



Prefrontal Cortex, Emotion, and Approach/Withdrawal Motivation

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Abstract

This article provides a selective review of the literature and current theories regarding the role of prefrontal cortex, along with some other critical brain regions, in emotion and motivation. Seemingly contradictory findings have often appeared in this literature. Research attempting to resolve these contradictions has been the basis of new areas of growth and has led to more sophisticated understandings of emotional and motivational processes as well as neural networks associated with these processes. Progress has, in part, depended on methodological advances that allow for increased resolution in brain imaging. A number of issues are currently in play, among them the role of prefrontal cortex in emotional or motivational processes. This debate fosters research that will likely lead to further refinement of conceptualizations of emotion, motivation, and the neural processes associated with them.

Human emotion has not always been a popular topic for brain researchers interested in the cortex. Twenty-five years ago, the vast majority of studies focused on cognition, with relatively little research addressing emotion. Interest in emotion has increased exponentially, however, with the term ‘affective neuroscience’ (Davidson & Sutton, 1995) now competing with the term ‘cognitive neuroscience’. In recent years, studies have moved beyond investigating emotion and cognition as separate phenomena toward acknowledging their complex coupling under many ordinary circumstances, developing experimental paradigms that examine their relationships, and even wondering whether they are fundamentally distinguishable (Blair et al., 2007; Gray, 2004; Kalisch, Wiech, Critchley, & Dolan, 2006; Miller, 1996; Mohanty et al., 2007; Pessoa, 2005). Emotion is now not merely one of many facets of brain structure and function to be better understood but a core domain for understanding brain mechanisms more broadly. For example, the study of emotion has become an important target of research attempting to uncover neural processes associated with psychopathology.

Modeling Brain Function in Emotion

Early research in this area tended to treat emotion and its physiological support as a unitary phenomenon. However, this view of emotion has not been supported (e.g., Reisenzein, 1983). For example, a number of researchers (Lang, Bradley, & Cuthbert, 1990; Osgood, Suci, & Tannenbaum, 1957; Russell, 1980) have suggested that emotion is best represented on a circumplex (two orthogonal axes). The first axis, commonly labeled the valence axis, represents the pleasantness/unpleasantness of emotion, and the second axis represents the degree of arousal associated with the emotion. Therefore, emotional stimuli, processes, memories, action plans, and central and peripheral support physiology are differentiable in terms of both valence and intensity. For example, happiness and fear are both high in arousal but differ in valence, whereas happiness and calmness are both positive in valence but differ in level of arousal.

Early studies of brain mechanisms involved in emotion were often hampered by conceptualizing emotion monolithically, rather than as a set of distinct but related processes. As research has come to distinguish discrete emotional processes it has also become possible to identify more precisely some of the neural structures and functions involved in these processes. For example, seminal studies in neuropsychology suggested differential involvement of right and left hemispheres in emotional processing (for reviews, see Davidson, 1983, 1984; Heller & Levy, 1981; Tucker, 1981). However, findings were mixed and often contradictory, with some studies suggesting primary right hemisphere involvement and some studies suggesting left.

Because early research studying neural correlates of emotion tended to treat emotion as unidimensional, the possibility that pleasant and unpleasant emotional valence would be associated with different brain areas was overlooked. Furthermore, pleasant and unpleasant valence were not always distinguished or differentiated from arousal, and often, only unpleasant stimuli were used. When emotional valence was systematically taken into consideration, a somewhat more consistent pattern of neural activity emerged, linking the right hemisphere with unpleasant emotion and the left hemisphere with pleasant emotion (Davidson, 1983; Heller, 1986, 1990). Considering the emotional valence associated with experimental stimuli thus proved to be an important step in obtaining a clearer picture of hemispheric involvement in emotional processes.

