Neurobiology of Emotion Perception I: The Neural Basis of Normal Emotion Perception

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There is at present limited understanding of the neurobiological basis of the different processes underlying emotion perception. We have aimed to identify potential neural correlates of three processes suggested by appraisalist theories as important for emotion perception: 1) the identification of the emotional significance of a stimulus; 2) the production of an affective state in response to 1; and 3) the regulation of the affective state. In a critical review, we have examined findings from recent animal, human lesion, and functional neuroimaging studies. Findings from these studies indicate that these processes may be dependent upon the functioning of two neural systems: a ventral system, including the amygdala, insula, ventral striatum, and ventral regions of the anterior cingulate gyrus and prefrontal cortex, predominantly important for processes 1 and 2 and automatic regulation of emotional responses; and a dorsal system, including the hippocampus and dorsal regions of anterior cingulate gyrus and prefrontal cortex, predominantly important for process 3. We suggest that the extent to which a stimulus is identified as emotive and is associated with the production of an affective state may be dependent upon levels of activity within these two neural systems. Biol Psychiatry 2003; 54:504–514 © *2003 Society of Biological Psychiatry*

Key Words: Emotion, limbic, amygdala, ventral, dorsal, prefrontal

Introduction

Critical to survival is the ability to identify quickly in the environment emotionally salient information, including danger and reward, and to form rapid and appropriate behavioral responses (Darwin 1872/1965). Although it is clear that the presence of an emotion involves physiologic arousal, appraisal, subjective experience, expression, and goal-directed behavior (Plutchik 1984), there is at present no generally accepted theoretical framework for human emotion and limited understanding of the neurobiological basis of the different processes underlying emotion perception. In this critical review, by examining the findings from recent animal, human lesion, and functional neuroimaging studies, we have aimed to identify the neural basis of a series of different neuropsychological processes important to the understanding of normal human emotional behavior.

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Neuropsychological Processes Underlying Emotion Perception

Early theories proposed to explain the neuropsychological basis of emotion perception (Cannon 1929; James 1884) emphasized the importance of feedback from bodily responses to an emotionally salient stimulus in determining the nature and extent of emotional feeling, but they did not distinguish between the identification of the emotive stimulus and the affective state produced in response to this. Appraisalist theories of emotion (Arnold 1960; Lazarus 1991), and current researchers (Clore and Ortony 2000), have emphasized that appraisal or identification of stimulus salience, which may occur with or without conscious awareness (Lazarus 1991), precedes the generation of emotional response. Emotion perception can therefore be understood in terms of the following processes occurring after the initial presentation of an emotive stimulus, which then allows the generation of complex affective states, emotional experiences (feelings), and behaviors: 1) the appraisal and identification of the emotional significance of the stimulus; 2) the production of a specific affective state in response to the stimulus, including autonomic, neuroendocrine, and somatomotor (facial, gestural, vocal, behavioral) responses, as well as conscious emotional feeling, which may bias process 1 toward the identification of specific categories of emotional stimuli; we would also argue for a third process, 3) the regulation of the affective state and emotional behavior, which may involve an inhibition or modulation of processes 1 and 2, so that the affective state and behavior produced are contextually appropriate (Figure 1).

In this review, we discuss the findings of studies with animals and humans, including studies of patients with focal brain lesions, stimulation studies, and those employing functional neuroimaging techniques, which have helped to determine the nature of the neural correlates of these different processes underlying emotion perception.

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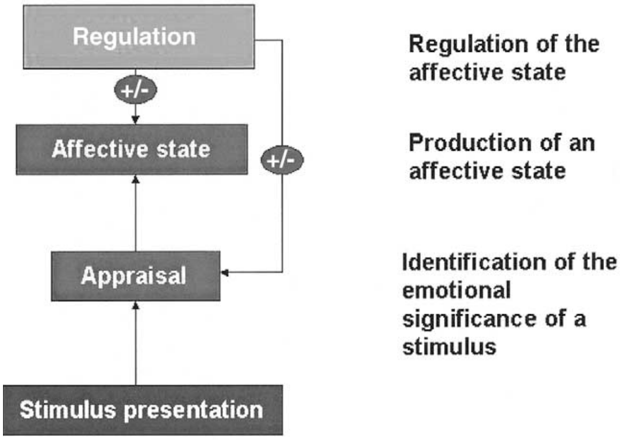

