Emotion-Modulated Performance and Activity in Left Dorsolateral Prefrontal Cortex

John D. Herrington, Aprajita Mohanty, Nancy S. Koven, Joscelyn E. Fisher, and Jennifer L. Stewart University of Illinois at Urbana–Champaign Marie T. Banich University of Colorado

Andrew G. Webb, Gregory A. Miller, and Wendy Heller University of Illinois at Urbana–Champaign

Functional MRI (fMRI) was used to examine the relationship between processing of pleasant and unpleasant stimuli and activity in prefrontal cortex. Twenty volunteers identified the colors in which pleasant, neutral, and unpleasant words were printed. Pleasant words prompted more activity bilaterally in dorsolateral prefrontal cortex (DLPFC) than did unpleasant words. In addition, pleasant words prompted more activity in left than in right DLPFC. Response speed to pleasant words was correlated with DLPFC activity. These data directly link positive affect, enhanced performance, and prefrontal activity, providing some of the first fMRI evidence supporting models of emotional valence and frontal brain asymmetry based on electroencephalography (EEG).

Keywords: emotion, positive affect, dorsolateral prefrontal cortex, functional MRI, brain asymmetry

Emotion influences cognition in a variety of ways. Perhaps one of the most well-established findings is that positive affect enhances performance on certain types of tasks. Dramatic procedures to induce positive affect are not required for this effect, with most studies having used simple experimental manipulations such as giving participants a small, unanticipated gift or having them watch a funny film, read a cartoon, or experience success in a task (Ashby, Isen, & Turken, 1999; Gray, Braver, & Raichle, 2002). In

John D. Herrington, Aprajita Mohanty, Nancy S. Koven, Joscelyn E. Fisher, and Jennifer L. Stewart, Department of Psychology, University of Illinois at Urbana–Champaign; Marie T. Banich, Department of Psychology, University of Colorado; Andrew G. Webb, Department of Electrical and Computer Engineering and Beckman Institute, University of Illinois at Urbana–Champaign; Gregory A. Miller, Departments of Psychology and Psychiatry and Beckman Institute, University of Illinois at Urbana–Champaign; Wendy Heller, Department of Psychology and Beckman Institute, University of Illinois at Urbana–Champaign.

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Correspondence concerning this article should be addressed to Wendy Heller, Department of Psychology, University of Illinois, 603 East Daniel Street, Champaign, IL 61820 or Gregory A. Miller, Biomedical Imaging Center, Beckman Institute, University of Illinois, 2100 S. Goodwin, Urbana, IL 61801. E-mail: w-heller@uiuc.edu or gamiller@uiuc.edu

addition, the effect has been shown to hold for people of different ages and circumstances (e.g., college students, adolescents, physicians, business executives) in different contexts (Greene & Noice, 1988; Isen, Daubman, & Nowicki, 1987).

Positive affect has the most impact on an aspect of executive function that can be described as the flexible and strategic manipulation of information to solve a problem or reach a goal (Ashby et al., 1999; Stuss & Levine, 2002). For example, positive affect fosters performance on tasks of flexible problem solving (Isen et al., 1987). When people are asked to generate words fitting a letter or a category, positive affect is associated with increased verbal fluency (Greene & Noice, 1988; Isen & Daubman, 1984). Positive affect is also associated with enhanced perspective-taking abilities, as measured by assessments of group strategizing involved in such tasks as integrative bargaining (Carnevale & Isen, 1986). In addition, tasks are perceived as more complex under positive affect conditions, which can lead to the formation of associations and representations between task components that would otherwise be less salient (Kraiger, Billings, & Isen, 1989).

Recent studies highlight the role of neuropsychological mechanisms in the relationship between positive affect and enhanced executive function. Working memory and processes of information monitoring and updating (Gray, 2001) are considered to be fundamental components of executive function (Banich, 2004). Gray (2001) found that participants who had seen a pleasant film clip performed better on a verbal working memory task. Gray also demonstrated greater fMRI activity in a portion of left dorsolateral prefrontal cortex (DLPFC; Gray et al., 2002). Perlstein, Elbert, and Stenger (2002) also found a relationship between DLPFC activity and stimulus valence. Participants were presented with an array of pleasant or unpleasant pictures followed immediately by a single pleasant or unpleasant picture and were asked to indicate whether

the second picture was present in the previously viewed picture array. Pleasant pictures as targets prompted more right DLPFC activity than did unpleasant pictures (information regarding activity in left DLPFC was not reported).

The studies of Gray et al. (2002) and Perlstein et al. (2002) are consistent with decades of research suggesting that executive functions such as self-monitoring, associative learning, and sequencing depend on prefrontal regions of the brain, particularly DLPFC (Cohen, Braver, & O'Reilly, 1996; Fuster, 1989; Owen, Evans, & Petrides, 1996; Rajkowska & Goldman-Rakic, 1995; Stuss & Levine, 2002). The role of DLPFC in the selection of information that is most task relevant is also revealed by lesion (Perret, 1974), positron-emission tomography (PET; Pardo, Pardo, Janer, & Raichle, 1990), and fMRI (Banich et al., 2000a, 2000b; Milham, Banich, Claus, & Cohen, 2003; Milham et al., 2001, 2002) studies of the Stroop task. In this task, individuals must identify the ink color in which a color word is presented. Such a task is attentionally demanding, because words are read more automatically than ink color is identified. Executive control is required to select the task-relevant but less salient information related to ink color. Thus, these studies link DLPFC to the shifting and maintenance of attentional set in the context of competing attentional demands (Banich, 2004; Milham et al., 2003). These findings are corroborated by substantial clinical evidence regarding the difficulties encountered by individuals with deficits in lateral frontal lobe function when negotiating novel, unconstrained tasks, such as anticipating future events or choosing among multiple problem-solving strategies (for a review, see Banich, 2004; also see Fuster, 1989; Nathaniel-James & Frith, 2002; Shallice & Burgess, 1991).