However, fundamental discrepancies continued to be seen among a number of methodological approaches. For example, research using electroencephalography (EEG; a measure of the electrical activity of the brain) and neuropsychological task performance presented an inconsistent picture regarding right hemisphere activity in depression. Flor-Henry (1976) reported that depression was associated with performance impairments on right hemisphere neuropsychological tasks. Because decreased activity in a brain area has been linked to worse performance on neuropsychological

tasks specialized to that area (for review, see Heller, Nitschke, Etienne, & Miller, 1997b), these impairments are thought to reflect decreased right hemisphere activity. However, Schaffer, Davidson, and Saron (1983) subsequently reported greater right than left prefrontal EEG activity in depression. Discrepancies such as this led Davidson and others (e.g., Davidson, 1984; Heller, 1986; Tucker, 1981) to raise the possibility that different patterns of activity could characterize prefrontal and posterior cortical regions. For example, a number of researchers proposed that emotional state is specifically associated with activity in prefrontal cortex (PFC), whereas the evaluation of spatial and emotional information is associated with activity in right temporal-parietal cortex (Borod et al., 1998; Davidson, 1992; Heller, 1990). If negative emotional experience is associated with increased right PFC activity, then depression would be characterized by rightward prefrontal asymmetry. However, the right hemisphere tasks employed by Flor-Henry are associated with processing of posterior brain regions, which may be less active, perhaps even inhibited by right PFC, during negative emotional experience. In this case, poor performance on such tasks (Flor-Henry, 1976) would no longer conflict with findings of increased PFC activity for depression (Schaffer et al., 1983). In summary, research on emotional processes and the neural systems associated with these processes has evolved by incorporating an increasingly complex understanding of both the psychological and neural aspects of emotion.

Prefrontal Asymmetries and Approach/Withdrawal

Further development in the understanding of emotion arose from research on motivational processes. For example, Lazarus (1991a, 1991b; Novacek & Lazarus, 1990) proposed a theory of emotion in which motivational processes play a central role. In this theory, motivational processes are engaged to evaluate potential benefit or harm. Emotions such as pride, love, or happiness would arise when a situation is regarded as beneficial, and anger, anxiety, or sadness would arise when a situation is regarded as harmful. This means that motivational evaluation is a necessary step for the occurrence of emotion.

A large body of research on the relation between emotion and motivation has postulated the existence of two overarching motivational systems that organize behavior. One system involves behavior prompted by a possible desirable outcome, whereas the other involves behavior prompted by a possible aversive outcome. A number of such models have been proposed, including Dickinson and Dearing's (1979) Aversive/Attractive systems, Gray's (1994) Behavioral Activation/Behavioral Inhibition systems, and Lang et al.'s (1990) Appetitive/Defensive systems (for reviews, see Davidson & Irwin, 1999; Elliot & Covington, 2001; Lang et al., 1990). Davidson (1983) proposed a similar model linked to research on frontal EEG asymmetry during emotional states. He posited that frontal asymmetry was not related to the valence of an emotional stimulus but rather to the motivational

system that is engaged by that stimulus. He proposed that the left PFC is involved in a system facilitating approach behavior to appetitive stimuli, whereas the right PFC is involved in a system facilitating withdrawal behavior from aversive stimuli. To explain prefrontal asymmetries for valenced emotional processing, this model assumes that processing related to emotional valence itself is not lateralized in PFC. Rather, emotion-related lateralization is observed because emotions contain approach and/or withdrawal components. Therefore, emotion will be associated with a right or left asymmetry depending on the extent to which it is accompanied by approach or withdrawal behavior (Davidson, 1983).

Subsequently, Davidson, Marshall, Tomarken, and Henriques (2000) hypothesized that the approach and withdrawal systems would be associated with pre-goal attainment emotions; that is, emotions that are typically generated while attempting to achieve a goal. For example, the approach system would be associated with enthusiasm but not contentment, which would be considered a post-goal attainment emotion. On this view, emotion should be understood in the context in which it arises. Different contexts can provide information about the function of an emotion. Miller and Kozak (1993) and Lang et al. (1990) also emphasized the importance of function-in-context in understanding emotion.

