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Corticolimbic Mechanisms in Emotional Decisions

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Midline frontolimbic networks are engaged in monitoring simple actions. They may also provide evaluative control for more complex decisions. Subjects read a trait-descriptive word and responded either “yes” or “no” within 1,500 ms whether it was self-descriptive. By 300 ms, an electrophysiological discrimination between good and bad words was seen over centromedial regions of the frontal lobe for both friend and self-decisions. By 350 ms, an interaction effect between evaluation and endorsement appeared, and by 500 ms, activity specific to self-evaluation was seen in both anterior and posterior midline sites. An evaluative decision thus begins by recruiting motivational and semantic influences within limbic networks, and these influences appear to shape the development of the decision within multiple neocortical regions.

Recent cognitive neuroscience research has gathered important evidence on the self-regulatory functions of the frontal lobe, particularly in relation to cognitive processes of memory and attention. For example, cerebral blood flow and metabolism studies have confirmed the activation of frontal cortex in human working memory in which representations of sensory cues are maintained to guide responses (Courtney, Petit, Haxby, & Ungerleider, 1998). This research is consistent with electrical recordings from monkey frontal cortex (Fuster, 1989; Wilson, O’Scalaidhe, & Goldman-Rakic, 1993), suggesting that the mnemonic substrate of human cognition has evolved from more elementary mechanisms of primate working memory.

Although many of the recent frontal lobe findings involve activation of neocortical regions, there are also consistent activations of paralimbic frontal cortices, including the anterior cingulate cortex. Particularly when tasks demand attention, or when they require the coordination of cognitive resources, activation of the anterior cingulate is a consistent finding (Posner, 1992; Posner & Petersen, 1990). These results have suggested that the anterior cingulate is a pivotal structure in the frontal executive control of attention (Posner & Dehaene, 1994). An alternative interpretation of the anterior cingulate is that this area of limbic motor cortex is engaged when there are conflicting response demands (Carter, Mintun, & Cohen, 1995). Although electrophysiological research shows that the anterior cingulate becomes active when errors are detected (Dehaene, Posner, & Tucker, 1994; Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Gehring, Coles, Meyer, & Donchin, 1995; Gehring, Goss, Coles, Meyer, & Donchin, 1993; Gevins et al., 1989; Luu, Collins, & Tucker, 2000), some findings suggest that increased anterior cingulate activity may be observed in the absence of errors when experimental conditions create conflicting demands for the motor response (Carter et al., 1998).

Corticolimbic Networks in Evaluating Actions

The ability to monitor errors and regulate actions accordingly has long been an important clue to the

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executive function of the frontal lobe (Luria, Pribram, & Homskaya, 1964). Integral to the executive process is the capacity for assessing the significance of an error and weighing this significance in relation to personal goals (Konow & Pribram, 1970). Research with electroencephalographic (EEG) measures on tasks requiring rapid motor responses has revealed a number of effects in the frontal lobe that may shed light on the relation of limbic to neocortical processing.

When subjects make an error on a speeded task, a negativity develops over the frontal midline immediately after the response (peaking at about 90 ms postresponse). Because this negativity, termed the *Ne* (Falkenstein et al., 1991), or error-related negativity (ERN; Gehring et al., 1993), begins to develop at the time of the response, it appears to reflect a monitoring or control process that operates in parallel with the response organization rather than subsequent to it. By examining a dense array EEG recording, Dehaene et al. (1994) found that the ERN was localized to medial frontal cortex, consistent with a source in the anterior cingulate gyrus, or supplementary motor area (Dehaene et al., 1994). Considering blood flow evidence that the anterior cingulate is active when subjects must decide between conflicting responses (Carter et al., 1995), Carter and associates interpreted the ERN as additional evidence of the engagement of the cingulate gyrus under conditions of response conflict (Carter et al., 1998).

Although conflict monitoring must be an integral component of the executive functions, the importance of evaluation in response monitoring has been recognized in several recent ERN experiments as well. For example, Luu et al. (Luu, Collins et al., 2000) recruited subjects who were high in negative affect, a summary psychometric dimension including components of anxiety and hostility. In the beginning of the experiment, when their performance indicated they were highly motivated, the high-negative affect subjects showed larger ERNs than the low-negative affect subjects. However, later in the experiment, when their performance and self-report indicated that they had disengaged from the experiment, the subjects high in negative affect showed smaller ERNs (Luu, Collins et al., 2000). Although the nature of the subject's motivational engagement was thus critical to the effects of negative affect on the ERN, it was specifically negative affect and not positive affect that determined the individual differences in the ERN in this experiment (Luu, Flaish, & Tucker, 2000).

When subjects are given feedback on their success in estimating a time interval, an ERNlike component is seen to the feedback stimulus (Miltner, Braun, & Coles, 1997). We observed a similar effect when presenting feedback on performance on a spatial memory task (Tucker, Hartry-Speiser, McDougal, Luu, & deGrandpre, 1999). In addition, when subjects viewed a bad target in this task, there was a focal negativity over the midfrontal region in comparison with the response to a good target. The engagement of medial frontal regions not only for feedback stimuli but for the initial discrimination of bad versus good targets suggests that the ERN may be engaged not only by error-monitoring and motor conflict but by evaluative decisions more generally (Tucker et al., 1999).

To separate the evaluative or affective response to feedback from the response-correction process, Luu and Tucker (2003) delayed the feedback on performance in a response-compatibility task in which spatially compatible and incompatible responses were required to be performed quickly. Because feedback (letter grades A, C, or F on the speed of response) was delayed for five trials, it could not be used to adjust responses but still elicited an evaluative response. The response to feedback elicited a medial frontal feedback-related negativity, as in the Miltner et al. (1997) study, and the errors elicited a medial frontal ERN. Although the head surface electrical topographies of these effects were similar, source analysis suggested that they stem from different regions of the cingulate gyrus. Whereas dipole sources in both the ventral anterior cingulate gyrus and the dorsal or midcingulate gyrus were required to model the ERN accurately, the feedback-related negativity was fully accounted for by activity of the midcingulate source.

Evidence of differential responses in specific regions of the cingulate gyrus has also appeared in hemodynamic neuroimaging studies. Bush, Luu, and Posner (2000) reviewed a number of studies in which emotional responses were associated with activity in the more ventral (subgenual) region of the anterior cingulate gyrus, whereas task demands on conflict or cognitive effort engaged more dorsal regions of the anterior cingulate. Further suggestion of the importance of the ventral anterior cingulate in emotional responses was provided by Mayberg et al. (1999), who observed that depressive patients showed not only increased activity in the subgenual anterior cingulate region in a positron emission tomography (PET) study but also showed an inverse relation between subgenual cingulate activity and activity in right dorsolateral frontal cortex. In contrast, depressives who responded favorably to treatment showed a decrease in subgenual cingulate activity and an increase in right dorsolateral frontal activity. Mayberg et al. proposed that there may be a reciprocal balance between neocortical (dorsolateral frontal) and limbic (subgenual anterior cingulate) networks. In depression, the balance may shift toward excessive emotional constraint associated with limbic dominance.

Corticolimbic Networks in Cognitive Evaluation

These several findings suggest that activity in limbic regions of the frontal lobe may apply emotional influences on cognition that may be exaggerated in psychopathology, but that may be important to the adaptive control of normal cognition as well. The theoretical question raised by these results is why the motor control pathways (anterior cingulate, supplementary motor area) and their associated limbic circuits appear to be so important to the evaluative control of cognition. The answer may be that cognition is not a disembodied mental faculty but an emergent function of the self-regulation of the brain's sensory and motor systems (Jackson, 1879). The limbic base of the motor pathway may recruit arousal and evaluative controls not only for concrete actions but also for abstract cognition (Brown, 1977).

In terms of psychological mechanisms, classical cognitive studies have shown that evaluative judgments form a foundation for semantic representations. Factor analytic studies suggest that an evaluative (good–bad) dimension consistently explains how words are used to convey meaning, even in abstract, subtle, or aesthetic decisions (Osgood, Suci, & Tannenbaum, 1957). It may be at the level of this evaluative semantic dimension that limbic networks shape decision making in everyday situations.

In terms of neural mechanisms, limbic circuits have long been recognized as important to integrating emotional responses with cognition (Papez, 1937). An important effect of brain lesions may be to exaggerate emotional responses through releasing limbic and subcortical mechanisms from cortical control (Monrad-Krohn, 1924; Tucker, 1981). Recent models of frontal lobe regulation of emotion have recognized the importance of understanding frontolimbic interactions (Davidson, 2002).

In terms of neural connectivity, progress in neuroanatomical studies over the last several decades (e.g., Pandya & Yeterian, 1985) has provided a new framework for understanding the connectivity that mediates corticolimbic interactions (Tucker, 2001). At the core of the brain is the limbic system, regulated by motivational influences from the hypothalamus (Swanson, 2000). The limbic cortices receive extensive hypothalamic projections, supporting the functions of the cingulate cortex in visceromotor control and the insular cortex in viscerosensory control (Neafsey, Terreberry, Hurley, Ruit, & Frysztak, 1993). Surrounding this limbic core is a "shell" of cortical modules that is the primary sensory and motor neocortices (Pandya & Yeterian, 1985) that interface with the environment. Research on memory has shown that consolidation of new memories requires some traffic between specific (sensory and motor) neocortical networks and the general (motivational) limbic networks (Squire, 1986). The implication of this architecture is that memory and cognition must arbitrate between the visceral core of the brain, which provides evaluative and motivational control, and the somatic shell, which provides articulation of affects and motives into specific perceptions and actions (Tucker, 2001).

Applying this general model to a more specific formulation of anterior cingulate contributions to evaluative decisions, we proposed an explanation for why limbic motor cortex (the anterior cingulate) is active early in an evaluative (good–bad) decision (Tucker et al., 1999); a decision is an implicit urge toward action. Even when there is no overt action, the visceromotor base of the motor pathway provides an incipient, emotionally charged motor impulse. This impulse or urge serves as a primitive, vectoral motive (Werner, 1957), which then forms both an evaluative basis and an implicit prediction for the developmental control of the decision as it is actualized within frontal neocortical networks (Brown, 1977). From this perspective, the pseudodepression and lack of motivational initiative seen with mediodorsal lesions (Blumer & Benson, 1975) show the effect of impairing the limbic motivational base of behavior. Similarly, the psychomotor retardation seen in severe depression (American Psychiatric Association, 1994) shows how an impaired mood level disrupts the hedonic engagement of the motor impulse: Although the impulse to action may often have a positive hedonic emotional charge, the increased ERN in subjects high in negative affect (Luu et al., 2000) or with obsessive–compulsive disorder (Gehring, Himle, & Nisenson, 2000) suggests that anxiety or negative affect may be an essential impetus to action in midline frontal circuits as well. The fact that electrical responses are observed from the limbic motor region of frontal lobe when stimuli are evaluated for their motivational significance (Luu, Tucker, Derryberry, Reed, & Poulsen, 2003; Tucker et al., 1999) is consistent with the proposal that cognitive evaluation engages a latent, visceral urge to action. If so, then electrical field changes in dorsomedial frontal cortex may reflect the dynamic regulation of the incipient evaluative response not only under conditions of immediate response control, as in the ERN, but in any emotionally significant decision process.