Figure 1. The main processes important for emotion perception: 1) Appraisal and identification of the emotional significance of the stimulus; 2) Production of a specific affective state and behavior in response to the stimulus; and 3) Regulation of the affective state and emotional behavior, which may involve an inhibition or modulation of processes 1 and 2, indicated by the negative and positive signs in the circles, so that the affective state, emotional experience, and behaviors generated are contextually appropriate.

Identification of the Emotional Significance of the Stimulus

Animal Studies

Many of these studies have been helpful in determining neural regions associated with behavioral responses to emotive stimuli (i.e., the combination of processes 1 and 2), whereas other studies have attempted to examine regions associated predominantly with process 1. These have demonstrated the importance of the amygdala in the initial response to emotionally salient stimuli. Cells in the amygdala responding selectively to faces and eye gaze direction have been identified in studies of nonhuman primates (Brothers and Ring 1993). Other studies have implicated the insula in the initial response to emotive stimuli. The anterior (agranular) insula shares extensive, reciprocal anatomic connections with the amygdala (Augustine 1996) and forms part of a network of structures involving the ventromedial prefrontal cortex, amygdala, hypothalamus, and periaqueductal gray that appears to participate in perceiving and organizing autonomic responses to aversive or threatening stimuli (Alexander et al 1990; Ongur and Price 2000).

Humans: Stimulation Studies and Focal Brain Lesions

In humans, paradigms employed to examine neural correlates of this process have included the recognition of emotionally salient material (e.g., eye gaze and facial expression identification). Stimulation studies (Heit et al 1988) and those of patients with amygdala lesions (Young et al 1995) have implicated the amygdala in the response to fearful stimuli presented in visual (Adolphs et al 1994; Phelps and Anderson 1997) and auditory (Scott et al 1997) modalities, whereas examination of a patient with a focal insula lesion has implicated the insula in the recognition of facial and vocal expressions of disgust in humans (Calder et al 2001). Patients with Huntington's disease, in whom there is degeneration of the caudate nucleus, also demonstrate impairment in the recognition of facial expressions of disgust (Sprengelmeyer et al 1996). Stimulation of the insula in humans is associated with the perception of unpleasant tastes (Penfield and Faulk 1955).

Humans: Functional Neuroimaging Studies

These have demonstrated increased blood flow and activation within the amygdala in response to unfamiliar faces (DuBois et al 1999), during the detection of eye gaze (Kawashima et al 1999), and to presentations of fearful (e.g., Breiter et al 1996; Morris et al 1996; Phillips et al 1997, 2001; Wright et al 2001), sad (Blair et al 1999), and happy facial expressions (Breiter et al 1996). Other studies have demonstrated activity within the amygdala to emotive scenes (Taylor et al 2000) and film excerpts (Reiman et al 1997).

The amygdala has been implicated in the response to visual presentations of threatening words (Isenberg et al 1999), fearful vocalizations (Phillips et al 1998), unpleasant olfactory (Zald and Pardo 1997) and gustatory (O' Doherty et al 2001b) stimuli, in the memory of emotional information (Cahill et al 1996; Canli et al 2000), and in the enhanced perception of emotionally salient information (Anderson and Phelps 2001). Other studies have indicated a habituation of the amygdalar response to visual displays of emotionally salient information (Phillips et al 2001; Wright et al 2001) and gender differences in the development of these amygdalar responses (Killgore et al 2001; Thomas et al 2001).

These findings suggest a specific role for the amygdala in the modulation of vigilance and attention to emotionally salient information per se (Davis and Whalen 2001), which may occur via projections from the central nucleus of the amygdala to cholinergic neurons, which lower cortical neuronal activation thresholds and potentiate cortical information processing (Whalen 1998).