Hemispheric Asymmetries and Valence/Arousal

Taking a different approach to integrating the reported findings on emotion-related lateralization, Heller (1986, 1990, 1993) proposed that the circumplex model of emotion could be represented biologically. To account for PFC asymmetries, Heller proposed that pleasant valence is associated with more left than right activity, whereas unpleasant valence is associated with more right than left activity. Heller's model invoked the arousal dimension of the circumplex model to make sense of reported posterior asymmetries (for reviews, see Banich, Stolar, Heller, & Goldman, 1992; Heller, 1990; Heller & Nitschke, 1998; Keller et al., 2000). It was proposed that activity in the right posterior region of the brain is associated with the arousal component of emotion, with greater activity in this brain region reflecting greater levels of self-reported and sympathetic nervous system activity.

Whether the findings for prefrontal asymmetries are better accounted for by motivational or valence dimensions, or even whether such a choice is necessary, is an open question (see below for review). However, a unique role in arousal for the right posterior region has been supported in various ways and has subsequently been used to explain patterns of brain activity associated with depression and anxiety (for reviews, see Engels et al., 2007; Keller et al., 2000; Levin, Heller, Mohanty, Herrington, & Miller, 2007). Emotion-related arousal has been found to co-vary with activity in right-posterior regions in a variety of studies using diverse methodologies, such as studies of lesion-damaged patients, EEG, and positron emission

tomography (e.g., Hugdahl, 1995; Wacker, Heldmann, & Stemmler, 2003; Wittling, 1990; for reviews, see Heller, 1990; Heller, Nitschke, & Lindsay, 1997a). In addition, research has consistently found an association between reduced right parietal activity and depression (especially with anxiety partialled out; e.g., Bruder et al., 1997; Flor-Henry, 1979; Keller et al., 2000; Uytendhoef et al., 1983; for review, see Levin et al., 2007) and between increased right parietal activity and anxiety-related arousal (e.g., Engels et al., 2007; Heller et al., 1997b; Kentgen et al., 2000).

Prefrontal Asymmetry: Motivation or Valence?

Although Davidson's (1983) and Heller's (1986, 1990) proposals have stimulated programs of research based on the respective models, most of this research has not distinguished emotional valence from motivational direction, because most pleasant emotions are thought to be coupled with approach motivation, and most unpleasant emotions are thought to be coupled with withdrawal motivation. For example, both Davidson's and Heller's model would predict enthusiasm, a pleasantly valenced, approach-related emotion, to be associated with leftward asymmetry in prefrontal activity, whereas disgust, an unpleasantly valenced, withdrawal-related emotion, would be associated with rightward asymmetry in prefrontal activity. This is an example of how models that seem to diverge conceptually can often overlap in terms of their empirical predictions. This overlap makes it difficult to judge which model better captures the phenomena under consideration, in this case, the relation between emotion, motivation, and prefrontal asymmetry, or even how distinct the models are.

In situations such as this, it is necessary to identify areas where the predictions of the two models diverge. In the case of Davidson's (1983) and Heller's (1986, 1990) models, anger is associated with conflicting predictions and thus can be used to compare the accuracy of the two models. The predictions conflict because anger is commonly assumed to be unpleasantly valenced yet also frequently approach-related (Berkowitz, 1999; Davidson, 1984). Davidson's approach/withdrawal model predicts that, to the degree that anger is associated with approach behavior, it should co-occur with left prefrontal activity, whereas Heller's valence/arousal model predicts that, to the degree that anger is associated with unpleasant valence, it should co-occur with right prefrontal activity. A program of study by Harmon-Jones et al. has examined this issue (for review, see Harmon-Jones, 2004) and has associated approach-related anger with leftward prefrontal EEG asymmetry, consistent with the predictions of the approach/withdrawal model (e.g., Harmon-Jones & Allen, 1998; Harmon-Jones, Lueck, Fearn, & Harmon-Jones, 2006; Harmon-Jones & Sigelman, 2001; Harmon-Jones et al., 2002). Several researchers have replicated this finding (Hewig, Hagemann, Seifert, Naumann, & Bartussek, 2004; Jensen-Campbell, Knack, Waldrip, & Campbell, 2007; Rybak, Crayton, Young, Herba, & Konopka, 2006;