The Present Study

We hypothesized that making complex evaluative judgments about human personality would engage similar regions of dorsal limbic cortex, as seen for the evaluation of simple events and actions. Specifically, based on the medial frontal electrophysiological responses to evaluative feedback on performance in the above research (Luu, Collins et al., 2000; Tucker et al., 1999), we hypothesized that evaluation of bad traits would be associated with a focal surface-negative electrical field over centromedial frontal cortex in the 300–400 ms interval, whereas evaluation of good traits would be associated with relatively positive-surface electrical waves in medial frontal region in this interval. Although some evidence suggests that surface-negative fields indicate local cortical activation, whereas surface-positive fields indicate inhibition (Rockstroh, Elbert, Canavan, Lutzenberger, & Birbaumer, 1989), we framed the current hypothesis empirically, based on the medial frontal "evaluative negativity" seen to bad targets and the relative positive-medial frontal electrical field to good targets in the video game in our previous study (Tucker et al., 1999). The hypothesis was tested with a priori statistical contrasts directed toward midline scalp electrode sites at this time interval.

In addition to making self-evaluative judgments, we asked subjects to read the same trait words (see Appendix) in a separate condition and decide whether each trait applied to a well-known friend. This manipulation provided a contrast to separate evaluative processes unique to self-evaluation from those used to evaluate personality characteristics generally. A number of studies have shown that primate frontal networks show motor and preparatory responses while observing the actions of others (Iacoboni et al., 1999). In addition, there is evidence of cingulate activation in social observation of pain. Human subjects showed activation in anterior cingulate networks in response to viewing another person being pricked with a pin (Hutchinson, Davis, Lozano, Tasker, & Dostrovsky, 1999). We hypothesized that evaluative decisions about a friend would engage the same evaluative networks of the brain as self-evaluation, but at a lower intensity because of the lesser emotional significance of evaluating the friend than evaluating the self. In a control condition, subjects were asked just to read each word and press a button, with no decision required.

Given the importance of the orbital frontal lobe (ventral limbic cortex and its neocortical extensions) as a self-regulatory counterpart to mediodorsal networks both in the lesion evidence and in the theoretical models, we also directed a post hoc analysis to frontopolar and ventrolateral electrical fields that may emanate from the ventral pathways of the frontal lobe. In dense array event-related potential (ERP) experiments, orbital and frontopolar effects have been particularly important to response control demands of the task (Potts & Tucker, 2001). Given the clinical evidence on the importance of the orbital frontal lobe in impulse control (Blumer & Benson, 1975; Tucker & Derryberry, 1992), we speculated that orbital frontal pathways may be engaged in inhibiting responses, such as to bad trait words.

Method

Overview

In an initial study, 30 University of Oregon student subjects generated trait words describing favorable or unfavorable personality characteristics that were familiar to young adults at the time. These words were combined with a larger set of trait words from personality research (L. R. Goldberg, 1993). The full item set was then rated by five judges who selected a set of words ($N = 393$) that were vividly descriptive and understandable by students and other community samples. In a separate norming study, these words were rated by 56 different student subjects on five psychometric dimensions. In the dense array EEG–ERP experiment, a new sample of 44 students rated each trait word as descriptive of the self or a friend, or they simply read the word, as EEG was collected.

Trait Word Generation Study

Beginning with a list of trait descriptors used by personality researchers (L. R. Goldberg, 1993), we attempted to add words that would reflect the daily language of the students at the University of Oregon. We started by asking 30 subjects to generate words describing three people they respected, admired, and would like to be and three people they disliked and would not like to be. Subjects were asked to generate 20 words for each person, and they were encouraged to list more than 20 words if they could. Subjects were instructed not to identify the people but to merely indicate their relation to each person. Subjects were also ensured that their responses would be confidential to encourage their honest description of people they liked or did not like. From this process, we gathered, 1,665 descriptive words.

This set of items was added to the 1,943 descriptive nouns from L. R. Goldberg's (1993) list, which was parceled into five sections. Five judges were given two sections each. The judges selected from the list words that they felt the general undergraduate population could understand. The words were also selected on the basis of their descriptiveness, and short words (six letters or fewer) were preferred. Words were selected that would represent either a positive or a negative descriptor (given that some descriptors used for a "liked" person in the previous rating study might have been negative as well as positive). Words that were not selected by at least one judge were dropped from the norming phase. A total of 393 words were retained from this procedure.

Trait Descriptor Norming Study

In the norming phase, 56 subjects provided word norms for the following five scales: (a) a comprehension scale, (b) a social desirability scale, and ratings of how accurate the word was for (c) a person the subject knew well and liked, (d) a person the subject knew well and disliked, and (e) a person the subject knew well but neither liked or disliked. Each subject rated all 393 words on a 5-point scale for one of the dimensions. The number of subjects rating each scale were as follows: 13 for Scale 1, 11 for Scale 2, 11 for Scale 3, 9 for Scale 4, and 12 for Scale 5.

The first criterion was that of word comprehension, ranging from 1 to 5, with 1 being easily recognizable and understandable. A value of 2 was used as the maximum for inclusion.

When subjects rated people they liked (or did not like), it is possible that some negative traits would be appropriate for the liked person (and some positive traits appropriate for the disliked person). To test whether the desirability scores correlated positively with like-accuracy-descriptor scores and negatively with dislike-accuracy-descriptor scores, correlational analyses were conducted. As expected, high desirability scores were positively correlated with like-accuracy-descriptor scores and negatively correlated with dislike-accuracy-descriptor scores. The Social Desirability scale ranged from 1 (*very undesirable*) to 5 (*very desirable*). To ensure that good trait words would have positive valence, only those with a Social Desirability score above 3.5 were included. For the bad trait words, the criterion was a social desirability score less than 1.75. From the word set meeting these criteria, 192 words were selected (half positive, half negative) to construct four trial blocks of 48 words each.

Dense Array EEG Study: Subjects and Task

The subjects in the EEG experiment were 44 University of Oregon psychology students (24 women and 20 men), who were fully informed about the purpose of the research, which was to study the brain processes in making decisions about emotionally significant words. For each of the three conditions of the experiment (self, friend, read-only), the same 192 trait descriptive words were presented in four subblocks of 48 words each. For the self condition, the subject was asked to answer yes or no whether the word applied to him or her most of the time. For the friend condition, the subject was asked to choose a close friend and decide whether each word applied to that friend most of the time. For an additional control condition, the subject simply read the words and pressed alternate keys to advance to the next trial. The order of the three conditions was counterbalanced across subjects.

Trial Procedure

As each word was presented, subjects pressed a button as quickly as possible for each word to indicate "yes" or "no" whether the word described them (or the friend). Rapid decisions were required to fix the timing of the evaluative process in a stereotyped sequence that would allow examination with the ERP averaging of the EEG. The sequence began with a fixation point ("+") for 2,000 ms, then the word was presented for 500 ms, then 1,000 ms was allowed for a response before the next trial began. After a block of 10 practice trials, most subjects were able to decide and respond quickly enough to meet the timing requirement of the trial sequence. If not, the practice block was repeated.

EEG Acquisition

The EEG data were recorded with the 128-channel Geodesic Sensor Net (Tucker, 1993). This device arrays EEG electrodes in a regular distribution across the head surface, with an approximately 3-cm intersensor distance (see Figure 1). The EEG was digitized at 250 samples per second, with a 0.1–50-Hz bandwidth and a vertex recording reference. After artifact

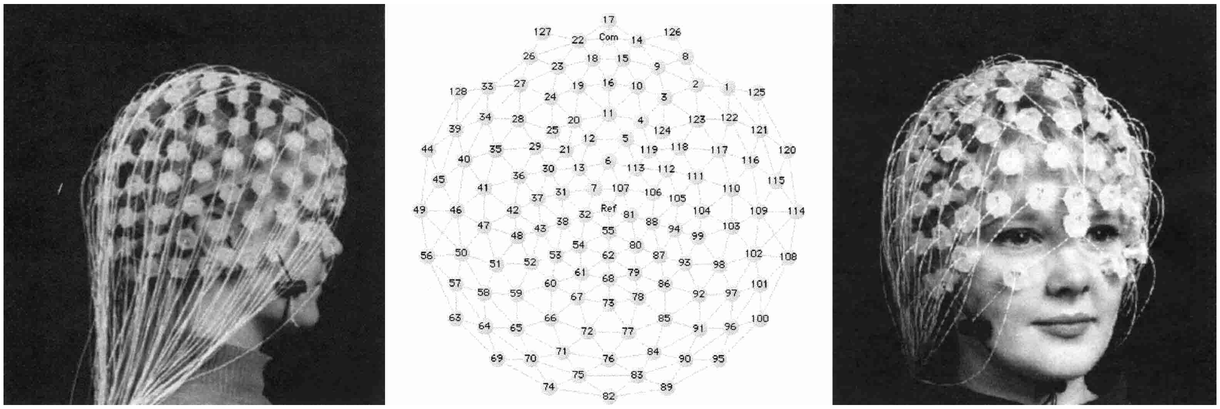

Figure 1. The 128-channel Geodesic Sensor Net (left) arrays electroencephalographic sensors across the head surface in an even distribution. The polar projection of the channel locations (middle) is arranged in a view down on the head, with the nose at the top. Com = isolated common; Ref = recording reference.

rejection, the data were rereferenced to the average reference (Tucker, Liotti, Potts, Russell, & Posner, 1994), averaged to create ERPs, and then examined with both topographic waveform plots (e.g., see Figure 2) and surface electrical field animations (maps every 4-ms sample; selected frames shown in Figure 3) for each experimental condition. Individual subjects' data were examined to evaluate artifacts and to determine the variability of experimental effects across conditions. Estimates of radial current density were made with the Laplacian transform (second spatial derivative of the surface voltages) of the grand averages (averaged waveforms across subjects) to characterize the features of the head surface electrical fields that can be attributed to superficial cortical sources (Perrin, Bertrand, & Pernier, 1987).