Whereas DLPFC activity has been linked to executive function in fMRI studies, it has been linked to affective processing in electroencephalography (EEG) studies. In particular, positive affect has been associated with activation of frontal regions including DLPFC, particularly in the left hemisphere (Baxter et al., 1989; Davidson, 1992; Davidson & Henriques, 2000; Harmon-Jones & Allen, 1997). Indeed, these and additional EEG findings have formed the basis of at least two theories of the neuroscience of emotion in which left anterior activity is hypothesized to accompany approach motivation as well as pleasant valence (as defined by the circumplex model; Davidson, 2002; Heller & Nitschke, 1998). As predicted by these models and the evidence implicating DLPFC in executive function, the deficits in goal representation and attentional resource allocation commonly seen in depression are in part thought to be mediated by decreased activity in left prefrontal cortex, particularly in left DLPFC (Nitschke, Heller, Etienne, & Miller, 2004; see also Davidson, Pizzagalli, Nitschke, & Putnam, 2002; Heller & Nitschke, 1997; G. E. Miller & Cohen, 2001). In addition to these findings of hemispheric asymmetries in frontal regions for pleasant and unpleasant emotional valence, Heller and Nitschke (1998) reviewed research suggesting that depression is associated with a bilateral decrease in anterior activity. One might expect that if depression is associated with both bilateral and lateralized differences in frontal lobe functioning, positive affect would, conversely, be associated with bilateral and lateralized increases in activity. Apparently, no study has directly examined this possibility.

Despite the number of EEG studies providing evidence of anterior asymmetry in favor of left frontal regions for positive affect, these findings have generally not been replicated using hemodynamic neuroimaging (Wager, Phan, Liberzon, & Taylor, 2003). However, the absence of main effects and interactions for prefrontal activity may not be a true null finding. The interpretation of neuroimaging studies examining hemispheric brain asymmetries has been complicated by methodological inadequacies (Davidson, 1998, 2002; Davidson & Irwin, 1999). Davidson (1998) drew attention to the fact that few studies were examining frontal asymmetries using appropriate analysis of variance (ANOVA) designs that examined the interaction between group (typically, depressed vs. nondepressed individuals) and hemisphere. Few studies of frontal asymmetries in emotion have gone beyond the use of voxel-by-voxel statistics (rather than clusterlevel or region of interest [ROI] statistics), and many have focused solely on whether an active area met a particular statistical threshold in one hemisphere as well as the other, without examining significant differences between activity in the hemispheres. The same criticism can be leveled against imaging studies that examine main effects and interactions between hemisphere and emotional valence. As pointed out by Reid, Duke, and Allen (1998), the pursuit of hemispheric asymmetries in EEG signals "reflects the theoretical emphasis [of EEG methods] on the complementary functioning of the left and right hemispheres" (p. 391), whereas the hemodynamic imaging studies they cited examined brain activity across groups but not hemispheres.

Despite reason to believe that positive affect would influence executive function with concomitant changes in activation of DLPFC, few studies have directly examined their conjoint effects. Furthermore, no research has made the distinctions between valence and arousal that Heller (1993; Compton, Heller, Banich, Palmieri, & Miller, 2000; Heller, Nitschke, & Miller, 1998) has suggested in previous research are crucial with regard to brain activity for emotion processing. A number of studies using factor analytic and multidimensional scaling approaches have established that basic emotions (e.g., happiness, fear) can be characterized by a two-dimensional structure with axes representing valence (pleasant vs. unpleasant) and arousal (Ekman, Levenson, & Friesen, 1983). Together, these axes form what is known as the circumplex model of emotion. Positive and negative affect are terms that emerge from a rotation of the circumplex model that subsumes arousal (Watson & Tellegen, 1985). In previous research (Heller, 1993; Heller, Koven, & Miller, 2003; Heller et al., 1998), it has been argued that prefrontal asymmetries are associated specifically with valence, not arousal. Hence, in order to understand the mechanisms underlying the purported relationship between positive affect and prefrontal function, it will be important to parse the emotional information used to elicit brain activity into valence and arousal contributions.

In the present study, we examined frontal asymmetries in processes associated with emotional valence, arousal, and executive function by implementing voxel-by-voxel statistics and using the results to perform subsequent ROI analyses across hemispheres and individuals. By focusing across-hemisphere analyses on a region of DLPFC demonstrated to be active within the sample, rather than relying solely on per-voxel evidence of activity that meets a significance threshold in one hemisphere but not the other, the present study represents a rigorous test of anterior brain asymmetries in emotion.

