# Chapter 10
# Circuits of Emotion

*Emotion always has its roots in the unconscious and manifests itself in the body.*

—Irene Claremont de Castillejo.

A book on brain is incomplete without a discussion of what emotions are, where, if they can be localized, they are located in the brain, and how brain handles them. Emotions pose a peculiar problem to the neuroscientist. They are vague and elusive. They evade precise definition and rigorous characterization. There are other aspects of brain function, like the sensory-motor function, for example, that are a child's play to the neuroscientist compared to the challenge offered by emotions. Vision is doubtlessly a complex problem. How does the brain process form, static and dynamic, or color and other primitive properties? Or how does it identify a complex entity like the grandmother? Which parts of the brain participate, in what precise fashion, when I scan a crowded image for a familiar face? These are obviously difficult questions, because the domain of study is complex and involves immense detail; not because it is vague. Similar comments could be made on other types of sensory function—hearing, touch, smell, and taste. We can split sounds into frequencies, or categorize touch in terms of light, deep, or vibratory touch. We can describe the chemistry of smell and taste. Likewise, our motor system, the part of the brain that generates our movements, offers no difficulty in basic definition, quantification, and measurement of motion. The difficulty lies in the extraordinary detail involved in describing movements and the circuits that control them. But such is not the case with emotions. Where do we begin in our search for a science of emotions? Do we seek out brain areas of love and hate? Do we look for neurons whose firing rates code for precise intensities of the spectrum between pleasantness and ecstasy? Is there a hierarchy of emotions, with primary emotions represented in the lower layers, and more complex emotions in the higher layers? Such naïve line of questioning would have worked with lesser aspects of brain function. But, if our aim is to get a neurobiological grip on emotions, we must tread more carefully.



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## Ancient Emotions

Although emotions themselves are as ancient as man and mind, a science of emotions, in the sense of modern Galilean science, is perhaps only over a century old. Earlier explorations into the world of emotions occurred in the domains of literature, poetry, philosophy, art, culture, and even religion.

There is no precise translation for the word emotion in ancient Indian philosophy. A large body of original Indian philosophical literature was written in Sanskrit. The Sanskrit terms that come closest to emotion are *bhava* (feeling) and *samvedana* (sensation/experience). But bhava has a manifold connotation and can be loosely translated as mood, outlook, perspective, or even attitude. Bhagavad Gita, an essential text in Indian spiritual literature, comments on emotions in quite negative terms when it refers to desire (*kama*), anger (*krodha*), greed (*lobha*), delusion (*moha*), pride (*mada*), and jealousy (*matsarya*) as the six inner enemies that must be identified and vanquished. It exhorts the individual to shun love (*raga*), or the attachment that it causes, as much as hatred (*dvesha*) since both are two sides of the same coin, and ultimately lead the individual to attachment to the object of love/hate, culminating in sorrow and bondage. The only love that is approved and admired is the love that is directed toward God, and such love is discussed and described at great length in various ancient Indian writings. The Narada Bhakti Sutras, a treatise on devotional love, speaks of nine stages of blossoming of love turned toward God. Patanjali yoga sutras, a treatise on systematic inner development, warns that love (*raga*) and hate (*dvesha*) are afflictions (*klesa*) of the mind, impediments to spiritual progress. Thus, due to its dominant preoccupation with a goal that is otherworldly, Indian philosophy does not seem to indulge in emotions but only talks of their transcendence and sublimation.

But Indian theory of aesthetics, the theory of rasas, seems to take a more considerate and inclusive view of emotions. The word *rasa* means "juice" literally, but is used in the sense of "essence," the essential qualities and colors of experience. The theory of rasas, which first appears in Natyasastra, an ancient treatise on the science of dance and drama, speaks of eight primary rasas. These are love (*sringaram*), humor or mirth (*hasyam*), fury (*raudram*), compassion (*karunyam*), disgust (*bibhatsam*), horror (*bhayanakam*), valor (*viram*), and wonder (*adbhutam*). Each of these rasas or emotions is associated with a color and even a deity. For example, the color of love is light green (not pink!) with Vishnu, the god of preservation and sustenance, as its presiding deity. The color of terror is black, presided over by Kala, the god of death and destruction. To the list of eight rasas, a ninth—known as *shantam*, which stands for peace and tranquility—was added around the eleventh century. Two more—*vatsalyam* (love or fondness of a senior person toward a junior) and *bhakti* (devotion to God)—were added subsequently. The evolving list of emotions in Indian tradition shows that there is finality to the list.

Western philosophy seems to grant to emotions a more consistently respectful status. Plato, one of the great thinkers of ancient Greece, describes, in his Republic, that the human mind has three components—the reasoning, desiring, and emotional parts. Plato's student Aristotle, with his penchant to pronounce upon things at length without any objective support, gave a long list of emotions: anger, mildness, love, enmity (hatred), fear, confidence, shame, shamelessness, benevolence, pity, indignation, envy, emulation, and contempt. Spinoza a philosopher of seventeenth century, with strong theological leanings, posits that emotions are caused by cognitions. Affects, the word that Spinoza used for emotions, like hate, anger, envy, etc., follow their own laws just as everything else in nature. He rejected the notion of free will, since the will, which is presumed to be free, has a hidden cause, which in turn has another cause, and so on ad infinitum.

## Emotions in Psychology

Thus, philosophical or aesthetic inroads into the subject of emotions were based on introspection, insight, and speculation and often lack an objective basis. Therefore, the number and classification of emotions had no finality or definiteness and varied with place, epoch, and cultural milieu. But then the need for an objective basis and a universal framework is a peculiar need of modern science and does not constrain art or philosophy. Even a preliminary attempt to find universal emotions must go beyond common cultural knowledge and anecdotal information arising out of immediate nativity, and warrants a comparative study of emotions in a range of world cultures. Keeping in line with the traditions of objectivity, attempts were made to classify emotions based on facial expressions, which can serve as sensitive markers of emotions. Based on a study of universal patterns in facial expressions, Sylvan Tomkins had arrived at a list of eight basic emotions—surprise, joy, interest, fear, rage, disgust, shame, and anguish. Although it is tempting to compare some of these emotions with the rasas of Indian aesthetics (rage = raudram; fear = bhayanakam, etc.), one can easily get carried away by such analogies. Since all cultures share the same neurobiology, it is not surprising that there are some emotions shared by all. But the difficulty arises if we seek a uniquely universal list of emotions. Based on analysis of universal facial expressions, Paul Ekman proposed the following six basic emotions: surprise, happiness, anger, fear, disgust, and sadness. The close resemblance to the typology of Sylvan Tomkins is easily noticed.

An interesting attempt to organize emotions hierarchically, not relying completely on facial expressions as the basis, was made by Robert Plutchik. In Plutchik's system, there are basic emotions and their combinations which generate "higher order" emotions. There are eight basic emotions arranged in the form of a circle (Fig. 10.1). Each of the basic emotions has a corresponding basic opposite emotion (joy—sadness, fear—anger, and so on). Angular distance of emotions on the circle is a measure of their similarity—nearby emotions are more similar. The basic emotions can be combined, a pair at a time, to produce mixed emotions called dyads. Blends of emotions that are at adjacent positions on the circle are called first-order dyads. The blend of joy and trust/acceptance corresponds to friendliness. Fear and surprise produce alarm. Combinations involving emotions with one other intervening emotion

**Fig. 10.1** Robert Plutchik's wheel of eight basic emotions


are called second-order dyads. For example, a combination of joy and fear results in guilt. There are also third-order dyads constructed by combining basic emotions with two spaces between them. Plutchik's system was able to accommodate a good number of complex and subtle emotions in an elaborate framework.

But for the fact that there is no objective, neurobiologically rooted, quantitative basis, Plutchik's system of emotions gives a considerable insight into interrelationships among emotions. It might serve as a guideline, a map for any future endeavor directed toward creation of a comprehensive neural theory of emotions. Its placement of emotions on a wheel, with opposite or complementary emotions located on opposite ends of the wheel is reminiscent of the "color wheel" used by artists to comprehend color. Colors too are organized in a simple circular map—the color wheel—and segregated into primary, secondary, and complementary colors. In fact, there are several such systems. In one such system, known as the red-green-blue (RGB) system, the primary colors are red, blue, and green. Their complementary colors are cyan, magenta, and yellow, respectively. To test this, stare at a red square for a little while (about 30 s) and then shift your gaze to a white background. You will see an afterimage of the red square, which will turn out to be a cyan square, hovering in your sight. Cyan is what you get when you subtract red from white, and is therefore complementary to red. It is tempting to compare this transformation of a color into its complement, to a similar conversion of emotions, to the manner in which love, when spurned, turns into its opposite, hate. These distracting speculations aside, color classification of the kind mentioned above is based on extensive study of human visual perception, a field known as visual psychophysics. In addition, these studies are also corroborated by the study of responses of the photoreceptors in the eye, and a whole range of neurons spread over the visual hierarchy from the retina to higher visual cortical areas. Perhaps, Plutchik's classification is actually fashioned on the lines of color theory. But then such correspondence is at the best an analogy, an insightful metaphor, and nothing more. A theory of emotions that is rooted in the brain will necessarily have to be a very different beast.

How do we begin to construct a neural theory of emotions? How do we tether the tempests of emotion to the calm, motionless ground of the brain? To begin to answer these questions we must, first, notice a serious omission in the aforementioned approaches to emotion. Emotions are basically very different from thoughts. The contents of an emotional experience are very different from the contents of a sensory-motor experience. The products of cognition can perhaps be neatly segregated into bins, with convenient labels. Anyone who has struggled with the difficulty of figuring why they feel what they feel in certain emotional moments knows that emotions do not lend themselves to such easy analysis. A deep reason behind this difficulty is that emotions do not limit themselves to the brain and mind—they spill over into the body, and demand its implicit participation. When a mathematician is lost in thought in the tranquil solitude of a pleasant night, her brain is perhaps feverishly active but the body might remain calm, motionless, allowing the brain its full play. But when a young man struggling to utter his first words of endearment to the girl of his love, what he experiences is a tumultuous state of mind that is accompanied by the pounding of the heart, the sweating of palms, frozen and disobedient limbs, the flushing of the face, dilated pupils, and so on. It is as though the whole body is struggling to express those first feelings of fondness. Describing the outward signs of a devotee experiencing divine ecstasy, Vaishnava devotional literature mentions sudden perspiration, choking, tears, and horripilation. Thus, our cogitations are purely mental, cerebral. Our emotions, on the other hand, carry the brain and the body in a single sweep.

We now turn our attention to the nature of the bodily changes that accompany an emotional experience. Accelerated cardiac activity, perspiration, and dilation of the pupils are effects of a part of the nervous system known as the sympathetic nervous system. It coordinates what is described as a flight-or-fight response in the body. When an animal prepares to fight a predator and defend itself, its sympathetic systems try to muster all its somatic resources in a desperate attempt. Pupils are dilated so as to enable the animal to take in as much visual information as it can to aid its defense. Heart accelerates to meet the additional energy demands of the body engaged in fight. Perspiration in the skin increases so as to shed extra heat produced. Therefore, in addition to the cognitive information about the object of the emotion, be it love, hate, anger, or fear, the emotional experience involves a whole range of sympathetic effects in the body.