Statistical Analysis

All statistical and source analyses were conducted with the scalp voltage (rather than with current density) data. Planned contrasts between the experimental conditions were made with repeated measures analyses of variance (ANOVAs) on the channels and time intervals of interest (primarily the medial frontal sites in the 300–400-ms interval) from each subject's data, with significance levels corrected for sphericity (Greenhouse–Geisser) for factors with more than two levels. For the a priori contrasts, the significance level for ANOVAs and *t* tests were set to $p < .05$, and for the exploratory analyses, the significance level was set to $p < .01$. These significance levels were used to examine the patterning of results in the random-effects simulation dataset (described below).

Exploratory analyses of the brain responses to the experimental manipulations were carried out through visual inspection of each condition's data, with topographic waveform plots and surface electrical field animations, and through both main and interaction effect experimental contrasts with the Student's *t*-test electrical field animations. For each time sample and each channel, the *t* test expresses the difference between two experimental conditions, normalized by the variance across subjects. Interaction effects reflect the difference between condition differences. The electrical field *t*-test animations are then created by interpolating head surface maps and animating them over time (Tucker et al., 1994). The color palette for the *t*-test maps was set to reflect the significance levels of the *t* contrasts.

To calibrate the interpretations for the chance patterns of significance (in space and time), based on the multivariate distribution characteristics of this sample of subjects, a random effects dataset was created by reversing the sign of every other subject's averaged ERP, thus fixing the condition mean ERP waveform to zero but retaining the variance across subjects. This procedure shows the number and spatial patterning of results that can be expected by chance at each significance level, given the distribution characteristics of the specific dataset, and was used to inform the post hoc interpretation of the experimental results. The random effects results occasionally showed spatially coherent regions of significant effects, but these were never consistent over time for the tens of milliseconds seen with the experimental results. However, because of the number of contrasts with the dense array data, caution is warranted in interpreting post hoc effects until they are replicated.

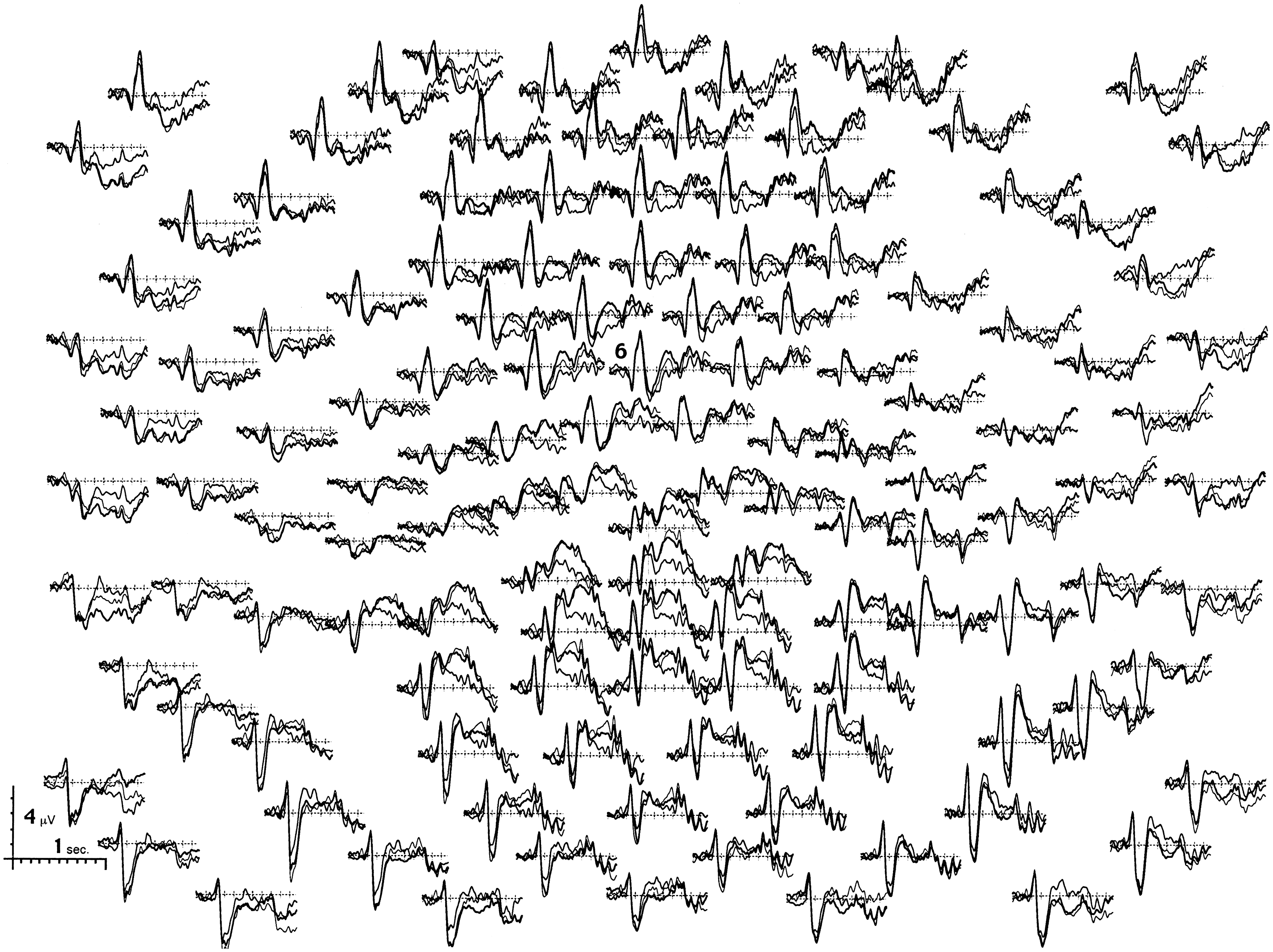

Figure 2. Waveform plots for all channels, with an average reference derivation, arranged in a topographic pattern to show the spatial relation of the electric fields. This plot shows the averaged event-related potential collapsed over word valence and endorsement for the self-evaluation (thick line), friend evaluation (thin line), and read-only (medium line) conditions. Channel 6 (corresponding to FCz in the 10–20 system) is marked to aid orientation.

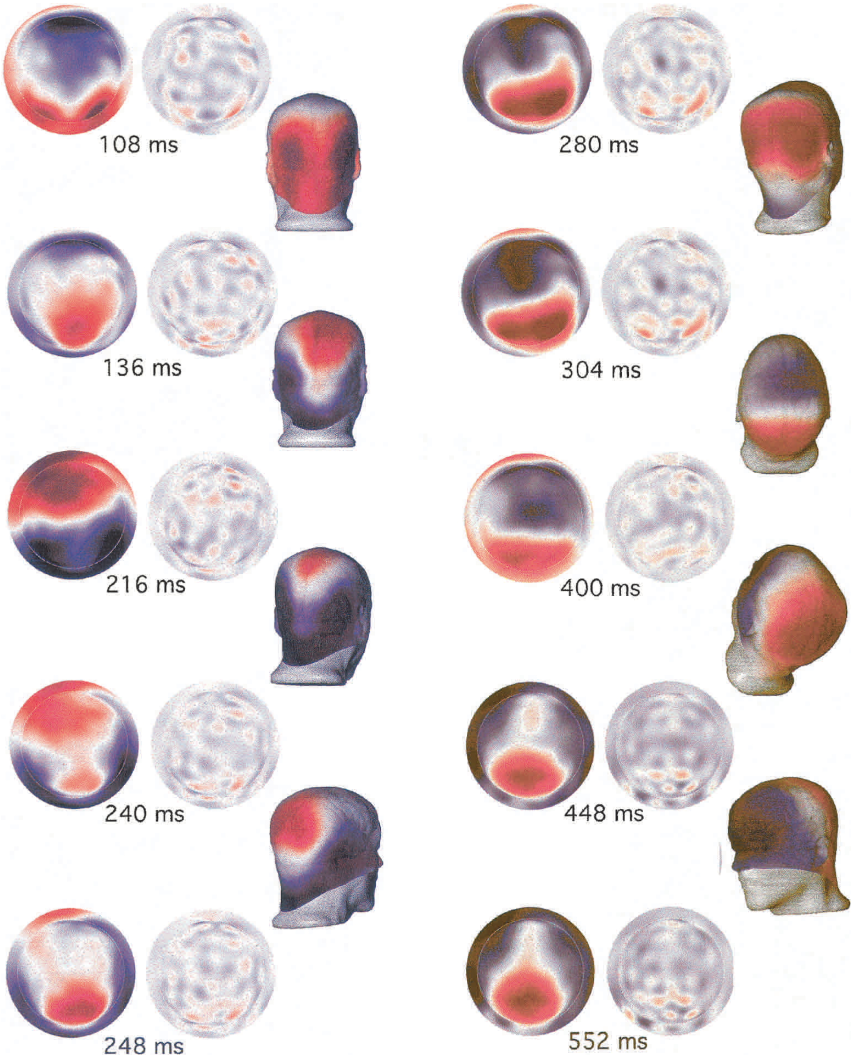

Figure 3. Selected frames from the grand-average electrical field animations to show the averaged event-related potential (ERP) features that were common across experimental conditions (these data represent "yes to good word," collapsed over rating conditions). For each time sample, the circle on the left is the voltage map, with red positive, white zero, and blue negative. For all voltage maps, the palette range is set to ±2 *SD*s of the voltage excursions over the epoch. The circle at the right is the Laplacian estimate of radial current source density. For both circle maps, there is an inner circle reflecting a polar projection of the head above the canthomeatal (eye-to-ear) line and an outer ring reflecting the "unwrapped" projection of the data below this line. The three-dimensional head model shows the realistic surface distribution for each of these intervals in the averaged ERP.