Wacker et al., 2003; for null results, see Waldstein et al., 2000). Furthermore, Harmon-Jones et al. have examined the influence of perceived control, and presumably therefore motivation to act, on anger-related asymmetry in prefrontal activity. They compared anger evoked in situations where participants did or did not believe they were able to influence the occurrence of a potential negative outcome (Harmon-Jones, Sigelman, Bohlig, & Harmon-Jones, 2003). Although reported anger levels did not differ for the two conditions, enhanced leftward prefrontal asymmetry was observed only when participants were motivated to attempt to influence the potential outcome. The results of this study suggest that anger is associated with greater leftward prefrontal asymmetry when it is accompanied by preparation for approach behavior. Thus, it may not be anger per se that is associated with leftward asymmetry but the approach motivation that often (but not inevitably) accompanies it.

Although a strong link has been established between approach-related anger and leftward frontal asymmetry in support of the motivational model, asymmetry associated with non-approach-related anger has been less studied and could provide more information to support or discredit the motivational model. It has been argued that not all anger is associated with approach motivation and that withdrawal-related anger (which involves suppressing outward facial and verbal expression of anger as well as leaving anger-provoking situations) is orthogonal to approach-related anger (e.g., Deffenbacher, 1992; Knight, Chisolm, Paulin, & Waal-Manning, 1988; Spielberger, 1988, 1999). If both approach- and withdrawal-related anger are associated with asymmetry in favor of the left hemisphere, then the motivational model of emotion would not be supported, because it would predict that withdrawal-related anger would be linked to asymmetry in favor of the right hemisphere. Conversely, anger is sometimes associated with positive valence, further complicating reliance on anger to adjudicate differences between the models.

Available data are mixed. Hewig et al. (2004) found no relationship between withdrawal-related anger and asymmetry in favor of either hemisphere, whereas two studies have found that anger, regardless of motivational direction, was associated with asymmetry in favor of the left hemisphere (Stewart, Levin, Heller, Sass, & Miller, forthcoming; Wacker et al., 2003). In the study by Wacker et al. (2003), motivational direction (approach and withdrawal) and emotion (fear and anger) were independently manipulated, and prefrontal asymmetry was examined. Independent of motivational direction, anger induction was associated with greater changes toward leftward asymmetry than was fear induction. High levels of anger, regardless of motivational direction, were related to more leftward prefrontal asymmetry. Stewart et al. (forthcoming) examined resting EEG asymmetry for groups high in trait anger that differed in approach- and withdrawal-related motivational tendencies. Results indicated that anger groups, regardless of motivational direction, displayed greater left frontal asymmetry than did control participants. These results are not well explained by either

approach/withdrawal motivation or pleasant/unpleasant valence notions, suggesting that refinement of the models might be needed to fully account for the relationship between frontal asymmetry, motivation, and emotion.

Research has tended to support aspects of both Heller's (1986, 1990) and Davidson's (1983) models. Although these models have often been treated as if they are in competition, this is not necessarily the case. They may capture distinct aspects of human function and may be better thought of as complementary or as simply distinct (e.g., Coombes, Cauraugh, & Janelle, 2007; Wacker et al., 2003). An examination of the psychological phenomena that these models attempt to explain suggests this possibility. The approach/withdrawal model focuses on neural activity associated with goal-related emotion and thus on (at least potential) overt actions (e.g., approach to or withdrawal from a situation). The valence/arousal model focuses on emotional stimuli and information processing, rather than behavioral sequelae.