Therefore, we observe that emotional experience consists of two components: a cognitive registration of the object of emotion, the loved one, or a fearful predator, and so on, which serves as a stimulus for the emotion, and the bodily response. But where do we place the feeling that goes with emotion? Is the feeling of panic or love produced by the first contact with the stimulus, or does it develop as a result of the bodily response? In other words, is the feeling a result or a cause of the bodily response? This interesting chicken-and-egg question about the origins of emotional feeling played an important role in the evolution of ideas about emotion. Our intuitive guess, emerging out of a commonsensical understanding of ourselves and the world, would be that the feeling comes first, with the bodily changes following in its wake. But an eminent nineteenth-century American psychologist, William James, seemed to think otherwise. When James published an article titled "What is an Emotion?" in 1884, he unwittingly fired the first shot in a long-drawn battle among several competing theories of emotion. He asks the question more pointedly: do we run from a predator because we are afraid, or does the act of running produce fear? What comes first—the feeling of fear, or the bodily response? James proposed that the feeling is a result of bodily response. To state his proposal in his own words:

> My theory … is that the bodily changes follow directly the perception of the exciting fact, and that our feeling of the same changes as they occur is the emotion. Commonsense says, we lose our fortune, are sorry and weep; we meet a bear, are frightened and run; we are insulted by a rival, are angry and strike. The hypothesis here to be defended says that this order of sequence is incorrect … and that the more rational statement is that we feel sorry because we cry, angry because we strike, afraid because we tremble … Without the bodily states following on the perception, the latter would be purely cognitive in form, pale, colorless, destitute of emotional warmth. We might then see the bear, and judge it best to run, receive the insult and deem it right to strike, but we should not actually feel afraid or angry.

There are two possible accounts of the cause and effect relationships of an emotional response:

(1) Stimulus (predator) → feeling (fear) → bodily response (running)
(2) Stimulus (predator) → bodily response (running) → feeling (fear)

James chose option #2 over what seems acceptable to common knowledge, option #1. James' theory is primarily emphasizing the importance of bodily or physiological response to emotional experience. Without the feedback of physiological response, emotional experience would be bland, placid, and incomplete. Each type of emotion would be accompanied by physiological responses that are distinct and unique to that emotion. A votary lost in her rapture of God may choke and shed tears of joy but is not likely to run, while an individual under an attack by a predator takes to his heels. It is this distinctness in bodily response that gives the emotion its distinct color.

Carl Lange, a Danish physician, developed a theory of emotions that closely resonates with ideas of James. Like James, Lange also believed that emotions are caused by physiological responses. But unlike James, he emphasized the specific role of vasomotor responses. Therefore, the theory that emotional feeling is caused by the physiological response is referred to as James–Lange theory (Fig. 10.2).

James's ideas received wide acceptance by psychology community for several decades. However, in 1920s, first notes of dissent began to be heard. One of the first to oppose James' ideas was William Cannon, a physiologist at Harvard medical school. Cannon developed the idea of homeostasis originally proposed by Claude Bernard, a French physiologist. Claude Bernard proposed that the internal environment of the body is actively maintained at constant conditions by the action of nervous system. We now know that the autonomic branch of the nervous system is mainly responsible for maintenance of such internal constancy. Cannon elaborated this idea and studied the nervous mechanisms underlying homeostasis. He coined the term

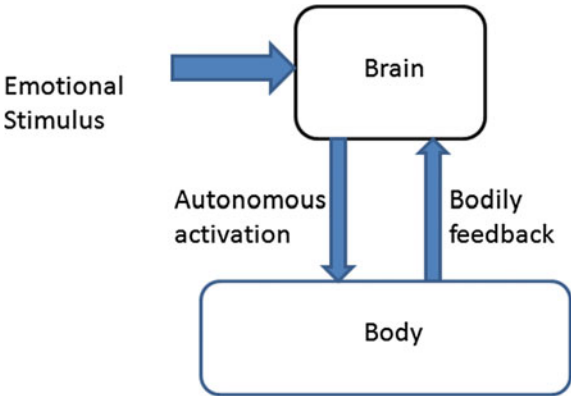


**Fig. 10.2** James–Lange theory of emotion. Emotional stimulus received by the brain produces autonomous activation in the body, which when fed back to the brain causes emotional experience

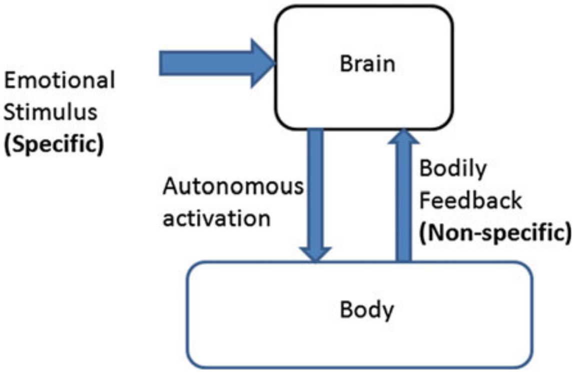


**Fig. 10.3** Cannon–Bard theory pointed out that the bodily feedback is the same irrespective of emotional stimulus, thereby dealing a deadly blow to James–Lange theory

fight-or-flight, mentioned above, which refers to the response of an organism under attack. Cannon believed that the fight-or-flight response is mediated by the autonomic nervous system, particularly the sympathetic nervous system. A peculiarity of the sympathetic nervous system is that it responds in a general way, irrespective of the stimulus, a property known as mass discharge. No matter what the nature of the stimulus is, sympathetic activation produces a full-blown response involving accelerated heart rate, perspiration, piloerection, and so on. Cannon noted that independent of the type of the emotional experience, the bodily, sympathetic response is the same. This observation struck a serious blow to James–Lange theory which depended on the physiological response to provide specificity to emotional experience. Cannon felt that the factors that give specificity to emotional response must be sought after in the brain, or in the parts of the brain that receive the feedback from ongoing physiological responses in the body; they cannot be found in the bodily responses themselves. Cannon developed these ideas jointly with physiologist Phillip Bard. The resulting theory is called Cannon–Bard theory of emotions (Fig. 10.3).

A resolution of the standoff between James–Lange and Cannon–Bard theories of emotion came much later in the '60s. Part of the reason behind the delay was the behaviorist thinking that had a strong influence on psychology throughout a good part of twentieth century. Behaviorists held that all that an organism does must be expressed in terms of behavior and nothing else. Subjective elements like thoughts, feelings, and emotions are non-existent in behaviorist view. Insertion of these subjective notions in psychology was felt to be contrary to the objective standards of science. Prominent behaviorists like B. F. Skinner, Edward Thorndike, and John Watson rejected all introspective methods and resorted solely to experimental methods in which behavior can be clearly defined and quantified. It was perhaps necessary to take such a rigid stand on matters pertaining to the mind, since it was a time when appropriate tools for probing the brain were not available. In the absence of the right tools, researchers resorted to fuzzy speculation about mental processes marring the development of science. In such a setting, the question of the causes of emotional feeling was not considered a serious scientific question. A framework that refused to accommodate feelings in the first place naturally found the origins of feeling irrelevant. But a new wave began in the second half of twentieth century. The behaviorist movement started giving way to the cognitive revolution. The cognitivists sought to explain all mental functions in terms of cognitions, in terms of a well-defined sequence of internal processes by which an organism responds to an external stimulus. The question of causes of feeling, particularly the factors that are responsible to the specificity in emotional experience, began to be given fresh attention.

Two social psychologists at Columbia University, Stanley Schachter and Jerome Singer, set out to investigate the standoff in the two key rival theories of emotion. They discovered that each of the rival theories was partly true. The physiological response was indeed important just as James had suggested, but it lacked specificity just as Cannon pointed out. A range of emotional experiences is associated with a common set of physiological responses—sweaty palms, pounding heart, and so on. The heightened state of arousal is indeed essential for the intensity of emotional experience. But it turns out that specificity comes from somewhere else. The immediate external conditions, the social context, the stimulus, determine the specific emotion that is actually felt (Fig. 10.4). The pounding heart and sweaty hands could signal feelings of joy if what you have in front of you is a person that you love, and feelings of morbid fear if it is a hissing snake. Schachter and Singer set out test their hypothesis with an experiment.

The subjects in this experiment were kept in the dark regarding the ultimate objective of the experiment, to make sure that knowledge of the objective does not bias and color the emotional responses of the subjects. Subjects were told that the experiment was about testing the effects of vitamins on vision. Specifically, they were told that a vitamin compound called Suproxin was being tested. But actually some of the subjects were given a ½ cc dose of epinephrine, a drug that activates the sympathetic nervous system; the remaining subjects were given saline water as placebo. Those who were given epinephrine were further segregated into three groups: the "informed," the "ignorant," and the "misinformed" group. The "informed" group was told that the drug can have side effects like increased heart rate, thereby allowing them an explanation of the experiences they were going to have. The "ignorant" group were told nothing. The "misinformed" group was told that they were going to

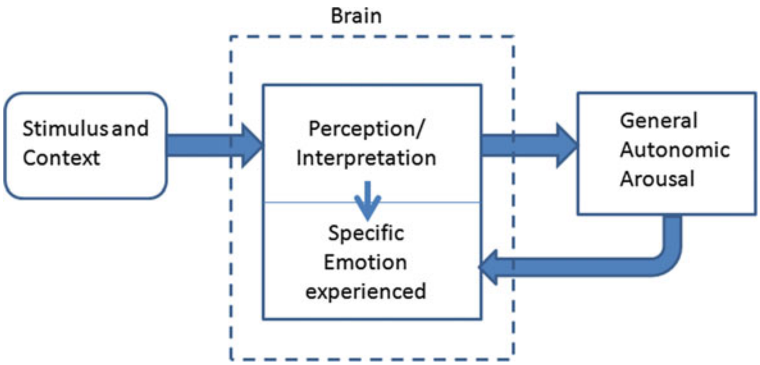


**Fig. 10.4** Schachter and Singer theory of emotion: specific emotional experience is produced by a combination of cognitive interpretation of the specific emotional/sensory stimulus and the general autonomic arousal

have side effects that had no relation to those they were really going to experience. With the conditions of arousal of the subjects thus controlled, the experimenters also arranged for appropriate forms of emotionally significant stimuli. Two trained actors were engaged to act before the subjects in "euphoric" or "angry" manner. At the end of the experiment, the subjects were evaluated regarding the nature and intensity of their experience. Participants who were given the drug that produced sympathetic activation felt a greater sense of arousal than those who were given a placebo. Furthermore, among those who experienced such higher arousal, the ones who were exposed to "euphoric" display reported feelings of euphoria, and those exposed to "angry" displays had feelings of anger. Thus though the arousal was the same, the specific feelings depended on the external conditions. The experiment thus provided strong support to Schachter and Singer theory.