Source Analysis Strategy

Dipole source analysis (Scherg, 1989) was conducted on the grand averages with the Brain Electrical Source Analysis package (MEGIS, GmbH, Munich, Germany) to characterize the major features of the voltage surface topography and to test the hypothesized localization of the a priori statistical tests. The rationale was to begin with a source model that characterized the major electrical events of the visual ERP. Additional sources were then evaluated that could explain the differential brain response to the experimental manipulations. By the principle of mutual exclusion (M. Scherg, personal communication, May 2001), a strong logical test can be applied to each incremental source that is added to an adequate base source model. If the original sources are adequate, then there is no variance in the electrical field to be explained by the additional sources, and the contribution of the additional sources to the reduction of residual variance will be negligible. The principle of mutual exclusion has proved particularly useful with dense array data sets. Whereas with sparse (e.g., 32-channel) recordings, the addition of an unnecessary dipole to a source solution may result in instability caused by pathological (ambiguous) interactions among the sources in explaining the sparse set of potential recordings; with a dense array (128 or 256) recording, dipole sources can be fit to the obvious sensory or motor potentials, and then additional sources can be tested sequentially and systematically because the original model remains highly stable.

In the present study, a source analysis was first developed for the early visual (P1, N1) components common to all conditions. Next, additional sources were added for the later ERP components, including the P300 modeled by temporoparietal sources (e.g., see Figure 10). Then, for each of the major condition differences revealed by the *t*-test contrasts, sources were examined that may have contributed to those task differentiations (e.g., good vs. bad words, yes vs. no responses) by modeling the *t*-test contrasts directly. The sources suggested by the *t*-test contrasts were then added to the initial electrical source model to determine whether they contributed meaningful variance to the condition source models and to the condition discriminations. Following the principle of mutual exclusion, only sources that substantively improved the overall model were reported as reasonable explanations of the experimental-condition differences.

Results

Behavioral Analysis

The mean number of endorsed items per condition did not differ between the sexes (males = 39.3, females = 33.7), $F(1, 42) = 2.14$, $p > .15$, or between the rating conditions (self-rating = 36.3, friend rating = 36.0), $F(1, 42) < 1$; nor did sex and rating condition interact, $F(1, 42) < 1$. There was, however, the expected main effect of valence, such that good words (those with positive valence) were endorsed more often ($M = 46.0$) than bad words (those with a negative valence; $M = 26.3$), $F(1, 42) = 46.96$, $p < .01$.

An ANOVA with the response times (RTs) showed a significant interaction of endorsement (yes–no) with evaluation (good–bad), $F(1, 42) = 5.75$, $p < .03$. Yes responses to good words were 20 ms faster (mean RT = 679 ms) than no responses to good words (mean RT = 699 ms). We found intermediate latencies for responses to bad words (mean RT for yes responses = 694 ms; and mean RT for no responses = 691 ms). There were no significant differences in RTs between males and females, self- or friend-rating condition, or good and bad words. Self-rating responses (mean RT = 687 ms) were similar to friend-rating responses (mean RT = 695 ms), and positively valenced words (mean RT = 689 ms) were similar in RT to negatively valenced words (mean RT = 693 ms). There was a significant main effect of endorsement (yes responses faster than no responses), which was modified by a significant interaction with valence, $F(1, 42) = 5.75$, $p < .03$, such that endorsements of good trait words were faster (mean RT = 679 ms) than rejections of good words (mean RT = 699 ms). For bad trait words, however, the response speed was similar for endorsed (mean RT = 694 ms) and rejected (mean RT = 691 ms) words.

Common Topography and Source Model for the Visual ERP

The general features of the visual ERP were common to all experimental conditions and were consistent with those seen for foveal single word stimuli in previous dense array studies (Curran, Tucker, Kutas, & Posner, 1993; Johnson & Hamm, 2000; Tucker et al., 1994). These common effects can be seen for the average-referenced topographic waveform plots shown for the self, friend, and read-only conditions in Figure 2. Selected surface maps from the electrical field animations are shown in Figure 3. Inspection of the animated surface topographies showed that the first obvious effect was the appearance of two bilateral P1 foci over occipitoparietal areas, beginning at 72 ms and peaking at 116 ms. These were modeled with equivalent regional (3-moment) dipoles in the occipital region. The superficial cortical activity associated with the P1 foci can be seen in the current density map for the 108-ms sample. The current density measure is sensitive to electrical activity immediately under the skull, primarily from the superficial areas of the cortical gyri (Tucker et al., 1994).

The P1 foci merged medially at about 140 ms. Source analysis suggested the medial posterior effect (136 ms) was due to a posterior cingulate or midline parietal generator. At this time, the N1 appears, at inferior occipital sites, modeled by bilateral inferior occipital temporal sources, and it is initially left-lateralized. This observation is consistent with the observation that the N1 to foveal words is typically left-lateralized when subjects are reading for meaning rather than making nonsemantic judgments, such as perceptual discriminations with letter features (Compton, Grossenbacher, Posner, & Tucker, 1991; Tucker et al., 1994). In the present data, the N1 then became right-lateralized at about 210 ms, at which time the frontal P2 peaked (Potts & Tucker, 2001), stronger over the left frontal region. In the animated head surface maps, the bilateral negative foci of the N1 then shifted in topography, inferiorly and toward the temporal lobe, possibly reflecting the sequential activation of adjacent networks of the ventral visual pathway (Tucker et al., 1994). By 240 ms, the negativities of this wave progressed to the lateral inferior temporal regions in both hemispheres, an effect that is only seen with the 128-channel sensor array because of its coverage of the lower skull and neck. In the next 40 ms or so, the positivity over frontal regions appeared to reduce to the midline then shift posteriorly along the midline toward the back of the head. By 300 ms, this now posterior positivity (the "P1 reprise"; Tucker et al., 1994) separates laterally into two overlapping foci slightly superior to the initial P1 locations. The Laplacian estimate of current density actually showed stronger activity at bilateral superficial occipital sites than had occurred for the P1. Also during this interval, and apparently coincident with the P1 reprise, a weak negative focus appeared at the vertex, or just posterior to it. By 400 ms, the P1 reprise waned, and a second posterior, more parietal positivity took form, coincident with the characteristic inferior frontal negativity of the P300, or late positive complex (LPC; Tucker et al., 1999; Tucker et al., 1994). In the particular condition shown in Figure 3 (yes responses to good words), the parietal positivity of the LPC appears to extend to the frontal midline (448 and 552 ms).

Analysis of Overall Condition (Self, Friend, Read) Differences

Inspection of the condition differences in this overall ERP showed, as expected, a smaller LPC for the read-only condition than for the self- and friend-rating conditions (which were fairly similar). The comparison of these conditions for the 400–800-ms interval of the LPC (see Figure 2) shows that the medial parietal positive wave of this effect is somewhat left-lateralized and it inverts particularly strongly over right anterior temporal and frontal sites (suggesting a right-lateralized source for this voltage pattern). In addition, the friend and especially the self-ratings showed an extension of the LPC toward the frontal midline in the 400–600 ms-interval. To examine the reliability of these grand-average condition differences, we conducted a Rating (self, friend, read) × Valence (good, bad) × Endorsement (yes, no) repeated measures ANOVA on the midline and parasagittal sites (the electrodes on either side of the midline showing the LPC effect in Figure 2), with channel groupings for caudality (anterior, posterior) and laterality (left, middle, right). Consistent with the data in Figure 2, there was a significant rating difference, and this effect interacted with the laterality of the LPC, $F(6, 172) = 6.47, p < .001$, such that the asymmetry of the LPC in Figure 2 is seen for both self and friend but not read conditions (see Figure 4). We observed a higher order interaction of this overall LPC test for the Rating × Valence × Endorsement × Laterality interaction, $F(4, 172) = 2.88, p < .04$. The means for this interaction showed that, whereas the overall tests showed self and friend conditions to be similar, there was a clear valence differentiation in the midline frontal sites for the self condition only. This effect was clarified by the a priori analyses focused on the midline sites described below.

A Priori Analyses on Midline Frontal Sites

Within this overall form of the averaged ERP to these words, we conducted an ANOVA to test the hypothesis that frontal midline sites would discrimi-

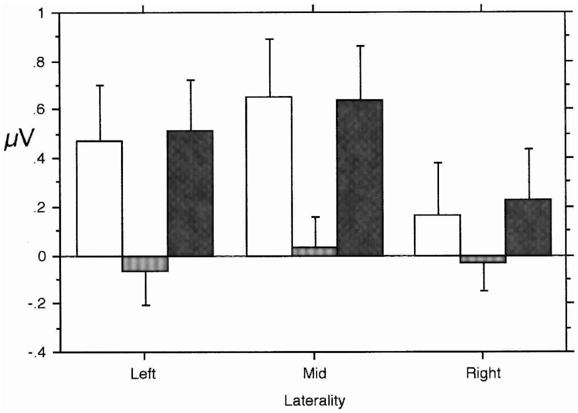

Figure 4. Condition means for the Condition × Laterality interaction for midline and parasagittal channels for the late positive complex (LPC). The LPC is observed for both friend and self-evaluation conditions but only minimally for the read-only condition, and when the LPC is observed, it is left-lateralized at these sites. Open bars represent the friend condition; gray bars represent the read-only condition; solid bars represent the self condition.

nate between good and bad trait words. As in previous research (Tucker et al., 1999), these condition differences at centromedial scalp sites were of small or moderate amplitude but were statistically reliable. None of the endorsement or valence or their interaction effects interacted with the rating procedure until about 450 ms, such that the initial effects appeared to apply equally to decisions made about the self and the friend. There was a temporal sequence to the onset of the experimental effects, with a valence (good–bad) main effect appearing first, at 304 ms, then a Valence × Endorsement interaction appearing at 344 ms, followed by an endorsement (yes–no) main effect at 436 ms.