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In the present study, we assessed the relationship between emotion and task performance using a modified version of the color-word Stroop task that included pleasant and unpleasant words. The emotional Stroop task differs from the standard colorword Stroop task in that there is no direct conflict between the relevant (word color) and irrelevant (word meaning) stimulus dimensions. However, a number of studies have shown changes in response time when the irrelevant stimulus dimension is an emotional word, indicating that the emotional Stroop task is effective in manipulating attention (Williams, Mathews, & MacLeod, 1996). The central hypothesis in the present study was that the positive affect condition would improve performance on this task and that this improvement would be associated with increases in DLPFC activity. Furthermore, a review of EEG and hemodynamic imaging studies regarding frontal asymmetries and emotional valence supported a prediction that positive affect would be accompanied by an asymmetry in favor of left DLPFC that would be superimposed on a bilateral increase in DLPFC activity (Heller & Nitschke, 1998). Although the viewing of a mixture of pleasant and unpleasant emotional words would not be expected to alter mood state in general, studies have shown that emotional words modulate attentional processes and influence overt behavior in this task despite the fact that participants are asked to ignore the meaning of the words (Compton et al., 2003; Mohanty et al., 2005; Williams et al., 1996). Of interest in the present experiment was whether exposure to even a mild emotional stimulus incidental to a task requiring executive control would provide evidence in favor of brain asymmetries for positive emotion.

Method

Participants

Participants were 20 paid volunteers (11 women and 9 men) recruited from the university community through flyers and e-mails (mean age = 21.5 years). All were right-handed, native speakers of English with self-reported normal color vision.

Task and Stimuli

For each trial, participants were asked to indicate as quickly and accurately as possible the color in which a word was presented (red, yellow, green, or blue) by pressing one of four buttons. Word presentation and response recording were controlled by MEL 2.0 (Micro Experimental Laboratory 2.0; Psychology Software Tools, Pittsburgh, PA). Stimuli were displayed with the use of LCD goggles (Magnetic Resonance Technologies, Willoughby, OH).

Data were acquired in a single run lasting approximately 11 min. Each trial consisted of a 300-ms fixation cross followed by a 1,700-ms word presentation. Trials followed a blocked design in which sets of 16 pleasant, neutral, or unpleasant words alternated. A blocked design was chosen because emotional words result in better attentional capture when presented in a blocked fashion than when presented in mixed blocks of emotional and neutral words (Compton et al., 2003; Dalgleish, 1995; Holle, Neely, & Heimberg, 1997; Koven, Heller, Banich, & Miller, 2003). Fixation blocks occurred at the beginning, middle, and end of the run and consisted of a low-intensity fixation cross presented for 300 ms followed by a full-intensity fixation cross presented for 1,700 ms. The order of blocks was counterbalanced across participants to control for valence-modulated order effects.

Word stimuli consisted of two emotion word lists (one for pleasant and one for unpleasant words) and two neutral word lists. The pleasant blocks

consisted of words such as DESIRE and EXCITE, the neutral blocks consisted of words such as MATH and TIME, and the unpleasant blocks consisted of words such as HATE and SAD. Emotion words were selected on the basis of published ratings of valence and arousal (Bradley & Lang, 1998). The pleasant and unpleasant word conditions were selected to rate highly on the arousal dimension but to differ from one another on the valence dimension (see Compton et al., 2003, for a table containing the mean valence and arousal ratings of the pleasant and unpleasant conditions). Each neutral list was constructed to match either the pleasant or the unpleasant word list as closely as possible in word length, familiarity, imageability, and concreteness (Toglia & Battig, 1983). Words within each neutral list were selected to be semantically related, as the pleasant and unpleasant words were semantically related within each list. Words were randomly ordered within their respective lists, and each color appeared equally often for each word type.

Imaging Equipment and Acquisition Parameters

MRI data were acquired using a General Electric Signa 1.5 Tesla scanner (Milwaukee, WI) equipped for echo-planar imaging (EPI). A bite bar was attached to the head coil in order to minimize head movement. During the experimental run, 445 functional images were acquired using a gradient-echo EPI sequence (repetition time = 1,517 ms; echo time = 60 ms; flip angle = 90°). Fifteen contiguous axial slices (slice thickness = 7 mm, no gap, in-plane resolution = 3.75×3.75 mm) were acquired parallel to the anterior and posterior commisures. Prior to the EPI sequence, 15- and 26-slice T1-weighted gradient-echo structural scans were acquired for anatomic localization and registration.

MRI Data Analysis

Functional image processing and analyses were implemented using FEAT (FMRI Expert Analysis Tool; from the Oxford Centre for Functional Magnetic Resonance Imaging of the Brain [FMRIB]'s Software Library [http://www.fmrib.ox.ac.uk/fsl]). Each fMRI time series was motion-corrected, high-pass filtered (to remove drift in signal intensity), intensity-normalized, and spatially smoothed using a 3D Gaussian kernel (full width at half maximum = 7 mm) prior to analysis.

Statistical maps were generated for each participant's time series data by applying a regression analysis to each intracerebral voxel (Woolrich, Ripley, Brady, & Smith, 2001). The fitted model was designed to predict observed brain activity from explanatory variables representing pleasant and unpleasant trial blocks separately, convolved with a gamma variate function to more accurately model the hemodynamic response (Aguirre, Zarahn, & D'Esposito, 1998; Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000). Each explanatory variable in these analyses yielded a voxel-by-voxel map of parameter estimates (β) representing the correlation between the explanatory variable and the observed data. Beta values representing the pleasant and unpleasant word conditions were contrasted with one another to generate voxel-by-voxel contrast parameter estimate maps. These maps were then converted to t statistic maps by dividing each individual β by its standard error. Finally, each voxel in the t statistic maps was converted into a z statistic by comparing each t value to a Gaussianized t distribution that follows a z distribution.