Functional neuroimaging studies have implicated the insula in delay fear conditioning (Buchel et al 1999) and during the anticipation of an aversive stimulus (Phelps et al 2001), suggestive of a role for this structure in conveying the representation of aversive sensory information to the amygdala. The insula, together with the ventral striatum and thalamus, has also been implicated in the identification of displays of disgust, with studies providing evidence for the role of the insula in the identification of facial expressions of disgust (Phillips et al 1997) and in taste perception (Small et al 1999).

Production of an Affective State and Emotional Behavior

Animal Studies

The existence of brain regions specialized for reward processing was initially suggested by studies showing that rats responded operantly to stimulation of specific sites to the exclusion of other activities (Olds and Milner 1954). These included the midbrain dopaminergic projections from the ventral tegmental area into the nucleus accumbens shell region and the medial prefrontal cortex (Spanagel and Weiss 1999). In primates, regions important for reward processing have been identified as the nucleus accumbens, which lacks distinct microscopic and macroscopic borders with the anteroventral putamen and ventromedial caudate (Heimer and Alheid 1991), other areas of the ventral putamen, and the medial portion of the caudate head, which receive projections from the amygdala and the orbital and medial prefrontal cortex (Ongur and Price 2000).

The amygdala has also been implicated in the production of emotional states and behaviors. Bilateral lesions of the temporal lobes (Kluver and Bucy 1939), and, particularly, the amygdala (Zola-Morgan et al 1991) result in significant changes in social behavior in monkeys, including hyperorality, social disinhibition, and an absence of emotional motor and vocal reactions usually associated with emotional states. Amygdala lesions in monkeys result in decreased autonomic responses to emotionally salient stimuli and during anxiety-provoking situations (Bagshaw et al 1965), decreased attention and vigilance and impaired fear conditioning (Gallagher et al 1990), and attenuated freezing and flight (Blanchard and Blanchard 1972). Electrical stimulation of the amygdala increases plasma levels of corticosterone, autonomic symptoms of fear and anxiety, and attention, vigilance, and freezing behavior (Applegate et al 1983; Kapp et al 1994), whereas infusion of a γ-aminobutyric acid (A) (GABA-A) antagonist into the amygdala increases blood pressure and heart rate (Sanders and Shekhar 1991).

Animal studies have also highlighted the role of the insula in the production of affective states. Studies of rats have implicated the insula in conditioned taste aversion (Dunn and Everitt 1988), whereas lesions that include the anterior insula and adjacent ventrolateral prefrontal cortex reduce fear reactivity to contextual stimuli but do not affect contextual stimuli acquisition or response extinction (Morgan and LeDoux 1999).

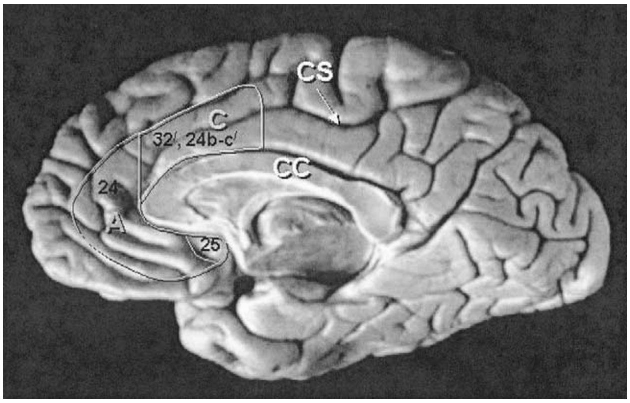

Figure 2. Approximate boundaries of the putative affect and cognitive divisions of the anterior cingulate gyrus. The affective division (A) is a ventral region of the anterior cingulate cortex comprising subgenual anterior cingulate gyrus (Brodmann area 25), Brodmann area 33, and pregenual anterior cingulate gyrus (rostral regions of Brodmann area 24). This division is outlined in the figure. Brodmann areas 25 and rostral area 24 are also labeled. The cognitive division of the anterior cingulate gyrus (C) comprises caudal and dorsal regions, including Brodmann areas 24b′-c′ and 32′, and is outlined in the figure. The corpus callosum (CC) and cingulate sulcus (CS) are also indicated on the figure.