Valence effect. There were no significant differences in the ERPs for good versus bad words until the 304-ms sample, at which time a difference appeared at centromedial sites. The mean surface topographies across subjects for the good and bad trait words at 304 ms are shown in Figure 5. The primary difference in the electrophysiologic activity in evaluating good versus bad traits at this time was greater relative negativity for bad traits at the centromedial sites, as hypothesized. The map in the center of Figure 5 shows the valence t test, with the color palette adjusted for significance level for this mean difference (good minus bad) with this sample size. As is typical for medial frontal discriminations (Luu, Flaish et al., 2000;

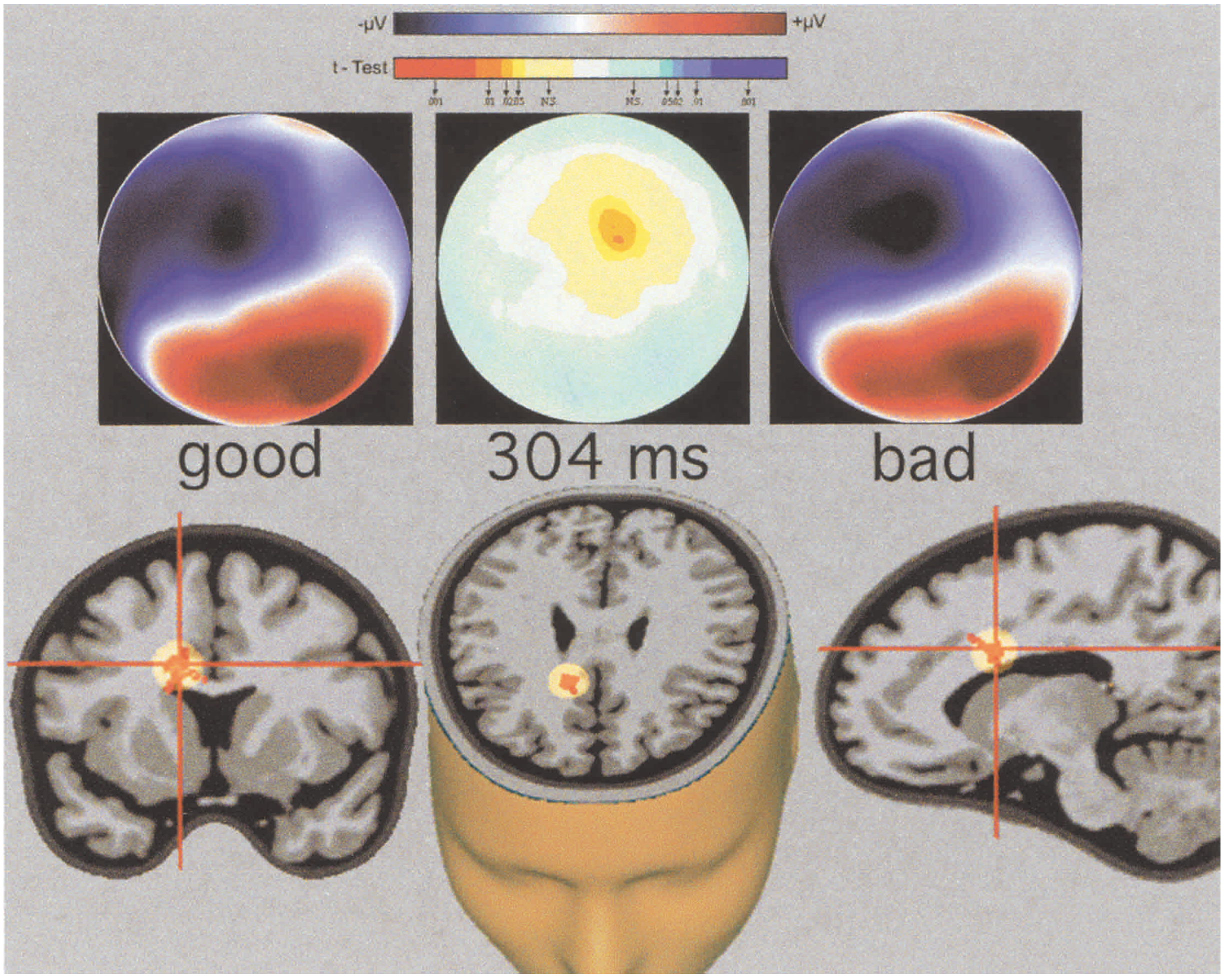

Figure 5. Voltage maps (red, white, blue) for good versus bad trait words at 304 ms. The good minus bad difference map (normalized to Student's t values) in the center is represented with a palette calibrated by significance levels for this sample size (N = 44). Below is the dipole source model fit to this condition difference, with a source localized in the dorsal anterior cingulate cortex (possibly the lower bank of the cingulate sulcus) of the right hemisphere.

Tucker et al., 1999), the condition difference is a small but consistent electrical effect superimposed at centromedial sites on the broad parietal positivity (and inferior frontal negativity) that first characterized the P1 reprise at 280 ms and then the developed P300 or LPC, beginning about 300 ms. Examination of this medial frontal valence effect in individual subjects' data showed that it became fairly consistent across subjects by 304 ms and remained stable until about 332 ms. The grand-average waveforms for the medial frontal sites (around Channel 6) are shown in Figure 6. A repeated measures ANOVA (Valence × Endorsement, collapsed over friend and self-ratings) on the 304–332-ms interval for the right medial frontal locations shown in Figure 5 (Channels 5, 119, 6, 113, 112, 107, 106) showed that the valence main effect was significant, $F(1, 87) = 7.38, p < .01$.

This was the first experiment in which we observed an early medial frontal discrimination to be lateralized; all previous findings with the ERN or evaluative responses have been medial and roughly symmetric. The scalp asymmetry itself is not a strong lateralization sign; a source on the medial wall of the left frontal lobe could produce a right-lateralized surface field. However, the dipole analyses fit to the whole head EEG sampling (described below) were consistent with this right-lateralization of the evaluative (good–bad) discrimination at this early time point.

As with this initial valence effect, the repeated measures ANOVAs continued to parallel the *t* tests closely in each comparison. Examining representative sites, additional ANOVAs showed that the valence main effect remained significant, $F(1, 87) = 7.31, p < .01$, at the 344-ms sample at the centromedial (central midline) site (Channel 6), at 344 ms at the frontopolar sites (Channels 9 and 15), $F(1, 87) = 4.44, p < .04$, and at 424 ms at the centromedial site, $F(1, 87) = 4.50, p < .04$.

We conducted electrical source analysis on the initial valence contrast at 304 ms, as characterized by the *t*-test topography (good minus bad) at this time (see Figure 5, center). The equivalent dipole for this effect

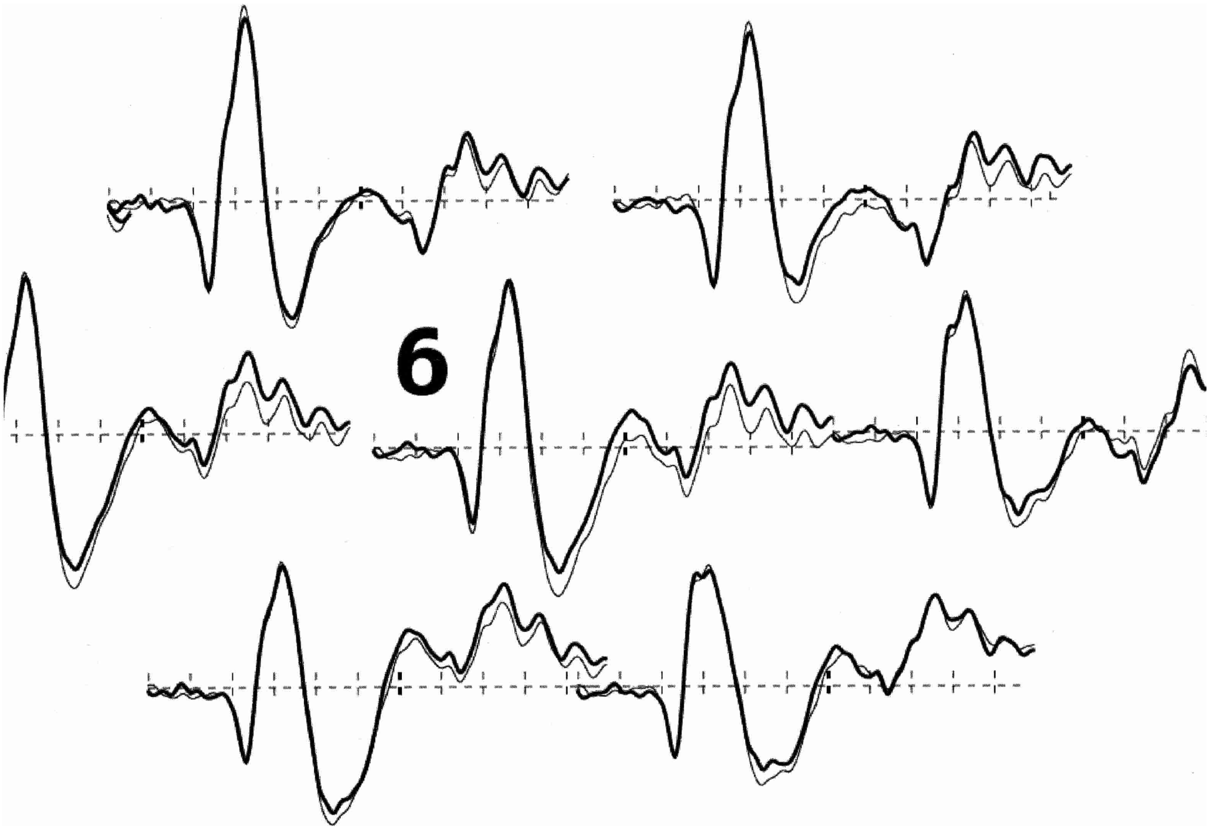

Figure 6. Waveforms for the medial frontal sites (Channel 6 shown for orientation) for the good (thick line) and bad (thin line) words, showing the time course of the valence discrimination.

was localized to the dorsal anterior cingulate cortex of the right hemisphere (see Figure 5, bottom), possibly consistent with a source in the lower bank of the anterior cingulate sulcus. Given the radial appearance of the condition contrast electrical field (see Figure 5, center), a source in the cingulate sulcus would have the correct orientation (whereas a source in the cingulate gyrus would point medially and thus not create a radial surface topography). As a test on the viability of this source, we added this dipole to the overall dipole model for the averaged ERP, as developed for the common topography for all conditions of this experiment (see Figure 3). Under the principle of mutual exclusion, if a source does not contribute explanation to the data, it will receive zero-moment weight when added to a plausible source configuration. The anterior cingulate source shown in Figure 5 showed minimal weight until around the 300-ms point, at which time it received a substantial weight in the overall model and it measurably reduced the residual variance. This result suggested that the modeling of the difference topography (i.e., the *t* test) revealed a plausible source that, although small in amplitude, differentiated meaningfully between the experimental conditions.