Let us take stock of where we stand at the moment in our search for a satisfactory theory of emotions. James–Lange's proposal that emotional experience depends on the feedback from the body was countered by Cannon–Bard theory which pointed out that the autonomic state is nonspecific and therefore cannot account for specificity in emotions. Schachter and Singer theory confirmed parts of both and achieved some sort of reconciliation between the two theories by demonstrating that bodily feedback intensifies emotional experience but does not provide specificity, which seems to arise out of a cognitive interpretation of external stimuli and social context. If bodily feedback only intensified emotional experience, the latter must have arisen even before the autonomic response in the body had developed. This aspect of delay in autonomic responses was pointed out by Cannon also who noted that autonomic responses are too slow to account for emotional feelings. Therefore, it remains to be clarified, how and where do the feelings occur?

The second half of the twentieth century is an era of cognitive science and cognitivist thinking about mind and brain function. There was an attempt to resolve every known psychological process into its component steps and the sequence in which those steps occur. A similar approach was directed toward study of emotions too. This led to the birth of appraisal theory of emotions, which posits that emotional feeling depends on cognitive appraisal or evaluation of the external conditions.

A strong proponent of the appraisal theory was Magda Arnold (1903–2002), a brilliant psychologist and a remarkable individual who lived for a ripe age of 99. Her major work on emotions was Emotion and Personality, a two-volume work that was published in 1960. In this work, she sought to study the brain circuitry that subserves perception, motivation, and emotion.

The broad idea behind linking emotion to cognitive evaluation may be expressed with an illustration. Consider the experience of facing a job interview. Assume that at the time of the interview you were in a financial tight spot and needed the job desperately. Consider that the first few brilliant answers impressed the interviewers and your job prospects began to glow. You could not contain the excitement and could feel your heart pounding away. But a sudden query thrown by a chap, who was sitting quietly at one end of the table until then, put you on the spot. As you scrounge the depths of your memory for an answer that is hard to find, your evaluations of the current situation start to nosedive. You get that sinking feeling and your tongue runs dry. But suddenly, by a stroke of luck, an answer flashed in your mind, and interview board found your reply so convincing that they ask you when is the soonest you can join. Your evaluations soar once again. The emotional roller coaster ride that you have been on during those few tens of minutes is predominantly steered by your interpretations and evaluations ("Is it good for me, or is it dismal?") of your immediate situation. Thus, the emotion that is experienced depends on the cognitive appraisal or evaluation (is it good for me or bad?) of the immediate context.

Richard Lazarus, a psychologist at the University of Berkeley, took the appraisal theory of emotions further. Emotion, he argued, is the result of an appraisal that people make, about their immediate surroundings, about the situation they are facing, and the meaning of that situation to their well-being and survival. Lazarus also developed a theory of coping in which the appraisal is linked to stress. According to his theory, stress has more to do with how the subject felt about his resources than the subject's actual situation. Thus, the appraisal, or an emotional evaluation, can become more important than the reality of the situation. Such a view of emotions shows the phenomenon of denial in a new light. Patients who are engaged in denial about their health condition are found to fare better than those who had a realistic assessment. Their favorable appraisal, even though removed from their reality, is helping them cope with their condition. In a book titled, Stress, Appraisal and Coping, co-authored with Susan Folkman, Lazarus explored the relationship with stress and coping. Effective appraisal, which leads to successful coping, helps you cope with stress. When the appraisal is ineffective, and coping fails, stress builds up and manifests in a range of pathological effects ranging from physiological disturbance and impaired social functioning.

Richard Lazarus described appraisals in terms of something positive or negative happening (or happened, or going to happen) to the concerned individual. For example, fear represents an immediate and overwhelming physical danger. Sadness represents an irrevocable loss that had already happened, whereas happiness represents a progress made toward a desirable goal. Disgust represents a state in which one is too close to an object or an idea that is difficult to assimilate. Such a treatment of emotions and their appraisal lends itself, as we will see in the subsequent sections, to creation of a more neurobiologically grounded theory of emotions.

Several others have followed the tradition of appraisal theory that is based on the premise that cognitive appraisals are the very essence of emotions. This cognitive component of emotions seems to make emotions easily analyzable. The theory maintains that through introspection, the results of which can be elicited by interrogation, it is possible to analyze and understand the contents of emotion. A study by appraisal theorists Craig Smith and Phoebe Ellsworth asks subjects to assess a past emotional experience in terms of several emotional dimensions (like pleasantness, effort involved, etc.). For example, pride may be associated with a situation involving pleasantness and little effort, while anger is linked to unpleasantness and a lot of effort. Thus, it seemed to be possible to resolve emotions to their bare essentials simply by introspection and verbal report of the same.

Thus, a cognitive approach to the problem of understanding emotions seemed to have achieved a tremendous success, paradoxically, by reducing emotions to a cognitive phenomenon. A major complaint that is often leveled against early cognitive science and its allied fields like artificial intelligence is that they have successfully banished emotions from their purview. A robot or a computer system with emotions is often seen a creation of science fiction, as a wonder that cognitive science and computer science can only aspire to create, but hitherto failed to achieve. In making emotions a part of the cognitive reckoning, the appraisal theorists seemed to have bent backward and committed an opposite error. By reducing emotions to verbal analyses and self-reports, they seemed to have expelled the charm, the intrigue, the sweet or terrible unpredictability, from emotions. If emotions can be seen and read out so clearly, like a piece of text under a table lamp, they would not be emotions in the first place. A good theory of emotions must allow them their right to be mysterious, at least in part. This mysterious aspect of emotions began to be unraveled through the link between emotions and the unconscious.

## The Unconscious Depths of Emotions

Consider the following striking experiment that highlights the irrelevance of cognition to emotional preference. Subjects were shown some emotionally neutral, nontextual patterns like the Chinese ideograms in two rounds. The set of patterns shown in the first round may be labeled as "previously exposed" and those shown in the second round as "novel." The patterns—old and new—are jumbled and presented to the subjects who were then asked to choose the patterns they find more preferable. The subjects chose some but could not rationalize their decision. It turned out that the subjects chose the ones they were "previously exposed" to. But in a given mixed set, the subjects could not tell the two sets apart. They only knew subconsciously that the first set was preferable over the second.

This is a simple instance where conscious cognitive appraisal was not involved in the formation of emotional responses. There was an underlying reason behind the subjects' choices which the experimenter knew, but was hidden from the view of their cognitive appraisal. Experiments like this one and many others were performed by Robert Zajonc, a social psychologist, to show that emotional appraisal need not be cognitive. The reasons of an emotional appraisal could be hidden from any cognitive reckoning. What shaped the preference was what was known as "subliminal exposure," an unconscious exposure to a stimulus.

A lot of experiments of the above kind were based on different ways of reaching the unconscious, bypassing the cognitive self. One way to do so in the visual domain is to present a visual stimulus so briefly that it fails to form a conscious registry. In one experiment, the subjects were shown some emotionally significant pictures (like a smiling or a frowning face), albeit too briefly (5 ms) to be registered consciously by the subjects. This pattern, known as the priming pattern, was followed by a masking stimulus which prevents the subjects from consciously recalling the original pattern. After a further delay, the target pattern, an emotionally neutral pattern, like the Chinese ideograms for example, was presented. The presentation of priming pattern $\rightarrow$ mask $\rightarrow$ target pattern was repeated over many patterns. The subjects were asked regarding the patterns they preferred. It turned out that they preferred those for which the primes had an emotionally positive significance (like a smilie). But when probed regarding the reasons behind their choice, the subjects were unable to make their reasons explicit. Once again subliminally presented stimuli shaped emotional preferences without informing the conscious self.

This ability by which humans show evidence of perceiving a stimulus though they report no conscious awareness of that stimulus has been dubbed subliminal perception. Such perception has nothing to do with emotions per se. Earliest studies in this area date back to 1800s and early part of twentieth century. In these studies, for example, people were presented with visual stimuli from such a distance that it is nearly impossible to identify the stimuli. Or they were presented with auditory stimuli too weak to comprehend. They were then asked to identify the stimuli. In one such study, the subjects were presented with visual stimuli which could be single letters or single digits with equal probability, and were asked to guess the class (digit or letter) of the stimulus. The subjects reported that they were guessing but guessed at levels much higher than chance level.

Cases of subliminal perceptions have also been discovered in patients who underwent surgery under general anesthesia. As a matter of principle, general anesthesia is administered such that the patient is completely oblivious of what has happened during the surgery. This is often confirmed by checking with the patient once the patient is back to consciousness. The patient often denies remembering anything that happened during that time. But more delicate methods of probing have revealed that patient retained memories of stimuli presented under conditions of general anesthesia. For example, in one such study, the patients were played sounds of certain words (e.g., guilt, prove, etc.) repeatedly when under general anesthesia. Once they came back to consciousness, they were given word stubs like gui-, pro-, and so on and asked to fill the blanks. The patients chose the words they “heard” under general anesthesia to fill the missing parts of the words.

There were claims that the power of subliminal perception was exploited by companies to influence consumers and induce them to buy their products. One such claim which was published in 1957 was made by James Vicary, a market researcher. Vicary described an experiment in which a large number of patrons were exposed to two advertising messages: “Eat popcorn” and “drink coco-cola” while they were watching a movie in a theater in New Jersey. According to Vicary’s report, the messages were flashed only for 3 ms, a duration too brief for conscious recognition. Over a 6-week period during which these messages were presented, the sales of popcorn rose by 57.7% and that of coke by 18.1%! Vicary’s study was described in a popular book titled “the hidden persuaders” by Vance Packard. The book described how companies manipulate the minds of consumers persuading them to buy their products, and how politicians use the same tactics to influence voting patterns. All this led to public outrage and resulted in creation of a law that prohibits use of subliminal perception in advertising.

Thus, the phenomenon of subliminal perception shows that conscious perception of a stimulus is not necessary to exhibit behavior that depends on the stimulus. Such stimuli can influence emotional preferences and decision-making, while completely evading conscious perception. Existence of subliminal perception turns out to be perhaps the strongest counterargument to appraisal theory of emotion. Conscious, cognitive appraisal cannot be the whole story with emotions. At the same time, AI-style approaches that hope to reduce emotional processes to a set of clean, well-defined procedures, and design machines that posses (cognitive!) emotions, are foredoomed. Subliminal perception strongly urges us to fundamentally rethink our strategy of understanding emotions.