Cortical Asymmetry of Emotion: Implications for Cognition

A variety of aspects of executive function may be related to hemispheric asymmetry in frontal lobe function (Banich, 1997). For example, the left PFC has been associated with performance on verbal executive function tasks, whereas the right PFC has been associated with performance on spatial executive function tasks (e.g., Smith, Jonides, & Koeppe, 1996; Smith & Jonides, 1999). Given the overlap in patterns of brain asymmetry for executive function and emotion, a number of researchers have proposed that emotional/motivational states bias performance on tasks that require executive functions specialized to the affected hemisphere (Gray, 2001; Heller & Nitschke, 1997; Levin et al., 2007; Shackman et al., 2006; Tomarken & Keener, 1998). Therefore, pleasant emotion/approach motivation is theorized to improve performance on verbal tasks, because both involve left PFC. The mechanism by which this bias is produced is not fully understood, and several theories have been proposed (e.g., Ashby, Isen, & Turken, 1999; Heller & Nitschke, 1997; Tomarken & Keener, 1998).

Supporting the proposal that emotional/motivational states will differentially bias performance on different executive function tasks, Gray (2001) found a double dissociation between the effects of inducing pleasant emotion/approach motivation and unpleasant emotion/withdrawal motivation on performance in spatial and verbal working memory (WM) tasks. Specifically, performance on the verbal task was enhanced by the induction of pleasant emotion/approach motivation and impaired by the induction of unpleasant emotion/withdrawal motivation. In contrast, performance on the spatial task was enhanced by the induction of unpleasant emotion/withdrawal motivation and impaired by the induction of pleasant emotion/approach motivation.

Herrington et al. (2005) examined neural correlates of emotion/motivation on tasks recruiting executive function. Participants engaged in an

emotion-word version of the Stroop paradigm, wherein they identified the colors in which pleasant/appetitive, neutral, and unpleasant/aversive words were printed. Functional magnetic resonance imaging (fMRI) was used, and activation in hemispheres was compared statistically (almost never done in the fMRI literature, though routine in the EEG literature). Results revealed that pleasant/appetitive words elicited more activation in left than right dorsolateral PFC (DLPFC), an area associated with representing stimulus valence (Engels et al., 2007; Perlstein, Elbert, & Stenger, 2002) and selection of task relevant information (Banich et al., 2000a, b; Milham, Banich, Claus, & Cohen, 2003; Pardo, Pardo, Janer, & Raichle, 1990; Perret, 1974). In addition, response speed to pleasant/appetitive words was correlated with activation in DLPFC, suggesting that this region has a role in the emotional modulation of task performance.

Gray, Braver, and Raichle (2002) also used fMRI to examine neural correlates of the influence of emotion/motivation on tasks recruiting executive function, with a seemingly conflicting pattern of results. Gray et al. (2002) employed a task similar to that of Gray (2001), wherein emotion/motivation was induced, after which participants engaged in verbal and spatial WM tasks. Evidence of hemispheric specialization for type of WM was found both in dorsolateral and ventrolateral PFC, where verbal stimuli were associated with relative left hemisphere activation, and spatial stimuli were associated with relative right hemisphere activation. In addition, evidence of hemispheric specialization associated with the valence of emotion/motivation induction was found in DLPFC, although the pattern of activation was opposite to that expected. Unpleasant emotion/withdrawal motivation induction evidenced higher activity in left DLPFC, whereas pleasant emotion/approach motivation induction evidenced higher activation in right DLPFC. Gray et al. (2002) explained this by positing that emotion/motivation induction asymmetrically increases the efficiency of the relevant neural processes. For example, they proposed that pleasant emotion/approach motivation induction increases neural efficiency in left PFC. Therefore, tasks recruiting this hemisphere would induce less activation.

