*Research Article*

# Frontal Brain Asymmetry and Reward Responsiveness

## A Source-Localization Study

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ABSTRACT—*The influence of approach and avoidance tendencies on affect, reasoning, and behavior has attracted substantial interest from researchers across various areas of psychology. Currently, frontal electroencephalographic (EEG) asymmetry in favor of left prefrontal regions is assumed to reflect the propensity to respond with approach-related tendencies. To test this hypothesis, we recorded resting EEG in 18 subjects, who separately performed a verbal memory task under three incentive conditions (neutral, reward, and punishment). Using a source-localization technique, we found that higher task-independent alpha2 (10.5–12 Hz) activity within left dorsolateral prefrontal and medial orbitofrontal regions was associated with stronger bias to respond to reward-related cues. Left prefrontal resting activity accounted for 54.8% of the variance in reward bias. These findings not only confirm that frontal EEG asymmetry modulates the propensity to engage in appetitively motivated behavior, but also provide anatomical details about the underlying brain systems.*

Within several domains of psychology, much research has been devoted to understanding how two fundamental dimensions of behavior, approach and avoidance, influence emotions, reasoning, and other mental processes (e.g., Chen & Bargh, 1999; Henriques & Davidson, 2000; Tripp & Alsop, 1999). Unfortunately, little is known about the neural substrates underlying approach and avoidance behaviors and their relations to cognitive and affective processes.

Emerging evidence suggests that frontal regions in the two hemispheres are differentially involved in the experience of emotion and expression of motivated behavior. Studies involving patients with brain lesions (Narushima, Kosier, & Robinson, 2003) and emotional disorders (Davidson & Henriques, 2000), electroencephalography (EEG; Coan & Allen, 2004), and functional neuroimaging (Pizzagalli, Shackman, & Davidson, 2003) indicate that the left and right frontal regions are crucially involved in approach-related and withdrawal-related affect, respectively.

On the basis of these findings and animal work demonstrating that the prefrontal cortex (PFC), particularly its dorsolateral regions, is critically involved in on-line maintenance of affective representation necessary to guide behavior (Kobayashi, Lauwereyns, Koizumi, Sakagami, & Hikosaka, 2002; Wallis & Miller, 2003), Davidson (2004) proposed that left PFC regions are implicated in a system that facilitates appetitive behavior and certain forms of affect that are approach related. Thus, individual differences in tonic levels of activation in this system are hypothesized to reflect a diathesis involved in modulating an individual's propensity to experience approach-related affect and to engage in appetitively motivated behavior. In a study consistent with this notion, subjects with greater resting left-sided frontal activity (as reflected by lower power within the alpha EEG band, 8–13 Hz) were found to select more pleasant stimuli in a later judgment task compared with subjects with greater resting right-sided frontal activity (Sutton & Davidson, 2000). As 60% of the variance in frontal EEG alpha asymmetry is thought to reflect a latent trait (Hagemann, Naumann, Thayer, & Bartussek, 2002), these findings suggest that tonically increased left-lateralized activity may predispose an individual to information processing biases toward positive cues.

In the present study, we aimed to extend this literature in two important ways. First, although theoretical arguments predict that individual differences in frontal EEG asymmetry are associated with differences in propensity to engage in appetitively motivated behavior, few studies have specifically assessed this link (Sutton & Davidson, 2000). Second, although frontal EEG

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asymmetry has been typically found at midfrontal (F3/4), anterior frontal (Fp1/2), or lateral frontal (F7/8) sites, little is known about underlying intracerebral sources.

To address these two issues, we investigated relations between baseline EEG data and recently published behavioral data from our laboratory. In a behavioral study, Henriques and Davidson (2000) studied the effect of incentives on performance during a verbal memory task and found that healthy control subjects changed their pattern of responding in both the reward and the punishment conditions, compared with a neutral condition; this strategy led to maximization of earnings. Of primary importance for the current study is the finding that even among these healthy subjects, substantial individual differences in reward bias emerged. To test the hypothesis that individual differences in reward bias are related to differences in resting left prefrontal activation, we used low-resolution electromagnetic tomography (LORETA; Pascual-Marqui et al., 1999) to compute the intracerebral electrical sources underlying EEG alpha activity recorded at the scalp.

## METHOD

### Participants

Eighteen subjects (38.6 ± 13.6 years; 10 females) recruited from the community participated. Subjects were right-handed (Chapmans' Handedness Inventory score between 13 and 17; Chapman & Chapman, 1987), were free of psychotropic medications, and had no current or past Axis I pathology in themselves or first-degree relatives. Subjects gave informed written consent to a protocol approved by the local institutional review board.