For analyses across participants, z maps representing the difference between pleasant and unpleasant word conditions for each participant were registered into a common stereotactic space (Talairach & Tournoux, 1988) with the use of automated linear registration software (FLIRT [FMRIB's Linear Image Registration Tool] from FMRIB's Software Library). Statistical analyses were carried out with MEDx 3.4 by implementing a paired t test comparing each participant's z map to zero (i.e., no difference between the two conditions). For ease of interpretation, the resulting t values for each voxel were then converted into z statistics following a Gaussianized t distribution. This analysis was intended to isolate specific

regions for subsequent ROI analyses. The probability of obtaining false positives was minimized by applying a statistical threshold of p < .01 and a cluster threshold of 20. This combination of thresholds results in a false positive probability of .00001 for each voxel (Forman et al., 1995, p. 642, Table 2)

In order to test the hypothesis regarding the conjoint effects of emotion, laterality, and executive function, an ROI analysis was implemented to examine activity in DLPFC. As specified above, a significantly active cluster was identified in left DLPFC for the pleasant word condition. This cluster was then used to define the homologous ROI in the right hemisphere. Average *z* scores were calculated for this ROI within each participant's *z* map representing significant activity during pleasant, neutral, and unpleasant word conditions. A repeated measures ANOVA was carried out on these ROI scores to examine main effects and interactions for word valence (pleasant, neutral, and unpleasant) and hemisphere within this ROI.

Brain Activity and Reaction Time Relationships

Average reaction times (RTs) for pleasant and unpleasant words were computed for each participant. Differences in RT were tested using a paired *t* test. Separate linear regressions were computed to determine whether RTs to pleasant and unpleasant words could predict left, right, and combined DLPFC activity.

Results

Brain Activity

As an initial step, a regression analysis with two explanatory variables representing each valence condition (pleasant, unpleasant) was carried out on the fMRI intensity values for each voxel for each participant. The resulting beta values for the two conditions were statistically compared to produce a beta map representing the difference between the two conditions. The beta maps for each participant were converted to z maps for subsequent analysis.

A paired t test was used to compare each difference score against zero collapsed across participants, and the number of contiguous voxels that reached statistical significance was computed. This analysis revealed a number of significantly active regions (see Table 1), including a cluster of activity for pleasant words in left DLPFC (see Figure 1). The center of mass for this cluster was located at x = -32, y = 24, and z = 42 in Talairach and Tournoux's (1988) coordinate space. The cluster was located in inferior and middle frontal gyri, with small intrusions into superior frontal and precentral gyri (between the z coordinates of 20 and 62).

In the Valence (pleasant, neutral, and unpleasant) \times Hemisphere ANOVA for this DLPFC ROI, the ordering of levels for the valence factor meant that orthogonal trend components provided planned comparisons distinguishing valence and arousal. The linear trend contrasted pleasant with unpleasant stimuli (i.e., valence), and the quadratic trend contrasted the combination of pleasant and unpleasant stimuli with neutral stimuli (i.e., arousal). The linear valence effect confirmed more bilateral DLPFC activity for pleasant words than for unpleasant words, F(1, 19) = 7.57, p = .01. The linear Valence \times Hemisphere interaction showed that this valence effect was larger in left than in right DLPFC, F(1, 19) = 5.90, p = .03, as is apparent in the graph in Figure 1. Post hoc t tests confirmed the simple main effect of valence in the left, t(19) = 4.17, p = .001, but not the right, t(19) = 1.12, ns, DLPFC

ROI. There was no main effect of hemisphere, F(1, 19) = 0.68, ns, nor were there any effects involving quadratic trends (arousal).

Reaction Time

The average RT for pleasant words (M=725 ms, SD=93 ms) was slightly faster than the average RT for unpleasant words (M=727 ms, SD=95 ms), in a manner analogous to the group fMRI analysis above. This difference did not approach significance, t(19)=0.21, ns. However, an analysis using data from a behavioral study in our laboratory with a much larger sample found significantly faster responses for pleasant stimuli in a similar paradigm, t(159)=-2.07, p=.04 (Koven et al., 2003). The absence of a behavioral finding in the present study therefore likely reflects the present limited sample size rather than an ineffective manipulation of word valence.

Brain Activity and Reaction Time

Zero-order correlations between RT for pleasant words and either bilateral or lateralized DLPFC activity during the pleasant word condition were not significant. On the basis of theorizing regarding the need to distinguish valence and arousal dimensions of emotion in research on brain activity (Compton et al., 2000; Heller, 1993; Heller, Etienne, & Miller, 1995; Heller & Nitschke, 1998; Heller, Nitschke, & Lindsay, 1997; Heller et al., 1998, 2003), we computed composite variables in order to statistically separate these constructs. RTs for pleasant and unpleasant words were averaged to capture the variance associated with emotional arousal, whereas the RT for unpleasant words was subtracted from the RT for pleasant words to capture the variance associated with pleasant valence. These variables were then entered into a hierarchical regression predicting activity in bilateral DLPFC during the pleasant word condition. In combination, the two RT measures (arousal reflected in the RT average and valence reflected in the RT difference) accounted for a substantial 39% of the variance in DLPFC activity, F(2, 17) = 5.44, p = .02. Increased DLPFC activity was associated with faster RTs for pleasant valence, t(17) = -2.94, p = .01, but not with RT for emotional arousal, t(17) = 1.62, ns. A similar regression was carried out for left DLPFC only. The full model accounted for 28% of the variance, F(2, 17) = 3.33, p = .06, with increased activity associated with slower RTs for emotional arousal only, t(1) = 2.08, p = .05. The RT for pleasant valence, although in the expected direction, was not significantly associated with left DLPFC activity, t(1) =-1.11, p = .28. A similar analysis for the right DLPFC did not show a significant effect for the full model (23%), F(2, 17) = 2.48, ns, though the association between pleasant valence and RT was in the same direction as that of the left DLPFC. In summary, the behavioral data revealed a relationship between faster RTs for pleasant valence and bilateral DLPFC activity, though this relationship was not strong enough to reach significance for left or right DLPFC in isolation.