There is an even more dramatic form of sensory phenomenon in which the subject denies any conscious experience of the stimulus but exhibits behavior that depends on reception and processing of the stimulus. A class of patients who suffer from a condition called blindsight report no visual awareness but are capable of displaying visually based behavior. One of the earliest patients of blindsight was DB, a patient at National Hospital at London. DB had his occipital lobe surgically removed as a treatment to remove a tumor that invaded it. Although DB reported that he could not see anything, he could perform a lot of visual tasks. For example, he could reach out to objects with remarkable accuracy. When shown a grating pattern, he could tell if the lines are oriented one way or the other. Since the early studies on DB, a large number of blindsight subjects have been studied confirming the phenomenon. Analogous conditions in touch (“numbsense”) and even hearing (“deaf hearing”) have also been found. This unconscious sensory capacity, which occurs when the corresponding sensory cortex is damaged, is believed to be possible because certain relevant deep brain structures, like thalamus, for example, are intact. Since most sensory information goes to thalamus before it proceeds to cortex, it is likely that thalamic representations of sensory inputs are responsible for this kind of unconscious sensory capacity.

Let us pause for a moment to take bearings on our journey through various influential theories of emotions. We began with James–Lange theory that emphasizes the importance of bodily response for emotional experience. But Cannon–Bard theory points out that the bodily response occurs rather late, and also argues that it lacks the specificity required for various emotions. Schachter and Singer theory reconciled the two theories by proving that though bodily response is important (it intensifies emotional experience), specificity does not come from it. Specificity comes from a conscious evaluation and interpretation of external conditions and social context. This paved way to appraisal theory and the thinking shifted in a major way from bodily response to cognitive evaluations. Subliminal perception and related results brought about correction of a different kind. Between the cognitive self and the bodily self, it posited an unconscious self that can influence and determine the contents of emotions. A greater synthesis, with James–Lange approach at one end of the spectrum, and that of the appraisal theorists at the other, seems to be the need of the hour.

In our quest to understand emotions, we seem to have got ourselves stuck in the body–unconscious–cognition axis. If a grand synthesis is our ultimate goal, we are not likely to succeed merely by collecting more data that support various theories located somewhere on this axis. We need to get out of this axis in the first place and search in a very different direction. Indeed, there is a direction, a line of attack on the problem of emotions that we have ignored in the story of emotions that we have narrated so far. The theory, or the spectrum of theories of emotions that we have so far visited, is predominantly psychological. Beyond the initial references to involvement of autonomic responses in emotion, our considerations have been, almost exclusively psychological, not really neural. The influence of behaviorism led us away from drives and motivation and other ghosts in the brain. The influence of cognitive science taught us the language of appraisal, and a strong reliance on introspection, from the point of view of the subject, and verbal report, from the point of view of the experimenter. The physical brain, the ganglia, the nuclei, the neurons, and the gossamer wiring that links them did not become a part of the reckoning. A theory of emotions that does not mention brain is not likely to get very far.

Part of the reason behind this gross omission is perhaps the subconscious (?) feeling that emotions are an exclusive prerogative of humans, conscious and intelligent, and cannot be unraveled by any means other than linguistic, cognitive investigation, and analysis. The legend and folklore that surrounds the claims of pet owners about the boundless love that their pets shower on them is not often sufficiently convincing to the scientifically inclined. But it is an unmistakable sign of vanity to deny the entire animal world their share in emotions, when we ourselves are a precarious outgrowth of aeonic animal evolution. Therefore, it seems to be eminently logical to reconsider the problem of emotions from two points of view: (1) from that of the brain and nervous system, and search for substrates of emotional activity in the brain, and (2) that of emotions as they occur in animals. Though a complete and comprehensive neural theory of emotions does not exist as yet, we will see that a familiarity with neural components of emotional activity offers some solid leads toward such grand synthesis.

## Animal Emotions and Facial Expressions

Earlier in this chapter, we have seen how Sylvan Tompkins, Paul Ekman, and others have classified emotions purely on the basis of facial expressions. We have mentioned this class of studies as some of the first in line that led to the development of psychological theories of emotion. But there is a study of emotions based on facial expressions, one that is much older than that of Sylvan Tompkins, and one that is perhaps the first of its kind. This study performed by Charles Darwin considered facial expressions in both humans and animals, and showed universal similarities across a range of species. An approach to emotions that discusses them in both humans and animals in a single breath necessarily paves way to a whole different direction of thinking, a direction that would perforce lead to a neurobiology of emotions.

But Darwin's original question was not to study emotions, human or animal, but to understand the forces that shape the evolution of species. Rejecting the religious idea that God had created different species afresh at various stages in the history of the Earth, Darwin set out on a worldwide voyage, famously called the "Voyage of the Beagle," to look for evidence. He brought back with him a large mass of biological evidence, in the form of specimens like teeth and feathers, bones and nails, and fossils of all types. His studies convinced him that biological organisms were not created arbitrarily afresh without a precedent, but have evolved gradually through the history of the Earth. Certain biological traits are inherited from generation to generation. Children do resemble their parents and often inherit certain traits. But certain new traits also emerge in new generations, traits that did not exist before. Children do not look identical to their parents. Sexual reproduction is not only a preserver of old traits, it is a source of new ones. Thus, Darwin observed that change is a natural process of evolution. But what is the logic behind this change? What is the direction of its progress? In answer to this question, Darwin thought of how animal breeders tend to pair certain breeds together in order to produce offspring with suitable traits. The criteria for interbreeding that determine the choices of a breeder include more milk, more meat, more speed and strength, greater resistance to disease, or simply longer life. Thus optimizing certain traits is the direction in which the controlled evolution shaped by a breeder proceeds. By extension of this idea to nature at large, Darwin visualized that species compete for the limited natural resources in a struggle to survive. Thus, species that are fit in a given natural habitat tend to survive, passing on their traits to their offspring. Mother Nature, like a grand Breeder, selects the species that are the fittest for survival in a given milieu. This "natural selection" is the cornerstone of Darwin's theory of evolution.

But Darwin felt that not only physical features but personality traits and behavioral features could also be inherited. Particularly, Darwin observed that there are universal ways of emotional expression, through countenance and bodily gestures, that cut across cultures and species. He captured his observations on this subject in a volume titled "*The Expression of the Emotions in Man and Animals*," in which he expounds three principles of expression:

The first principle, dubbed the principle of serviceable associated habits, states that certain bodily movements or actions are habitually associated with certain states of mind. Through repeated association between the states of mind and accompanying actions, expression becomes habitual, and sometimes even outlives its original purpose.

The second principle, known as the principle of antithesis, may be simply stated as follows. If a state of mind #1 is exactly opposite in nature to state of mind #2, the expression of the former will be exactly opposite to those of the latter.

The third principle which reads, "*The principle of actions due to the constitution of the Nervous System, independently from the first of the Will, and independently to a certain extent of Habit*," needs some translation since he uses a rather archaic language, very different from that of contemporary neuroscience. Here, he talks about certain reflexive, innate motor traits that are hard-wired in the nervous system, and have nothing to with the action of the will, or formation of habit.

Darwin gives a large number of examples to support these principles. A perplexed man tends to scratch his head as if the external act is going to provide relief to his internal crisis. Accordance with another's view is expressed by a nod, while opposition is expressed by shaking the head. A person describing something horrible shuts his/her eyes, or shake his/her head, as if trying "not to see or to drive away something disagreeable." A person trying to recollect something tends to raise his/her eyebrows attempting actually to look for it. Interestingly, in this context, Darwin comments that "a Hindoo gentleman," a person of Indian origin, also agrees that the trait of lifting eyebrows during mental recall is common even in the subcontinent.

Darwin also observes that certain motor traits are inborn even among animals. Young ponies show inherited gait patterns, like ambling and cantering. A certain moth species (humming-bird Sphinx moth), soon after its emergence from its cocoon, is seen to hover above a flower, inserting its proboscis into the orifices of the flower. Certain species of pigeons display peculiar patterns of flight which could not have been learnt. In addition to such general motor traits, Darwin also observes innate patterns of expression of emotion. In face of a mortal threat, it is common among a variety of animals, and also humans, to urinate and defecate. Piloerection is a common form of emotional expression found in many animal species including rats, bats, cats, lions, and so on. A remnant of this primordial expression in humans is goosebumps, a manner of emotional expression that could indicate an elated state of mind, or one of sheer horrors. A state of rage that is accompanied by snarling, hissing, spitting, baring of canines, and other gestures is found in both animals and humans. Quoting from Shakespeare, Darwin presents an illustration of how an agitated state of mind could be expressed in an elaborate, quaint bodily ritual:

Some strange commotion
Is in his brain; he bites his lip and starts;
Stops on a sudden, looks upon the ground,
Then, lays his finger on his temple: straight,
Springs out into fast gait; then, stops again,
Strikes his breast hard; and anon, he casts

**Fig. 10.5** Similarity in human and simian facial expressions

His eye against the moon: in most strange postures
We have seen him set himself.—*Hen. VIII*., act 3, sc. 2.

The observation that humans and animals share certain forms of emotional expression urges to look for common origins (Fig. 10.5). We need to figure out methods of emotion research that could be applied equally to humans and animals. The methods described hitherto were predominantly cognitive, with a strong dependence on verbal report and introspection. These psychological methods were certainly fruitful in case of human emotions, but will be irrelevant to unravel animal emotions. If traits of emotional expression were inherited by us from our animal past, the basis of that inheritance can only be found in our brain which has evolved from a mammalian brain, or a primate brain, more specifically, and look for correspondences between shared cerebral features and shared manner of emotional expression. Even if we are ambivalent in granting animals the luxury of subjective emotions, we have no option but to allow them emotions in their objective expression. A new line of investigation into the nature of emotions now opens up. This line of study will have to consider a neural basis for emotional expression. After romancing with feelings, appraisals, conscious and unconscious, and cognitive evaluations for too long, we realize it is now time to return to the bodily basis of emotions. And when we consider the body, the brain will follow in its wake automatically, autonomically.

## Emotions Right in the Middle

Some of the earliest efforts to find the "centers of emotion" in the brain came from a Russian physiologist named Vladimir Bekhterev. Conducting experiments on animals in which parts of the brain were ablated, Bekhterev looked for signs of emotional attenuation. As a result of such experiments, in 1857, Bekhterev concluded if the brain is lesioned or "truncated" above an important structure called thalamus, emotional responses remained nearly intact. Thalamus is an important hub through which most sensory data (except olfactory and gustatory information) passes, before it arrives at appropriate targets in the cortex. This strategic anatomical location of thalamus had earned this structure the title "gateway to the cortex." Bekhterev concluded that thalamus is the center of emotion. But this line of work went unnoticed for nearly three decades. In 1892, Friedrich Goltz followed up Bekhterev's work. Goltz was interested in studying the contributions of the cortex to motor output. He studied decorticated animals, a special neuroanatomical preparation in which the entire cortex is disconnected surgically, and found that they exhibited a lot of normal functions of nervous system like sleep–wake cycle, temperature rhythms, spinal reflexes, response to sensory stimuli, and so on. Most importantly, they showed normal responses to painful stimuli. Though it was not possible to attribute experience of pain to these animals, they obviously exhibited reflexes of pain. Although the use of decorticated animals could have become a fruitful line of work in emotion research, unfortunately this tradition was ignored for some time when Walter Cannon entered the scene.