### Task and Procedure

Data for the present study were derived from a larger study of depression involving measurement of resting brain electric (EEG) and metabolic (positron emission tomographic, PET) activity, structural magnetic resonance imaging (MRI), and neuropsychological assessment. Unlike prior studies on this sample that have compared EEG, PET, and structural MRI data of control and depressed subjects (Pizzagalli et al., 2002, 2004), the current study tested whether, in control subjects, intracerebral electrical sources underlying scalp-recorded EEG alpha activity were linked to an individual's propensity to respond with approach-related tendencies, a topic not investigated before.

#### *Signal Detection Task*

After completing the state and trait forms of the Positive and Negative Affect Schedule (PANAS; Watson, Clark, & Tellegen, 1988), subjects received instructions for a signal detection task, which consisted of a verbal recognition task performed under three payoff contingencies: neutral, reward, and punishment (Henriques & Davidson, 2000). Six blocks (two for each condition) were presented according to an order randomized across subjects. At the beginning of each block, subjects were informed of the payoff contingencies. Each block consisted of three parts: First, 24 five- and six-letter target words were presented in lowercase (height = 1.0–1.5 cm) for 400 ms each (interstimulus interval, ISI = 200 ms). Immediately thereafter, a color distractor task (20 trials) was presented to prevent rehearsal of the target words. For this task, subjects were instructed to determine whether two circles displayed consecutively for 100 ms (ISI = 2,000 ms) were of the same color. Finally, in the discrimination task, 24 target and 24 distractor words were presented for 700 ms each in a randomized order, and subjects were instructed to press one of two buttons to indicate whether or not each word had been presented before. For each trial, visual feedback of "correct response" or "incorrect response" was provided. In the neutral condition, accuracy feedback was displayed, but there were no monetary consequences. In the reward condition, subjects earned $0.10 for each correct identification of a target. In the punishment condition, subjects lost $0.10 (from an initial credit of $2.50) for each missed target identification. For both the reward and the punishment conditions, accuracy feedback was displayed along with the amount of money the subject had earned thus far in the block.

#### *EEG Data*

The EEG recording involved 10 (5 eyes-closed, 5 eyes-open) contiguous 3-min trials, as previously described (Pizzagalli et al., 2004). For 12 subjects, the signal detection task was performed in the morning, and the EEG recording occurred in the afternoon of the same day. Because of scheduling issues related to the PET measurement, 6 subjects underwent EEG recording at a later session (on average, 13.5 days later).

### Data Acquisition

#### *Signal Detection Task*

NeuroStim software (Neurosoft, Inc., El Paso, TX) was used to present the signal detection task on a computer.

#### *EEG Data*

A Grass Model 12 Neurodata system using Model 12C preamplifiers was used to amplify the EEG and electro-oculogram (EOG) data using a bandpass of 1 through 300 Hz and a 60-Hz notch filter. Data were then digitally low-pass filtered at 100 Hz and digitized on-line at 250 Hz. EEG data were recorded from 28 scalp sites (10/20 system plus FC3/4, FC7/8, CP5/6, PO3/4, and FPz; reference: left ear) using a modified Lycra electrode cap (Electro-Cap International, Inc., Eaton, OH; impedances $< 5$ KΩ). Horizontal and vertical EOGs were recorded through two additional channels ($< 20$ KΩ).

### Data Reduction and Analysis

#### *Signal Detection Task*

For each subject, hit rate (HR) and false alarm rate (FAR) were determined. Following Snodgrass and Corwin (1988), we

computed response bias (RB) as follows: $RB = FAR/[1 - (HR - FAR)]$. This formula creates a range of RB scores from 0.0 (conservative) to 1.0 (liberal), with a score of .5 indicating no bias. RB was computed for each block and then averaged within payoff condition. Finally, to adjust for individual differences in baseline response, we calculated a difference score between RB in each payoff contingency and the neutral condition (Henriques & Davidson, 2000). We refer to these difference scores as reward bias (reward − neutral) and punishment bias (punishment − neutral).

*EEG Data*

After artifact detection, all available artifact-free 2,048-ms EEG epochs (on average, 151.7 epochs per condition across subjects, $SD = 99.6$) were extracted from the eyes-closed trials and subjected to conventional spectral analyses. On the basis of prior research implicating baseline alpha activity in predicting performance on affective (e.g., Sutton & Davidson, 2000; Wheeler, Davidson, & Tomarken, 1993) and cognitive (e.g., Glass & Riding, 1999) tasks, as well as the potential functional dissociation between lower and upper alpha activity (Kubicki, Herrmann, Fichte, & Freund, 1979), we restricted analyses to alpha1 (8.5–10.0 Hz) and alpha2 (10.5–12.0 Hz) bands. Resting alpha activity was used as an inverse indicator of activation (Shagass, 1972), in accordance with a large body of literature on individual differences in tonic frontal EEG asymmetry (for reviews, see Coan & Allen, 2004; Harmon-Jones, 2003). Thus, stronger intracerebral sources of alpha activity were interpreted as decreased activity.