Discussion

The present study is the first to provide evidence simultaneously integrating pleasant emotion, executive function, and changes in hemodynamic brain activity. Our findings show that exposure to

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Table 1
Regions Activated by the Emotional Stroop Task

Region	Talairach coordinates for center of intensity				
	x	У	z	Peak z score	Cluster size (no. of voxels)
	Pleasant wor	ds > unpleas	ant words		
Frontal					
Middle frontal gyrus ^a	-34	24	42	3.66	634
Middle frontal gyrus	-28	68	18	2.63	24
Inferior frontal gyrus	-34	24	0	3.47	521
Inferior frontal gyrus	26	20	-12	3.17	57
Inferior frontal gyrus	-56	44	4	2.93	50
Inferior frontal gyrus	34	22	6	4.02	212
Superior frontal gyrus	-10	76	6	2.78	21
Superior frontal gyrus	16	18	66	2.73	20
Medial frontal gyrus	-4	24	46	4.03	338
Anterior cingulate gyrus	18	10	32	3.05	103
Parietal					
Superior parietal lobule	-36	-54	60	2.85	22
Posterior cingulate	-12	-50	18	3.13	40
Occipital					
Inferior occipital gyrus	-30	-74	-2	3.82	64
Cuneus	20	-82	10	3.15	96
Cuneus	-8	-80	8	2.53	20
Cuneus	2	-100	20	3.31	51
Orbital gyrus	-32	-68	30	3.03	34
Temporal					
Inferior temporal gyrus	58	-42	-16	3.57	72
Inferior temporal gyrus	58	-14	-16	3.50	43
Middle temporal gyrus	56	-48	6	3.93	186
Superior temporal gyrus/insula	-40	-16	0	3.82	1,064
Superior temporal gyrus	58	0	-6	3.02	37
Superior temporal gyrus	-42	20	-22	2.87	28
Lingual gyrus	-12	-72	-8	3.35	239
Parahippocampal gyrus	30	-18	-18	3.02	22
	Unpleasant w	ords > pleas	ant words		
Frontal					
Middle frontal gyrus	46	46	24	3.40	34

Note. Clusters of activity for pleasant > unpleasant and unpleasant > pleasant contrasts. All voxels are significant at p < .00001 with a cluster size threshold of at least 20 contiguous voxels. Only significant clusters within cortical gray matter are listed.

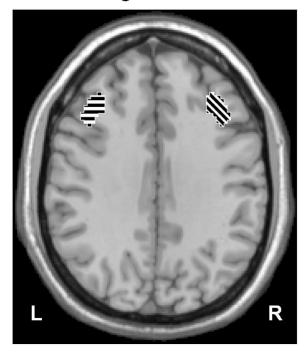
pleasant stimuli results in increased activity bilaterally and especially in left DLPFC, a region implicated in a variety of tasks related to executive function. It is important to note that this association of DLPFC with pleasant stimuli is in addition to any activation by negative words matched for arousal value. Thus, the association is not simply related to the processing of words or emotional stimuli in general but is specific to pleasant words. The strategy of focusing on a specific area of prefrontal cortex shown to be active when individuals were exposed to pleasant words and then analyzing the same region in the opposite hemisphere was successful in finding hemispheric asymmetries in favor of the left hemisphere for pleasant relative to unpleasant words. Furthermore, the main effect of valence across left and right DLPFC ROIs confirms that this hemispheric asymmetry was superimposed on a bilateral increase in activity for pleasant relative to unpleasant words, as hypothesized (Heller & Nitschke, 1998).

In the present study, predicted effects of positive affect were obtained when participants exposed to pleasant words were asked to ignore the stimuli and to make a judgment about the color of the word. Hence, the emotional character of the stimuli provided no information directly relevant to performance on the task itself. The evidence for substantial effects on brain activity and associated RT despite the lack of overt processing of the emotional stimulus demonstrates that emotional valence nonetheless influences cognitive function. In addition, the findings suggest that the effects of valence are not dependent on measurable or persistent change in overall mood. The lack of a statistically significant difference between pleasant and unpleasant compared with neutral words indicates that activity in this area is related specifically to emotional valence rather than emotional arousal.

The differentiation of pleasant and unpleasant words was more robust for brain activity than for behavioral responses. However,

^a Left dorsolateral prefrontal cortex cluster used to define region of interest.