A division of the anterior cingulate gyrus, the "affective" division, has been consistently associated with emotional behavior. This ventral region of the anterior cingulate cortex comprises the subgenual anterior cingulate gyrus (Brodmann area 25), Brodmann area 33, and the pregenual or rostral anterior cingulate gyrus (rostral regions of Brodmann areas 24; Devinsky et al 1995; Figure 2). It has extensive connections with the amygdala, periaqueductal gray, mediodorsal and anterior thalamic nuclei, nucleus acumbens and ventral striatum, and has been associated with autonomic function and emotional behavior (Devinsky et al 1995; Paus 2001). Lesions of this region significantly impair the ability of the autonomic system to respond to conditioned stimuli, abolish conditioned emotional vocalizations to painful stimulation (Frysztak and Neafsey 1991), and result in reduced aggression, shyness, emotional blunting, reduced motivation, and changes in maternal–infant interactions (MacLean and Newman 1988). Stimulation of this region is associated with changes in autonomic and endocrine function (Buchanan and Powell 1993).

Orbital and medial (ventromedial) prefrontal cortex has also been implicated in the production of emotional states and behavior. The orbitofrontal cortex includes Brodmann areas 11, 12, and 13 and the medial portion of area 47, and may also be defined as including subgenual and pregenual portions of the anterior cingulate gyrus, Brodmann areas 25, 24, and Brodmann area 32 (Price 1999). It has direct connections from the basolateral nucleus of the amygdala (Davis and Whalen 2001) and appears to play a critical role in the representation of the reward value of a stimulus and the way in which this representation guides goal-directed behavior (Rolls 1999).

Orbitofrontal cortex lesions in monkeys produce emotional changes, including reduced aggression to humans, changes in food-selection behavior, and an impaired ability to break a learned association between a stimulus and a reward (Meunier et al 1997). Single-unit recordings of orbitofrontal cortical neurons in rats have demonstrated that these neurons respond when information regarding the reward value of stimuli relayed from the basolateral nucleus of the amygdala is required to guide behavior (Schoenbaum et al 1998). Orbitofrontal cortical neurons in monkeys have been demonstrated to respond during taste (Rolls 1995) and smell (Critchley and Rolls 1996) perception, but also to visual stimuli associated with reward (Thorpe et al 1983). The orbital cortex has also been shown to play a role in inhibiting sympathetic autonomic and defensive behaviors elicited by amygdala stimulation (Timms 1977), whereas left ventromedial prefrontal cortical lesions have been demonstrated to inhibit autonomic, behavioral, and endocrine responses to fear-conditioned stimuli and restraint stress (Sullivan and Grattan 1999).

Humans: Stimulation Studies and Focal Brain Lesions

In humans, paradigms employed to examine the neural correlates of affective states have included studies of mood induction, fear conditioning, and decision-making to maximize reward. Another type of paradigm, backward masking, has been employed to examine this process at the unconscious level. Here, although emotionally salient material is presented without the conscious awareness of the observer, appraisal may occur at the unconscious level, so that the observer develops an unconscious emotional response (Esteves and Ohman 1993).

Amygdala lesions in humans result in emotional blunting (Aggleton and Brown 1999) and reduced fear conditioning (Bechara et al 1995), and abnormal activation of the amygdala in patients with temporal lobe epilepsy leads to a behavioral pattern reminiscent of fear (Gloor 1992). Whereas electrical stimulation of the amygdala in humans results in autonomic reactions associated with feelings of fear (Gloor 1992), stimulation of the insula is associated with the perception of unpleasant tastes and nausea (Penfield and Faulk 1955).

Lesions of the affective division of the anterior cingulate gyrus in humans can result in a variety of different changes in emotional behavior, ranging from apathy and depression to disinhibition and anxiety (Angelini et al 1981; Levin and Duchowny 1991). Stimulation of this division evokes autonomic and visceromotor changes and different types of emotions in humans (Bancaud and Talairach 1992). Emotional changes are also common, with spontaneous emotional vocalization sometimes occurring, in patients with cingulate seizure foci (Bancaud and Talairach 1992).