In the next step, LORETA (Pascual-Marqui et al., 1999) was used to estimate intracerebral electrical sources underlying alpha1 and alpha2 activity recorded at the scalp. LORETA computes current density (i.e., the amount of electrical current flowing through a solid) without assuming any number of active sources.[1] The LORETA solution space (i.e., the locations in which sources can be found) is composed of 2,394 cubic elements ("voxels," 7 × 7 × 7 mm) and is limited to cortical gray matter and hippocampi, as defined by a digitized MRI available from the Montreal Neurologic Institute (MNI; Montreal, Quebec, Canada). Following established procedures (Pizzagalli et al., 2004), we normalized LORETA activity to a total power of 1 before the statistical analyses.

**Statistical Analyses**

The main goal of this study was to assess links between frontal EEG asymmetry and reward responsiveness. Accordingly, a correlational approach was used.

*Whole-Brain Analyses*

Because LORETA data were not normally distributed across subjects and voxels, Spearman's rank correlations between current density and reward bias (reward − neutral) and between current density and punishment bias (punishment − neutral) were computed at each voxel. Findings were considered significant at $p < .005$, as prior studies using permutation procedures have shown that this threshold provides adequate protection against Type I errors (Pizzagalli et al., 2002).

*Specificity Analyses*

To assess the specificity of findings in terms of condition (reward vs. punishment), laterality (left vs. right), and band (alpha1 vs. alpha2), we used the Meng test for dependent correlations (Meng, Rosenthal, & Rubin, 1992). As in prior studies (Pizzagalli et al., 2004), current density was first averaged across voxels within a cluster and then entered in further analyses. For the laterality tests, homologous clusters were defined by reversing the $x$ (left-right) coordinate.

## RESULTS

**Whole-Brain Analyses**

For alpha1, only one voxel in the posterior cingulate gyrus ($x = -3$, $y = -25$, $z = 36$; Brodmann's area, BA, 31) showed a significant correlation between current density and reward bias ($\rho = -.65$, $p < .005$). No significant findings emerged for punishment bias. Because of the limited spatial extent of this finding, no further analyses were performed with alpha1.

For alpha2, no significant findings emerged when considering punishment bias. For reward bias, 31 positive and 59 negative Spearman correlations were significant ($p < .005$). As shown in Figure 1 and Table 1, these voxels fell into six distinct clusters: three in the left dorsolateral PFC (Clusters 1, 2, and 3), one in the left parietal lobe (Cluster 4), one in the medial orbitofrontal cortex (OFC; Cluster 5), and one in the right temporal lobe (Cluster 6). All but Cluster 6 showed significant negative correlations between current density and reward bias (see Fig. 2 for correlations involving Clusters 1, 3, and 5).

**Specificity Analyses**

*Condition Specificity*

For each cluster, the Meng test was used to assess whether the correlation between current density and reward bias was significantly different from the correlation between current density and punishment bias. For Clusters 1, 2, and 5, the correlation between alpha2 and reward bias was significantly more negative than the one between alpha2 and punishment bias ($p < .05$; see Table 2).

*Laterality Specificity*

Meng's tests were run to determine whether the correlation between reward bias and current density in a given cluster was

[1] Important cross-modal validation has come from studies combining LORETA with functional MRI (Mulert et al., 2004; Vitacco, Brandeis, Pascual-Marqui, & Martin, 2002), structural MRI (Worrell et al., 2000), PET (Pizzagalli et al., 2004; cf. Gamma et al., 2004), and intracranial recordings (Seeck et al., 1998). LORETA core assumptions, its mathematical implementation, and additional technical details, including relations between scalp-recorded EEG and LORETA data, have been described extensively (Pascual-Marqui et al., 1999; Pizzagalli et al., 2002, 2004).