Valence × Endorsement interaction. By 344 ms, the *t*-test animations and ANOVAs showed that the initial valence discrimination was joined by a Valence × Endorsement interaction, $F(2, 86) = 9.23$, $p < .004$. At first, this interaction initially seemed to explain the valence effect. However, examination of the *t*-test topographies for the two effects suggested that, although both involved centromedial sites, the initial topography of the valence effect suggested a radial source (see Figure 5), and this was characteristic for the valence effect for the 50 ms or so that it was maintained (see Figure 6). In contrast, the animations of the Valence × Endorsement *t*-test topography showed that the medial frontal positivity for this more complex contrast effect (see Figure 7, center) was exactly coincident in time course with a medial posterior negativity, implying that both surface fields were produced by a source in the mid or posterior cingulate gyrus. Consistent with the surface topography, a dipole source model for the *t*-test contrast for the Valence × Endorsement interaction at 344 ms showed a tangential source in the mid-to-posterior region of the cingulate cortex (see Figure 7, bottom).

Examination of the experimental-condition voltage topographies from which this interaction effect arose (see Figure 7, top) showed that at this 344-ms sample, strong medial frontal negativities were produced by saying no to a good word and saying yes to a bad word. Interestingly, these are both the more negative emotional appraisals of the personality-decision task.

Examining the time course of the Valence × Endorsement interaction in the *t*-test animations showed that this effect was sustained over 100 ms from its appearance at about 340 ms. The repeated measures ANOVA for this interaction at the medial frontocentral sites showed it was first significant at 344 ms, maintained at 424 ms, $F(2, 86) = 7.96$, $p < .01$, and began to wane by 436 ms, $F(2, 86) = 6.11$, $p < .02$. This interaction reappeared at about 500 ms and became highly significant in the *t*-test contrasts, with a more radial medial frontal surface topography.

Exploratory Analyses of Orbital Frontal Sites

The *t*-test animations showed that an endorsement main effect (yes vs. no responses) appeared at about 400 ms at frontopolar sites. In the ANOVAs on frontopolar sites, the endorsement contrast became strong by 436 ms, $F(2, 86) = 20.01$, $p < .0001$; and it remained highly significant until the end of the epoch (700 ms), that is, the mean RT, $F(2, 86) = 13.40$, $p < .001$.

The topography of the endorsement effect is seen for the 436-ms sample in Figure 8. The general parietal-positive-inferior-frontal-negative topography of the P300 remains at this sample, and the endorsement (yes vs. no) difference emerges as a focal effect, with a relative surface positivity for yes responses, versus surface negativity for no responses, at the midline frontopolar sites. Source analysis of this condition contrast suggested that the frontal brain activity related specifically to the response decision could be accounted for by a source in the right orbital cortex.

Whereas the endorsement discrimination begins exclusively at the frontopolar sites, by 500 ms it has extended dorsally, and the electrical field animations showed this progression to extend up the frontal midline by 600 ms. From 600 to 700 ms, the endorsement effect remained highly significant not only at both frontopolar (described above) but at centromedial, $F(2, 86) = 20.64$, $p < .0001$, sites as well.

Self-Evaluation Contrasts

None of the above effects differed between self- and friend ratings (and none appeared in the read-only condition). At about 475 ms, however, the electrical activity for the self-evaluation procedure showed significant discriminations that we did not observe for the friend evaluation. An ANOVA on the medial frontal sites shown in Figure 6 (Channels 6, 13, 113, 7, 107) for the 475–525-ms interval showed this differentiation of self-evaluation activity as a significant

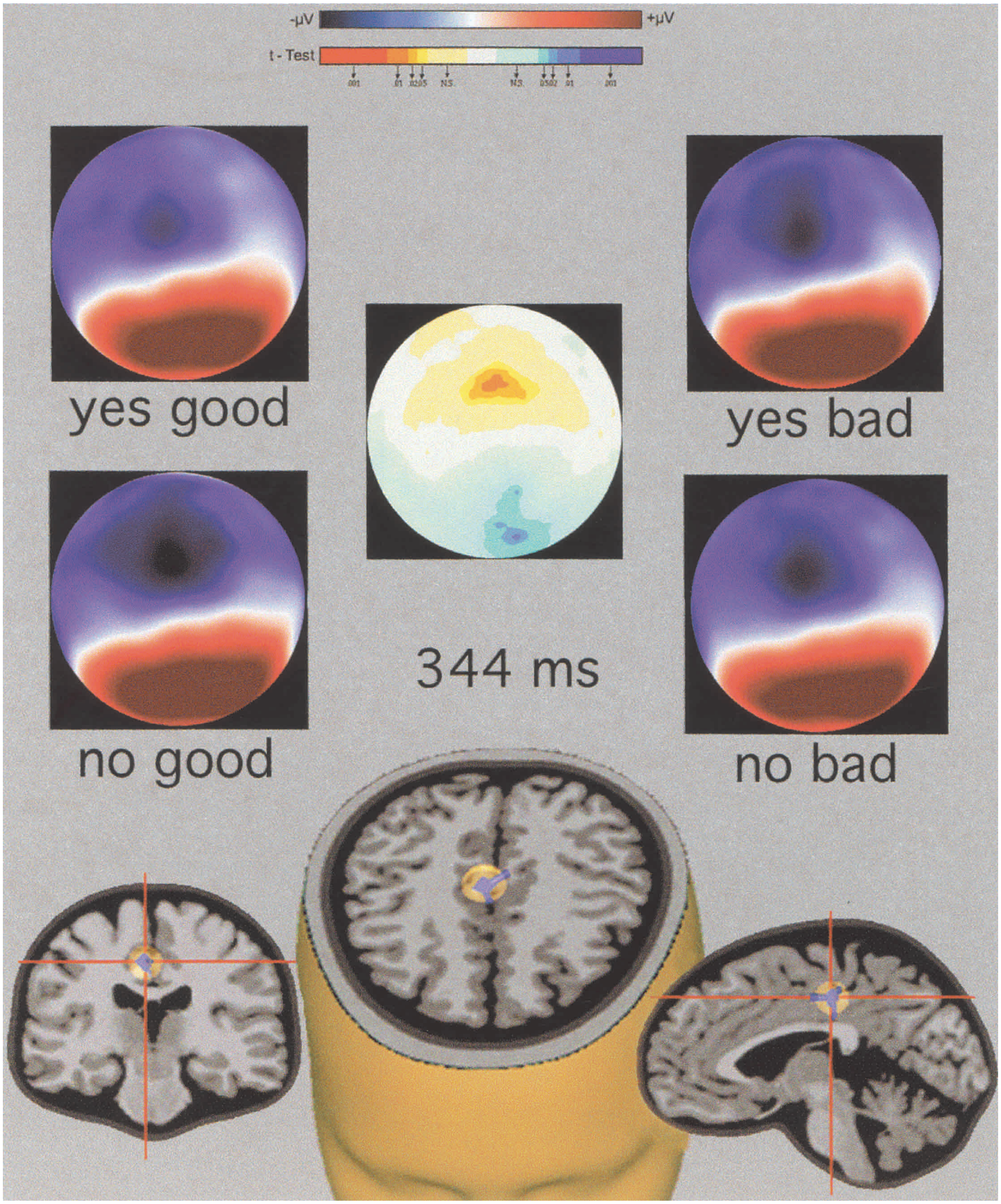

Figure 7. Discrimination of good versus bad trait words at 344 ms as a function of responding yes versus no (collapsed over self- and friend ratings). The *t* map in the center now describes the interaction of valence and endorsement (i.e., mapping the difference of differences). The largest contributions to this effect seem to come from saying yes to a bad trait and saying no to a good trait, with enhanced centromedial electrical responses in both cases. A source model suggests that, on average, this effect can be attributed to activity in a tangential source in the mid-to-posterior cingulate cortex.

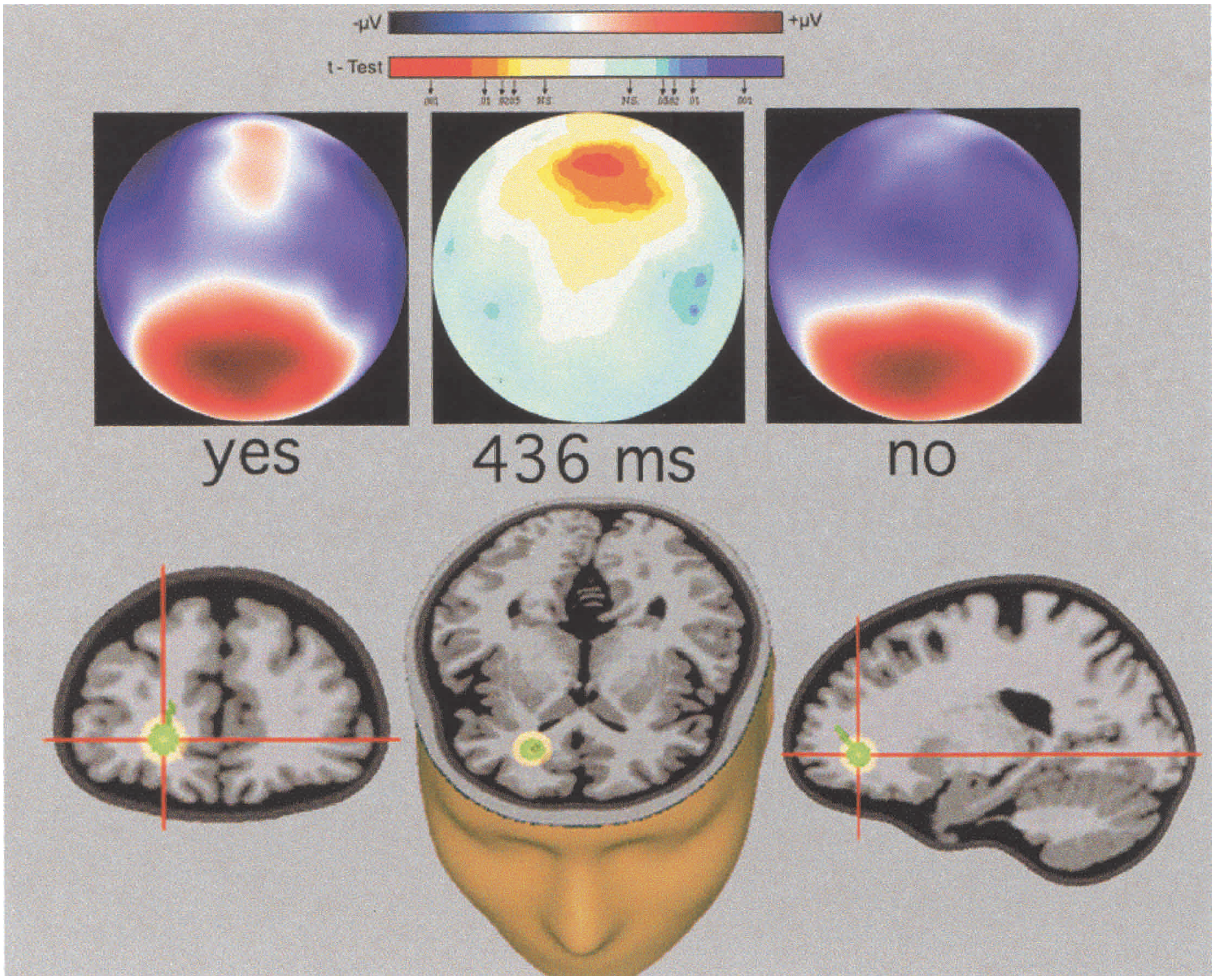

Figure 8. Frontopolar endorsement contrast at 436 ms. The contrast *t* map in the center shows the yes-minus-no contrast. The voltage maps to the left and right show that this contrast reflects an enhanced frontopolar negativity for the no response compared with enhanced frontopolar positivity for the yes response. The dipole source analysis of this effect suggested it could be explained by activity in the right orbital frontal region.