The findings of Gray et al. (2002) and Herrington et al. (2005) underscore the fact that emotional phenomena can have implications for task performance, particularly in the domain of executive function (for review, see Levin et al., 2007). Potentially contributing to the apparently discrepant findings for the two studies are differences in stimulus presentation and engagement. Gray et al. (2002) presented emotional stimuli before performing the executive function tasks, intended as a mood induction. Therefore, participants were not processing incoming emotional information during the cognitive tasks. In contrast, in Herrington et al. (2005), emotional stimuli were part of the task itself and thus would have fostered simultaneous processing of fresh emotional information. Another difference was that Herrington et al.'s (2005) task allowed participants to ignore emotional aspects of the stimuli (in fact, task performance was likely better the more participants

ignored the emotional information); thus, mood-induction effects may have been much weaker. Even if similar emotional processes occurred in both studies, different stages in the time course of these processes were assessed. Patterns of cortical activation are likely to vary over the time course of these processes. Each of these potential explanations highlights the importance of taking into consideration multiple aspects of emotion, including differences in their temporal properties, in the design of emotional tasks (e.g., Davidson, 1998). Not doing so may lead to seemingly discrepant findings between studies that may reflect true differences but for reasons other than those under study (e.g., different facets of the time course of processes are captured, and these are taken to reflect the whole of the time course of these processes).

Neural Correlates of Appetitive and Aversive Stimulation

Another line of research has differentiated neural activity occurring while evaluating and selecting among potential appetitive and aversive outcomes from neural activity occurring while experiencing an appetitive or aversive outcome (e.g., being rewarded vs. punished). Based on this distinction, neural activity occurring during evaluation and decision-making reflects, in part, emotional responses that, based on past experiences, bias individuals toward choosing certain options and away from choosing other options (Damasio, 1996). Conversely, the neural activity occurring while outcomes are being experienced reflects, in part, emotional responses such as pleasure that serve to reaffirm the accuracy of prior choices or emotional responses, such as regret, that evoke re-evaluation of the information used to make choices (Coricelli et al., 2005). Research examining neural correlates of appetitive and aversive decisions and outcomes has implicated a consistent set of brain regions that likely function as a network. For example, dorsal anterior cingulate cortex (dACC) has consistently been found to be involved in decisions between two potentially aversive outcomes (Blair et al., 2006; Kim, Shimojo, & O'Doherty, 2006) and in adapting behavior after a predicted rewarding outcome has not occurred (Bush et al., 2002; Williams, Bush, Rauch, Cosgrove, & Eskandar, 2004). dACC has also been implicated in the occurrence of regret when non-pursued options are found to be more advantageous than the option chosen (Coricelli et al., 2005). Therefore, dACC seems to be consistently involved in decisions to minimize potential loss.

Some consistency in medial prefrontal cortex (MPFC) involvement has been found as well. Activity in this region has been associated with decision-making between two potentially appetitive outcomes (Blair et al., 2006), as well as reflecting the magnitude of potential gain from an appetitive outcome (Rogers et al., 2004). In addition, activity of MPFC has been related to the experience of appetitive outcomes, particularly to errors in predicting these outcomes (Blair et al., 2006; Elliott, Newman, Longe, &

Deakin, 2003; Kim et al., 2006). Therefore, MPFC activation has been consistently related to decisions between, and the experience of, appetitive outcomes.

Orbitofrontal cortex (OFC) activity has been consistently linked with choices between appetitive outcomes (Arana et al., 2003; Rogers et al., 2004; Yacubian et al., 2006) as well as with errors in predicting these outcomes (Jensen et al., 2007; Yacubian et al. 2006). However, OFC has also been associated with the experience of, and decisions regarding, aversive outcomes. In fact, different areas of OFC have been found to respond differentially to appetitive or aversive outcomes (O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001; O'Doherty, Dayan, Friston, Critchley, & Dolan, 2003). This research, coupled with studies suggesting that OFC is involved in inhibiting behavior when the demands of the task have changed (Mogenson, Brudzynski, Wu, Yang, & Yim, 1993; Price, Carmichael, & Drevets, 1996; Rolls, 1995), suggests that OFC is involved in monitoring important outcomes in order to detect when behavior should be altered.

