

Brain-Behavior Relationships in Systems of Emotion

By Diane H. Engelman, Ph.D., October 2005

I. Introduction

LeDoux (1996) has said that until one is asked to define emotion, everyone knows what it is. Appreciating and understanding the complexity and meaning of emotion requires careful thought and examination.

Paraphrasing Webster's Unabridged Dictionary's definition of emotion: it is an affective state of consciousness in which fear, hate, sorrow, and joy is experienced. It is to be distinguished from: volitional and cognitive states of consciousness including any feelings of fear, hate, sorrow, love, or joy. Emotion is usually accompanied by physiological changes such as increased respiration or heartbeat, often with overt physical manifestations such as shaking or crying. When one compares this definition to a contemporary comprehensive neuropsychological perspective, Webster's definition appears out-dated and narrow in scope.

In the neuropsychological literature, Hagemann, Waldstein, and Thayer (2003) gave a working definition of emotion that is focused on its functional aspects. They characterize affect as a human response to an event from the environment that facilitates action for rapid mobilization. These authors add that emotion incorporates behavioral, cognitive, and autonomic sub-systems. These multiple response processes, coordinated efficiently, facilitate behavior that is goal-directed and allows for flexible adaptation to continually changing environmental demands.

Plutchik (1984) describes emotions as responses to relevant catalysts involving cognitive perception (appraisal), motoric behavior (expressive), feelings (subjective experience), physiological arousal, and behavior (goal-directed). Birbaumer & Ohman (1993) and Oatley & Jenkins (1996) concur, stating that emotion involves a complex combination of affective, cognitive, behavioral, and physiological responses. Panksepp (2003) noted that emotion included motor-expressive, sensory-perceptual, autonomic-hormonal, cognitive-attentional, and affective-feeling aspects.

Defining emotion has historically been and remains today a controversial and complex endeavor. From an evolutionary perspective, emotions have developed over time to play adaptive and diverse roles for human beings. Affect is considered a vital biologic source of data necessary for processing information related to experience and stimuli (Schulkin, J, Thomson, Barbara L., and Rosen, J.B., 2003). Emotions and their related facial expression (as part of affective response) are socially adaptive tools used for communication (Erickson and Schulkin, 2003).

For the purposes of this paper, the neuropsychological factors central to the production of emotion will be considered first. Second, the underlying neuroanatomical, neurophysiological and biochemical substrates of emotion will be explored. Third, individual differences in the experience of emotion will be considered. Fourth, factors influencing the development or expression of the neuropsychological abilities involved in emotion will be delineated. Finally,

there will be a discussion and analysis of the various models and hypotheses under consideration.

II. Neuropsychological Factors of Emotion

There are several important factors to consider related to the neuropsychology of processing emotion. Factors specifically associated with brain organization include: (a) laterality or interhemispheric - right versus left cerebral hemisphere; and (b) caudality - anterior vs. posterior brain structures; or (c) verticality - neocortical vs. limbic/subcortical diencephalic areas. Most of the functional asymmetry studies of the human brain have used unilateral brain-damaged patients as compared to normal adult subjects.

Previously, research in this area (functional asymmetry) related only to cognitive functions, despite clinical observations supporting the notion that some emotional behaviors were also linked to certain locations in the brain. Contemporary studies have demonstrated that patients with left or right-sided brain damage experience aspects of emotional behavior that coincide with underlying brain function rather than with symptomatology that is secondary to injury (Borod, 1993).

Recent research has demonstrated that both subcortical and cortical regions of the brain play important roles in emotional experience and behavior (Banich, 2004). Compatible with these results is evidence that many emotional processes occur outside one's conscious awareness yet careful thought can and does influence emotional response. In other words, emotions spontaneously arise and can be modulated by cognitive assessment of a given situation. Banich (2004) stated emotions can arise spontaneously, bypassing our conscious control (e.g., when we fall in love). But they can also be modulated by our appraisals of the situation (e.g., whether or not this person's characteristics make him or her a good potential mate) (p. 397).