Rating × Valence × Endorsement interaction, $F(2, 86) = 4.53$, $p < .01$. The means comparison for this effect (see Figure 9) shows that certain valence and endorsement contrasts are only observed during self-evaluation. There is a negativity for the read-only rating that does not differ across the valence and endorsement conditions. There is a small positive deflection for the good-yes condition for friend ratings. There is then both a small positivity for the bad-no condition and a large positivity for good-yes for the self-evaluation procedure. Consistent with this analysis, the Endorsement × Valence Student's *t*-contrast maps examined separately for each rating procedure for this interval showed neither friend nor read only were associated with significant contrasts, whereas, the self-evaluation procedure did produce a significant interaction (see Figure 10, top center). The condition mean topographies in Figure 10 are consistent with the ANOVA summary means, showing that saying yes to good words and no to bad words engaged a positivity in the medial frontal lobe during the self-evaluation procedure. The surface topography of this interaction contrast at 476 ms suggests that the condition differences arose from sources in anterior as well as posterior cingulate cortex. This interpretation of the scalp fields was confirmed through dipole modeling with Brain Electrical Source Analysis. As shown in Figure 10 (bottom), a source in the anterior cingulate cortex was necessary to add to the model to characterize the anterior extent of the midline positiv-

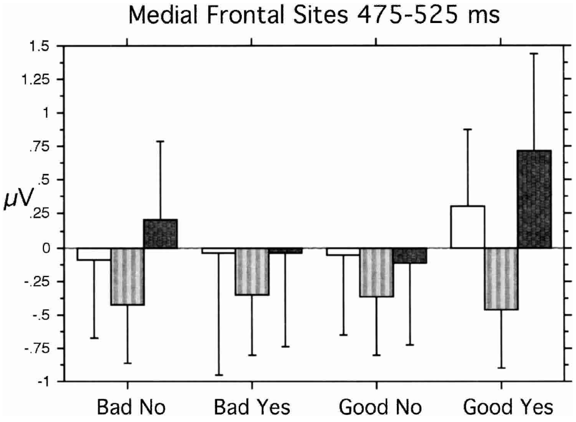

Figure 9. Condition means for the Rating × Valence × Endorsement interaction. The read-only (gray bars) control produces a negativity during this interval that does not discriminate valence or endorsement, whereas both friend (open bars) and self-rating (solid bars) result in an enhanced positivity for the good-yes condition. This positivity for good-yes is stronger for self- than for friend rating. Self-rating also results in a positivity to the bad-no condition that was not seen for the friend rating.

ity that was particularly striking for the yes-to-good condition. As with the anterior cingulate source for the valence effect at 304 ms, we added the source model for the self-specific Valence × Endorsement interaction contrast (see Figure 10, top center) to the overall dipole model for the common ERP to determine whether it added significant variance. Whereas the posterior cingulate activity could be accounted for by sources already in the model, which were necessary to model common temporoparietal and posterior cingulate activity in the early ERP, the anterior cingulate source received a substantial unique-moment weight in the recomputed model, suggesting it effectively explained not only the interaction contrast but also the source activity underlying the individual experimental conditions.

Discussion

As the subjects in this study made evaluative decisions about themselves or their friends, electrical activity at midline frontal sites provided the first signs of the developing decision process. Consistent with previous evidence that evaluation of significant events engages the anterior cingulate and associated dorsomedial frontal cortex (Luu, Flaish et al., 2000; Miltner et al., 1997; Tucker et al., 1999), the first electrophysiological discrimination reflecting the meaning of the words in the present study was seen in the centromedial region of the head at about 300 ms. As hypothesized on the basis of the previous results, this discrimination showed a greater relative surface positivity of a radial source in the anterior cingulate cortex for good words versus greater relative surface negativity for bad words. In the present data, this initial medial frontal discrimination appeared to be right-lateralized, both in the surface topography and in the dipole source analysis.

By 344 ms, the valence discrimination remained, and the statistical contrasts showed an interaction effect had developed that predicted the decision to respond to good versus bad words. This interaction effect also produced a voltage topography over the midline centromedial frontal region (see Figure 7, top), but it was more posterior than the initial valence discrimination, with a tangential rather than radial pattern. A dipole source model suggested that this initial evidence of a decision in relation to trait word valence engaged neural activity in the middle or posterior regions of the cingulate gyrus (see Figure 7, bottom).

These results add to the growing evidence of functional differentiation within the cingulate cortex (Bush et al., 2000; Luu & Tucker, 2003). After these initial midline effects, post hoc analyses suggested that a discrimination between yes and no responses appeared over anterior, ventral regions of the frontal lobe at about 400 ms, suggesting that an additional control over the action, and perhaps the decision, was applied by the orbital frontal cortex. As with the initial valence evaluation, this endorsement effect was lateralized to the right hemisphere. At about 475 ms, a second interaction effect (whether to say yes or no to good vs. bad words) appeared over both anterior and posterior cingulate cortex (see Figure 10), but only for the self-evaluation procedure. Finally, in contrast to the read-only condition, the evaluation of words in relation to both the self and the friend engaged a large LPC, extending from 400 to 700 ms, in the posterior cingulate gyrus and associated temporal and parietal cortices.

We speculate that this progression of activity in the cingulate gyrus and linked networks of the neocortex indicates that a decision involves a developmental progression within corticolimbic networks (Brown, 1977). This progression begins as the perception resonates with a primitive representation of affective valence in the anterior cingulate cortex (about 300 ms). There is then an initial integration of this representation with the response decision in more posterior networks of cingulate cortex (about 350 ms). Next, a separate recruitment of networks moderates the re-

Figure 10. Contrast with Student's *t* test for the Valence × Endorsement interaction effect for the self-evaluation procedure, shown here at 476 ms. As suggested by the topography of the *t*-test animation, this effect required sources in both anterior cingulate and posterior cingulate (or parietal) regions. The source model below shows multiple dipoles for the common visual event-related potential, including temporal (pink); inferior occipital (brown); posterior cingulate, or midparietal (green); and frontopolar (blue). The anterior cingulate source (orange with yellow halo) was weighted in the model with a strong moment at the 476-ms sample. This anterior cingulate source seems to be somewhat more superficial than that for the 304-ms sample.

sponse choice in orbital frontal networks (about 450 ms). A combined response of anterior and posterior cingulate cortices then specifically discriminates the valence and response choice for self-evaluation (500 ms; see Figure 10). Finally, there is a general context-updating integration process extending to 700 or 800 ms in posterior cingulate and associated temporal and parietal cortices. These network operations are undoubtedly operating in parallel. However, the fact that their time course is stereotyped suggests that motivation and cognition are organized through developmental mechanisms that build representations across linked networks through finite intervals of time.

These theoretical speculations raise several neurophysiological questions, including the interaction of limbic with neocortical networks, the functional relation between anterior and posterior cingulate cortices, the balance between cingulate and orbital frontolimbic circuits, and the functional significance of positive versus negative cortical field potentials over the medial frontal lobe. These results also raise psychological questions about the nature of an evaluative representation, including whether it has inherent links to arousal mechanisms, how it might shape the decision process, and how it may emerge from elementary mechanisms of action regulation.

Functional Roles of Limbic and Neocortical Networks

Recognizing that there are inherent limits to the confidence of source localization, the source model suggested that the initial discrimination of the word meaning, differentiating good from bad, was observed in the anterior cingulate cortex at about 300 ms. Within 50 ms, medial electrical activity showed a statistical discrimination of the interaction of word valence (good–bad) with response choice (yes–no), and both the source modeling and the surface topographies suggested that this effect was localized within more posterior cingulate networks.

It may be significant that the initial affective discrimination was observed in limbic networks. The cingulate gyrus and associated mediodorsal neocortex form a structured hierarchy of functional networks. In this hierarchy, the limbic regions are densely interconnected with each other and with subcortical motivational circuits. In contrast, the adjacent neocortical networks become increasingly differentiated and isolated, to the point that primary sensory and motor cortices are highly specialized “islands” of cortical modules (Barbas, 1995; Pandya & Yeterian, 1985; Tucker & Derryberry, 1992). Given this connectional architecture, the limbic and paralimbic networks can be expected to form holistic and undifferentiated representations, in contrast to the more specialized and differentiated representations within the sensory or motor neocortices. These holistic or syncretic representations may be well-suited to initial, global evaluative concepts that are then developed into more explicit decisions as they are articulated into specific actions or propositions (Tucker & Derryberry, 1992; Werner, 1957).

Because psychologists and neuroscientists typically begin their analysis with sensation, and then consider the pathways to memory and response decisions, the direction of traffic in corticolimbic pathways is often assumed to be neocortex-to-limbic (e.g., V1-to-hippocampus). However, the connectivity is as dense and as well-organized in the opposite, limbifugal or limbic-to-neocortex direction (Pandya & Yeterian, 1984). Some cognitive studies have emphasized that the process of perception must start with memory, as expectancies shape the incorporation of sensory data (Shepard, 1984). Recent recordings from limbic and visual neocortex in monkeys (Naya, Yoshida, & Miyashita, 2001) have provided support for the limbic-cortical direction of processing. When the monkey responded to a perceptual cue, the order of activity was visual cortex then limbic cortex. When the monkey responded to a cue to remember a visual stimulus, the order was limbic then visual cortex. Naya et al. proposed that the subsequent activation of visual cortex reflects recruitment of the visual memory by the limbic cortex.