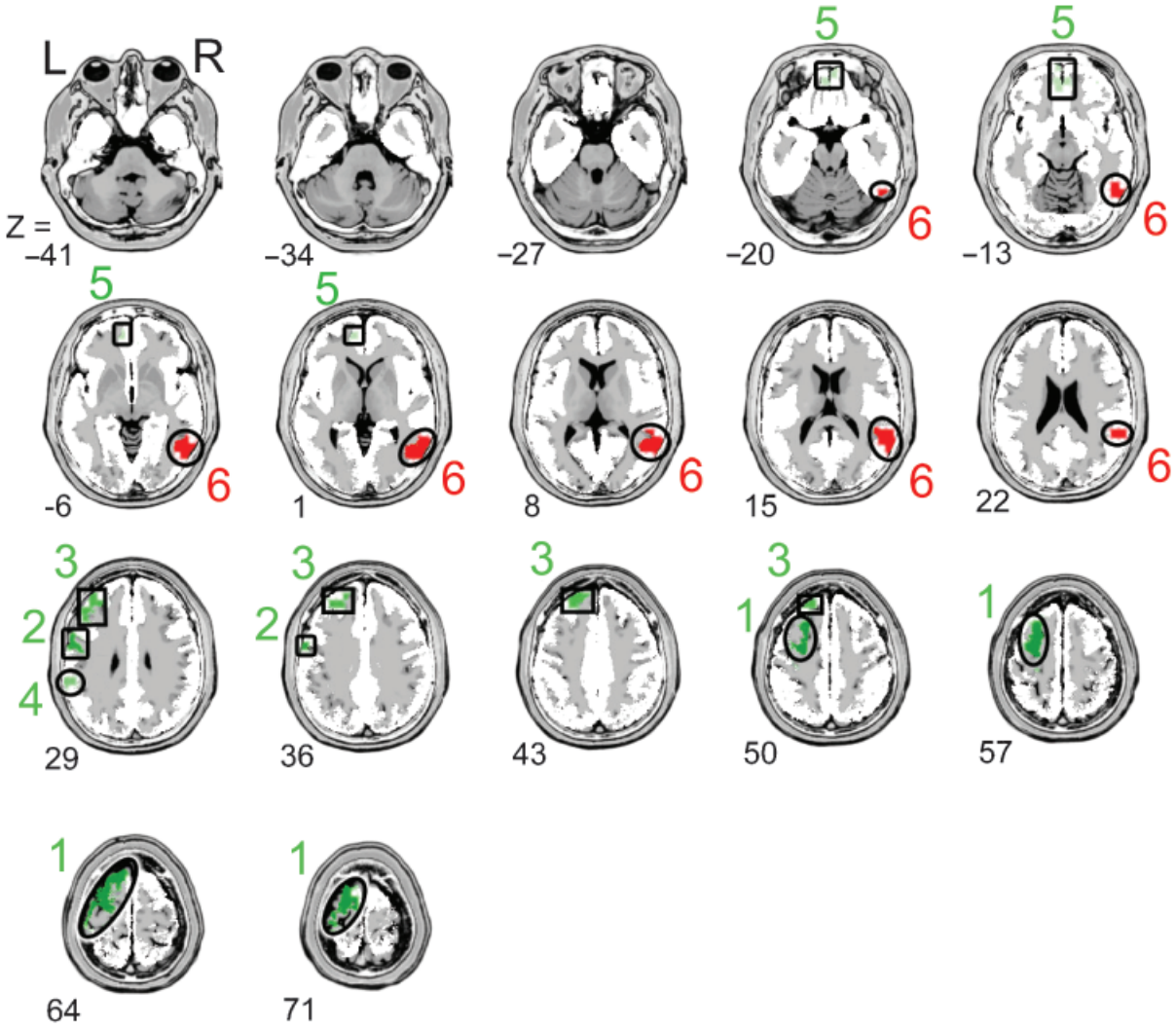


**Fig. 1.** Whole-brain analyses showing voxel-by-voxel correlations between alpha2 (10.5–12 Hz) current density and reward bias for 18 healthy subjects. Seventeen axial brain slices (head seen from above, nose up; L = left, R = right) are shown in steps of 7 mm from the most inferior level ($z = -41$) to the most superior level ($z = 71$). Coordinates are in millimeters (Montreal Neurologic Institute, MNI, brain template), and the origin is at the anterior commissure. The clusters discussed in the text are outlined and identified by number; red denotes the cluster with positive correlations between alpha2 current density and reward bias (Cluster 6), and green denotes the clusters with negative correlations between alpha2 current density and reward bias (Clusters 1–5). The color intensity is arbitrary and used merely to differentiate clusters spatially.

significantly different from the correlation between reward bias and current density in the homologous cluster in the opposite hemisphere (Cluster 5 was excluded). The difference was significant for all clusters except Cluster 3 (all $ps < .05$; see Table 3). In an alternative approach, an asymmetry index score (left − right) was computed by subtracting alpha2 current density between homologous regions (again, Cluster 5 was excluded). For Clusters 2 ($\rho = -.55$), 3 ($\rho = -.58$), 4 ($\rho = -.70$), and 6 ($\rho = .52$), the Spearman correlation between reward bias and this asymmetry index score was significant (all $ps < .025$). Thus, relatively diminished alpha2 current density in the left compared with right PFC was associated with stronger reward bias (Fig. 3).

*Band Specificity*

Meng's tests were run to compare the correlations between alpha1 activity and reward bias and the correlations between alpha2 activity and reward bias. For all six clusters, these correlations were significantly different (all $ps < .05$; see Table 4).