While decorticated animals were continued to be omitted, emotion researchers often used a so-called "cat and dog" paradigm in experimental studies of emotion. In this setup, the cat is placed inside a cage and the dog is placed outside. The dog is angry and frustrated that it is prevented from reaching the cat. The cat is afraid and exhibited signs of fear response. Cannon found this setup inconvenient for careful physiological measurement. When the animals are in such an excited condition, it is difficult to measure circulatory and other autonomous responses like blood pressure, temperature changes, etc. Measurement, taken when the animals become calm again, defeat the original purpose. Cannon found that the decorticated preparation is full of potential for understanding substrates of emotions in the brain.

One of the first things that Cannon noticed about decorticated animals is that, under provocation, these animals showed a range of responses bundled as rage response consisting of retraction of ears, unsheathing of claws, arching of the back, growling, and so on. This evidence flew in face of James–Lange theory which maintained that cortex is necessary to process sensory information and produce motor output appropriate for emotional response. Cannon felt the need to distinguish this rage response from the one that occurs in an intact animal and coined a new term to describe the rage expressed by a decorticated animal—"sham rage." Cannon was joined by his student Phillip Bard in his efforts to precisely establish the substrates of emotion. Their joint efforts resulted in Cannon–Bard theory of emotion (Fig. 10.6). Together, they ablated brain at various levels and systematically descended toward the diencephalon—a brain region that consists of two key structures, thalamus, and hypothalamus. They noticed that rage response was significantly attenuated when parts of hypothalamus were lesioned. Animals in which hypothalamus was destroyed did show some aspects of rage response—snarling, crouching, hissing, unsheathing of claws, etc.—but the responses did not occur in a coordinated fashion as they occurred in an animal with intact hypothalamus.

The crucial role of hypothalamus in coordinating rage and other emotionally significant responses have been unraveled through electrical stimulation experiment,

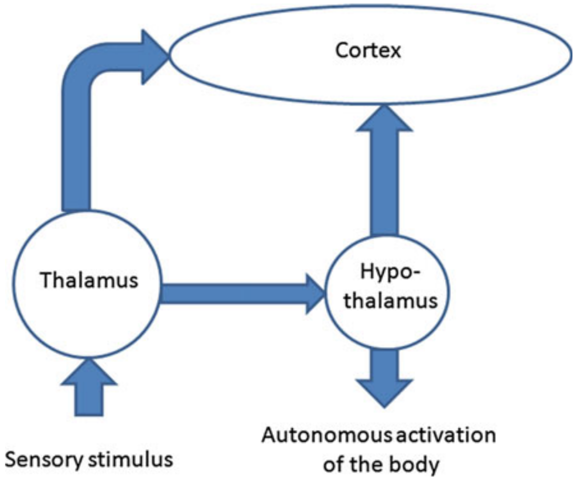


**Fig. 10.6** A schematic of Cannon–Bard theory of emotion processing. Hypothalamus is a key coordinating center for emotional expression; cortex is considered the site of emotional experience. In James–Lange theory, physiological response is the cause of emotional experiences. Contrarily, in Cannon–Bard theory, hypothalamus triggers both bodily response and emotional experience in the cortex

analogous to cortical stimulation experiments performed by Penfield. In experiments of this kind, electrodes were placed at various points in the brain of a caged experimental animal. The animal is free to press a lever that is placed next to the cage. When the lever is pressed, a mild current is delivered to the animal's brain through the implanted electrode. Stimulation of certain sites in the brain caused such a sense of reward or pleasure that the animal depressed the lever hundreds of times in an hour. Interestingly, the animal found this experience of self-stimulation preferable even over offerings of food. Sites of this type were found in parts of hypothalamus, the lateral and ventromedial nuclei.

Other sites were found in hypothalamus where stimulation produced a strong aversive response in the animal, as if the stimulus were punitive. Stimulation here elicited responses of pain, terror, and sickness. A rage response was characteristically elicited by stimulation of punishment centers, exhibiting hissing, spitting, crouching, snarling, and other classic features of rage. Such "punishment centers" were found particularly in the periventricular parts of hypothalamus, the parts that overlie ventricles, and also thalamus. It is noteworthy that when both reward and punishment centers were stimulated, activation of the punishment centers inhibited the reward centers, and there was a predominance of fear and pain response.

The fact that hypothalamus is an important control center for coordinating emotional responses, the fact that it receives inputs from thalamus, and the fact that thalamus is involved in unconscious sensory processing open a window of opportunity that could possibly reconcile the standoff between James–Lange theory and Cannon–Bard theory. It could also begin to conveniently accommodate both the cognitive appraisal approach to emotions and the unconscious aspect of that appraisal. When sensory input winds its way through the nerves, it first arrives at the thalamus and proceeds onward to the sensory cortex, where it produces the corresponding sensory awareness. A part of the information that arrives at the thalamus is also conveyed to hypothalamus which evaluates the emotional or affective significance of the sensory information and triggers appropriate bodily responses. The hypothalamus in turn projects to the cortex. Thus, the cortex is now a proud recipient of two streams—the direct stream from thalamus which conveys sensory information, and the indirect stream via the hypothalamus which supplies the emotional appraisal. The combination of these two forms of information in the cortex is probably the precondition for the feeling that goes with an emotional response.

This simplified depiction of emotional processing as it is played out in the circuit consisting of thalamus, hypothalamus, and the cortex has several merits. It agrees with James–Lange theory in part, in that it does not say that conscious experience is responsible for bodily responses. For in the above description, it is the unconscious processing occurring at the level of the diencephalon (thalamus + hypothalamus) that initiated the bodily response. It agrees in part with Cannon–Bard theory, since it does not invoke the feedback from the body, to account for emotional experience. In fact, the above picture does not even include such feedback. Next, it accommodates cognitive appraisal, since such appraisal can be said to be occurring in hypothalamus which has access to the sensory information available in thalamus. But it also stresses the unconscious aspect of such appraisal since the processing occurs at the level of thalamus and hypothalamus.

But hypothalamus is not the whole story of emotions. It is a good place to begin with, and is indeed a key player. But there is a whole world of brain structures, cortical and subcortical, that are involved in emotional processing. Let us begin with a brain area involved in emotions, an area that is right in the middle of the brain, and was a source a lot of progress and controversy in emotion research.

## The Middle Kingdom of Emotions

Imagine the shape that is produced when the fists formed by your two hands are brought together so that the middle phalanges of the four fingers come into contact. This shape that looks like a 3D object with two halves, or "hemispheres," divisible right in the middle by a vertical plane that separates the two fists, has a convenient resemblance to the hemispheres of the brain. The visible parts of the surface of this double fist, the back of the hand and the lower phalanges of the fingers, are comparable to the lateral cortex of the brain, the part of the cortex that is visible from outside. The parts of the double fist that are in contact—the middle phalanges of the four fingers—are comparable to a cortical region that is located right in the middle of the brain, hidden from the external view. This part of the cortex, the medial cortex, has been named by the famous French neurologist Paul Broca as le grand lobe limbique, or the great limbic lobe in plain English. Broca thought of the limbic lobe as the fifth lobe, after frontal, parietal, temporal, and occipital lobes. Another reason he distinguished the limbic lobe from the other lobes is that this part of the brain is hardly convoluted, like the other four lobes. Since its appearance resembled the cortices of lower animals, he felt that limbic lobe corresponded to "bestial" nature in us. Another reason behind attribution of "bestiality" to this cortical area is its link to sense of smell, which earned this brain area the title of rhinencephalon (meaning "smell brain"). Smell is an important driving force in an animal's life and behavior. Smell is a strong guiding power in foraging for food, flight from a predator, and sexual arousal. Anatomist CJ Herrick, who did seminal work on the evolution of brain, felt, as Broca did, that the lateral cortex must be distinguished from the medial cortex, on evolutionary terms. He proposed that, whereas the older medial cortex is involved in emotion processing, the newer lateral cortex, called the neocortex ("neo" means new), is responsible for higher cognitive functions in humans.

There are other reasons for considering the association between the medial cortex, particularly a part of the medial cortex known as the anterior cingulate cortex, and emotions. An early case—and a royal one at that—of this link dates back to the seventeenth century. It involved a knight called Caspar Bonecurtius, who suffered from severe apathy. He sat in a place whole day long, unresponsive to his surroundings. Toward the end of his life, he spoke very little, and whatever little he spoke was not very meaningful. After his death, postmortem revealed a tumor in his anterior cingulated gyrus. Even in the middle of the last century, it was known that electrical stimulation or ablation of anterior cingulate cortex is accompanied by transient changes in emotional behavior. These findings led to a drastic practice of surgical removal of anterior cingulate in order to cure "severely disturbed mental hospital" patients. Damage to anterior cingulate also resulted in depression, apathy, delirium, and other affective disorders.

Another unlikely structure that was found to play a role in emotion processing was hippocampus. We have seen, in Chap. 5, that hippocampus is a site of memory consolidation. It is a place where memory resides temporarily, before it is shipped to long-term stores in the cortex. This mnemonic function does not give any clue to its role in emotions. But the link between hippocampus and emotions was first recognized from studies of cases of rabies. Rabies is a viral disease that affects the brain by causing inflammation. The symptoms may begin as headaches and fever, but expand to anxiety, insomnia, agitation, paranoia, terror, and consummating in delirium. The virus particularly attacks hippocampus.

Another disease—epilepsy—also links hippocampus to emotion processing. Epilepsy is a brain disorder characterized by seizures caused by uncontrolled spread of synchronized neural activity across the brain. These seizures are often preceded by an aura, a prior feeling, a sort of a warning sign that predicts a seizure. Interestingly, the auras are often accompanied by inexplicable fear, a sense of déjà vu (it happened before), and even a bad taste in the mouth.

Thus, a certain coarse knowledge of the above mentioned cerebral components of emotion processing was known even in the early decades of the twentieth century. Seizing upon these ideas, James Papez, an anatomist at Cornell University, made a bold attempt to expand the simple scheme of Cannon–Bard theory into a more elaborate circuit of emotions—the eponymous Papez circuit. The Cannon–Bard scheme primarily has two pathways: one proceeding directly from the thalamus to the cortex, and the other, a detour, that bifurcates from the thalamus and proceeds to the cortex but via an important hub of emotion processing—the hypothalamus. The essence of these two branches is preserved in Papez circuit. Papez thought of these two branches carrying two fundamentally different streams of experience. The branch from thalamus to the cortex is thought to carry the stream of thought, while the detour from the thalamus to hypothalamus carried the stream of feeling. A broad distinctive feature of Papez circuit compared to the Cannon–Bard scheme is the presence of feedback from the cortex to hypothalamus; Cannon–Bard scheme only had a forward influence from hypothalamus to the cortex. These general differences and interpretations apart, what really put the Papez circuit on a pedestal is that it is primarily a neural circuit. Drawing from the available knowledge of the neural substrates of emotion at that time, he linked some specific neural structures in a circuit and proposed it as an engine of emotions. The new structures he added to Cannon–Bard scheme are hippocampus and cingulate cortex, for reasons mentioned above. Let us quote Papez himself on how he thought this circuit functions:

> The central emotional process of cortical origin may then be conceived as being built up in the hippocampal formation and as being transferred to the mamillary body and thence through the anterior thalamic nuclei to the cortex of the gyrus cinguli. The cortex of the cingular gyrus may be looked upon as the receptive region of the experiencing of emotions as the result of impulses coming from the hypothalamic region, the same way as the area striata is considered as the receiver of photic excitations coming from the retina. Radiations of the emotive processes from the gyrus cinguli to other regions of the cerebral cortex would add emotional coloring to the psychic processes occurring elsewhere. This circuit may explain how emotional processes may occur in two ways: as a result of psychic activity and as a result of hypothalamic activity.