In the present data, there were clear activations in visual areas before temporal (late N1) and limbic (anterior and midcingulate) activity. However, the initial discriminations of word valence appeared in a limbic region, the right anterior cingulate cortex, with substantial activity evident in posterior cingulate and orbital regions before the response was organized in motor neocortex. We interpret this limbifugal direction of activity in frontal networks to reflect a microdevelopmental progression, from global evaluative representations in limbic networks toward greater specification of decisions in prefrontal and premotor areas. An evaluative role for limbic cortical networks is consistent with classical theory on the function of limbic regions in providing motivational evaluation of the action plan as it unfolds in frontal cortex (Nauta, 1971). The recent molecular tracer studies of diencephalic projections to the cerebral hemispheres have shown that projections from the hypothalamus are focused on limbic cortex (Swanson, 2000). This evidence of hypothalamic regulation is well-suited to Nauta's emphasis on the motivational and evaluative functions of limbic cortices that provide executive guidance to the behavioral and cognitive plans unfolding in frontal cortex.

Response Monitoring and Activity in Orbital Regions

After the interaction of word valence and endorsement response appeared over the central scalp, apparently reflecting activity in the midcingulate region, it was electrical activity at the frontopolar scalp that predicted whether the subject would say yes or no to the trait word. Interestingly, this effect was specific to the response decision and did not interact with word valence. In previous research, a frontopolar effect termed the *P2a* was found to be enhanced when subjects attended to object features of a stimulus array (identifying letters and shapes) rather than to the spatial locations (Potts & Tucker, 2001). Because the orbital frontal lobe extends the object processing of the ventral corticolimbic pathway (Wilson et al., 1993), the specific enhancement of the frontopolar electrical field by object attention provides functional evidence that this frontopolar electrical field reflects activity in orbital frontal cortex (Potts & Tucker, 2001). The dipole model for the endorsement effect in the present data (see Figure 8) pointed to a right orbital frontal cortex source as critical for discriminating between the yes and no response choices. Given the clinical evidence of personality disinhibition with orbital lesions (Blumer & Benson, 1975), we can speculate that the orbital activity in the current data reflects an inhibitory monitor on the action plan, operating in parallel with, or perhaps downstream to, the medial frontal decision process.

Interpreting Averaged Brain Waves

An important question is the polarity of the electrical effects: why good targets (Tucker et al., 1999) or good words (in the present results) are associated with more positive surface electrical waves at medial frontal sites and bad targets and bad words are associated with more negative electrical potentials. Recently, Gehring and Willoughby (2002) have observed a similar effect as subjects evaluated the outcome of bets in a gambling task. Losses were associated with medial frontal negativities, even when subjects had made a correct, nonerroneous bet (which could minimize the loss but not eliminate it). It may be that the anterior cingulate gyrus and associated frontal networks are engaged by emotionally significant events regardless of valence because of demands for motor initiation, cognitive effort, and autonomic arousal (Paus, 2001). Bad words and bad outcomes may engage more of this nonspecific demand for arousal and visceral self-regulation (Tucker, 2001). It may be that the valence discrimination reflects a response of the anterior cingulate network to the distress engendered by the bad targets, bad words, and losses (Luu, Collins et al., 2000). Or it may be that the medial frontal networks of the archicortex are normally biased toward the hedonic impulse for action (Tucker et al., 1999), such that the relative medial frontal positivity in saying yes to good words is the modal response, and the medial frontal negativities reflect ventral limbic (Tucker & Derryberry, 1992) or dopaminergic (Holroyd & Coles, 2002) input to the anterior cingulate cortex that is important not only in errors but in any painful or defensive response.

Interpreting the electrical positivity or negativity in ERP experiments in this way typically assumes there is a consistent transient electrical potential on each trial and that trial averaging cancels the (non-phase-locked) background EEG to be removed. For many years, some EEG researchers have questioned this assumption of event-related averaging (Basar, Basar-Eroglu, Rahn, & Schurmann, 1991). Recent analyses of how the visual ERP emerges from the oscillatory rhythms of the EEG (Makeig et al., 2002) are clarifying the EEG dynamics underlying the averaged response, demonstrating that much of what has been described as the N1 component of the averaged visual ERP occurs through phase-resetting of the posterior alpha rhythm. In examining the individual EEG epochs of the medial frontal ERP, we observed that error trials were often associated with oscillatory activity in the theta band (Luu & Tucker, 2001). In addition, these theta oscillations engaged lateral motor cortex in alternating waves with the midline cortex, and the alternations were particularly strong on error trials (Luu & Tucker, 2001). In recent analyses of the unaveraged EEG from the Luu & Tucker (2001) experiment, the ERN could be seen to arise from phase-resetting of midline frontal theta, as the alignment of the theta waves caused by the resetting resulted in phase alignment that survived the averaging process (Makeig et al., 2003).

In animal studies, limbic theta has been found to organize learning and plasticity, such that phase-resetting of the theta rhythm is an important mechanism for network coordination (Luu & Tucker, 2003). For example, the input from the hippocampus to the posterior cingulate gyrus oscillates at the theta rhythm, and this input is important in representing the context in which learning is appropriate (Gabriel, 1990). Particularly important to the recent human ERP studies on error and evaluative responses is the observation by Gabriel and associates that, whereas the posterior cingulate updates a representation of the learning context in a gradual fashion, the anterior cingulate is responsible for rapid adaptation to new learning contingencies (Gabriel, 1990; Gabriel et al., 1996). Such rapid adaptations to unexpected and motivationally significant events may explain the mechanisms of the cingulate cortex underlying the human medial frontal negativities for both action monitoring and evaluative decisions (Luu & Tucker, 2003).

The Visceral Basis of Decisions

The present results add to the growing evidence that electrical responses in the medial frontal lobe are created not only in the control of immediate motor actions but also by the representation of motivational significance. The anterior cingulate cortex is not only an essential structure of the dorsal motor pathway (Vogt, Finch, & Olson, 1993) but it is also responsible for cortical control of visceromotor function (Neafsey et al., 1993). Interpreting the functional significance of the limbic base of the frontal lobe may therefore require consideration of motivational and visceral functions as integral to the executive control of action (Luu & Tucker, 2001, 2003; Paus, 2001; Tucker, 2001). It may be that electrical activity is seen in this motor pathway during the process of stimulus evaluation because the evaluation itself is an incipient action. An evaluation of an event may not be a logical operation but may emerge from the evolved motivational mechanisms of action regulation. Within the dorsal frontolimbic pathway, there appears to be a mode of elaborating limbic and subcortical influences so as to create the visceromotor basis for predicting an action that is consistent with the current model of the behavioral context (Luu & Tucker, 2003). In normal motor operations, this form of control may lead to a projectional feedforward mode of action regulation (G. Goldberg, 1985). When the dorsal pathway is lesioned, the loss of the hedonic impulse may be seen in the syndromes of akinetic mutism and pseudodepression (Blumer & Benson, 1975; Hecaen, 1964). Similarly, the intrinsic alliance of mood and impulse are seen in the loss of the behavioral impulse in a normal depressed mood, and this alliance becomes undeniable in the psychomotor retardation of severe clinical depression. In the positive direction, elation excites impulses, both in the behavioral exuberance of normal elation and in the distracted impulsivity of pathological mania (Tucker & Williamson, 1984). Represented within the archicortical motor control networks of the cingulate cortex, and balanced by constraint within the paleocortical motor control networks of the orbital frontal lobe, an evaluation may be of an action in its early developmental stage. A good thing may be perceived and represented through the process of a small elation and predictive confirmation of the motive urge to approach and the loss of a good thing as a small depression and motive deflation. In both cases, limbic contributions to decisions may occur as subcortical projections of the arousal and visceral regulatory systems apply immediate motivational regulation to the developing corticolimbic mechanisms of the decision process.

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Appendix

Trait Words

Good Traits

ACTIVE
ALERT
ASTUTE

BLUNT
BOLD
BRAINY
BRAVE
BREEZY
BRIGHT
BRISK
BUBBLY

CALM
CANDID
CANNY
CASUAL
CHASTE
CHATTY
CHIC
CHOOSY
CIVIL
CLEVER
COY

DAPPER
DARING
DEEP
DEMURE
DEVOUT
DIRECT

EAGER
EARTHY
EXACT

FIERY
FIRM
FRANK
FRISKY
FRUGAL

GENTLE
GIVING
GUTSY

HEARTY
HEROIC
HONEST
HUMANE
HUMBLE

JAUNTY
JOLLY
JOVIAL
JUST

KIND
KINDLY

LIVE
LIVELY
LOVING
LOYAL
LUCID

MANLY
MERRY
MILD
MORAL

PEPPY
PERKY
PERT
PLACID
PLUCKY
POETIC
POISED
POLITE
PROMPT
PROPER
PROUD

QUIET

RUGGED

SERENE
SEXY
SHREWD
SOCIAL
SOLEMN
SPEEDY
SPRY
SPUNKY
STABLE
STEADY
SUAVE
SUNNY

TENDER
TIDY

URBANE

VERBAL
VIRILE
VIVID
VOCAL

WARM
WARY
WISE
WITTY

ZANY

Bad Traits

ABRUPT
ALOOF

BIASED
BITTER
BLAND
BOSSY
BOYISH
BRASH
BRUTAL

CATTY
CLINGY
CLUMSY
COARSE
COCKY
COLD
CRABBY
CRANKY
CRUEL
CURT
FICKLE
FIERCE
FUSSY

GLIB
GREEDY
GRUFF
GRUMPY
GUSHY

HARSH
HASTY
HECTIC

ICY
INWARD

LAX
LAZY
LEWD
LOUD

MEEK
MESSY
MOODY
MORBID
MOROSE
MOUSY
MULISH
MUSHY

NAIVE
NARROW
NERVY
NOISY
NOSEY

PETTY
PICKY
POUTY
PRIM

RASH
RIGID
ROWDY
RUDE
SASSY
SAUCY
SEVERE
SHOWY
SHY
SILENT
SLICK
SLOPPY
SLY
SMUG
SNEAKY
SNOOTY
SOMBER
SOUR
STERN
STINGY
STORMY
STRICT
STUFFY
SUGARY
SULKY
SULLEN
SURLY

TAME
TESTY
TIMID
TOUCHY
TRICKY

UNFAIR
UNKIND
UNRULY
UNWARY
UNSURE
UNWISE

VAGUE
VAIN

WEEPY
WHINY
WORDY

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