### Regression Analyses

A simultaneous regression analysis revealed that LORETA current density in the three left PFC clusters accounted for 54.8% of the variance in reward bias, $F(3, 14) = 5.66, p < .009$. To assess whether relations between left PFC current density and reward bias were mediated by self-report measures of positive affect, we ran three hierarchical regression analyses. In the

**TABLE 1**

*Summary of Regions Showing Significant Correlations Between Reward Bias and Alpha2 (10.5–12 Hz) Current Density*

| Region (cluster number) | Highest correlation | Coordinates (*x*, *y*, *z*) | BA | Side | Number of voxels | Mean correlation |
|---|---|---|---|---|---|---|
| 1: middle frontal gyrus | −.84**** | −24, −11, 50 | 6 | Left | 31 | −.77**** |
| 2: precentral gyrus | −.69*** | −59, 3, 29 | 6 | Left | 4 | −.66*** |
| 3: superior frontal gyrus | −.77**** | −17, 38, 50 | 8 | Left | 14 | −.68*** |
| 4: inferior parietal lobule | −.72*** | −59, −39, 29 | 40 | Left | 2 | −.71*** |
| 5: orbital gyrus | −.68*** | −3, 52, −20 | 11 | Medial | 8 | −.66*** |
| 6: superior temporal gyrus | .75*** | 60, −53, 8 | 22 | Right | 31 | .69*** |

**Note.** Coordinates given are in millimeters (Montreal Neurologic Institute, MNI, brain template), with the origin at the anterior commissure; *x* ranges from negative on the left to positive on the right, *y* ranges from negative in posterior regions to positive in anterior regions, and *z* ranges from negative in inferior regions to positive in superior regions. For each cluster, the number of voxels exceeding the statistical threshold ($p < .005$) is reported; the mean Spearman correlation is averaged across all voxels belonging to the cluster. Cluster 1 is in left middle-superior frontal and precentral gyri, Brodmann's areas (BAs) 6 and 8 (10.63 $cm^3$); Cluster 2 is in left precentral gyrus, BA 6 (1.37 $cm^3$); Cluster 3 is in left superior-middle frontal gyrus, BAs 8, 9, 10, and 46 (4.80 $cm^3$); Cluster 4 is in the left inferior parietal lobule, BA 40 (0.69 $cm^3$); Cluster 5 is in orbital and medial frontal gyri, as well as the ventral anterior cingulate cortex, BAs 10 and 11 (2.74 $cm^3$); Cluster 6 is in right inferior-middle-superior temporal gyri, inferior parietal lobule, and middle occipital, supramarginal, and fusiform gyri, BAs 3, 19, 21, 22, 37, 39, and 40 (10.63 $cm^3$).
***$p < .005$. ****$p < .001$.

first, state Positive Affect (PA) scores were entered in the first step, and current density in the three left PFC clusters was entered in the second step. The second analysis was the same except that trait, rather than state, PA scores were entered in the first step. In the third regression analysis, state PA was entered in the first step, trait PA was entered in the second step, and current density was entered in the third step. Results showed that left PFC current density continued to explain unique variance in reward bias even when controlling for state PA scores, $\Delta R^2 = .45$, $\Delta F(3, 13) = 4.61$, $p = .021$; trait PA scores, $\Delta R^2 = .36$, $\Delta F(3, 13) = 3.76$, $p = .038$; or both, $\Delta R^2 = .37$, $\Delta F(3, 12) = 3.53$, $p = .049$.

### Control Analyses

*Behavioral Data*

Additional analyses were run to fully explore links between LORETA and behavioral data (Table 5). First, reward and punishment bias had similar means, variances, and ranges, indicating that the correlational findings reported earlier were not due to differences among the conditions in task strategies or psychometric properties. Second, no differences in $d'$ (Macmillan & Creelman, 1991) emerged among the neutral, reward, and punishment conditions, suggesting there were no differences in the ability to accurately distinguish words presented during the verbal memory task (all pair-wise $|ts|(17) < 1.66$, all $ps > .10$). Finally, for all conditions, no significant correlations emerged between RB and $d'$ (neutral: $r = -.33$; reward: $r = -.14$; punishment: $r = -.36$; all $ps > .14$).

*EEG Data*

Fisher tests revealed no differences in correlations between behavioral and LORETA data for subjects performing the verbal memory task on the day of the EEG recording versus a later time ($|Z| < 1.53$, n.s.). Moreover, no significant differences in alpha2 or behavioral data were seen between male ($n = 8$) and female ($n = 10$) participants, or among subjects performing the punishment ($n = 8$), reward ($n = 6$), or neutral ($n = 4$) condition first. Thus, the links between EEG and behavioral data were not affected by gender or counterbalancing.

## DISCUSSION

The goals of the present study were to investigate (a) whether resting EEG alpha activity was associated with reward bias in a separate verbal memory task performed under varying incentive (monetary) conditions and (b) the EEG sources that underlie approach-related behavioral tendencies. Using a promising source-localization technique to estimate intracerebral sources underlying scalp-recorded brain electric activity, we found that alpha2 current density in three left dorsolateral PFC regions, the medial OFC, and the left parietal lobe[2] was negatively correlated with reward bias, suggesting that higher activity in these regions (reflected in lower alpha2 current density) was associated with a stronger reward bias on the task. Thus, subjects with increased resting medial OFC and left PFC activity had a higher propensity to define an ambiguous stimulus as a target when reward was involved than did subjects with lower activity within these regions.[3]

[2]Because we had no a priori hypotheses for the involvement of left parietal regions in reward bias, we do not discuss the role of this region in this process further.