In Papez' view, the cingulate cortex is like a window between the cortex in general and the emotional circuit under the hood. Activity in the cingulate cortex, triggered by inputs from the hypothalamus (via anterior thalamic nuclei), spreads to other cortical areas. These inputs from cingulate cortex to sensory-motor cortex give the ongoing experience there an emotional color. Hypothalamic influences downward to the endocrine system and the autonomous system, produce bodily responses as in Cannon–Bard theory. A new element of Papez circuit, compared to the Cannon–Bard scheme is the feedback from the cingulate cortex to hypothalamus, via hippocampus. Thus, by supplying the neurobiological substance to Cannon–Bard approach, the Papez circuit had a profound influence on our understanding of emotion processing. But Papez circuit had an important emotion module missing. Ironically, some of the earliest work on this new module was published in 1937, the year in which Papez first published ideas about his circuit of emotions (Fig. 10.7).

## Almond Fears

In the '30s, Heinrich Kluwer, a professor at the University of Chicago, was studying visual cognition in monkeys. He was particularly interested in the effect of a hallucinogen called mescaline. As a part of his research, he tried the drug on himself and described some of his findings in a little book called *Mescal, the Divine Plant*.

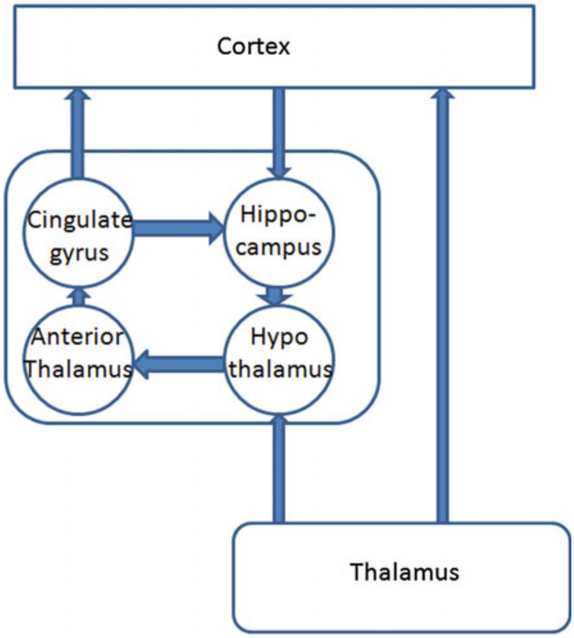


**Fig. 10.7** Papez' circuit of emotions

Kluwer noticed that hallucinations that form part of the aura experienced by patients undergoing temporal lobe seizures resembled the hallucinations induced by mescaline. So he wanted to see if mescaline acted on the temporal lobe to induce those seizures. To check this idea, he wanted to remove temporal lobes in experimental animals and see if mescaline's ability to induce hallucinations will be blocked by the surgery. With the help of neurosurgeon Paul Bucy, he got this surgery—called temporal lobotomy—performed on monkeys. The results of the experiment turned out to be negative: the monkeys with temporal lobes removed continued to respond to mescaline as normal monkeys did. But what was interesting about the experiment was that the lobotomized monkeys showed some strange behavioral changes, which were summarized by Kluwer as follows:

1. Psychic blindness or visual agnosia: the ability to recognize and detect the meaning of objects on visual criteria alone seems to be lost although the animal exhibits no or at least no gross defects in the ability to discriminate visually.
2. … strong oral tendencies in the sense that the monkey insists on examining all objects by mouth.
3. hypermetamorphosis: There is a tendency to attend and react to every visual stimulus.
4. profound changes in emotional behavior, and there may even be a complete loss of emotional responses in the sense that… anger and fear are not exhibited. All expressions of emotions… may be completely lost.

5. …striking increase in amount and diversity of sexual behavior. It exhibits forms of autosexual, heterosexual or homosexual behavior rarely or never seen in normal monkeys.
6. a remarkable change in dietary habits… tendency to consume large quantities of …[meat].

The above-listed complex set of symptoms was bagged together and described as Kluwer–Bucy syndrome. Both the cause (removal of temporal lobe) and the effect (the many-sided syndrome) are complex. The experiment does not provide a specific insight into the possible role of temporal lobe in emotional behavior, though it is clear that damage to temporal lobe indeed causes emotional disturbances. Therefore, efforts were on to localize the lesion further, and see if specific lesions could produce specific symptoms. As a part of this effort, Josephine Semmes from Yale and Kao Liang Chow from Harvard showed that lesions of temporal cortex produced "psychic blindness," which refers to serious deficits in visual discrimination. Subsequently, Karl Pribram and Muriel Bagshaw showed that damage to deeper structures of temporal lobe, primarily the amygdala, produced the emotional changes (tameness, changes in sexuality, and eating) associated with Kluwer–Bucy syndrome. These findings put the spotlight on amygdala as an additional structure involved in emotion processing. Existence of amygdala was known even in the nineteenth century. The structure earns its name from the Greek word that denotes almond, referring to the almond-like shape of amygdala. But not much was known about amygdala's function until the studies of Kluwer and Bucy and the research that followed. It remains to be seen how the new structure is related to the rest of the emotion circuit hitherto understood—the Papez circuit.

The story of our first efforts at gaining a functional understanding of amygdala begins with behavioral experiments on fear conditioning. In Chap. 1 of this book, we briefly encountered Russian physiologist Ivan Pavlov's pioneering experiments on conditioning. The essence of this experiment was to learn a novel stimulus–response pair with the help of a pre-existing stimulus–response pair. When a plate of meat is offered to a hungry dog, the animal exhibits the natural response of salivation. In the terminology of conditioning literature, the plate of meat is an unconditioned stimulus (US). Before conditioning, the animal does not salivate in response to a neutral stimulus like the sound of a bell. But when the bell is rung a little before the meat is presented, the animal learns to respond by salivation even in response to the bell, which is now called a Conditioning Stimulus (CS). Salivation in response to CS is known as Conditioned Response (CR). Conditioning experiments are interesting since they represent simplest, and precisely quantifiable forms of learning, which are hoped to serve as prototypes to more sophisticated forms of learning that humans are capable of.

A variation of Pavlovian conditioning is fear conditioning, in which animals exhibit the so-called *fear response*, instead of salivation, in response to a painful or an aversive stimulus. A striking aspect of fear response is total immobility, as opposed to a more intuitive escape response in face of danger. This immobility or freezing may be thought of as a preparation for a subsequent escape, or a temporary strategy to prevent the predator from attacking, since predators often respond to movement. Fear response is associated with appropriate autonomous changes like increased heart rate and respiration, dilated pupils, etc.

In a typical fear conditioning experiment, a rat placed in a cage is first exposed to a sound followed by a mild electric shock. In the initial stages, the animal responds to the shock by freezing but ignores the sound. But when the sound and shock are repeatedly presented in that order, with a fixed delay, the animal begins to freeze in response to the sound. Joseph LeDoux and colleagues set out to unravel the circuitry that subserves fear conditioning. Their investigation naturally led them to amygdala which turns out to be an important hub in coordination of fear conditioning.

LeDoux and colleagues began their search for the branch, or the junction point at which the stream of sounds climbing up from the ear to the cortex meets the autonomous outflow that coordinates the fear response. The auditory stream begins its journey in the inner ear, where the vibrations produced by the sounds are converted into electric signals. These signals wind their way up toward the cortex passing several way stations, at various levels of the nervous system. First among these stations is the cochlear nucleus located in the brain stem, followed by inferior colliculus, another way station located slightly higher up in the midbrain. As the auditory information climbs further, it arrives at the thalamus, or more specifically the auditory thalamus, which refers to the thalamic nucleus responsible for receiving and relaying auditory information to the auditory cortex. Now what is the takeoff point on this auditory pathway at which a part of the auditory stream bifurcates and arrives at parts of the emotional circuitry that coordinates fear response?

Lesion experiments showed that damage to auditory cortex had no effect on fear conditioning, while damage to auditory thalamus or any way station below thalamus prevented fear conditioning. Thus, the auditory information must be branching out from the auditory thalamus to a target, other than the auditory cortex, through which it is coordinating fear responses. LeDoux and colleagues applied a classic neuroanatomical technique known as tract tracing to find out this new target. A question that neuroanatomists often find asking themselves is: does region A in the brain project to another region B? Or, conversely, does the region B receive inputs from region A? In an attempt to answer this question, a special visualizing substance called a tracer is injected into region A. The tracer then winds its way through the fibers connecting A to B. The wiring that connects B to A can then be visualized by standard staining methods. Similar methods applied to the auditory thalamus showed that this region projects to four different targets, one of which was amygdala. Which of these targets is responsible for fear conditioning? To answer this question, the research group systematically lesioned the four targets and checked for fear conditioning. Three of the targets had no effect on fear conditioning, but lesioning the fourth, amygdala, completely blocked fear responses.

We now know that a lesion of amygdala blocks fear conditioning. We also know how sensory information found its way to amygdala to trigger fear responses. But what exactly does amygdala do? How does it coordinate fear responses? A lot was known about the autonomic actions of amygdala long before the new direct connection between auditory thalamus and amygdala was discovered. Pioneering work by Bruce Kapp and colleagues in 1979 unraveled the autonomic effects of activation of a central core of amygdala, known as the central nucleus. This central nucleus of amygdala has, as it was later worked out by several researchers, connections to hypothalamus and other brainstem areas by which it can produce autonomic responses like freezing, blood pressure, heart rate, etc. By selective lesioning of parts of the central nucleus, it was possible to block specific aspects of the fear response, for example, to eliminate increased heart rate, while retaining the freezing response.

We now have a concrete realization of the Cannon–Bard scheme applied to fear conditioning. Sensory input bifurcates at the level of thalamus into two pathways one proceeding to the sensory cortex, creating the sensory experience of the stimulus that is the original cause of the fear response. It is the sensory stream of Papez's depiction. The other branch from the thalamus proceeds to the amygdala where through specific outgoing pathways produces a whole array of autonomic changes that constitute fear response. This latter branch may be described as a part of what Papez visualized as the feeling stream. But unlike in Cannon–Bard scheme, it is not a direct projection from the thalamus to hypothalamus, but a direct thalamic projection to amygdala, that triggers the fear response. Thus, amygdala turns out to be the kingpin in the world of fear conditioning.