Left and Right ROIs in DLPFC



Average ROI Z-Scores for Pleasant And Unpleasant Conditions

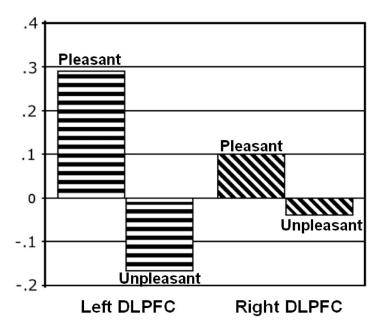


Figure 1. Differences in brain activity during presentation of pleasant versus unpleasant words. Left panel: Regions of interest (ROIs) used to quantify activity in left (L) and right (R) dorsolateral prefrontal cortex (DLPFC) on an axial image in radiological orientation (right hemisphere displayed on the left) at a z coordinate of 34 mm. Right panel: Mean z scores for pleasant and unpleasant word conditions in right and left DLPFC. Z scores representing the relationship between brain activity and pleasant or unpleasant word conditions were averaged for all voxels inside the DLPFC ROIs.

an analysis of a large sample in a behavioral study published elsewhere that used a virtually identical task revealed significant RT differences between pleasant and unpleasant words in the predicted direction (Koven et al., 2003). These behavioral data complementing the present finding of differences in DLPFC activity for pleasant versus unpleasant stimuli suggest that executive function can be influenced by the valence of an automatically processed task-irrelevant stimulus dimension even if the overt behavioral effects are subtle.

The present results suggest that established findings demonstrating the benefits of positive affect for executive function can be explained in terms of increased DLPFC activity and may have implications for understanding normal and abnormal neuropsychological function. For example, diminished positive affect may foster difficulties in performance on tasks dependent on executive function, as is commonly found among individuals with depression (Heller & Nitschke, 1998). The relationship between positive affect, executive function, and DLPFC activity that emerges from these data involves both bilateral and left-lateralized DLPFC increases. This is consistent with the results of EEG studies of the neuropsychology of emotion that examined prefrontal cortex activity (Baxter et al., 1989; Davidson, 1992; Davidson & Henriques, 2000; Harmon-Jones & Allen, 1997). However, EEG studies have not typically used localization and registration techniques sufficient to find changes in specific frontal regions that underlie

patterns of brain asymmetry in emotion processing. Conversely, despite the relatively good spatial resolution of present hemodynamic imaging methods, studies using these techniques have frequently failed to maximize their potential in analyzing brain asymmetries because of limited statistical models (Davidson, 2002; Davidson & Irwin, 1999). The present study suggests that EEG and hemodynamic imaging methods show convergent results in relation to frontal asymmetries in emotional function when appropriate statistical models and region selection procedures are used.

The present results have pragmatic implications for the assessment of executive function. It appears that even relatively mild emotional manipulations can influence brain activity in areas related to the maintenance and allocation of attentional resources. As a result, many tasks of executive function used in clinical and research contexts may be at least partially influenced by affective state. The neuropsychological profiles of individuals undergoing clinical assessment would be better characterized if the influence of emotion was considered systematically when collecting data related to executive function.

The present findings contribute to the ongoing debate about the relationship between cognition and emotion. Although some studies have been interpreted to indicate distinct areas of the brain that are involved in cognition and not in emotion (and vice versa), there are extensive logical and empirical grounds to suggest that the boundary between ostensibly cognitive and emotional processes is

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often ill-defined at best and may, under some circumstances, be nonexistent (G. A. Miller, 1996; Nussbaum, 2001). Given the complex interplay of putatively cognitive and emotional processes in real-world task performance, future neuroimaging studies should focus both on specific brain regions implicated in this interplay and on larger networks of regions that may function in concert to integrate executive processes that depend on what are sometimes distinguished as cognitive and emotional functions.

References

- Aguirre, G. K., Zarahn, E., & D'Esposito, M. (1998). The variability of human BOLD hemodynamic response. *NeuroImage*, 8, 360–369.
- Ashby, F. G., Isen, A. M., & Turken, A. U. (1999). A neuropsychological theory of positive affect and its influence on cognition. *Psychological Review*, 106, 529–550.
- Banich, M. T. (2004). Cognitive neuroscience and neuropsychology. Boston: Houghton Mifflin.
- Banich, M. T., Milham, M. P., Atchley, R., Cohen, N. J., Webb, A., Wszalek, T., et al. (2000a). fMRI studies of Stroop tasks reveal unique roles of anterior and posterior brain systems in attentional selection. *Journal of Cognitive Neuroscience*, 12, 988.
- Banich, M. T., Milham, M. P., Atchley, R. A., Cohen, N. J., Webb, A., Wszalek, T., et al. (2000b). Prefrontal regions play a predominant role in imposing an attentional "set": Evidence from fMRI. *Cognitive Brain Research*, 10, 1–9.
- Baxter, L. R., Schwartz, J. M., Phelps, M. E., Mazziotta, J. C., Guze, B. H., Selin, C. E., et al. (1989). Reduction of prefrontal cortex glucose metabolism common to three types of depression. *Archives of General Psychiatry*, 46, 243–250.
- Bradley, M. M., & Lang, P. J. (1998). Affective norms for English words (ANEW). Gainesville, FL: University of Florida, National Institute of Mental Health Center for the Study of Emotion and Attention.
- Carnevale, P. J., & Isen, A. M. (1986). The influence of positive affect and visual access on the discovery of integrative solutions in bilateral negotiation. *Organizational Behavior & Human Decision Processes*, 37, 1–13.
- Cohen, J. D., Braver, T. S., & O'Reilly, R. C. (1996). A computational approach to prefrontal cortex, cognitive control and schizophrenia: Recent developments and current challenges. *Philosophical Transactions* of the Royal Society of London B: Biological Sciences, 351, 1515–1527.
- Compton, R. J., Banich, M. T., Mohanty, A., Milham, M. P., Herrington, J. D., Miller, G. A., et al. (2003). Paying attention to emotion: An fMRI investigation of cognitive and emotional Stroop tasks. *Cognitive, Affective and Behavioral Neuroscience*, 3, 81–98.
- Compton, R. J., Heller, W., Banich, M. T., Palmieri, P. A., & Miller, G. A. (2000). Responding to threat: Hemispheric asymmetries and interhemispheric division of input. *Neuropsychology*, 14, 254–264.
- Dalgleish, T. (1995). Performance on the emotional Stroop task in groups of anxious, expert, and control subjects: A comparison of computer and card presentation formats. *Cognition & Emotion*, 9, 341–362.
- Davidson, R. J. (1992). Emotion and affective style: Hemisphere substrates. *Psychological Science*, 3, 39–43.
- Davidson, R. J. (1998). Affective style and affective disorders: Perspectives from affective neuroscience. Cognition & Emotion, 12, 307–330.
- Davidson, R. J. (2002). Anxiety and affective style: Role of prefrontal cortex and amygdala. *Biological Psychiatry*, *51*, 68–80.
- Davidson, R. J., & Henriques, J. (2000). Regional brain function in sadness and depression. In J. C. Borod (Ed.), *The neuropsychology of emotion* (pp. 269–297). New York: Oxford University Press.
- Davidson, R. J., & Irwin, W. (1999). The functional neuroanatomy of emotion and affective style. *Trends in Cognitive Sciences*, 3, 11–21.
- Davidson, R. J., Pizzagalli, D., Nitschke, J. B., & Putnam, K. (2002).