Another brain area associated with both potential appetitive and aversive outcomes is the striatum, a subcortical structure comprised of the dorsal striatum, which includes the caudate and putamen, and the ventral striatum, which includes the nucleus accumbens and olfactory tubercle. The dorsal striatum has been linked primarily to the prediction of potential appetitive outcomes and errors associated with that prediction (Coricelli et al., 2005; Delgado, Nystrom, Fissell, Noll, & Fiez, 2000; Elliott, Friston, & Dolan, 2000; Kim et al., 2006; Knutson, Fong, Bennett, Adams, & Hommer, 2003).

The ventral striatum, like the OFC, has been related to the prediction of both potential appetitive and aversive outcomes, along with errors associated with that prediction (e.g., O'Doherty, Buchanan, Seymour, & Dolan, 2006; Seymour, Daw, Dayan, Singer, & Dolan, 2007). There is evidence that separate regions of the ventral striatum respond preferentially to appetitive or aversive outcomes (Jensen et al., 2003). Activation in the ventral striatum has been associated with the predictability of outcomes, such that less predictable outcomes engender greater activation (Berns, McClure, Pagnoni, & Montague, 2001). This suggests that the ventral striatum is involved in the process of learning to predict the occurrence of unfamiliar, hence relatively unpredictable events. In addition, there is evidence that ventral striatal activation in response to potential aversive outcomes is not dependent on whether participants have the ability to act to avoid that outcome (Jensen et al., 2003). Therefore, the striatum seems to be involved in the prediction of potentially important and unfamiliar outcomes, regardless of the valence and controllability of these outcomes.

This line of research investigating the regulation of behavior to approach appetitive stimuli and avoid aversive stimuli has identified a network of relevant brain regions. Activity in the ventral striatum seems to reflect

monitoring of the environment for potentially important stimuli, whereas activity in dACC and MPFC reflect evaluation of these stimuli, and activity in OFC reflects the evaluation of decision outcomes in order to adjust future behavior accordingly. Further investigation is needed to fully explore how these brain regions, along with other regions, interact to evaluate situations and guide behavior to maximize potential gain and minimize potential harm.

Pizzagalli, Sherwood, Henriques, and Davidson (2005) provided a bridge between prefrontal cortical asymmetries for emotion/motivation and regions of the network associated with behavioral responses to appetitive and aversive stimuli. In this study, the authors employed a verbal WM task in which participants were presented with a set of words and later required to identify these target words embedded among distractor words. In one condition, participants were rewarded for correct responses, and in another condition, they were punished for incorrect responses. The authors calculated the degree to which participants were biased to identify words as target words when responses were either rewarded (reward bias) or punished (punishment bias). Reward bias was found to be positively related to EEG activity in left DLPFC and medial OFC. No relation was found between EEG activity and punishment bias.

This finding provides support for the association between approach motivation and left hemisphere asymmetry, as well as approach motivation and OFC. Conversely, the lack of association between punishment bias and EEG in right PFC is contrary to the pattern predicted by Davidson and colleagues (e.g., Davidson, 1983). However, given that this study utilized a task engaging verbal WM, which has been associated with activity in left PFC (Smith et al., 1996) and which is enhanced by induction of approach motivation (Gray, 2001), it is possible that, if a task engaging spatial working memory were used, the converse pattern would be found (punishment bias would be associated with EEG activity in the right hemisphere, and reward bias would not be associated with EEG activity at all). Therefore, it may be that prefrontal asymmetry is related to motivational or emotion valence according to the mapping of the tasks onto the respective specializations of the hemispheres.

Conclusion

Research on neural correlates of emotion and motivation has led to an increasingly complex understanding of the brain systems that implement these psychological functions. Technological advances such as dense-array EEG and fMRI have allowed this investigation to more precisely identify the neural circuits that are involved in the experience of, and processing related to, emotion and motivation (for review, see Miller, Elbert, Sutton, & Heller, 2007). These advances have moved our understanding of human brain organization from assuming simple, large-scale, hemisphere-level

phenomena to distinguishing differences between activity in relatively small and sometimes adjacent regions, such as differential responses to appetitive and aversive stimuli in different regions of the OFC (O'Doherty et al., 2001, 2003).