But a question that may be asked at this juncture is: what is the advantage of having two separate pathways, one for sensory experience and another for emotional response? In the words of Joseph LeDoux, why does the brain need the "high road" of the sensory pathway and the "low road" connecting thalamus and amygdala? First of all, is the auditory cortex even necessary for fear conditioning, since a copy of the auditory information is reaching amygdala through the "low road"? The answer is in the negative, since it was shown that tone–shock pairing could be achieved even without auditory cortex? Then what is the purpose of auditory cortex for fear conditioning?

In order to answer this question, Neil Schneidermann, Phil McCabe, and associates performed an experiment in which they tried to pair an auditory input that is more complex than a pure tone, with a shock. They presented two tones, $T_1$ and $T_2$, with nearby frequencies, say, $f_1$ and $f_2$. Only $T_1$ was paired with the shock, but not $T_2$. The animal has to discriminate the two tones and exhibit fear response only to the appropriate tone. The animal was able to learn this more complex form of fear conditioning only when the auditory cortex was intact. When the cortex was lesioned, the animal exhibited fear conditioning to both the tones. This is because the information that travels down the "low road" does not have the detail that is characteristic of the information of cortical input. The two tones would sound nearly the same in the thalamus $\rightarrow$ amygdala pathway. The two sounds are discriminated at the level of the auditory cortex.

But our question is still unanswered. Why are there two pathways? If the auditory cortex is more informative, why not get rid of the "low road" completely? For one, the low road consisting of the projection from thalamus to amygdala is much older, in evolutionary terms, than the neocortex. So it is a baggage inherited from lower rungs of evolution, going all the way to reptiles. The advantage of this lower path is speed. It takes only a few tens of milliseconds at the worst for auditory information to reach amygdala by the lower pathway. But it takes a few hundred milliseconds for the sound to be consciously registered in the auditory cortex. By the time the subject consciously perceives and identifies the auditory stimulus, the autonomous response triggered by amygdala would be well underway. By its very nature, a fear response is associated with an emergency situation, and rapidity of response is crucial. Therefore, evolutionary wisdom seems to have decided that it is better to act sooner, even if the action is based on coarse, approximate information, rather than opt for a leisurely response driven by conscious experience.

## Memorizing Fear

We have seen in Chap. 5 that damage to temporal lobe, particularly hippocampus, can cause serious memory impairments. The famous amnesic patient HM, who had undergone temporal lobectomy, had not only lost a good portion of his past memories (retrograde amnesia), he also had a difficulty in creating new ones (anterograde amnesia). The hippocampus is endowed with special neural infrastructure and the neurochemical mechanisms that enable this structure's memory-related operations. The kind of memory that hippocampus supports is known as declarative memory, a form of memory that can be consciously stored and retrieved. This form of memory must be distinguished from another memory system, the procedural memory, which refers to memory of motor skills. Procedural memories cannot be expressed or "declared" but are memories of nonconscious, implicit skills. This latter form of memory is subserved by a very different circuit known as basal ganglia. Thus, we have two parallel memory systems supported by apparently unrelated brain networks. But a closer study of damage to temporal lobe structures and the associated impairment of memory operations had unearthed a third form of memory, one that is also unconscious and had something to do with memory of emotions.

Edouard Claparede was a Swiss physician and child psychologist who lived in the earlier half of twentieth century. Claparede had an interesting amnesic patient who had retained some of the older memories but had lost all ability to create new ones. So all her experiences were short-lived and were erased within minutes. Claparede greeted her every day, afresh, while the patient never had a recollection of having met the doctor. As this ritual went on for some time, one day, when Claparede went to meet her, he extended his hand, as always, to greet her but with a pin concealed in his hand. The next day when he went to meet his patient, she again did not have a recollection of having met him, but simply refused to shake his hand. Claparede inferred that though his patient did not have the ability to remember conscious memories, she retained a memory of painful experiences, and of the fear response that the pinprick had elicited.

Not much was known in the days of Claparede about the neural substrates of this new emotional memory, a memory of pain and its consequential fear. But as knowledge of amygdala and its role in fear conditioning began to be accumulated toward the end of the last century, the observations pertaining to Claparede's patient seemed to make more sense. This patient, like HM, must have had a damaged hippocampus, which explains her amnesia of declarative kind. But perhaps her amygdala was intact, which allowed her to store memory of a painful experience. It is interesting that the patient had no conscious understanding of why she hesitated to shake hands with her doctor. It indicates that the fear memory, which was supported by amygdala, was an unconscious memory. Thus, we have here a third memory system in addition to the declarative and procedural types, the one subserved by amygdala. This last type of memory is an emotional memory.

Now if we look back at our fear conditioning experiment from the previous section, we may come to regard conditioning also as memory. The rat had retained the memory that the CS (bell) is associated with a painful consequence, not very different from the manner in which Claparede's patient remembered (unconsciously) that the seemingly harmless handshake actually had a painful consequence. But the memories supported by hippocampus and amygdala seem to be of a very different kind—one retains memories of words, events, and other explicit items, while the other retains an unconscious memory of painful experiences. Considering the close contiguity of amygdala and hippocampus in temporal lobe, is it possible that the two memory systems are aspects of a larger memory system?

We have ignored an interesting feature in our earlier accounts of fear conditioning in rats. In these experiments, when a neutral stimulus like a tone (CS) is paired repeatedly with a shock (US), the rat learns to show fear response to the CS. But another element can also enter the picture and can trigger fear response in the animal. In addition to the CS, the cage, the surroundings in which the conditioning experiment was conducted, can by itself act as a trigger that can precipitate fear response. After sufficient training, if the rat is brought back to the same cage where it was earlier trained, it immediately shows signs of fear response (freezing, increased heart rate, etc.) without the necessity of presenting the CS. This form of conditioning is called contextual conditioning, since the surroundings or the context serves as a kind of CS in this case.

Therefore, there are two factors that contribute to fear response—the CS and the context. One may wonder why the animal's nervous system chose to split the environmental events into the CS and the context, since both may be thought of as parts of a unitary environment in which the animal is situated. The animal is trying to figure out the events in its immediate vicinity that can predict the arrival of a painful occurrence. In this process, it is trying to isolate cause and effect relationships from its experience of the environment, and thereby construct a useful model of the world. A hallmark of a good model is economy of representation. If there is a specific neutral event that consistently predicts the subsequent occurrence of a painful event, the animal is wiser to specifically pair the neutral event with the painful event, while deemphasizing other surrounding stimuli. But when there is no such specific neutral event, then the animal is faced with a harder task of building a cause and effect model of whatever it has at hand—to treat the entire context as being predictive of the painful event. Therefore, it was observed that contextual fear conditioning is more prominent when there is no CS at all. For the same reason, to really test whether the animal is sufficiently conditioned to respond to the CS, the animal has to be moved to novel surroundings, to a different looking cage perhaps, and the experiment must be repeated. Damage to amygdala was found to block both types of conditioning. The animal responded to neither the tone nor the cage. But damage to hippocampus was found to selectively block contextual fear conditioning.

The role of hippocampus in contextual fear conditioning was verified even in human experiments. In one experiment, human subjects were immersed in a virtual reality environment which provided the context. The subjects were actually exposed to two such contexts: Context+ and Context−. Context+ was paired with a shock which served as US, as in the case of animal experiments. Fear response was measured using changes in skin conductance, a measure known as Galvanic Skin Response (GSR) linked to sympathetic activation. Contextual fear conditioning was observed in case of Context+ which was paired with shock. The subjects' brains were scanned using functional Magnetic Resonance Imaging (fMRI) technique while they performed the experiment. fMRI measures neural activity indirectly by measuring blood flow changes associated with neural activity in the brain. fMRI scans indicated significantly higher activation of hippocampus and amygdala in case of Context+ relative to Context− condition.

## Brain Mechanisms of Pleasure

Psychologists may visualize complex, multi-hued palettes of emotions; art folks may quibble about the perfect list of fundamental emotions; philosophers may hypothesize existence of exotic and unearthly emotions beyond the scope of common human experience. But if we descend to the level of the humble neuron, with its spikes and ion channels, there are only two very mundane emotions—pain and pleasure, the positive and negative that form the bedrock of all experience. Stimuli that elicit pain, the aversive stimuli, which make us run away from them, induce in us fear and panic. Stimuli that create pleasure in us, the appetitive stimuli, which make us want more of them, induce in us a sense of reward. Whatever emotional hues that may be must be constructed out of these binary colors, and are ultimately rooted in the gray axis that extends between reward (white) and punishment (black).

We have encountered the neural systems of fear response in the last section. Let us now visit the brain's engines of pleasure and reward. In 1954, two researchers, James Olds and Peter Milner, at Canada's McGill University, performed brain stimulation experiments in rats. Experiments in which brains were electrically stimulated in order to understand the responses elicited by the stimulation were known much before the studies of Olds and Milner. But in the experiments of Olds and Milner, the animals were given an option to stimulate themselves. When the animals pressed a level, tiny currents flowed through brain regions where the electrodes were implanted. The question that the researchers asked is: will the animals prefer to press the lever, or avoid it? The studies were conducted with the electrodes placed at various locations in the brain. It was found that when the electrodes were placed in two specific brain regions—the septum and nucleus accumbens—animals pressed the lever at a whopping rate of about 2000 times an hour! Some animals chose this stimulation over food, at the risk of severe starvation. Unwittingly Olds and Milner have hit upon a pleasure center of the brain. Studies scattered over several decades after the original findings of Olds and Milner have unraveled several other centers of pleasure in the brain. Examples of such studies include the stimulation experiments, described earlier in this chapter, which found pleasure centers in the hypothalamus. Studies that searched for brain areas that respond to pleasure have converged on certain key "hotspots" which include deep brain areas like nucleus accumbens, ventral pallidum, and brain stem, and cortical areas like orbitofrontal cortex, cingulate cortex, medial prefrontal cortex, and insular cortex.

In addition to the abovementioned cortical and subcortical pleasure centers, there is a small subcortical pool of neurons in the mesencephalon, known as the Ventral Tegmental Area (VTA) which plays a pivotal role in brain's pleasure processing. VTA has neurons that release a chemical called dopamine, a molecule that is so important for pleasure that it has been dubbed the "pleasure chemical." The relevance of dopamine for pleasure processing was first discovered indirectly when effects of blockage of dopamine transmission were studied. The pleasurable effect of stimulation of pleasure centers was found to be severely attenuated when dopamine antagonists, chemicals that block transmission, were administered. Dopamine antagonists were also found to attenuate the pleasurable experience that goes with addictive drugs like cocaine. Subsequently, it was found that both electrical stimulation of pleasure centers and addictive drugs stimulate neurons of mesencephalic dopamine centers. Not unexpectedly a more common desirable object like food also activated dopamine neurons. Application of dopamine antagonists attenuated this response to food stimuli also. These findings amply justify the title of "pleasure chemical" given to dopamine.

