversion versus introversion as well as the degree of neuroticism, a trait related to anxiety and mood.

In one study, subjects were shown emotionally positive or negative material. In response to positive stimuli, extroverts showed higher activity in the anterior cingulate cortex than did introverts. In a second study by Brian Haas, Canli, and their colleagues, the subjects were shown stimuli designed to elicit emotional conflict. When subjects viewed material containing high emotional conflict, those scoring higher in neuroticism showed higher activation in the amygdala and anterior cingulate cortex (Figure 20.2).

These types of data are sources of insight into the stable differences between extraverts and introverts and the manner in which mood can affect our perception of emotional stimuli. The results suggest that personality traits are indeed associated with activity in distinct cerebral regions. We return to this possibility at the end of the chapter.

Candidate Structures in Emotional Behavior

A consistent principle of neural organization is that multiple systems control virtually every behavior. Sensory information enters the cortex through multiple, distinctly different sensory channels. When stimuli have been processed, information travels through multiple parallel systems subserving different functions.

Processing Emotional Stimuli

Visual information from the occipital lobe follows a ventral route through the temporal lobe to play a role in object recognition and a dorsal route through the parietal lobe to play a role in the control of movement. In keeping with this

Figure 20.2
Neuroticism and Brain Activity
Changes in anterior cingulate activation in response to emotional conflict correlate positively with neuroticism. The investigators overlaid areas of significant activation, shown in red, on a template brain. EI = emotionally incongruent; EC = emotionally congruent. (Haas et al., 2007, p. 253.)
general principle of brain organization, we can speculate that multiple systems, both cortical and subcortical, contribute to the experience of an emotion.

Neural systems must process sensory stimuli as being significant to social behavior. Presumably, sensations are species specific for olfactory (pheromones), tactile (especially to sensitive body zones), visual (facial expressions), and auditory (phonemes, crying, screaming, and so forth) stimuli. Arguably, these socially significant stimuli are processed by the same systems that analyze other sensory inputs, but at least some sensory systems may be separate. Olfaction in cats provides a good example.

In many mammals, a receptor organ (Jacobson's organ) is specialized to analyze species-typical odors. When animals such as cats encounter certain odors (especially urine from other cats), they close their nostrils and appear to stare off into space with an odd look on their faces, a behavior known as flehmen (Figure 20.3). Actually, the cats are forcing the air through the roof of the mouth and into a special duct that is connected to the accessory olfactory system, allowing the air access to Jacobson's organ. (The accessory olfactory system functions to analyze species-specific odors and has direct connections to the hypothalamus and amygdala.)

Virtually the only odors that produce flehmen in cats are from other cats, including urine and ear wax but not feces. This neural system is thus specialized for species-typical odors. (Curiously, we have found that human urine also is often effective.) An interesting property is that the system shows habituation (repeated exposure to the same urine reduces the likelihood of flehmen), and cats appear able to remember the odors of familiar cats. Thus, they do not show flehmen to their own urine or to that of cats with which they live. Urine from novel cats will produce prolonged episodes of flehmen, and urine from familiar, but not co-resident, cats will produce shorter episodes.

Although little evidence points to such specialized systems for other senses, there is more evidence of specialized processing for emotionally relevant sensory information. Cells in the temporal lobes of monkeys are specially tuned for species-typical calls and are relatively insensitive to other sounds. Recall, too, the temporal cortical cells that are specialized for faces (see Chapter 15).

Higher-level systems possibly process other aspects of sensory information, including the internal generation of feelings. In addition to multiple systems that may encode specific species-typical information, a general cortical system may identify affective attributes of external stimuli. An interesting experiment by Michael Gazzaniga and Joseph LeDoux illustrates such a system. They presented split-brain subjects with visual information to one or the other visual field. A subject's task was to describe the stimulus verbally and to give it a rating on a five-point scale from "dislike very much" to "like very much."

The results are striking. As expected, only the items in the right visual field (and therefore sent to the left, speaking, hemisphere) were described accurately. In contrast, the five-point rating was identical for stimuli in each visual field. Clearly, the pathways that process the affective significance of the stimuli are distinct from the pathways that process their objective properties.

This distinction is reminiscent of the difference between knowing what a stimulus is and knowing where it is, as illustrated by blindsight (see Chapter 13). There may be a third system that processes affect. We have all recognized an odor, sound, or other physical stimulus, even though we cannot...
identify it at the moment. We may say that we have a “feeling” or “intuition” about the stimulus.

The effect is often true of sounds that may elicit a certain feeling because of the context in which we hear them normally. For example, music that is associated with being at some place or with some person may elicit emotional feelings when heard in another context, such as an elevator. We may not realize why we are suddenly melancholy or unusually happy. Recall from Chapter 18 that emotional memories are generally unconscious.

**Brain Circuits for Emotion**

Recall that, in the early 1930s, when the psychiatrist was beginning to study J.P., the limbic lobe (including the amygdala) and prefrontal cortex were identified as brain regions implicated in emotion. Although the original limbic structures identified by Papez in the late 1930s focused on the hippocampus and its connections with the hypothalamus, modern views of the limbic system include the amygdala and prefrontal cortex. Figure 20.4 shows the amygdala lying adjacent to the hippocampus in the temporal lobe, with the prefrontal cortex lying just anterior.

Figure 20.5A diagrams the contemporary notion of the extent of the limbic system, and Figure 20.5B schematically illustrates the limbic circuit. The hippocampus, amygdala, and prefrontal cortex all connect with the hypothalamus. The mammillary nucleus of the hypothalamus connects to the anterior thalamus, which in turn connects to the cingulate cortex. Connections from the cingulate cortex complete the circuit by connecting to the hippocampus, amygdala, and prefrontal cortex.

Although the entire circuit is important for emotional behavior, the amygdala and prefrontal cortex hold the key to understanding the nature of emotional

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**Figure 20.4**

**Emotional Circuitry** The limbic lobe, which encircles the brainstem, consists of the cingulate gyrus and hippocampal formation, the amygdala, the mammillothalamic tract, and the anterior thalamus.

**Figure 20.5**

**Contemporary View of the Limbic System** (A) An interconnected network of structures including the cortex, thalamus, hypothalamus, hippocampal formation, and amygdala forms the basis of emotional experience. (B) In a schematic representation of the major connections in the limbic circuit, the prefrontal and sensory regions connect with the cingulate cortex, hippocampal formation, and amygdala. The last two structures connect with different regions in the hypothalamus, which in turn connects with the cingulate cortex through the thalamus.
experience. We considered the anatomy of the prefrontal cortex in detail in Chapter 16, and so we will briefly examine only the amygdala here.