- Depression: Perspectives from affective neuroscience. *Annual Review of Psychology*, 53, 545–574.
- Ekman, P., Levenson, R. W., & Friesen, W. V. (1983, September 16). Autonomic nervous system activity distinguishes among emotions. Science, 221, 1208–1210.
- Forman, S. D., Cohen, J. D., Fitzgerald, M., Eddy, W. F., Mintun, M. A., & Noll, D. C. (1995). Improved assessment of significant activation in functional magnetic resonance imaging. *Magnetic Resonance in Medicine*, 33, 636–647.
- Fuster, J. M. (1989). *The prefrontal cortex* (2nd ed.). New York: Raven Press
- Gray, J. R. (2001). Emotional modulation of cognitive control: Approach—withdrawal states double-dissociate spatial from verbal two-back task performance. *Journal of Experimental Psychology: General*, 130, 436–452.
- Gray, J. R., Braver, T. S., & Raichle, M. E. (2002). Integration of emotion and cognition in the lateral prefrontal cortex. *Proceedings of the Na*tional Academy of Sciences, USA, 99, 4115–4120.
- Greene, T. R., & Noice, H. (1988). Influence of positive affect upon creative thinking and problem solving in children. *Psychological Re*ports, 63, 895–898.
- Harmon-Jones, E., & Allen, J. J. B. (1997). Behavioral activation sensitivity and resting frontal EEG asymmetry: Covariation of putative indicators related to risk for mood disorders. *Journal of Abnormal Psychology*, 106, 159–163.
- Heller, W. (1993). Neuropsychological mechanisms of individual differences in emotion, personality and arousal. *Neuropsychology*, 7, 476–489.
- Heller, W., Etienne, M. A., & Miller, G. A. (1995). Patterns of perceptual asymmetry in depression and anxiety: Implications for neuropsychological models of emotion and psychopathology. *Journal of Abnormal Psychology*, 104, 327–333.
- Heller, W., Koven, N. S., & Miller, G. A. (2003). Regional brain activity in anxiety and depression, cognition/emotion interaction, and emotion regulation. In K. Hugdahl & R. J. Davidson (Eds.), *The asymmetrical* brain (pp. 533–564). Cambridge, MA: MIT Press.
- Heller, W., & Nitschke, J. B. (1997). Regional brain activity in emotion: A framework for understanding cognition in depression. *Cognition & Emotion*, 11, 637–661.
- Heller, W., & Nitschke, J. B. (1998). The puzzle of regional brain activity in depression and anxiety: The importance of subtypes and comorbidity. *Cognition & Emotion*, 12, 421–447.
- Heller, W., Nitschke, J. B., & Lindsay, D. L. (1997). Neuropsychological correlates of arousal in self-reported emotion. *Cognition & Emotion*, 11, 383–402.
- Heller, W., Nitschke, J. B., & Miller, G. A. (1998). Lateralization in emotion and emotional disorders. *Current Directions in Psychological Science*, 7, 2–32.
- Holle, C., Neely, J. H., & Heimberg, R. G. (1997). The effects of blocked versus random presentation and semantic relatedness of stimulus words on response to a modified Stroop task among social phobics. *Cognitive Therapy & Research*, 21, 681–697.
- Isen, A. M., & Daubman, K. A. (1984). The influence of affect on categorization. *Journal of Personality and Social Psychology*, 46, 1206– 1217.
- Isen, A. M., Daubman, K. A., & Nowicki, G. P. (1987). Positive affect facilitates creative problem solving. *Journal of Personality and Social Psychology*, 52, 1122–1131.
- Koven, N. S., Heller, W., Banich, M. T., & Miller, G. A. (2003). Relationships of Distinct Affective Dimensions to Performance on an Emotional Stroop Task. *Cognitive Therapy and Research*, 27, 671–680.
- Kraiger, K., Billings, R. S., & Isen, A. M. (1989). The influence of positive affective states on task perceptions and satisfaction. *Organizational Behavior and Human Decision Processes*, 44, 12–25.