Another set of neuropsychological factors explored in the literature involves emotional components that distinguish processing modes referring to emotional comprehension (perception), experience, physiological arousal, expression, and goal-directed activity (Plutchik, 1984). Emotional components influence the way that emotion is processed, that is, the channel of communication. Human modes of communication typically comprise lexical/verbal, prosodic/intonational, facial, postural and gestural pathways (Borod & Madigan, 2004).

Additionally, basic individual emotions such as happiness, sadness, and anger versus levels of emotion that are dimensional are identified as important subjects of study in the neuropsychological literature. Examples of levels of emotion include "emotional valence" (pleasantness/unpleasantness) and "motoric direction" (approach/ withdrawal) (Borod, 2000).

Banich (2004) summarizes emotional factors as a set of processes that include attention, appraisal, perception, and feeling, as well as visceral and motor responses. Situations are perceived and interpreted as they relate to personal history and experience. Actions are taken once a situation has been evaluated. Examples include communicating or suppressing an emotional reaction (emotional regulation), orienting attention toward a stimulus, and readying oneself for action through bodily responses (e.g. fight or flight) (Banich, 2004).

III. Neuroanatomical Substrates of Emotion

Contemporary research has shown that emotion is a set of processes with no central location in the brain from which it (emotions) derives. Several regions of the brain are required to implement the functions of emotion. Activities are, therefore, coordinated and outputs are integrated under normal circumstances.

Numerous neuroanatomical structures have been identified in modulating emotion at the limbic, subcortical, and cortical regions of the nervous system. Theories have attempted to explain specialization of emotion in cerebral hemispheres for componential and modular processing (Borod, 1993). The componential nature of emotion focuses on identifying a number of structures related to affect that are linked for transmission of information from one system to the other (Gianotti, 2000).

Neuroanatomical structures that underly emotion include the limbic system, which is a circuit of structures, primarily subcortical, containing the amygdala, hippocampus, hypothalamus, cingulate cortex and other structures (Patterson, & Schmidt, 2003). In addition, there are subdivisions of the prefrontal cortex and the posterior areas of the brain implicated in emotion, such as the retrosplenial cortex, posterior cingulate, and parietal lobes (Banich, 2004).

Despite emphasis on different regions of the brain by various researchers it is agreed that human emotion is the result of interactions of these regions through meaningful interconnection.

A. Emotion: Subcortical Brain Regions

The amygdala is associated with learning the emotional significance of information and then affording an instinctive and expedient emotional reaction. The hippocampus is important in furnishing information that is context-specific, framing the emotional interpretation of a specific stimulus. Associated with flight or fight, the hypothalamus intercedes with physiological experience linked to states of emotion, like changes in the endocrine or nervous system function. Acting as an interface between emotion and cognition, the anterior cingulate is a strategic location for managing regions of the brain related to emotion and integrating the assessment of emotional experience with episodic memory (context specific and often autobiographical) (Banich, 2004).

B. Emotion: Cortical Regions

Associated with assessment of reward and punishment and adaptively responding to changes in these relationships is the orbitofrontal cortex. In the absence of immediately reinforcing incentives, the ventromedial prefrontal cortex is implicated in representing elementary positive and negative emotional states (Banich, 2004).

The dorsolateral prefrontal cortex seems most associated with the representation of goals in which basic positive and negative emotional states are the focus. This is important for both attentional control and working memory. In other words, in order to appropriately respond to one's environment, goal-directed behavior would be expected to be influenced by positive and negative emotional states. Unpleasant affective states would be related to the goal of withdrawing from a circumstance that produced the emotion, and a pleasant experience would be associated with the goal of approaching the circumstance that produced the emotion (Banich, 2004).

Banich (2004) added that these motivational states of withdrawal or approach have been linked to hemispheric asymmetries in the prefrontal cortex: right hemisphere activation is associated with withdrawal, and the left hemisphere is connected with approach. Negative feelings are linked more to right prefrontal than left prefrontal activity. Positive feelings have the reverse pattern, with more activity over the left than the right prefrontal cortex. Affiliated also with emotion, the insula corresponds to olfactory, gustatory, and autonomic functions.

Understanding of emotional information is mediated through the right parietal and parietotemporal regions of the brain. Modalities of comprehension include facial expression, tone of voice or categorizing situations (scenes) that are based on affective content. The ability to process and understand emotion in a face is thought to be a separate ability from identifying a specific person by viewing his or her face (Banich, 2004).