From the Greek, meaning “almond,” the amygdala is formed by three principal subdivisions—the corticomedial, basolateral, and central areas. Like the prefrontal cortex, the amygdala receives inputs from all sensory systems; in fact, excited, the cells of the amygdala, like those of the prefrontal cortex, require complex stimuli (such as faces). Many cells in the amygdala are multimodal; in fact, some respond to visual, auditory, somatic, gustatory, and olfactory stimuli, just as prefrontal cells do. The amygdala can therefore create a complex image of the sensory world, and we shall see later that this image is especially sensitive to stimuli that might be threatening or dangerous.

Frontal Lesions in Monkeys

Spouses or relatives often complain of personality changes in brain-damaged patients, but the parameters of these changes have been poorly specified in human subjects. Even the behavioral changes in people such as Phineas Gage (see Chapter 16) are described in general, subjective terms and seldom reported objectively. The results of research on animals, particularly nonhuman primates, make possible the identification of six behavioral changes associated with emotional processes after frontal lesions.

1. Reduced social interaction. Especially after orbitofrontal and anterior cingulate lesions, monkeys become socially withdrawn and even fail to reestablish close preoperative relations with family members. The animals sit alone; seldom if ever engage in social grooming or contact with other monkeys; and, in a free-ranging natural environment, become solitary, leaving the troop altogether.

2. Loss of social dominance. As reported in Chapter 16, after orbitofrontal lesions, monkeys that were formerly dominant in a group do not maintain their dominance, although the fall from power may take weeks to complete, depending on the aggressiveness of other monkeys in the group.

3. Inappropriate social interaction. Monkeys with orbitofrontal lesions fail to exhibit the appropriate gestures of submission to dominant animals and may approach any other animal without hesitation, irrespective of that animal’s social dominance. This behavior often results in retaliatory aggression from the dominant, intact animals. Similarly, when approached by dominant animals, monkeys with frontal lesions may simply ignore them or run away rather than performing normal submissive gestures such as allowing mounting.

4. Altered social preference. When a normal monkey is released into a large enclosure that has conspecifics behind a glass barrier, it will generally sit against the glass next to an animal sitting on the opposite side. Although normal animals prefer to sit beside intact monkeys of the opposite sex, monkeys with large frontal lesions prefer to sit with other frontal-lesion monkeys of the same sex, presumably because they are less threatening.

5. Reduced affect. Monkeys with frontal lesions largely abandon facial expressions, posturings, and gesturings in social situations. (Lesions of the
cingulate or visual association cortex seem to have no effect.) Thus, monkeys with frontal lesions show a drastic drop in the frequency and variability of facial expressions and are described as “poker faced.” This loss of facial expression is not a simple loss of muscle control of the face, because the animals do produce expressions, but not often.

6. Reduced vocalization. Lesions of the frontal cortex reduce spontaneous social vocalizations. Indeed, after anterior cingulate lesions, rhesus monkeys effectively make no normal vocalizations at all.

In general then, lesions of the monkey orbitofrontal cortex produce marked changes in social behavior. In particular, lesion monkeys become less socially responsive and fail to produce or respond to species-typical stimuli. Damage to the paralimbic cortex produces milder effects, the animals showing a reduction in social interaction. An important point is that, despite the significant changes in the sensory processing abilities of animals with visual association lesions, there appear to be very few obvious changes in their affective behavior.

The changes in emotional processes in monkeys with frontal lesions are especially intriguing, because they suggest that similar changes might be found in humans with frontal-lobe injuries. In particular, because monkeys fail to make appropriate vocal and gestural behaviors and fail to respond normally to those made by conspecifics, we can predict that humans with frontal-lobe injuries or abnormalities, such as those endured by J.P., will show similar changes in social behavior. Furthermore, disorders such as schizophrenia, which are characterized by significant changes in social interactions, also might be due to frontal dysfunction.

Premorbid Emotional Processes

The personality of a brain-injured patient at least partly depends on his or her premorbid (preinjury) state. A person who is depressive before the injury is likely to be depressive afterward; a person who is cheerful is likely to remain so. There has been no systematic study of this phenomenon, but, in our experience, there is far more intersubject variability in the emotional behavior of brain-damaged people than is revealed in most tests of their cognitive function.

A study on the social behavior of squirrel monkeys with frontal lesions is relevant here (Peters and Ploog, 1976). Although the researchers found many of the changes in social behavior previously observed by others, they also noted that some monkeys seemed less changed by their lesions. Two dominant monkeys received similar orbitofrontal lesions but, whereas one of them completely lost his dominant position, the other remained dominant but did not exert the dominance strongly. In a different social group, the second monkey might have been challenged and lost this position. Differences in the premorbid behavior of the lesioned monkeys, as well as in the group structure, appear to contribute to the change in social behavior after lesioning.

In contrast, when monkeys with frontal lesions are given neuropsychological learning tests, such as delayed-response tests, all animals typically show a much more similar behavioral change. This result is important because it is probably true of humans as well: the effects of brain damage on processes such as language and memory are more consistent than the effects on emotion. Stated differently, the premorbid personalities of human patients with cortical
injuries are likely to influence the extent of postinjury changes in emotional processes. This possibility has been completely neglected in research to date and adds a major complication as we try to make generalizations about emotional processes.

The relation between premorbid behavior and the effects of cerebral injury leads to the logical idea that there must be some difference in the details of brain organization in response to social experience. A promising finding is that the density of serotonin receptors in the orbitofrontal cortex of a monkey correlates with the animal's social status. In fact, in one study, a pharmacological increase in serotonin receptors was shown to alter social behavior and increase social status (Raleigh et al., 1991). This result may offer some explanation for how drugs that selectively block serotonin reuptake (for example, Prozac; see Figure 7.10) can alter social behavior in humans (see review by Panksepp et al. for more on this idea).

**Neuropsychological Theories of Emotion**

One theme runs through all modern theories of emotion: emotion and cognition are intimately related and likely entail overlapping neural systems. It therefore follows that changes in cognitive abilities will be related to changes in emotion and vice versa. (For a thorough review of theories of emotion, see Scherer.) Here, we outline three current theories that represent the major lines of thinking in cognitive neuroscience regarding emotion: Antonio Damasio's somatic marker hypothesis, Joseph LeDoux's cognitive-emotional interaction theory, and Guido Gainotti's lateralization theory. The reader is directed to books and reviews by these authors in the References at the end of this chapter.