[3]This study found no relations between right PFC activity and punishment, although such relations are expected from the approach-withdrawal model (Davidson, 2004; Harmon-Jones, 2003). Although the reasons for this null finding are not entirely clear, it is possible that the punishment manipulation was not powerful enough to induce withdrawal-related tendencies (subjects could avoid monetary loss through correct target identification).

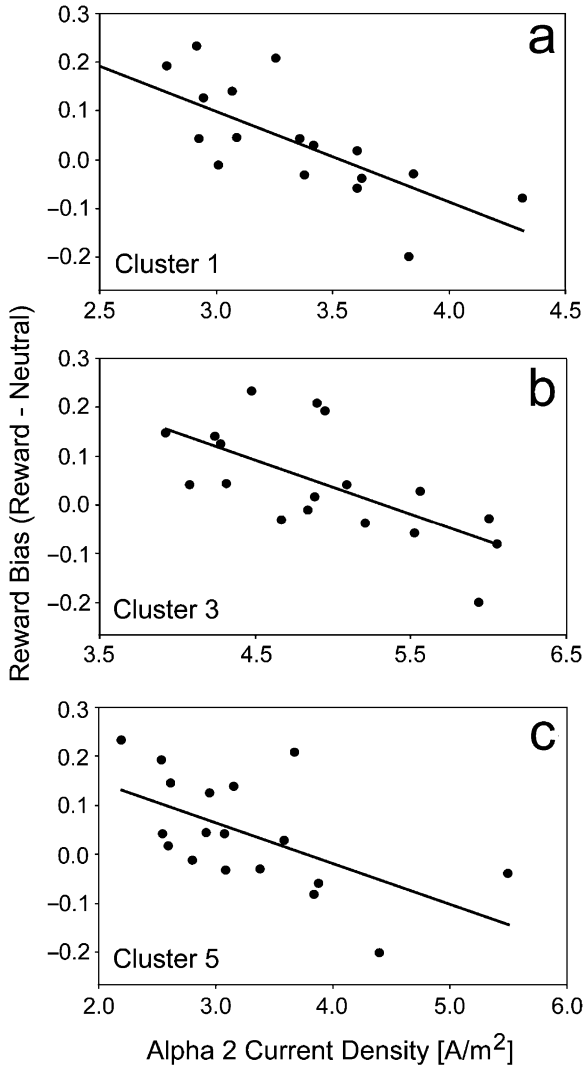


**Fig. 2.** Reward bias as a function of mean LORETA (low-resolution electromagnetic tomography) alpha2 activity in Cluster 1 (a), Cluster 3 (b), and Cluster 5 (c). For each cluster, the regression line is shown. See Table 1 for a description of the clusters. Higher alpha2 current density reflects lower activity. For the abscissa, values are scaled to amperes per square meter ($A/m^2$).

Three additional analyses highlighted the specificity of these findings. First, for clusters encompassing the superior frontal, middle frontal, and precentral gyri (Clusters 1 and 2), as well as medial PFC regions involving medial OFC and the ventral anterior cingulate cortex (Cluster 5), the correlation between alpha2 current density and reward bias was significantly different from the one between alpha2 current density and punishment bias. Second, correlations between reward bias and current density in the left PFC were significantly different from correlations between reward bias and current density in the homologous right PFC regions, suggesting that the findings were specific in terms of laterality; this laterality effect was replicated in an alternative approach using an intracerebral asymmetry index. Third, correlations involving alpha2 current density were significantly different from the ones involving alpha1 current density, indicating that the findings were specific to the upper alpha band. Overall, these findings indicate that relatively increased baseline activity in left dorsolateral PFC regions and medial OFC was associated with stronger reward responsiveness in a separate task performed later.

**TABLE 2**
*Analysis of Condition Specificity*

| Cluster | Spearman correlation: Reward bias and alpha2 activity | Spearman correlation: Punishment bias and alpha2 activity | Spearman correlation: Reward bias and punishment bias | Meng's test $Z$ |
|---|---|---|---|---|
| Cluster 1 | −.83**** | −.43 | .49* | −2.29* |
| Cluster 2 | −.64** | −.17 | .49* | −2.05* |
| Cluster 3 | −.65*** | −.36 | .49* | −1.34 |
| Cluster 4 | −.71*** | −.52* | .49* | −1.06 |
| Cluster 5 | −.65*** | −.16 | .49* | −2.17* |
| Cluster 6 | .77**** | .47* | .49* | 1.68 |

**Note.** Analyses involve correlations between alpha2 activity averaged across a given cluster and reward or punishment bias.
*$p < .05$. **$p < .01$. ***$p < .005$. ****$p < .001$ (two-tailed).