- Miezin, F. M., Maccotta, L., Ollinger, J. M., Petersen, S. E., & Buckner, R. L. (2000). Characterizing the hemodynamic response: Effects of presentation rate, sampling procedure, and the possibility of ordering brain activity based on relative thinking. *NeuroImage*, 11, 735–739.
- Milham, M. P., Banich, M. T., Claus, E. D., & Cohen, N. J. (2003). Practice-related effects demonstrate complementary roles of anterior cingulate and prefrontal cortices in attentional control. *NeuroImage*, 18, 483–493.
- Milham, M. P., Banich, M. T., Webb, A., Barad, V., Cohen, N. J., Wszalek, T., et al. (2002). The relative involvement of anterior cingulate and prefrontal cortex in attentional control depends on nature of conflict. *Cognitive Brain Research*, 12, 467–473.
- Milham, M. P., Erickson, K. I., Banich, M. T., Kramer, A. F., Webb, A., & Wszalek, T., et al. (2001). Attentional control in the aging brain: Insights from an fMRI study of the Stroop task. *Brain and Cognition*, 49, 277–296.
- Miller, G. A. (1996). How we think about cognition, emotion, and biology in psychopathology. *Psychophysiology*, *33*, 615–628.
- Miller, G. E., & Cohen, S. (2001). Psychological interventions and the immune system: A meta-analytic review and critique. *Health Psychol*ogy, 20, 47–63.
- Mohanty, A., Herrington, J. D., Koven, N. S., Fisher, J. E., Wenzel, E. A., Webb, A. G., et al. (2005). Neural mechanisms of affective interference in schizotypy. *Journal of Abnormal Psychology*, 114, 16–27.
- Nathaniel-James, D. A., & Frith, C. D. (2002). The role of the dorsolateral prefrontal cortex: Evidence from the effects of contextual constraint in a sentence completion task. *NeuroImage*, 16, 1094–1102.
- Nitschke, J. B., Heller, W., Etienne, M. A., & Miller, G. A. (2004). Prefrontal cortex activity differentiates processes affecting memory in depression. *Biological Psychology*, 67, 125–143.
- Nussbaum, M. C. (2001). Upheavals of thought: The intelligence of emotion. Cambridge, England: Cambridge University Press.
- Owen, A. M., Evans, A. C., & Petrides, M. (1996). Evidence for a two-stage model of spatial working memory processing within the lateral frontal cortex: A positron emission tomography study. *Cerebral Cortex*, 6, 31–38.
- Pardo, J. V., Pardo, P. J., Janer, K. W., & Raichle, M. E. (1990). The anterior cingulate cortex mediates processing selection in the Stroop attentional conflict paradigm. *Proceedings of the National Academy of Sciences*, USA, 87, 256–259.

- Perlstein, W. M., Elbert, T., & Stenger, V. A. (2002). Dissociation in human prefrontal cortex of affective influences on working memoryrelated activity. *Proceedings of the National Academy of Sciences, USA*, 99, 1736–1741.
- Perret, E. (1974). The left frontal lobe of man and the suppression of habitual responses in verbal categorical behavior. *Neuropsychologia*, 12, 323–330
- Rajkowska, G., & Goldman-Rakic, P. S. (1995). Cytoarchitectonic definition of prefrontal areas in the normal human cortex: II. Variability in locations of areas 9 and 46 and relationship to the Talairach Coordinate System. *Cerebral Cortex*, 5, 323–337.
- Reid, S. A., Duke, L. M., & Allen, J. J. B. (1998). Resting frontal electroencephalographic asymmetry in depression: Inconsistencies suggest the need to identify mediating factors. *Psychophysiology*, 35, 389– 404.
- Shallice, T., & Burgess, P. W. (1991). Deficits in strategy application following frontal lobe damage in man. *Brain*, 114, 727–741.
- Stuss, D. T., & Levine, B. (2002). Adult clinical neuropsychology: Lessons from studies of the frontal lobes. *Annual Review of Psychology*, 53, 401–433.
- Talairach, J., & Tournoux, P. (1988). Co-planar stereotactic atlas of the human brain. Stuttgart, Germany: Thieme.
- Toglia, M. P., & Battig, W. F. (1983). Handbook of semantic word norms. Hillsdale, NJ: Erlbaum.
- Wager, T. D., Phan, K. L., Liberzon, I., & Taylor, S. F. (2003). Valence, gender, and lateralization of functional brain anatomy in emotion: A meta-analysis of findings from neuroimaging. *NeuroImage*, 19, 513–531
- Watson, D., & Tellegen, A. (1985). Toward a consensual structure of mood. *Psychological Bulletin*, 98, 219–235.
- Williams, J. M. G., Mathews, A., & MacLeod, C. (1996). The emotional Stroop task and psychopathology. Psychological Bulletin, 120, 3–24.
- Woolrich, M. W., Ripley, B. D., Brady, M., & Smith, S. M. (2001). Temporal autocorrelation in univariate linear modeling of fMRI data. *NeuroImage*, 14, 1370–1386.

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