Single-neuron responses to aversive stimuli have been recorded in human ventral prefrontal cortex (Kawasaki et al 2001), and lesions to the orbitofrontal cortex result in impaired emotional expression identification (Hornak et al 1996) but also lead to disinhibition, impulsiveness, and misinterpretation of other people's moods (Damasio 1994; Hornak et al 1996). Lesions of ventromedial prefrontal cortex are also associated with impaired performance on gambling tasks designed to measure decision-making regarding high- versus low-risk options for monetary reward (Bechara et al 1998).

Humans: Functional Neuroimaging Studies

These have highlighted the role of the ventral striatum in craving (Breiter et al 1997), in the time-locked processing of reward prediction (Pagnoni et al 2002), in anticipation of reward (Knutson et al 2001), and in romantic love (Bartels and Zeki 2000). A positive correlation has also been reported between the euphoric response to dextroamphetamine and the magnitude of dopamine release in anteroventral striatal areas, indicating that the dopamine signal in these regions may be important for the formation of associations between salient contextual stimuli and internal rewarding events (Drevets et al 2001).

Other studies have demonstrated amygdala activation in response to induction of positive and negative emotional states (Reiman et al 1997), during fear-conditioning paradigms (Buchel et al 1999; LaBar et al 1998), and in response to presentations of fearful and angry facial expressions of which the observer had no conscious awareness (Morris et al 1998b; Whalen et al 1998).

The insula has been implicated in the generation of affective states in response to emotive stimuli. Physiologic activity increases in the anterior insula during the perception of pain (Casey et al 1996), during induced sadness and anticipatory anxiety in healthy subjects, and during lactate- or cholecystokinin-induced panic attacks in patients with panic disorder, during exposure to phobic stimuli in patients with animal phobias, during major depressive episodes in patients with major depressive disorder, and during exposure to trauma-related stimuli in posttraumatic stress disorder subjects (Charney and Drevets 2002). Studies have also highlighted the role of the insula during recall of internally generated emotion (Reiman et al 1997) and during the experience of guilt (Shin et al 2000), a complex emotion that, like the experience of shame, may involve self-directed disgust. There is therefore accumulating evidence for the role of the insula in mediating behavior to aversive, including disgust-related, stimuli.

Functional neuroimaging studies of healthy volunteers examining neural correlates of happy and sad mood induction have demonstrated increased blood flow and activation within the subgenual and pregenual anterior cingulate gyrus during mood induction compared with a resting state (Mayberg et al 1999; Shin et al 2000) and activation in the subgenual anterior cingulate gyrus in response to high rewards (Elliott et al 2000). The ventral anterior cingulate gyrus therefore appears to have an important role in the processing of emotional information during arousal and the production of affective states.

Other studies have implicated the orbitofrontal cortex in the production of affective states in humans. Increased blood flow and activation within the orbitofrontal cortex has been demonstrated during the perception of pleasant and unpleasant odors, flavors, and tactile stimuli (Francis et al 1999; O'Doherty et al 2001b; Zald and Pardo 1997; Zald et al 1998). Activation of the orbitofrontal/ventromedial cortex has also been reported during the perception of odors of foods not eaten to satiety compared with those of foods eaten to satiety (O'Doherty et al 2000), during the performance of gambling tasks (O'Doherty et al 2001a), during guessing and decision-making on the basis of reward value (Elliott et al 2000), and when engaging emotion processing during the consideration of moral dilemmas (Greene et al 2001). Finally, increased regional cerebral blood flow within the orbitofrontal cortex has been demonstrated during imagery of an event precipitating anger (Dougherty et al 1999; Kimbrell et al 1999) and during imagined restraint of physical aggression compared with imagined aggressive behavior (Pietrini et al 2000), although decreased cerebral blood flow to this region has been demonstrated during imagined physical aggression compared with neutral behavior (Pietrini et al 2000). Taken together with findings from animal studies, these findings implicate the ventromedial prefrontal cortex, and, in particular, orbitofrontal cortex, in the mediation of autonomic changes accompanying affective states produced in response to emotive stimuli or contexts, suggestive of a role for this region in the automatic regulation of emotional behavior.