Together with previous EEG studies highlighting links between tonic frontal brain asymmetry and individual differences in dispositional affect (Tomarken, Davidson, Wheeler, & Doss, 1992), well-being (Urry et al., 2004), behavioral approach tendencies (Harmon-Jones & Allen, 1997), reactivity to affective cues (Wheeler et al., 1993), and emotional regulation (Jackson et al., 2003), the present study adds to a growing literature suggesting that left prefrontal regions are critically implicated in an approach system that facilitates appetitive behavior and certain forms of affect that are approach related. Our findings extend this literature in several important ways.

First, they suggest that individual differences in baseline frontal brain activity lawfully predict subjects' propensity to modulate behavior as a function of incentives. Higher left pre-

**TABLE 3**
*Analysis of Laterality Specificity*

| Cluster | Spearman correlation: Reward bias and alpha2 activity in the cluster | Spearman correlation: Reward bias and alpha2 activity in the homologous cluster | Spearman correlation: Alpha2 activity in the cluster and in the homologous cluster | Meng's test $Z$ |
|---|---|---|---|---|
| Cluster 1 | −.83**** | −.15 | .22 | −2.87*** |
| Cluster 2 | −.64** | −.01 | .06 | −2.02* |
| Cluster 3 | −.65*** | −.18 | .30 | −1.78 |
| Cluster 4 | −.71*** | .25 | −.07 | −2.90*** |
| Cluster 5 | −.65*** | — | — | — |
| Cluster 6 | .77**** | .03 | −.18 | 2.44* |

**Note.** Analyses involve correlations between alpha2 activity averaged across a given cluster and reward bias.
*$p < .05$. **$p < .01$. ***$p < .005$. ****$p < .001$ (two-tailed).

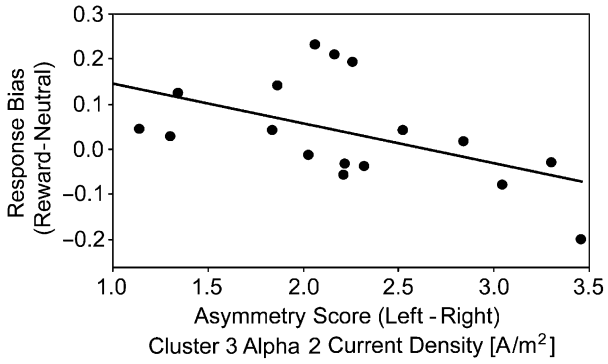


**Fig. 3.** Reward bias as a function of the asymmetry index score for LORETA (low-resolution electromagnetic tomography) alpha2 activity in Cluster 3. The regression line is also shown. The asymmetry index score was computed by subtracting alpha2 activity in the right hemisphere from alpha2 activity in the homologous cluster in the left hemisphere. On the *x*-axis, smaller values reflect relatively lower left than right alpha2 activity (i.e., relatively higher left activity). For the abscissa, values are scaled to amperes per square meter ($A/m^2$).

frontal activity recorded in a separate session was associated with a more liberal response style that led to maximization of earning. Second, the analyses revealed a high degree of specificity; no relations were observed between left prefrontal activity and punishment bias or between right prefrontal activity and reward bias. Third, the use of a distributed source-localization technique made it possible to identify, we believe for the first time, different territories within the PFC that underlie individual differences in approach-related behavior, or at least in the degree of reward responsiveness. Accordingly, higher baseline activity within three distinct regions in the dorsolateral PFC (BAs 6, 8, 9, 10, and 46) and in the ventromedial PFC (BAs 10 and 11) was associated with stronger reward bias. Fourth, regression analyses showed that subjects differing in PFC asymmetry reacted differently to emotional elicitors even when baseline mood was partialed out. Specifically, left PFC alpha2 current density predicted unique variance in reward bias even after controlling for state and trait positive affect.

**TABLE 4**
***Analysis of Band Specificity***

| | Spearman correlation | | | |
|---|---|---|---|---|
| Cluster | Reward bias and alpha2 activity | Reward bias and alpha1 activity | Alpha2 activity and alpha1 activity | Meng's test *Z* |
| Cluster 1 | −.83**** | −.16 | .52* | −3.43**** |
| Cluster 2 | −.64** | −.08 | .46 | −2.30* |
| Cluster 3 | −.65*** | .05 | .44 | −2.78*** |
| Cluster 4 | −.71*** | −.45 | .78*** | −1.96* |
| Cluster 5 | −.65*** | −.35 | .77*** | −2.04* |
| Cluster 6 | .77**** | .30 | .39 | 2.22* |

**Note.** Analyses involve correlations between alpha2 or alpha1 activity averaged across a given cluster and reward bias.
*$p < .05$. **$p < .01$. ***$p < .005$. ****$p < .001$ (two-tailed).

These findings are consistent with the hypothesis that individual differences in PFC activation are associated not with hedonic tone (e.g., positive affect), but rather with a propensity to show approach-related behavioral tendencies in response to specific cues. Conceptually, these results provide further evidence for a model in which individual differences in prefrontal activation asymmetry reflect a diathesis that modulates reactivity to emotionally salient cues (Davidson, 2004).

