

Affective and cognitive modulation of performance monitoring: Behavioral and ERP evidence

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This study investigates the effects of negative affect on performance monitoring. EEG was acquired during a lateralized, numeric Stroop working memory task that featured task-irrelevant aversive and neutral pictures between stimuli. Performance accuracy showed a right-hemisphere advantage for stimuli that followed aversive pictures. Response-locked event-related potentials (ERPs) from accurate trials showed an early negative component (CRN; correct response/conflict-related negativity) followed by a positive wave comparable to the Pe (error positivity). The CRN was bi-peaked with an earlier peak that was sensitive to aversive pictures during early portions of the experiment and a later peak that increased with error likelihood later in the experiment. Pe amplitude was increased with aversive pictures early in the experiment and was sensitive to picture type, Stroop interference, and hemisphere of stimulus delivery during later trials. This suggests that ERP indices of performance monitoring, the CRN and Pe, are dynamically modulated by both affective and cognitive demands.

Electrophysiological studies of performance monitoring have described a sequence of response-locked event-related potential (ERP) components, the ERN/Ne and Pe (error-related negativity/positivity), related to error detection. The ERN/Ne and Pe components, occurring within 400 msec after an executed response, show maximum amplitude over frontal-central cortical areas and have been observed after errors committed in numerous cognitive tasks (Falkenstein, Hoormann, Christ, & Hohnsbein, 2000). The ERN/Ne and Pe signals are thought to initiate compensatory effort toward minimizing subsequent errors. In support of this view, ERN/Ne and Pe features have been shown to correlate with corrective behaviors in response to stimuli presented subsequent to an error trial (Hajcak, McDonald, & Simons, 2003; Pailing, Segalowitz, Dywan, & Davies, 2002; Rabbitt & Vyas, 1970).

There has been controversy over whether the ERN/Ne and Pe signal the detection of discrepancy between the neural representation of a correct and that of an incorrect response, or an evaluative index of the degree of competition or conflict between response options. To resolve this issue, Gehring and Fencsik (2001) showed that the ERN/Ne was not sensitive to perceptual disparity between reafferent feedback about an incorrect response and the representation of the correct response. Rather, the ERN/Ne increased with similarity between correct and incorrect response options, supporting the idea that the ERN/Ne depicts relative conflict between competing response options (Gehring & Fencsik, 2001).

Studies have also described a response-locked ERP comparable to the ERN/Ne that increases after correct responses during task conditions that feature increased response conflict. This ERP has a latency range, morphology, and scalp distribution similar to those of the ERN/Ne and has been termed the *conflict-related negativity* (CRN; Luu, Flaisch, & Tucker, 2000; Vidal, Hasbroucq, Grapperon, & Bonnet, 2000). The ERN/Ne, Pe, and CRN may represent components of a neural response system to a more general class of conditions in which representations of goals, relevant stimuli, response options, or actions are poised to compete for ensuing attention and processing resources.

Several other ERPs, the stimulus-locked N2, and the feedback-related medial frontal negativity (MFN), also have scalp distributions comparable to the ERN/Ne, CRN and Pe and are similarly modulated by factors relevant to performance monitoring. The N2 occurs approximately 200 msec after presentation of task stimuli and shows increased amplitude for stimuli that convey increased conflict (Mathalon, Whitfield, & Ford, 2003; Van Veen & Carter, 2002). The MFN occurs approximately 200–300 msec after performance feedback and shows increased amplitude when the feedback indicates the loss of a reward or poor task performance (Gehring & Willoughby, 2002; Ruchow, Grothe, Spitzer, & Kiefer, 2002). The sensitivity of these components to information that is salient for assessing performance demands and requirements for adjustment of processing resources suggests that they represent processes similar to the ERN/Ne, Pe, and CRN. The analogous scalp distributions and overlapping functional sensitivity of the ERN/Ne, CRN, Pe, N2, and MFN suggest that these ERPs represent components of a neural response system in medial and lateral frontal brain regions

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that are sensitive to circumstances warranting reallocation of processing resources in cognitive and affective domains. This system may be theorized to promote reallocation of neural processing resources to produce behavior that maximizes coherence between cognitive and affective goals.