The ventrolateral prefrontal cortex can be defined as lateral and rostral regions of Brodmann area 47 and part of Brodmann area 45 and lies lateral to the orbitofrontal cortex on the ventral surface of the frontal lobes (Ongur and Price 2000). Human functional neuroimaging studies have demonstrated increased blood flow and activation within this region during a variety of tasks, including the induction of sad mood (Pardo et al 1993) and guilt (Shin et al 2000), during the recall of personal memories (Fink et al 1996) and emotional material (Reiman et al 1997), and in response to facial expressions displaying different negative emotions (Sprengelmeyer et al 1998), particularly when specific tasks are performed in response to the expressions (Lange et al 2003). The right temporofrontal junction and related right-sided ventrolateral prefrontal cortex have also been associated with autobiographical memory retrieval (Markowitsch 1997).

Regulation of Affective States and Emotional Behavior

Animal Studies

Studies have implicated the medial prefrontal cortex in the regulation of affective state and emotional behavior (Mega et al 1997). This region is strategically located between two broad trends or compartments in cortical evolution (Sanides 1970). The ventrolateral trend is reactive-based, operates by feedback, and is derived from archicortex (olfactory cortex). In addition to the response to emotional stimuli, ventral prefrontal regions appear to have a role in emotional behavioral regulation occurring at an unconscious or automatic level (e.g., the restraint of the acute stress response), via direct and indirect connections with subcortical structures, including the hypothalamus, amygdala, thalamus, ventral striatum, and brainstem nuclei (Kaufman et al 2000).

The mediodorsal trend is planning-based, operates by a feed-forward mechanism, and is derived from paleocortex (hippocampus). The hippocampus has been implicated in the inhibition of the stress response via inhibitory connections with many of the subcortical structures involved and activated in the stress response (Lopez et al 1999). Other studies have reported an association between recurrent stress and hippocampal neuronal damage, potentially resulting from exposure to higher levels of glucocorticoids (Salpolsky et al 1990) or stress-induced decreases of neurogenesis and/or brain-derived neurotrophic factor (see Sheline 2000).

Gray and McNaughton (2000) have proposed a more complex role for the hippocampus in affective state regulation, involving behavioral inhibition and centered on the septohippocampal system. This system has the capacity to facilitate but also inhibit defensive behavior and anxiety in response to threatening or potentially threatening environmental contexts. Other studies have emphasized the role of the hippocampus in spatial cognition (O'Keefe and Nadel 1978) and episodic memory (Squire 1992). Gray and McNaughton (2000) have attempted to unite these different roles into a single function of the hippocampus as a general-purpose comparator, with a central role in determining the extent of conflict between different goal-directed behaviors, in facilitating exploratory rather than defensive patterns of behavior, and allowing resolution of goal conflict.

Dorsal prefrontal regions are implicated in the performance of cognitively demanding tasks, in which attention is directed away from the emotional component of the stimulus or toward the context in which the stimulus is presented, and for planning-based regulation of emotional behavior with regard to future contexts (Tucker et al 1995). The division of the anterior cingulate gyrus that has generally been implicated in these tasks (e.g., discriminative attention, hence termed the "cognitive" division) comprises caudal and dorsal regions, including Brodmann areas 24b′-c′, and 32′ (Figure 2). It has connections with the lateral prefrontal cortex, primary motor cortex and supplementary motor area, the spinal cord, and red nucleus. Lesions of this region in animals are associated with increased impairments and errors in early stages of learning (Gabriel 1990), neuronal discharges within the region occur during avoidance learning, and studies of depth electrode recordings have implicated this region in error detection (Gemba et al 1986).