**Somatic Marker Hypothesis**

The core of Damasio's somatic marker hypothesis—that when a person is confronted with a stimulus of biological importance, the brain and the body change as a result—comes from William James's ideas. In the late nineteenth century, James began to argue that an emotion consists of a change in body and brain states in response to the evaluation of a particular event. For example, if you encounter a poisonous snake as you walk along a path, your somatic markers, including heart rate, respiration, and sweating, increase. You interpret these physiological changes as fear.

A prediction that we could make here is that a reduction in the bodily reaction to a stimulus should reduce the intensity of emotions. Figure 20.6 illustrates that people with spinal-cord injuries do indeed experience reduced emotionality, the loss being proportional to the level of injury.

Whereas James was really talking about intense emotions such as fear or anger, Damasio's theory encompasses a much broader range of bodily changes. For example, there may be a change in...
motor behavior, facial expression, autonomic arousal, or endocrine changes as well neuromodulatory changes in how the brain processes emotional information and other information. Hence, for Damasio, emotions engage those neural structures that represent body states and those structures that somehow link the perception of external stimuli to body states.

The somatic markers are thus linked to external events and influence cognitive processing. Damasio’s theory uniquely specifies that the neural control of emotions includes both the brain structures that represent body states and the activity of neuromodulatory systems that link them and can produce global changes in neural processing, including, at the extremes, depression or mania.

A key aspect of Damasio’s somatic marker hypothesis is that emotion is fundamental to the survival of the individual within a particular environment. The environment for mammals (certainly, for humans) includes not only the physical environment but also the social environment. Emotions therefore affect the survival of members of a social group.

The social aspect is of great importance in humans and includes the study of social development, social communication, and even culture. These topics have barely been addressed by neuroscientists, and virtually nothing is known about the neural underpinnings of social emotions such as jealousy, pride, and embarrassment. As the Snapshot on page 572 reveals, however, investigators are making strides in this area. Given that the frontal lobe has expanded so extensively in human evolution, social emotions probably require some form of frontal-lobe processing, but that they do so is conjecture at this point.

Finally, Damasio’s theory emphasizes that emotion is not only a fundamental experience for all higher animals but also a necessary experience for us to make rationale decisions—especially in situations in which a person faces risk or conflict, as described in the Snapshot on page 572. People with reduced emotions, such as frontal-lobe patients, thus show impairments in personal or social matters, especially when they include the possibility of risk or conflict. The role of our emotions, especially subtle emotional states, is obviously not always conscious, and thus we may be unable to account for why we behave in certain ways.

Cognitive–Emotional Interactions

LeDoux’s theory, like Damasio’s, is evolutionary. The general idea is that emotions evolved to enhance the survival of animals and, as the brain evolved, cognitive and emotional processes grew more and more interrelated. In contrast with Damasio, LeDoux has not tried to account for all emotions but rather has chosen one emotion—namely, fear—as an exemplar of how to study brain–behavior relations in emotion.

In LeDoux’s view, all animals inherently detect and respond to danger, and the related neural activities eventually evolve to produce a feeling—in this case, fear. When a mouse detects a cat, fear is obviously related to predation, and, in most situations, animals such as mice have fear related either to predation or to danger from other mice who may take exception to their presence in a particular place. For humans, however, fear is a much broader emotion that today is only rarely of predation but routinely includes stress—situations in which we must “defend” ourselves on short notice.
Human decisions are strongly influenced by emotions. Take regret, for example, an emotion associated with a decision that turns out badly. Typically, regret embodies a feeling that some outcome would have been better if we had made a different decision. Regret is a common experience, and people try to anticipate and avoid it by making choices they believe have a higher probability of a positive outcome. Recent imaging and patient data point to a key role of the orbitofrontal cortex in mediating the experience of regret.

Nathalie Camille and her colleagues presented normal subjects and orbitofrontal patients with a gambling task in which subjects were asked to rate their emotional states after making a choice that led either to a $50 or 200 win or to a $50 or $200 loss. When normal subjects learned that the choice led to a $50 win but an alternative choice would have led to a $200 win, they experienced a strong negative emotion, whereas learning that the alternative would have led to a $200 loss produced a feeling of relief.

After several trials, the subjects began to make choices that optimized profitable outcomes, even if smaller than they might have been, largely to prevent the feeling of regret at losing. In contrast, orbitofrontal patients reported no regret and did not adjust their behavior to minimize losses. The absence of regret in the orbitofrontal patients suggests that they failed to grasp the concept of being responsible for one’s own decisions—a concept that clearly biased the thinking of control subjects.

Georgio Coricelli and his colleagues used fMRI to investigate cerebral activity in control subjects when they participated in the gambling task. In the early stages of the task, the regret at choices was correlated with increased activity in the orbitofrontal and anterior cingulate cortex and the medial temporal regions. As the subjects began to make choices that reduced the probability of regret, increased activity in the orbitofrontal cortex and amygdala preceded the choices, a result that suggests that the same neural system mediates both the experience and the anticipation of regret (see the adjoining figure).

These studies show that the orbitofrontal cortex contributes to optimizing our life choices. They also show that it is possible to begin to understand individual differences in traits such as regret because they may be related to individual differences in orbitofrontal activity.


Modern humans face wide-ranging physical and psychological dangers, from sports injuries to terrorism, as well as more subtle dangers such as those posed by chronic stress. An important implication of the LeDoux theory is that our fear system includes both unconscious fear responses, such as the mouse's response to the cat, and conscious awareness of subjective feelings of fear. 

presumes, however, that the neural system underlying fear is similar in both cases and that the neural basis of fear can be studied by using a model system, which is fear conditioning.

Most behavioral studies of fear employ classical conditioning, the pairing of some initially neutral stimulus, such as a tone, with some biologically significant event, such as pain from a shock (see Chapter 18). Rats (and people) rapidly learn when a neutral stimulus is paired with a negative event (such as a shock). In this case, the auditory information (the tone) passes through the auditory pathways to the thalamus, which in turn sends the information to the cortex and to the amygdala, as illustrated in Figure 20.7.

The key brain structure in the development of conditioned fear is the amygdala, which sends outputs to stimulate hormone release and activate the ANS and thus generates emotion, which we interpret in this case as fear. Physiological measures of fear conditioning can rank autonomic functioning (for example, heart rate or respiration), and quantitative measures can rank behavior (for example, standing motionless) after the tone is heard.