### Putative Functional Dissociation Among PFC Regions

In this study, the dorsolateral PFC and medial OFC regions were both implicated in individual differences in reward responsiveness. Although studies in nonhuman primates have shown that neurons in both the dorsolateral PFC (Kobayashi et al., 2002; Tsujimoto & Sawaguchi, 2004) and the OFC (Roesch & Olson, 2004) fire during expectation of reward, recent data emphasize important functional specialization within the PFC.

In a recent study, Wallis and Miller (2003) found that neuronal activity in the dorsolateral PFC encoded both the amount of reward and the forthcoming behavioral response, whereas neurons in the OFC reflected only the amount of reward. Further, reward-based OFC activation peaked approximately 80 ms earlier than dorsolateral PFC activation, suggesting that reward information may be transferred from the OFC to the dorsolateral PFC to guide behavior.[4] A similar key role of the dorsolateral PFC in guiding behavior was demonstrated by Barraclough, Conroy, and Lee (2004). In their study, animals selected future choices on the basis of prior history of reward for choosing a given target and prior choices. Dorsolateral PFC neurons coded the integration of these two factors, which suggests that this region was instrumental for adaptive decision making in an unpredictable environment.

Studies with nonhuman primates have implicated the OFC in tracking relative preferences for rewarding stimuli rather than the physical properties of stimuli (Dias, Robbins, & Roberts, 1996). Interestingly, a recent meta-analysis suggests that medial OFC regions are critically implicated in reward monitoring, whereas lateral OFC regions are related to evaluation of punishers (Kringelbach & Rolls, 2004). Consistent with this functional specialization, the current study revealed associations between medial OFC regions and individual differences in reward responsiveness.

In sum, the dorsolateral PFC appears to be critically involved in maintaining goal representation and in anticipating future affectively charged events. The OFC, in contrast, appears to subserve evaluation of reinforcers and learning of stimulus-incentive associations and thus plays a key role in the motivational control of goal-directed behavior. The present findings suggest

[4]In the present study, of the nine correlations between pairs of PFC and OFC clusters, eight were significant ($rs > .53$, $ps < .025$), highlighting functional connectivity within frontal regions. The only exception was the correlation between Clusters 2 and 5.

**TABLE 5**
*Summary of Behavioral Results*

| | Condition | | | Difference score | |
|---|---|---|---|---|---|
| Measure | Neutral | Punishment | Reward | Reward – neutral | Punishment – neutral |
| Response bias | | | | | |
| Mean (*SD*) | .58 ± .17 | .59 ± .15 | .62 ± .16 | .04 ± .11 | .01 ± .11 |
| Minimum | .28 | .31 | .27 | −.20 | −.15 |
| Maximum | .85 | .83 | .91 | .23 | .24 |
| *d′* | | | | | |
| Mean (*SD*) | 1.24 ± 0.46 | 1.23 ± 0.45 | 1.12 ± 0.45 | −.012 ± 0.43 | −0.01 ± 0.42 |
| Minimum | 0.41 | 0.39 | 0.31 | −0.81 | −0.52 |
| Maximum | 2.07 | 2.35 | 2.26 | 0.56 | 1.08 |

that resting activity in these regions is associated with tendencies for approach-related behavior manifested through increased reward responsiveness. From a functional perspective, higher resting OFC and left PFC activity may increase readiness to develop approach tendencies, resulting in stronger reinforcement representations. In the context of this study, such a mechanism would account for the association between resting alpha2 activity and reward bias on the verbal memory task. Future studies measuring brain activity concomitantly with the emergence of a reward bias are needed to test this conjecture.

### Implications

Findings from the present study may provide valuable insight into questions that concern other fields of psychology. For instance, much investigation in social psychology has centered on the influence of approach and avoidance behaviors on emotions and reasoning (e.g., Chen & Bargh, 1999). However, except for a study by Gray, Braver, and Raichle (2002), little work has examined the neural generators underlying approach and avoidance behaviors and their relations to cognitive and affective functioning. This study helps to narrow the void by showing that individual differences in OFC and left PFC resting activity are associated with differential propensity to engage in appetitively motivated behavior. Similarly, although developmental psychologists know that children with attention deficit and hyperactivity disorder (ADHD) are hypersensitive to reward (e.g., Tripp & Alsop, 1999), not much is known about the underlying neural substrates. Our findings suggest that future research could utilize similar methodologies to identify ADHD subtypes characterized by reward hypersensitivity. Finally, clinical psychologists have described reward-processing dysfunction in various psychopathologies, including depression, schizophrenia, and substance abuse. The present identification of lawful relations between resting brain activity and reward bias may provide an objective tool for investigating the pathophysiology of these mental diseases and refining their phenotypic definitions.

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