Evidence suggests that the right hemisphere plays an important role in understanding the emotional meaning of visual information in general. These findings imply that emotional processing deficits can be profoundly debilitating because patients with damage to their right-hemisphere frequently lose their capacity for basic social skills. The right hemisphere also plays a critical role in prosody related to emotional feeling. In addition, the areas of the face that are controlled by the right hemisphere are thought to be more expressive than the left hemisphere. The left hemisphere is important for understanding emotion as it links affect to verbal meaning (Banich, 2004).

IV. Neurophysiological Substrates of Emotion

Banich (2004) commented that human beings typically experience an emotion as having a component "feeling" often associated with a physiological experience. This experience is accompanied by cognitive and sensory processes (attention, assessment) that enable human organisms to decipher and act upon cues from the environment.

Numerous neurophysiological systems have been identified in modulating emotion. According to Carlson (2004), three types of physiological components relate to an emotional response: behavioral, autonomic, and hormonal. He says that the behavioral component consists of muscle movements appropriate to a given situation (attack or run if threatened). Autonomic responses allow for behaviors that provide a quick response, with energy supplied for vigorous movement (heart rate increases, changes in the size of blood vessels shunting blood away from the digestive organs toward muscles). Hormonal changes support the autonomic response and are implicated in actions of flight or fight (emergency). Hormones are, in part, secreted to increase blood flow to the muscles and cause nutrients found in muscles to be converted to needed glucose. The adrenal cortex secretes steroid hormones which help to make glucose available to the muscles. Implicated in this hormonal linkage are epinephrine and norepinephrine which are secreted by the adrenal medulla.

Research has demonstrated that there are unique physiological signatures with different emotions (Levenson, Eckman, & Friesen, 1990). Banich (2004) noted that there are subtle but unique patterns of physiological change in the brain, electrodermal response, and patterns of heart rates that are associated with distinct emotional states.

Also important to our understanding of neuropsychology of emotion, neurons are genetically tailored to carry out many functions of the nervous system (Cozolini, 2002). Neurons are organized in increasingly complex (neural) networks. Of interest is that relatively few studies have simultaneously examined the central nervous system (CNS) and

autonomic nervous system (ANS) response during emotional experience (Hagemann, D., Waldstein, S. R., and Thayer, J.F., 2003).

Elementary background, of course, is that there are two basic divisions of the nervous system: the peripheral nervous system (PNS) and the central nervous system (CNS). The PNS includes the autonomic nervous system and the somatic nervous system. The PNS is involved in communicating between the CNS and the glands, sense organs, and the body (including the intestines, lungs and heart). The CNS includes the spinal cord and the brain.

The ANS has two branches: the sympathetic and parasympathetic nervous systems. In response to a threat or other forms of negative motivation, the sympathetic system is activated. The sympathetic system is balanced by the parasympathetic system which acts to conserve body energy and to repair damaged systems and immunological functions. As examples of the neuropsychology of emotion, both of these systems are important in creating attachment behavior and in mediating the effects of trauma and stress on the brain (Cozolini, 2002).

V. Neurochemical Substrates of Emotion

A research physiologist at Georgetown University, Candace Pert, Ph.D., explored a network of information that links body with mind by beginning to establish theories related to the biomolecular basis for our emotions (1997).

Elementary concepts described by Pert (1997), define peptides as tiny pieces of protein that are recognized as the first building material of life. Peptides consist of a string of amino acids joined together. When there are approximately 100 amino acids in the chain, the peptide is considered a polypeptide. After 200 amino acids, the material is called a protein. Receptors are molecules made up of proteins or peptides. According to Pert (1997), metaphorically speaking, amino acids are the letters of an alphabet while the peptides (including polypeptides and proteins), are the words made from the letters.