Damage to the amygdala interferes with fear conditioning, regardless of how it is measured. People with damage to the temporal lobe that includes the amygdala are impaired at fear conditioning, yet imaging studies show activation of the amygdala during fear conditioning (see, for example, LaBar et al., 1998). How does the amygdala “know” that a stimulus is dangerous? LeDoux proposes two possibilities. Both implicate neural networks, one genetically evolved and one shaped by learning.

Genetically based neural networks in the amygdala evolve with the animal (for example, the scent or appearance of a predator). Rats born in the laboratory, for example, show fear responses to the sound of owls or the scent of predators even though they have never encountered them. Most primates show intense fear of snakes on their first encounter, which suggests that a “snake detector” has evolved to sensitize us to stimuli associated with danger. Recall that John Downer’s split-brain monkey with one amygdala removed (see Chapter 17) had no fear of a snake from the side of brain lacking the amygdala but showed intense fear from the intact side.

Similarly, neurons in the amygdalae of primates evolved a sensitivity to negative facial expressions of others. This evolution makes sense because,
presumably, a cue to the presence of a threatening stimulus is the behavior of one's social group toward the stimulus.

Neural networks based in the amygdala likely also learn from experience about dangerous stimuli for which evolution could not prepare us. We may have learned, for instance, that a person wearing a certain type of insignia (such as one characteristic of a violent gang) is typically dangerous, whereas a person wearing another insignia (such as a police badge) is typically not dangerous.

LeDoux proposes that these circuits in the amygdala interact with cortical circuits to influence affective behavior. For example, if the amygdala functions to identify stimuli that signal danger, then the amygdala can act through the brainstem-activating systems to arouse the cortex and essentially to regulate cortical attention (awareness) to specific stimuli.

An important aspect of fear is context: a particular stimulus can be dangerous in one setting but not in another, and this distinction is clearly important to our behavior. A highly poisonous snake is extremely dangerous when suddenly encountered on a pathway but presents no danger behind a glass wall in a zoo. Furthermore, environmental contexts may acquire emotional properties through prior experiences (classical conditioning). If poisonous snakes are repeatedly encountered on a particular path in the woods, then the path itself becomes threatening.

Although the evidence is incomplete regarding exactly how context is associated with fear, the evidence is clear that hippocampal damage interferes with the development of contextual fear associations. How hippocampal activity normally acts to influence the association of context and fear remains to be understood.

How can the amygdala influence our thoughts about emotion-laden stimuli? People have all sorts of fears and worries that can interfere with everyday life, and, for some people, these fears become debilitating. People suffer from panic disorders, posttraumatic stress disorder, obsessive–compulsive disorders, anxiety disorders, and phobias. The extreme power of fear-related events to affect cognition suggests that evolution has crafted a powerful mechanism for forming such associations.

It is important in this context to recall that frontal-lobe patients show little anxiety or fear-related behavior. The orbital and medial prefrontal regions have significant reciprocal connections with the amygdala, suggesting that amygdalo-prefrontal circuits play a significant role in the formation of thoughts about fearful stimuli. The prefrontal cortex is possibly somehow modified in people with pathological fears and anxieties, making it difficult for them to extinguish learned fears or to suppress fears of evolutionarily significant events.

Cognitive Asymmetry and Emotion

We have seen in both Damasio's and LeDoux's theories that emotion entails cognitive appraisals. Because significant asymmetries exist in a variety of cognitive functions, it follows that related emotional systems also must be lateralized. This idea is not new and can be traced to at least the 1930s, when clinicians reported detailed observations of patients with large unilateral lesions, not-
ing an apparent asymmetry in the effects of left- and right-hemisphere lesions on emotional behavior. (Through the decades in neuropsychology, many versions of asymmetry theories of emotional control have been compiled, and the reader is directed to the reviews by Gainotti and by Tucker et al. for details.)

The best-known early descriptions, contemporary with J.P.’s case presented in the Portrait at the beginning of the chapter, are those of Kurt Goldstein, who suggested that left-hemisphere lesions produce “catastrophic” reactions characterized by fearfulness and depression, whereas right-hemisphere lesions produce “indifference.” The results of the first systematic study of these contrasting behavioral effects, by Gainotti in 1969, showed that catastrophic reactions were found in 62% of his left-hemisphere sample compared with only 10% of his right-hemisphere cases. In contrast, indifference was common in the right-hemisphere patients, found in 38% compared with only 11% of the left-hemisphere cases.

Significantly, however, Gainotti reported that catastrophic reactions were associated with aphasia and that indifference reactions were associated with contralateral neglect. A key point to remember in regard to Goldstein’s and Gainotti’s observations is that, if the left hemisphere is damaged extensively, then the behavior that we observe is in large part a function of what the right hemisphere can do. Thus, if we observe a catastrophic reaction after a left-hemisphere injury, one conclusion is that this behavior is coming from the right hemisphere. This conclusion leads directly to the idea that the right hemisphere normally plays a major role in the production of strong emotions, especially in emotions regarded as negative, such as fear and anger.

Gainotti concludes that the two sides of the brain play a complementary role in emotional behavior, the right hemisphere being more engaged in the automatic components of emotion and the left hemisphere in the overall cognitive control of emotion. The left hemisphere is presumed to have this general control because of language.

This idea is similar to one proposed by Gazzaniga, who suggests that a general control function of the speaking hemisphere characterizes the differences in thinking between humans and other animals. He calls the speaking hemisphere the “interpreter.” What he means is illustrated in an experiment using split-brain patients as subjects. Each hemisphere is shown the same two pictures, such as a picture of a match followed by a picture of a piece of wood. A series of other pictures is then shown, and the task is to pick out a third picture that has an inferred relation with the other two. In our example, the pertinent third picture might be a bonfire.

The right hemisphere is incapable of making the inference that a match struck and held to a piece of wood could create a bonfire, whereas the left hemisphere can easily arrive at this interpretation. Evidently, the speaking left hemisphere can make logical inferences about sensory events that the nonspeaking right hemisphere cannot make. Gainotti applies this general idea to emotion and concludes that the right hemisphere generates emotional feelings, whereas the left hemisphere interprets these feelings, presumably through its language abilities, and produces a conceptual (cognitive) level of emotional processing (affective behavior).
Asymmetry in Emotional Processing

Emotional and cognitive behavior overlap in all three principal neuropsychological theories of emotional behavior. We now turn our attention to studies that focus on the nature of this overlap. Since the 1990s, interest has shifted toward the Damasio and LeDoux theories, which focus on "site" within the cerebral hemispheres. But, in the 1970s and 1980s, there was considerable interest in cerebral asymmetry, the possibility that the two hemispheres play complementary roles in controlling emotional behavior. We briefly consider the asymmetry literature, providing examples of research on the production and interpretation of emotional behavior as well as on changes in personality associated with temporal-lobe lesions.