Dorsomedial and dorsal anterolateral prefrontal cortices include the dorsal region of Brodmann area 32 and rostral Brodmann area 9, bordering the dorsal anterior cingulate gyrus (Devinsky et al 1995), and lie medial to the dorsolateral prefrontal cortex. Lesions of the region equivalent to the dorsomedial prefrontal cortex in rats are associated with increased cardiovascular responses to fear conditioning, whereas electrical stimulation of this area is associated with a reduction in the behaviors associated with amygdala stimulation (Frysztak and Neafsey 1994).

Humans: Stimulation Studies and Focal Brain Lesions

In humans, lesions of the cognitive division of the anterior cingulate gyrus are associated with attentional deficits and impaired performance on tasks requiring controlled processing, including the generation of novel sequences and the selection of an unpracticed over a practiced response (Ochsner et al 2001). Other studies have demonstrated a focus within the dorsal anterior cingulate gyrus for the error-related negativity observed with event-related potentials and associated with errors during task performance (Dehaene et al 1994). Interestingly, error-related negativity has been reported to be higher in patients with anxiety disorders (Gehring et al 2000), and cingulotomy, involving lesions to dorsal regions, has been demonstrated to be a successful treatment for these patients (Cosgrove and Rauch 1995). These studies have therefore emphasized the role of the dorsal anterior cingulate gyrus in controlled processing and error monitoring in humans.

Humans: Functional Neuroimaging Studies

Several studies have demonstrated increased blood flow within dorsal, but decreased blood flow within ventral, anterior cingulate gyrus during performance of tasks requiring selective attention and novel response selection, and vice versa for performance of emotional tasks (Bush et al 2000; Drevets and Raichle 1998). In particular, these studies have emphasized the role of the dorsal anterior cingulate gyrus in effortful control (Raichle et al 1994) and in error and performance monitoring (Carter et al 1998). Other studies have implicated this region in conflict processing (Botvinick et al 1999) and in difficult task performance (Paus et al 1998).

Additionally, dorsal regions of the anterior cingulate gyrus are activated during the encoding of the perceived unpleasantness of pain (Casey et al 1994; Rainville et al 1997), anticipatory arousal and uncertainty (Critchley et al 2001a), the intentional regulation of autonomic arousal and performance of relaxation tasks (Critchley et al 2001b), and in the regulation and second-order mapping of internal bodily states (Damasio 1999). Increased blood flow has also been reported in dorsal and rostral regions of the anterior cingulate gyrus during attention to subjective emotional states and experiences (Gusnard et al 2001; Lane et al 1998), whereas inhibition of sexual arousal generated by viewing erotic stimuli has been associated with activation of right superior/dorsomedial prefrontal gyrus and right rostral anterior cingulate gyrus (Beauregard et al 2001). Finally, activity within regions along the border between the rostral anterior cingulate gyrus and the medial prefrontal cortex (the paracingulate gyrus) has been associated with mentalization and the representation of mental states of the self (Frith and Frith 1999). This area is consistently activated during self-reflective thought (Johnson et al 2002). Taken together, these findings suggest a role for dorsal and rostral regions of the anterior cingulate gyrus in attention to and effortful regulation of arousal associated with affective states, whereas the paracingulate gyrus appears to have a role in the reflective awareness of these phenomena (Lane 2000).

Studies have implicated the dorsomedial prefrontal cortex in the regulation of autonomic responses and arousal associated with affective states and emotional behavior, demonstrating in this region an inverse relationship between blood flow and measures of autonomic function and anxiety during performance of a novel cognitive task (Simpson et al 2001), decreased blood flow during the induction of sad mood in healthy volunteers (Mayberg et al 1999), and increased activation during self-referential judgments made when viewing emotionally salient stimuli (Gusnard et al 2001) and during anticipation of pain (Ploghaus et al 1999).

Other studies have demonstrated increased blood flow and activation within the dorsolateral prefrontal cortex (Brodmann areas 44 and 46), implicated in working memory (Goldman-Rakic 1987), to positive and negative facial expressions during the performance of explicit, emotion-labeling tasks compared with more implicit tasks (Hariri et al 2000). This region may therefore be associated with the representation and manipulation of nonemotive visuospatial and verbal components of emotional stimuli.