The key role of dopamine centers in pleasure or reward processing became clearer when anatomical investigations found that mesencephalic dopamine neurons project most of the other cortical and subcortical players of pleasure processing that we have listed above. Thus, it appears that the dopamine centers form the hub of the wheel of brain's pleasure system. In addition to extreme or laboratory inducers of pleasure like electrical stimulation, or addictive drugs, and the more common, primitive rewards like food, brain's pleasure system was found to respond to subtler forms of pleasure also.

The sight of a beautiful face is a source of pleasure, a fact that is used extensively in film, media, entertainment, and advertisement industry. Data from labor markets suggest that attractive individuals are more likely to get hired, promoted, and even paid more. In the ancient world, the influence of beautiful faces seems to have gone far beyond salary amplification, as was described potently by the Greek poet Homer when he wrote of "a face that launched a thousand ships." Homer was singing of the disastrous graciousness of Helen of Troy, whose beauty precipitated the Trojan war. Functional MRI scans of people watching pictures of beautiful faces unraveled the secret of this ancient power: the pictures activated the reward system of the brain, particularly nucleus accumbens and VTA.

The sighting of a beautiful face can, if certain favorable conditions prevail, lead to romantic love, courtship and, if more favorable conditions prevail, to marriage. Based on a survey of 166 modern societies, it was found that romantic love is present in 147 cultures. The negative result obtained in case of the remaining 19 cultures, it was found in retrospect, was because the survey did not ask appropriate questions in those cases. Thus, romantic love seems to be a universal phenomenon with probable neurobiological bases. To test how brains respond to romantic love, Arthur Aron, Helen Fisher, and Lucy Brown took functional MRI scans of lovers. The subjects were shown pictures of their partners and some other individuals with whom the subjects did not have a romantic relationship. One of the key brain areas that were activated when the pictures of romantic partners were shown was once again VTA. In addition, other centers in the brain's reward system—insula, putamen, and globus pallidus—were also activated. These findings strongly suggest that love is such a powerful motivational force probably because it activates the reward system of the brain.

Notwithstanding the popular claims of the beneficial effects of humor on health, and the unsubstantiated celebration of humor's medicinal properties by popular adages ("laughter is the best medicine"), it would be universally accepted that humor is pleasurable. How then does brain respond to humor? In a functional MRI study that aims to answer this question, the subjects were shown 49 cartoons which were rated previously by a separate group as funny and non-funny. Brain areas that were preferentially activated when the funny cartoons were shown include the dopamine cell network of the mesencephalon and nucleus accumbens. Once again something pleasurable is found to activate brain's reward system.

Money is one of the most potent pleasure inducers, a power that ancient Greeks deified as Mammon, a prince of Hell. Wolfram Schultz and colleagues set out to study the effect of money on the brain using functional imaging. The subjects were shown certain complex images some of which were "correct." The subjects were asked to respond to the correct ones by clicking a mouse button. The subjects found out what the "correct" images were by the response from the experimenter. When the subjects responded to "correct" images, the experimenter simply said "OK" or actually gave a monetary reward. The study found that brain's reward centers (orbitofrontal cortex and midbrain centers) were preferentially activated when the subjects received monetary reward relative to the case when they received a neutral "OK".

Thus, a large number of studies have unraveled how the brain responds to the many forms of pleasure or rewarding stimuli. But what does the brain *do* with these responses? How does it act upon them? Pure happiness, unhinged from all earthly cares, may be the holy grail of the poet and the philosopher, but the fact that brain's pleasure responses are found not just in poets and the philosophers but in the brains of the rest of us, and also in others perched on the lower rungs of the evolutionary ladder like rats and monkeys, shows that the brain might have some serious purpose for its responses to pleasure. And why should it not? Pleasure or a persistent form of the same, happiness, is a strong motivator. People work for it, go to great lengths to achieve it, and guard it often at great expense. Thus, it is very likely that brain regions that respond to pleasure or rewards use these responses to decide on actions that can increase those rewards in future, or suggest actions that can explore and discover avenues for achieving those rewards.

These intuitions began to be confirmed by recordings from VTA neurons taken by Wolfram Schultz and colleagues. In these experiments, which were conducted in three stages, electrodes were inserted in the VTA of a monkey, and the animals, in this case monkeys, were allowed to reach out to a food object, a piece of apple, hidden inside a box. When the animal touched the piece of apple, dopamine neurons starting firing away at a higher than normal frequency as expected. Thus, by direct recording from dopamine neurons, and not more indirectly by functional imaging, it was confirmed that dopamine neurons respond to food rewards. In order to confirm that the stimulus that elicits dopamine cell responses is the food object, and not something else, the experimenters kept the box empty on a few occasions. When the monkey's hand touched the bare wire in the middle of box, without the piece of apple, there is no dopamine cell response.

In the second stage of experimentation, the experimenters paired the presentation of food with a neutral stimulus like the ringing of a bell. A bell is first rung, and then, after a delay, the animal is allowed to grab the food in the box. Thus, the ringing of the bell is *predictive* of the opportunity to get the reward. This time the dopamine neurons showed a briefly heightened firing rate right at the time when the bell is rung, but there was no change in firing rate when the food was obtained. Thus, it appeared that the firing of dopamine neurons represents not actual rewards but *future rewards* that the animal is expecting to obtain.

The experiment was slightly altered in the third stage. The bell was rung and the dopamine neurons briefly increased their firing rate as before, but at the time of presentation of food, the experimenter cheated the animal and did not place the food in the box. Therefore, when the animal extended its hand to reach out for the fruit, it found the box empty. At this time, there was a brief reduction in the firing rate of VTA dopamine neurons. It is as though this brief fall in firing rate represents the "disappointment" that the animal might have experienced when the food reward that it was expecting to arrive at certain instant did not occur, or when its expectations did not match with the reality. Thus, the third stage of the experiment suggested that the firing of dopamine neurons indicates not the present or future reward but the discrepancy between the expected future reward and the actual future reward.

These findings gave an important clue regarding what the brains might be doing with dopamine cell responses to rewards. Imagine an experimental animal that is permitted to press one of two buttons—A and B. Pressing button A fetches a reward (say, a piece of apple), whereas when button B is pressed nothing happens. When the animal presses button A, dopamine neurons increase their firing. This signal enables the animal to learn to choose A over B so as to continue to get more reward. Thus, the dopamine signal helps the animal to choose rewarding actions over unrewarding ones.

Although it is a dramatic simplification, choosing rewarding options over unrewarding ones is what decision-making is all about. Whether the decisions refer to larger problems of human life (what job? which partner? etc.) or the simpler ones of an experimental animal (which button?), decision-making is essentially about choosing rewarding actions. This ability by which an organism learns to map stimuli to actions with the help of feedback from the environment in the form of rewards (or their opposite—punishments) is known as *reinforcement learning*. A lot of animal and human behavior can be explained using concepts of reinforcement learning.

Thus, the purpose of the brain's reward system is not just to create a sense of *joie de vivre* but something more fundamental, essential to the survival of the organism, namely, decision-making. The reward system is a sort of a navigational system enabling the organism course through the labyrinthine paths of life, taking rewarding turns and avoiding punitive ones.

We are now left with an important question for which unfortunately there is no easy answer. What is the relationship between the fear or punishment system, that we encountered in the earlier parts of this chapter, and the reward system just described? The reward and punishment system form the yin and yang of the brains emotional network, interacting and informing each other. But it is difficult to precisely delineate anatomical boundaries to these two systems for several reasons. Dopamine neurons which are generally considered to respond to rewards are also found to be responding to aversive or punitive stimuli. Similarly, the amygdala, which has been introduced earlier in this chapter as a substrate for fear conditioning, was also associated with reward signaling. A comprehensive understanding of brain's emotional network, with a precise mapping of each anatomical substrate to reward or punishment processing, does not exist as yet. With all the subtlety and elusiveness that is characteristic of emotions, it may be several decades before emotion researchers arrive at such a comprehensive understanding.

## Summary

We have presented an outline of how our engines of emotions work. Brain's emotion circuits are located somewhere in the middle, in the limbo between neocortex that is the stage of sensory-motor experiences, our cognitions, and other higher functions, and the low lying areas of the brain stem and spinal cord where there are centers that control our autonomic function. When we have an emotional experience, a part of the sensory stream that climbs toward the cortex bifurcates at the level of thalamus and finds its way into the emotion hubs like hypothalamus or amygdala. Activation of these centers produces two radiating influences one traveling downward and another climbing upward. The downward stream produces a wide array of autonomic responses which add to the intensity of emotional experience. The upward stream enters the cognitive, conscious world of the neocortex through the cortical window of cingulate cortex and create the emotional experience, or rather color the ongoing cognitive, sensory experience with the intensity of emotions. Thus, the element that strongly emerges in emotional experience is the connection between the higher cortical experience and the body, a connection that is established, powerfully with the densely connected hubs of the emotion circuits. The connection with the body is more easily understood in case of animals, where the function of emotion circuits is related to primitive operations like fleeing a predator, or foraging for food. These operations obviously have a meaning to the entire organism and therefore involve a significant part of the brain and appropriate activation of the internal organs. It appears that these primitive functions of the nervous system, in their more sublime action in us, are experienced as emotions and feelings. Sensory experience is primarily limited to the sensory areas. Cognitive function engages a larger spectrum of areas, like the association areas of the posterior cortex, and the prefrontal area, in addition to the relevant sensory areas. But an emotional experience, in a sense, is not only a whole brain experience but, with its effects on circulatory, endocrine, gastroenteric, and other internal systems, evolves to be a whole body experience.

But the story of neurobiology of human emotions is far from being complete. A lot of data about emotion circuits has come from animal studies and it is nontrivial to extend these findings to make sense of human emotions. There is still quite a distance between emotions as they are understood by neurobiologists and emotions as they are depicted in the jargon of psychologists. Emotions in neurobiology are of a more primitive kind—fear, rage, satiety, pleasure, and so on, particularly in the forms that are quantifiable, measurable. But more sophisticated emotions like guilt, resentment, or gloating, emotions of the kind that show up on the outer rim of Plutchik's wheels, have not yet found their rightful place in the ganglia and goo of the real, living brain. How the primary emotional colors of fear and pleasure are transformed into the rich rainbow hues of higher human emotions is a puzzle that emotion researchers will be grappling with for a considerable time in the future. Perhaps part of the problem lies in the manner in which we seek a solution. Our approach which tries to give a name to every subtle shade of emotion, and look for neural substrates to that label, is probably fundamentally flawed. Perhaps emotions are fundamentally nonlinguistic, and therefore any attempt to neatly segregate them into clean verbal categories is probably foredoomed. Until a comprehensive neurobiological theory of higher emotions emerges on the scene, these speculations are all that we are left with. But before we give up on emotions with the argument that they are nonlinguistic, we must first consider the linguistic aspects of the brain, and describe how brain wields the power of language, a power that forms the basis for our proud position on the ladder of evolution.

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