More recently, Schulkin, J., Thompson, B.L., and Rosen, J.B. (2003) note that chemical pathways, such as those involving angiotensin, corticotrophin- releasing hormone (CRH), and oxytocin (all neuropeptides), play a vital role in the organization of emotion. They are represented in both the peripheral and central nervous systems. These authors identify the amygdala as a major part of the taste/visceral connection to the brainstem. These pathways are visceral and underlie motivated emotional behavior. Schulkin et al. (2003) add that neuropeptides play a vital role in the organization and expression of adaptive responses found along the gustatory-visceral axes. Angiotensin, corticotrophin-releasing hormone (CRH), and oxytocin are found in many of the sites along the taste/visceral pathways.

Janig (2003) explored neurochemical coding which is important to our understanding of emotion. He defined this type of coding as the coexistence of a "classical" transmitter and one of a set of neuropeptides in neurons associated with a specific target tissue. This pattern of coding is frequently used to identify varying functional populations of autonomic neurons.

Neurochemical coding of autonomic neurons is a powerful tool used experimentally in the analysis of pathways of the autonomic nervous system. In other words, this "tool" is used in the context of understanding the chemical neuroanatomy of the autonomic nervous system. The functions of most neuropeptides are currently unknown however a few are beginning to be understood. Janig (2003) stated that in the current literature it is assumed that neuropeptides act as neurotransmitters (also called transmitter, neuromodulator, co-transmitters). Nonetheless, he

adds that the presence of a neuropeptide in an autonomic neuron, the release of that neuropeptide during nerve stimulation, and the presence of the receptors for the same neuropeptide on the target cells (neurons or effector cells) do not reveal whether the neuropeptide is normally or even pathophysiologically used during the neural regulation of that target tissue (p. 143).

Neurons related to emotion, communicate with one another via neurotransmitters (chemical messengers). Because neural networks use different sets of neurotransmitters, specific psychotropic medications will impact differently on emotional symptoms (Cozolino, 2002). Monoamines, neuropeptides, and amino acids are chemicals that serve as neurotransmitters. Neuromodulators (including estrogen, cortisol, testosterone, and other steroids) regulate neurotransmitter effects on receptor neurons. For example, the major excitatory amino acid in the brain is glutamate. Functionally, glutamate is related to N-methyl-D-aspartate (NMDA) and appears to be vital to neural change and learning. NMDA receptors seem to be involved in enhancing connections between the plasticity of neural networks and neurons (Cowen & Kandal, 2001; Malenka & Siegelbaum, 2001).

The monoamines which include serotonin, dopamine, and norepinephrine also have an important role in the regulation of emotional and cognitive processing. All of these monoamines are generated in different locations of the brainstem. Via the ascending neural network, they are carried upward through the limbic system to the cortex.

Produced in the substantia nigra and other areas of the brainstem, dopamine is a vital neurotransmitter important to motor action and the reward system. Too much dopamine may result in mood changes, increased motor behavior, and frontal lobe functioning that is disturbed. Symptoms that may result include apathy, memory impairment, and depression. Damage to the substantia nigra is likely to result in a deficit of dopamine and possibly to the development of Parkinson's disease. Interestingly, it is believed by many people that schizophrenia is caused by an excess of dopamine that overloads one's sensory processing capabilities (Cozolino, 2002).

Norepinephrine, in this case, produced in the locus coeruleus, is a major component of the fight-flight system of the brain, and is important to our understanding of stress and trauma. High levels of norepinephrine may result in vigilance, attacking or defense behavior, and anxiety. At the same time, norepinephrine can enhance memory for traumatic and stressful events.

Serotonin plays a role in the sleep-wake cycle and arousal and is widely distributed throughout the brain. It is generated in part, in the raphe nucleus. Serotonin mediates mood and emotion. Antidepressant medications like Paxil and Prozac (Selective Serotonin Reuptake Inhibitors) cause higher levels of serotonin to be available in the synapses by inhibiting its reuptake. They also create greater activation of serotonergic neural networks (Cozolino, 2002).

As noted earlier, neuropeptides are a group of neurotransmitters that include oxytocin, vasopressin, enkephalines, endorphins, and neuropeptides-Y. Working together with neuromodulators, these compounds regulate pleasure, reward systems, and pain.

Endorphins additionally modulate monoamines. Endorphins produced by the body (endogenous endorphins) act as analgesia in conditions of physical pain. They are also involved in self-abusive behavior and dissociation. Vitally important to the organization and growth of the brain is the relationship between the neuropeptides and the monoamines (Cozolino, 2002).