The Production of Emotional Behavior

Mood is inferred largely from affect—facial expression, tone of voice, and frequency of talking—and so it is sensible to measure these behaviors first in an analysis of emotional behavior in brain-damaged people. Table 20.1 summarizes a range of measures of emotional behavior. The general picture is that left-hemisphere lesions, especially left-frontal-lobe lesions, produce a flattening of mood and, in many people, an appearance of depression, especially after strokes that produce language difficulties.

Facial expression is one of the most obvious cues to emotion in humans, and overall studies of neurological patients find a reduction in the frequency and intensity of facial expressions in people with anterior lesions relative to those

| Table 20.1 Summary of experiments on the production of emotional behavior in neurological patients |
|-------------------------------|------------------------------------------|-----------------------------------------------|
| **Behavior**                  | **Characteristics**                      | **Basic Reference**                           |
| Clinical behavior of patients with natural lesions | Catastrophic reactions from left-hemisphere lesions; indifference from right-hemisphere lesions | Gainetti, 1969; Goldstein, 1939 |
| Facial expression             | Reduced by frontal lesions               | Kolb and Miler, 1981                          |
|                              | Reduced by right-hemisphere lesions      | Buck and Duffy, 1980; Barod et al., 1986      |
| Spontaneous speech            | Asymmetry altered                        | Bruyer, 1986                                  |
|                              | Decreased by left-frontal-lobe lesions; increased by right-frontal-lobe lesions | Kolb and Taylor, 1981 |
| Tone, or prosody, of speech   | Right-hemisphere lesions impair mimicry of emotional states | Tucker et al., 1977; Kent and Rosenbek, 1982 |
| Temporal-lobe traits          | Temporal-lobe personality                | Bear and Fedio, 1977; Waxman and Geshwind, 1974; Fedio and Martin, 1983 |
| Sodium amytal                | Catastrophic reactions to left injection; indifference reactions to right injection No evidence of asymmetric effects | Terzian, 1964; Rossi and Rosandini, 1974 |
|                              |                                          | Rowetta, 1960; Kolb and Milner, 1981          |
with more-posterior lesions. For example, in a series of studies, one of us (Kolb) and colleagues found that whether facial expressions are measured in terms of frequency, quantitative scoring of facial-movement elements, or subjective rating by judges, both left- and right-frontal-lobe patients show a reduction in facial expression relative to temporal-lobe groups (Figure 20.8A). This result is obtained whether the expressions are spontaneous or posed.

In contrast with the reduction in facial expression from both left- and right-frontal-lobe lesions, the effects of side of the lesion on spontaneous talking in frontal-lobe patients differ. Right-frontal-lobe lesions appear to increase talking markedly, whereas left-frontal-lobe lesions decrease it (Figure 20.8B). Without doubt, loss of facial expression and changes in talkativeness would be perceived by friends and relatives of frontal-lobe patients as marked changes in personality.

Spoken language carries two types of information: content and prosody. Typically, content is a function of the left hemisphere, and there is reason to suspect that tone of voice is a function of the right. For example, when Don Tucker and his colleagues asked patients to express particular affective states such as anger, happiness, and sadness as they read emotionally neutral sentences, patients with right-hemisphere lesions produced the sentences with relatively flat affect compared with patients with left-hemisphere lesions. This absence of tone in speech has been termed aprosodia, and it can be measured on a wideband spectogram (see Kent and Rosenbek, 1982).

Abnormalities in tone of voice in right-hemisphere patients led Elliott Ross to propose a set of aprosodias analogous to aphasias in left-hemisphere speech (Table 20.2). For example, motor aprosodia, an inability to produce affective components of language, is proposed to result from damage to Broca’s area in the right hemisphere. Sensory apraxia, a deficit in the interpretation of the emotional components of language, is presumed to result from damage to the region in the right hemisphere analogous to Wernicke’s area. Ross’s proposal may have merit and deserves serious reconsideration, but, at present, it is without much scientific support. Furthermore, like aphasias, which are virtually never purely of one type, aprosodias may not be as pure as Ross has suggested.
Table 20.2 Ross’s proposed classification of apraxias

<table>
<thead>
<tr>
<th>Type</th>
<th>Spontaneous Prosody and Gesturing</th>
<th>Prosodic Repetition</th>
<th>Prosodic Comprehension</th>
<th>Comprehension of Emotional Gesturing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Motor</td>
<td>Poor</td>
<td>Poor</td>
<td>Good</td>
<td>Good</td>
</tr>
<tr>
<td>Sensory</td>
<td>Good</td>
<td>Poor</td>
<td>Good</td>
<td>Poor</td>
</tr>
<tr>
<td>Global</td>
<td>Poor</td>
<td>Poor</td>
<td>Poor</td>
<td>Poor</td>
</tr>
<tr>
<td>Conduction</td>
<td>Good</td>
<td>Poor</td>
<td>Good</td>
<td>Good</td>
</tr>
<tr>
<td>Transcortical motor</td>
<td>Poor</td>
<td>Good</td>
<td>Good</td>
<td>Good</td>
</tr>
<tr>
<td>Transcortical sensory</td>
<td>Good</td>
<td>Good</td>
<td>Poor</td>
<td>Poor</td>
</tr>
<tr>
<td>Mixed transcortical</td>
<td>Poor</td>
<td>Good</td>
<td>Poor</td>
<td>Poor</td>
</tr>
<tr>
<td>Anomic (alexia with agraphia)</td>
<td>Good</td>
<td>Good</td>
<td>Good</td>
<td>Poor</td>
</tr>
</tbody>
</table>

Interpretation of Emotional Behavior

Emotional behavior might appear to be abnormal not only because a person is unable to produce the appropriate behavior (expression, say) but also because he or she misinterprets the social or emotional signals coming from others. The importance of interpretation symptoms in understanding personality change after injury has led to the development of a variety of clinical tests of emotional perception, which are summarized by Joan Borod and her colleagues. As summarized in Table 20.3, right-hemisphere lesions produce deficits in a range of measures, especially including the comprehension of humor, as well as the judgment of mood, both in tone of voice and facial expression.