These findings implicate dorsal prefrontal cortical regions in effortful regulation of attention and affective states in humans, but they also associate ventral prefrontal cortical regions, in particular rostral/ventral anterior cingulate gyrus, in the regulation of autonomic responses.

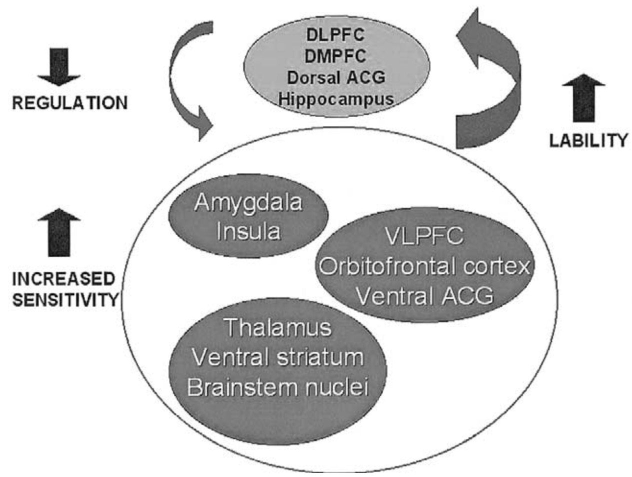

Figure 3. Schematic diagram depicting neural structures important for the three processes underlying emotion perception. A predominantly ventral system is important for the identification of the emotional significance of a stimulus, the production of an affective state, and autonomic response regulation (depicted in dark gray), whereas a predominantly dorsal system (depicted in pale gray) is important for the effortful regulation of the resulting affective states. A reciprocal functional relationship may exist between these two neural systems (curved arrows). VLPFC, ventrolateral prefrontal cortex; DLPFC, dorsolateral prefrontal cortex; DMPFC, dorsomedial prefrontal cortex; ACG, anterior cingulate gyrus.

Conclusions: Neural Systems for Emotion Perception

In this review, we have described findings from studies employing a variety of techniques and specific experimental paradigms, which have helped to increase understanding of the neural basis of neuropsychological processes important for emotion perception, namely: the identification of the emotional significance of an environmental stimulus; the production of an affective state and emotional behavior; and the regulation of the affective state and emotional behavior, allowing the generation of contextually appropriate, complex affective states, emotional experiences (feelings), and behaviors. Although there is a difficulty in designing paradigms to examine the neural correlates of each of these three processes individually, comparison of findings from studies employing paradigms examining one or more of these processes does suggest the presence of neural systems subserving each of these processes. Findings also indicate that specific neural regions may be important for more than one process. For example, both the amygdala and insula are important both for identification of the emotional significance of a stimulus in the environment and the production of an affective state and emotional behavior.

Overall, findings suggest that these processes may be dependent upon the functioning of two neural systems: a ventral and a dorsal system. The ventral system, including the amygdala, insula, ventral striatum, and ventral regions of the anterior cingulate gyrus and prefrontal cortex, is important for the identification of the emotional significance of environmental stimuli and the production of affective states. It is additionally important for automatic regulation and mediation of autonomic responses to emotive stimuli and contexts accompanying the production of affective states. The dorsal system, including the hippocampus and dorsal regions of the anterior cingulate gyrus and prefrontal cortex, regions where cognitive processes are integrated with and can be biased by emotional input, is important for the performance of executive functions, including selective attention, planning, and effortful rather than automatic regulation of affective states. Finally, evidence from studies examining ventral and dorsal anterior cingulate gyral activity suggests a reciprocal functional relationship between these two neural systems (Figure 3).

Taken together, these findings allow us to suggest that the extent to which a stimulus is identified as emotive and is associated with the production of an affective state and/or emotional behavior may be dependent upon levels of activity within a ventral neural system, important for the rapid appraisal of emotional material, production of affective states, and autonomic response regulation, and a dorsal system, important for effortful regulation of resulting affective states. Specific abnormalities in the functioning of either or both of these two neural systems may therefore be associated with abnormalities in emotional behavior and regulation and result in the generation of symptomatology characteristic of different psychiatric disorders.

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