In summary, neurochemicals form a dynamic network of information that links body and mind. As Cozolini (2002) said, availability and production of neurochemicals shape all of our experience -from bonding and affect regulation to cognitive processing and our sense of well-being (Cozolino, 2002, p. 74). An important spin off from this knowledge is that psychopharmacology can regulate these neurochemicals in an effort to control symptoms of psychological or psychiatric suffering (Gitlin, 1996).

VI. Individual Differences- Emotion and Affective Style

Patterns of regional brain activity are associated with different types of emotions. Anxiety is more often seen with right than left posterior cortex activity, while sad moods are usually accompanied by more right than left prefrontal cortex activity. Findings such as these suggest that individuals may differ in their characteristic tendencies to demonstrate different patterns of regional brain activity. For this reason, people may also differ in a number of psychological and personal dimensions, including "affective styles" (Davidson, 2001), their sensitivity to threats or incentives (Sutton, 2002), and/or their risk for psychopathology (Heller, Schmidtke, Nitschke, Koven, & Miller, 2002).

Individual differences in emotional reactivity are sometimes referred to as affective styles. Examples of affective style include: whether a person responds to a circumstance with a pessimistic or optimistic outlook; how fast a person calms down after an emotional challenge or scare; or even dispositional mood. Linked to these individual differences in affective style is asymmetry in both frontal and posterior regions of the brain (Banich, 2004).

EEG data suggest that people are different in the degree to which they demonstrate more right than left or left than right prefrontal activity during a baseline resting condition. Dispositional moods can be predicted through these asymmetries. Left frontal activity is associated with a more positive or optimistic view of situations while a greater reactivity to negative stimuli seems to be linked to more right frontal activity (Banich, 2004).

Interestingly, a healthier immune system and greater resistance to illness are linked to greater left frontal activity. The differential responses to stress cited were in 10-month old infants. It was found that infants upon separation from their mothers were more likely to cry if they had more right than left prefrontal activity. Also, children with more right than left prefrontal activation were more likely to be socially wary. Similar patterns in rhesus monkeys have been described. When these monkeys had more right than left prefrontal activation, they also showed higher levels of cortisol, the stress hormone (Davidson, 2001).

In addition, risk for psychopathology can be predicted through individual differences in asymmetries of posterior brain regions (Heller, Schmidtke, Nitschke, Koven, & Miller, 2002). There have been a number of studies (using EEG results and behavioral measures) with college students demonstrating that anxiety is associated with increased right hemisphere activity, while depression is associated with reduced right hemisphere activity (Banich, 2004).

Confounding this picture, the left temporal lobe, prefrontal cortex, and right hemisphere have all been implicated in schizophrenia. In addition, there appears to be a disconnection between the frontal and temporal regions of the brain with people who have symptoms of schizophrenia.

Aspects of anxiety characterized by panic symptoms and fear are linked to the right hemisphere, while aspects of anxiety characterized by worry are linked to the left hemisphere.

Depression has been associated with less left than right prefrontal activity, overall activity reduction in the prefrontal cortex, and decreased activation of the right hemisphere (posterior regions). These characteristics lead to poorer performance with executive functions (including inhibition, updating and shifting set) and visuo-spatial tasks (Banich, 2004).

VII. Factors Influencing the Development or Expression of Emotion

The survival value of emotions is obvious. Many emotions are not comfortable to experience, but despite the discomfort, the body needs to mobilize its resources when threatened. Taking protective action such as aggression (fight) or withdrawal (flight) are vital behaviors. It is necessary that these reactions occur quickly. Responses are often made before a person has time to consider conscious cognitive evaluations or decisions about an event (LeDoux, 1996). It is interesting and logical to note that animal researchers suggest that some of the areas of the brain strongly implicated in human emotion appear to be older in terms of evolutionary development (Banich, 2004).

Research in human emotional development is challenging because of the huge variability observed between people and their emotional behaviors. Scherer (1994) stated that emotion may exist to enable humans to learn from their immediate experience and to go beyond innate simple stimulus-response reflexes. For this reason, he claims that emotional variability, and therefore difficulties inherent to the study of emotional development, should not be surprising.