The ability to be humorous and to comprehend humor is one of human-kind’s most intriguing behaviors and certainly contributes to personality and in

Table 20.3 Summary of experiments on interpretation of emotional behavior in neurological patients

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Characteristics</th>
<th>Basic Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Judgment of mood in others</td>
<td>Right-hemisphere lesions impair comprehension</td>
<td>Heilman et al., 1993</td>
</tr>
<tr>
<td>Judgment of propositional affect</td>
<td>Right-temporal-lobe lesions impair perception of intonation</td>
<td>Tompkins and Mateer, 1985</td>
</tr>
<tr>
<td>Comprehension of verbal humor</td>
<td>Left-hemisphere lesions impair comprehension</td>
<td>Kolb and Taylor, 1981</td>
</tr>
<tr>
<td>Matching emotional expressions</td>
<td>Right-hemisphere lesions impair performance</td>
<td>DeKosky et al., 1980;</td>
</tr>
<tr>
<td></td>
<td>Left-hemisphere lesions impair performance</td>
<td>Kolb and Taylor, 1981;</td>
</tr>
<tr>
<td>Judgment of emotional expressions</td>
<td>Bilateral amygdala lesions impair perception of negative expressions</td>
<td>Bowers et al., 1987;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Young et al., 1993;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Adolphs et al., 1999</td>
</tr>
</tbody>
</table>
a basic ingredient in social life. In a study looking at humor in patients with focal injuries in various areas of the brain, those patients with right-frontal injuries were the most affected in that they reacted less than other patients, with diminished laughter and smiling, and failed to get the punch lines of jokes (Shammi and Stuss, 1999).

We should note here that not only do right-frontal-lobe patients fail to comprehend humor, in our experience, their efforts at humor exhibit a perverse aspect. Figure 20.9 is the business card of a man who had a traumatic brain injury including damage to the right frontal lobe. This man was genuinely attempting to use humor to get business for his company.

Like humor, facial expression is a kind of social glue that bonds humans together: a lot of information is passed between and among us simply by the nuances of facial expression. Patients with lesions of the right temporal or right frontal lobe or both have difficulty recognizing facial expressions. To illustrate: subjects were asked to choose the appropriate facial expression for each of a set of cartoons in which one face was blank, as illustrated by social situations 1 and 2 in Figure 20.10 (Kolb and Taylor, 1988). As summarized in Figure 20.11A, both frontal- and temporal-lobe patients were impaired at this test but, curiously, there was no asymmetry: lesions of either hemisphere were equally effective in disrupting performance, regardless of the appropriate emotion (Kolb and Taylor, 2000).

One explanation is that, although the right hemisphere may be dominant for processing faces and facial expressions, the left hemisphere may play a role in understanding context. We noted earlier that Gazaniga's studies of split-brain patients led him to conclude that the left hemisphere acts as an "interpreter" of behavior. It may also be true of social situations.

---

**Figure 20.9**

**Humor of a Frontal-Lobe Subject** Depicted is the business card of a man who sold himself as an entrepreneur. Read carefully, the card says, "Holy cow, look at the ass on that tomato."

---

**Figure 20.10**

**Testing Social Cognition**

Examples of cartoon situations in which patients were asked either to produce the appropriate expression for the blank face or to choose the appropriate expression from several choices. See Figure 20.1 for a representative range of choices. (After Kolb and Taylor, 1988.)
Are different facial expressions (for example, frightened, happy) analyzed by different cerebral regions? Recall, for example, that the amygdala is believed to selectively perceive fear, and the results of studies by Ralph Adolphs and his colleagues show that subjects with bilateral amygdala lesions are impaired at recognizing negative expressions (such as fear) but not at recognizing happy faces. In a similar study, one of us (Kolb) and Laughlin Taylor showed that patients with unilateral frontal-lobe lesions were severely impaired at matching negative but not positive faces to the appropriate Ekman face. Patients with right, but not left, temporal or parietal lesions showed a similar pattern of deficits, as illustrated in Figure 20.11B.

Thus, facial expressions appear to be a single stimulus category; rather, different expressions may be processed separately in the brain. An fMRI study addressed this idea by comparing the cerebral activation for fear and disgust (Phillips et al., 1997). Given that expressions of disgust are normally related to bad-tasting food, the researchers predicted that the perception of expressions of disgust might include the gustatory cortex, which is located in the insula within the temporal lobe. Indeed, that is exactly what they found: fearful expressions activate the amygdala, whereas disgust expressions activate the insula.

**Temporal-Lobe Personality**

The general clinical impression is that temporal-lobe patients have a clear personality change. For example, patients and their friends were asked to complete rating scales of behaviors such as “anger,” “sadness,” or religiosity, and the patients were found to display a distinctive set of traits (Bear and Fedio, 1977), summarized in Table 20.4, sometimes referred to as “temporal-lobe personality” (see also Chapter 15).

The epileptic patients self-reported a distinctive profile of humorless sobriety, dependence, and obsession. Raters differentiated the temporal-lobe patients on the basis of nearly every trait in Table 20.4 but rated them most strongly on the traits described as “circumstantiality,” “philosophical interests,”
Table 20.4 Summary of characteristics attributed to temporal-lobe epileptics

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Emotionality</td>
<td>Deepening of all emotions; sustained intense manic–depressive disease</td>
</tr>
<tr>
<td>Elation, euphoria</td>
<td>Grandiosity, exhilarated mood; diagnosis of manic–depressive disease</td>
</tr>
<tr>
<td>Sadness</td>
<td>Discouragement, fearfulness, self-deprecation; diagnosis of depression; suicide attempt</td>
</tr>
<tr>
<td>Anger</td>
<td>Increased temper, irritability</td>
</tr>
<tr>
<td>Aggression</td>
<td>Overt hostility, rape attacks, violent crimes, murder</td>
</tr>
<tr>
<td>Altered sexual interest</td>
<td>Loss of libido, hypossexualism; fetishism, transvestism, exhibitionism,</td>
</tr>
<tr>
<td></td>
<td>hypersexual episodes</td>
</tr>
<tr>
<td>Guilt</td>
<td>Tendency to self-scrutiny and self-reproach</td>
</tr>
<tr>
<td>Hypomania</td>
<td>Attention to rules with inability to distinguish significant from minor</td>
</tr>
<tr>
<td></td>
<td>infractions; desire to punish offenders</td>
</tr>
<tr>
<td>Obsessionalism</td>
<td>Ritualism; orderliness; compulsive attention to detail</td>
</tr>
<tr>
<td>Circumstantiality</td>
<td>Loquaciousness; pedantry; being overly detailed or peripheral</td>
</tr>
<tr>
<td>Viscosity</td>
<td>Stickiness; tendency to repetition</td>
</tr>
<tr>
<td>Sense of personal destiny</td>
<td>Events given highly charged, personalized significance; divine guidance</td>
</tr>
<tr>
<td></td>
<td>ascribed to many features of patient's life</td>
</tr>
<tr>
<td>Hypergraphia</td>
<td>Keeping extensive diaries, detailed notes; writing autobiography</td>
</tr>
<tr>
<td></td>
<td>or novel</td>
</tr>
<tr>
<td>Religiosity</td>
<td>Holding deep religious beliefs; often idiosyncratic multiple conversions,</td>
</tr>
<tr>
<td></td>
<td>neystical states</td>
</tr>
<tr>
<td>Philosophical interest</td>
<td>Nascent metaphysical or moral speculations, cosmological theories</td>
</tr>
<tr>
<td>Dependence, passivity</td>
<td>Cosmic helplessness, “at hands of fate”; protestations of</td>
</tr>
<tr>
<td></td>
<td>helplessness</td>
</tr>
<tr>
<td>Humorlessness, sobriety</td>
<td>Overgeneralized ponderous concern; humor lacking or idiosyncratic</td>
</tr>
<tr>
<td>Paranoia</td>
<td>Suspicious, overinterpretative of motives and events; diagnosis of</td>
</tr>
<tr>
<td></td>
<td>paranoid schizophrenia</td>
</tr>
</tbody>
</table>