The research discussed in the present paper has provided a number of important lessons and directions for future researchers. First, it will be important for researchers to continue to distinguish between neural phenomena related to different aspects of emotional phenomena. Phenomena commonly called 'emotional' sometimes involve stimulus properties, types of processing, effect on putatively non-emotional processing, diverse central and peripheral physiological phenomena, and diverse overt verbal and motor behaviors. Relevant neural mechanisms are surely equally diverse. Second, it will be important to attempt to differentiate correlates of emotional and motivational processes to the extent possible. Research conducted on animals by Berridge et al. may provide further direction (for review, see Berridge & Robinson, 2003). This research has differentiated two processes involved in interactions with rewarding stimuli, specifically distinguishing pleasure and approach. This research suggests that emotional and motivational systems are separable on a fundamental level, although there may still be considerable overlap, and healthy function may depend on their interaction or balance. This view is very much in line with the perspective of Wacker et al. (2003) discussed above, wherein valence/arousal and approach/withdrawal concepts fit different aspects of the same data set.

Third, the research discussed in the present paper emphasizes the importance of being alert to unforeseen interactive effects involving the concepts being investigated, the type of task employed in the service of those concepts, and the neural mechanisms foregrounded by their combination. For example, when investigating asymmetry in brain activity related to motivational or emotional valence, it will be important to employ both spatial and verbal tasks. Otherwise, differential effects that are attributed solely to emotion or motivation may be an artifact, in part, of task demands. Furthermore, effects that would be evident during other tasks might be overlooked.

Finally, it can be assumed that the many dichotomous organizing principles and models currently prominent in the literature that address functional brain organization will continue to evolve. There is considerable overlap among them and a long history behind some of them. Much supporting data are already available for each; choices among them would be premature and will probably prove unnecessary. Attempts at conceptual integration (e.g., Coombes et al., 2007; Elliot & Thrash, 2002; Wacker et al., 2003) are needed. The structural and functional organization of the brain and the diversity of our paradigms offer enough degrees of freedom that each dichotomy may receive considerable support, but as data accrue the models are likely to become more complex and less distinct. Choosing among them will be less important than helping them mature.

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Short Biographies

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Gregory A. Miller has appointments as Professor of Psychology, Adjunct Professor of Psychiatry, Beckman Institute Cognitive Neuroscience Group Leader, and Richard and Margaret Romano Professorial Scholar at the University of Illinois at Urbana-Champaign and as Adjunct Professor of Psychiatry at the University of New Mexico. He has been a Guest Professor at the Universities of Tuebingen and Konstanz. He teaches courses on clinical neuroscience and psychopathology, clinical assessment and intervention, and psychophysiology. He publishes laboratory studies on brain mechanisms in psychopathology and conceptual review papers on relationships between psychological and biological phenomena in cognition, emotion, and psychopathology. He has been president of the Society for Psychophysiological Research and editor of *Psychophysiology*. He has an AB in Psychology and Social Relations from Harvard University and an MS and PhD in Psychology from the University of Wisconsin-Madison.

Wendy Heller is Professor of Psychology, director of Clinical Training, and associate department head in the Psychology Department at the University of Illinois. Her research investigates the role of the brain in emotion, personality, and psychopathology, particularly anxiety and

depression. She uses psychological theories to determine how fundamental emotion and personality constructs can be mapped onto brain systems to clarify both the neural mechanisms of emotion and models of emotion themselves. Her work has shown that emotion and cognition interact to influence both feelings and task performance and that different patterns of brain activity are associated with different patterns of cognitive functions in types of anxiety and depression. Her more recent work has examined individual differences in personality (e.g., schizotypy), motivation (e.g., approach/avoidance) and executive function and their relationship to brain function and psychopathology. She teaches neuropsychological assessment of children, adolescents, and adults, and is founder and director of the Neuropsychological Assessment Service at the Psychological Services Center at the University of Illinois. Heller holds a BA in Psychology from the University of Pennsylvania and an MA and PhD in Biopsychology from the University of Chicago.

Endnotes

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