Lane & Nadel (2000) suggest that emotional development may consist of the transformation from implicit, modular, and automatic responses to emotional states, responses, and consciously-controlled abilities. Including innate and unique temperamental (affective) styles, and differences between people in terms of emotional development, further variations in (emotional) behaviors are likely to occur. According to these authors, neuroscientific investigation in the future will show how this variation occurs and the ways in which emotional development goes awry (Lane & Nadel, 2000).

Important to this discussion is the notion that there are maturational and experience-induced changes in the circuitry of emotion and emotion regulation. In addition, developmental changes that occur in cognitive function influence the quality and quantity of the emotional response in terms of the appraisal process (Davidson, 2003).

Emotional learning is another area that is important for future research. Human beings learn blueprints or scripts about relationships during their childhoods. These scripts affect capacity for love and intimacy, emotional reactions, and ability in the face of adversity (stress) to maintain emotional equilibrium. It can be difficult to change adult patterns of emotional behavior, especially those patterns that were established in early childhood when emotional development was under-construction.

Empathy is an important area to explore with regard to emotional development. The capacity for empathy and emotional self-awareness are closely connected to one another. Successful social adaptation appears to require the capacity to maintain awareness of the feelings and needs of others, while concomitantly paying attention to one's own goals and needs (Baddeley, Della Sala, Papagno, & Spinnler, 1997).

Work in this area of developmental research is only beginning. The ways in which emotional patterns establish themselves in personality is an area needing further research. Additional questions are many, including why emotional constellations are resistant to extinction

or alteration and how therapeutic change affecting emotion can occur most efficiently. It has also been suggested that there be further research elucidating neural networks associated with emotional learning (Friston, Tononi, Reeke, Jr. et al., 1994) and exploring how emotional abilities develop or fail to develop. The intent of this kind of research hopefully will be, in part, at least, to provide information facilitating remediation in areas of emotional disorder, potentially having a meaningful impact on people's sense of well-being (Lane & Nadel, 2000).

VIII. Comparison of Models or Hypotheses of Emotion

Clearly, emotion is comprised of many different related but separate components. It is best understood not as a monolithic process but rather as a set of categories that are differentiated and relate to one another in a network of cortical and subcortical circuits. Subcomponents of these remarkably complex neuropsychological systems include actions involved in the production of autonomic, subjective and behavioral changes. These changes are associated with emotion, emotional cue recognition processes, channels that regulate emotion and the means required for retrieving events and remembering past emotional experience (Panksepp, 1998).

As I hope I have made clear, it is very difficult to define and quantify emotion. It is easier to identify structures in which injury disrupts emotional behavior, but it is more problematic to determine what role the various structures of the brain and associated bodily processes play in the broad scenario. To recount: 1) multiple neural systems control different parts of emotionally-based behavior; 2) key structures involved in emotional behavior include the amygdala and associated paralimbic cortex, the hypothalamus, and the frontal lobes, primarily the inferior frontal cortex; 3) emotional behavior is affected by changes in memory, language, movement, and perception, making it clear that there are vast cortical regions that take part in cognitive processing necessary for emotion production.

Additionally, emotion and cognition are related to each other intimately and are likely to be controlled by neural systems that overlap. This theme of overlapping functions seems to run through all the major theories of emotion.

Interestingly, Davidson (2003) identified seven sins in the study of emotion: "(1) Affect and cognition are subserved by separate and independent neural circuits; (2) Affect is subcortical; (3) Emotions are in the head; (4) Emotions can be studied from a purely psychological perspective; (5) Emotions are similar in structure across age and species; (6) Specific emotions are instantiated in discrete locations in the brain; and (7) Emotions are conscious feeling states (p. 129)."

Future progress in the study of emotion will critically depend upon the continued detailing of the neuroanatomical, neurophysiological, and neurochemical substrates of emotion. The field has come a long way since early studies separating cognition from emotion and the belief that affect was generated in isolation in discrete areas of the brain. Future studies will no doubt emphasize the complexity and dimensionality of emotional experience, its relationship to brain function altogether.

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Mailing Address: 1044 Sir Francis Drake Blvd., Kentfield, CA 94904