and “anger.” Furthermore, right- and left-temporal-lobe patients could be distinguished: the right-temporal-lobe patients were described as more obsessional, and the left-temporal-lobe patients as more concerned with “personal destiny.”

Social Cognitive Neuroscience

Social psychology, the study of social behavior in humans, has traditionally been at arm’s length from the study of brain function. Although the reasons for this estrangement are complex, a fundamental historical problem is that social psychology has focused on abstract constructs, such as moral dilemma, empathy, and cognitive dissonance, without any particular interest in how or what neural systems might underlie these inferred processes. The development of noninvasive imaging enabled social psychologists to look at brain activation while subjects engage in social cognitive tasks, as exemplified in the Snapshot...
on page 572 and elsewhere in this chapter, but it was necessary to develop models amenable to brain investigations.

We have seen in the preceding chapters that psychological constructs such as memory and language must be decomposed into chunks that can be related to brain processes. A similar process had to take place in social psychology to open a new door to research. Indeed, it has led to the emergence of a new field, social cognitive neuroscience, or social neuroscience, that encompasses all cognitive processes that take into account conspecifics either individually or as a group level.

Understanding Other’s Actions
In Chapter 15, we considered biological motion—movements that have particular relevance to a species, which, for humans, includes movements of the eyes, face, mouth, hands, and body (see the review by Langton et al.). These movements can have social meanings and, presumably, contribute to our impressions of the mental states of others. Cells in the superior temporal sulcus (STS) code such movements; thus, we can infer that the STS must be a part of any neural network that controls social cognition.

However, cells beyond the STS also function to understand actions. Recall from Chapter 9 that neurophysiological research on monkeys identified mirror neurons in the premotor cortex that are activated when a monkey either executes limb movements or observes the same movements in another. The mirror neurons can distinguish between biological and nonbiological movements, responding, for example, to the manipulation of an object by a hand but not by a mechanical tool such as a pair of pliers.

Subsequent studies of humans with the use of noninvasive imaging have confirmed that similar processes take place in the human brain and that mirror neurons may play a role not only in understanding actions but perhaps even intentions (see review by Agnew et al.). Indeed, J.P.’s missing brain tissue included the region with the mirror neurons. Recall from the Portrait at the beginning of this chapter that he appeared unable to understand the intentions of others.

Understanding Other’s Minds
We humans are social animals living in large groups. To thrive in such an environment requires a deft social intelligence that allows us to make sense of other people’s actions and to discern their intentions. This ability plays a primary role in social cognition, or theory of mind, which we defined in Chapter 15 as the ability to attribute mental states to self and others and to predict and understand people’s behavior on the basis of their mental states.

The attribution of intentions to others is so automatic in people that we humans seem compelled to attribute intentions and other psychological motives to nonhumans and even to abstract animations. Fulvia Castelli and colleagues showed subjects animations of triangles that were supposedly interacting (one triangle mocking another and so on) versus animations that were characterized as random. Functional magnetic resonance images showed that the attribution state increased activation in subjects’ medial prefrontal regions, their basal tem-
poral regions (fusiform gyrus and temporal poles adjacent to the amygdala), and their STS and occipital areas.

Subsequent studies consistently show that the medial frontal and orbitofrontal regions are activated when subjects try to outwit one another during games or are asked to identify traits such as trustworthiness in others. Joel Winston and his colleagues asked subjects either to judge whether a face was trustworthy or to indicate if it was that of a high-school or university student. Figure 20.12 shows that the amygdala and insula were activated in both conditions, but the STS and orbitofrontal cortex were activated only when there was an instruction to make judgments about trustworthiness.

The results of a number of imaging studies provide corroborating evidence of the frontal lobe's judgmental role in social cognition. For example, subjects were asked to reflect on the thoughts and feelings of characters in comparison with control tasks in which thoughts and feelings were irrelevant, and specific medial frontal activation was found (Fletcher et al., 1995; see also Gallagher et al., 2000).

Damage to the orbitofrontal cortex consistently produces personality changes characterized by impaired social judgment. Donald Stuss and his colleagues devised a task to examine the ability to infer visual experience from others (see also a study by Rowe et al., 2001). In the Stuss task, a patient was presented with two Styrofoam cups, one of which had an object hidden under it. The patient was not permitted to watch the placement of the objects, but, in one test condition, the experimenter's assistant was able to watch the object (a 25-cent coin) placement. The patient kept the money for correct choices, and the assistant kept it for incorrect responses made by the subject.

The patient knew that the assistant was aware of the location of the object and that the assistant stood to gain by the patient's making an error. On each trial, the assistant pointed to the wrong cup, the one without the money, and the patient then made his or her choice. This condition continued for 14 trials or until the patient made five consecutive correct responses. Ventral medial frontal lesions, particularly on the right, were impaired at detecting the deception. Remarkably, the patients in this study did not appear to realize that the assistant was trying to deceive them.

Research on autism and related disorders (for example, Asperger's syndrome) has led to the conclusion that one consistent deficit is an inability to understand the intentions and inner mental states of other people. Autistic people consistently fail theory-of-mind tasks, and Simon Baron-Cohen theorized that the extreme abnormalities in social cognition in autism result from an abnormality in an amygdala-orbitofrontal circuit. John Allman and his colleagues have proposed that the social disabilities in autism-spectrum disorders are partly due to the abnormal development of the von Economo neurons.

Recall from Chapter 10 that one difference in human and ape brains compared with other brains is the emergence of von Economo neurons, which are found in the anterior cingulate cortex and frontal insular cortex. Allman and his colleagues do not propose that the von Economo neurons are responsible
for theory of mind but rather that they are part of the frontal-lobe neural network that creates mental models of the thinking of others. This social-cognition network likely includes the amygdala, and evidence is accumulating that autistic people have consistent abnormalities in the cell density of the amygdala (for a review, see Courchesne et al; see also Chapter 24).

The Self and Social Cognition

We humans not only are aware of the actions and intentions of others but also develop a sense of our own; we are self-aware. Two distinct neural networks in frontal-lobe structures appear to be critical for generating the "self": (1) a right frontoparietal network and (2) a cortical midline network.

Humans and apes have a unique ability to recognize themselves—the self-face—in a mirror, and it has been known for more than 30 years that the right hemisphere of a split-brain patient can recognize the self-face and that the physiological reaction to the self-face is greater for the right than the left hemisphere (for a review see Uddin et al.). Both imaging and patient data provide evidence that recognition of the self-face is controlled by a right frontoparietal network.

Lucina Uddin and her colleagues showed, for example, that self-face recognition activates right frontal and parietal regions, as illustrated in Figure 20.13. Furthermore, the activated regions overlap with regions that contain mirror neurons, and the activated neurons have been proposed to provide a link between self-perception and associated mental states of the self and understanding the intentions of others. Uddin proposed that the frontoparietal mirror-neuron area acts as bridges between self and other, by co-opting a system for recognizing the actions of others to allow for recognition of the actions of self.

But the actions of self are only part of what we would call self-awareness. There is also a more abstract, mental, self. Matthew Lieberman has proposed that the processes that focus on one's own (or other's) mental states rely on medial frontal regions. In one study Jason Mitchell and colleagues asked subjects to perform one of two types of semantic judgement: "Does this description refer to a potential psychological state of the target (a person or a dog)?" or "Does this description refer to a physical part of the target?" FMRI shows that activation increased selectively in the medial frontal region in the psychological state condition regardless of whether the target was a person or dog. It is proposed that this medial frontal system acts to monitor psychological states in others as well as in the self.

Because the frontoparietal mirror neuron network and the medial frontal network seem to be involved in self-other representations, they likely interact to maintain self-other representations.
across multiple domains. The nature of this interaction and the details of how the self develops and changes is likely to be the source of considerable interest over the coming decade.

**Cognitive Control of Emotion**

Humans produce an amazing range of emotions, but we also have the cognitive capacity to control them. For example, we may have expectations about how a stimulus might feel (e.g., a syringe injection of penicillin) and our expectations can alter the actual feeling when we experience the event. Nobukatsu Sawamoto and colleagues found that nonpainful stimuli are perceived as painful when participants expect pain, and this is correlated with activation of the cingulate cortex, a region associated with pain perception.

The use of cognitive processes to change an existing emotional response has also recently been studied using noninvasive imaging. Kevin Ochsner and James Gross reviewed such studies and conclude that when subjects re-appraise self-emotions there is concurrent activation of the prefrontal and cingulate cortex. In one study the authors showed subjects aversive photos and instructed them to think about the personal relevance of each image as it appeared.

In one condition the subjects were asked to increase their negative affect and to increase their sense of subjective closeness to pictured events, imagining themselves or a loved one as the central figure in a photo. In a second condition they were to decrease their negative affect by increasing their sense of objective distance, viewing pictured events from a detached, third-person perspective. The investigators observed that both up- and down-regulating negative emotion recruits prefrontal and anterior cingulate regions.

In summary, the emerging field of cognitive social neuroscience is radically changing our understanding of how the brain participates in the complex social behavior of humans. Historical lesion studies tended to focus on the perception and production of social behavior, but the new perspective is allowing insights into the very nature of how the brain allows humans to think about themselves and one another.

**Summary**

**The Nature of Emotion**

Emotions, or affective behaviors, are easily recognized but very difficult to quantify. Similarly, it is easy to identify brain structures in which injury can disrupt emotional behavior but difficult to determine what role different structures play in controlling emotional behavior.

**Historical Views**

Darwin first drew attention to the biology of emotion but not until the late 1920s did physiologists begin to look for neural and endocrine correlates of emotion, and they emphasized the role of thalamic and hypothalamic structures. Papez expanded the putative neural networks to include forebrain structures of the limbic system. The important role of the cerebral cortex emerged only in the past 30 years.

**Studies in Normal Subjects**

Neural correlates of emotion in normal subjects began with an exploration of hemispheric asymmetries
in the control of emotion and a demonstration of a special role of the right hemisphere. More-recent investigations have demonstrated differential activity in the anterior cingulate cortex that is correlated with personality traits such as extroversion.

Candidate Structures in Emotional Behavior
As with other cognitive processes, multiple neural systems control different aspects of emotional behavior. The key candidate structures in emotional behavior include the frontal lobes, primarily the inferior frontal cortex, the amygdala and associated paralimbic cortex, and the hypothalamus. To the extent that changes in functions such as perception, movement, memory, and language affect our emotional behavior, we can see that the vast cortical regions taking part in cognitive processing also take part in producing emotion.

Neuropsychological Theories of Emotion
A theme that runs through all major theories of emotion, especially Damasio’s somatic marker hypothesis, LeDoux’s cognitive–social interaction theory, and Gazzaniga’s asymmetry theory, is that emotion and cognition are intimately related and are likely controlled by overlapping neural systems.

Asymmetry in Emotional Processing
Studies of changes in emotional behavior after cerebral injury focus largely on changes in the production and perception of emotions. Overall, lesions of the left and right hemispheres have different effects on emotional behaviors, and damage to the right hemisphere appears to produce larger effects. Asymmetry in the effects of cerebral injury should not overshadow the importance of cortical sites in understanding emotional behavior. Both the frontal lobes and the amygdala play special roles in emotional control, especially on behaviors related to producing and interpreting facial expression. The left amygdala appears to play a special role in generating one particular emotion—namely, fear.

Social Cognitive Neuroscience
This emerging field encompasses the neural correlates of all cognitive processes that take into account conspecifics, either individually or in groups. Such processes include understanding others’ actions and intentions, the development of sense of “self,” and the role of beliefs and expectations in emotional processing. The preliminary work has pointed to a fundamental role of the prefrontal and anterior cingulate regions in such processes.

References