The sensitivity of the ERN/Ne, CRN, Pe, N2, and MFN to affective changes such as the unease that arises with committing an error or the stress associated with heightened cognitive conflict or increased demand on processing resources or with the disappointment associated with the detection of an outcome that is worse than expected has not been determined. One study has concluded that awareness of errors was not critical for emergence of the ERN/Ne, relegating an aspect of primary error detection to subconscious cognitive and affective domains (Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001). Another study has suggested that ERN/Ne amplitude correlates with perceived inaccuracy during error commission, and a third has concluded that motivation to perform well heightens the sensitivity of the ERN/Ne, suggesting that both cognitive and affective processes mediate error detection and compensatory responses (Scheffers & Coles, 2000; Stemmer, Witzke, & Schönle, 2001). In a more recent study, Nieuwenhuis, Yeung, Holroyd, Schurger, and Cohen (2004) have shown that the classically affect-related MFN and cognition-related ERN were dynamically sensitive to utilitarian (loss) versus performance (error) feedback information, depending on which aspect of feedback was more salient, concluding further that they emerge from a common monitoring system (Nieuwenhuis et al., 2004). Affective personality traits have also been related to ERN magnitude in response to errors, providing further evidence that emotional processes are involved in performance monitoring (Pailing & Segalowitz, 2004). However, the specific influence or mechanism whereby emotional processes influence the ERPs implicated in performance monitoring has not been well characterized.

Several behavioral studies have described emotional influences on response selection and performance-monitoring functions, providing a useful exploratory framework for investigating the influence of affective changes on underlying ERPs like the ERN/Ne, Pe, and CRN. For example, in several studies using a lexical decision task, subjects showed accuracy improvements after errors or external feedback for stimuli presented to the LVF (right hemisphere) but no difference after errors or improvement after external feedback for stimuli presented to the RVF (left hemisphere), which was interpreted to reflect a generalized right-hemisphere error-processing advantage (Iacoboni, Rayman, & Zaidel, 1997; Kaplan, & Zaidel, 2001). There is also behavioral, patient, electrophysiological and neuroimaging evidence that the right hemisphere plays a dominant role in processing negative or withdrawal-related emotion (Derryberry, 1990; Hartikainen, Ogawa, & Knight, 2000; Müller, Keil, Gruber, & Elbert, 1999; Pizzagalli, Regard, & Lehmann, 1999; Schutter, van Honk, D'Alfonso, Postma, & de Haan, 2001; Schwartz, Davidson, & Maer, 1975; Simon-Thomas,

Role, & Knight, 2005; Tucker, Hartry-Speiser, McDougal, Luu, & deGrandpre, 1999). The primary affective shift associated with error commission, increased difficulty, and loss is in the negative direction. Therefore, right-hemisphere negative-emotion-related processing may drive the right-hemisphere error-processing advantage described above. *Habituation*, defined as the universal tendency to show diminished responses to initially salient or emotionally evocative stimuli that are not associated with significant consequences is also likely to be a factor in any study of emotion–cognition interaction. As experimentally induced emotional reactions diminish (Phan, Liberzon, Welsh, Britton, & Taylor, 2003), the relative influence of emotion on cognitive processing is also likely to change. Evaluation of the influence of emotion on performance-monitoring function requires consideration of hemispheric specialization for cognitive and emotional processes, as well as dynamic changes in the strength of emotion elicitation over time.

The ERN/Ne, CRN, Pe, N2, and MFN all show dipole source localizations that are consistent with a neural generator in various subregions of the anterior cingulate cortex (ACC) (Luu, Tucker, Derryberry, Reed, & Poulsen, 2003; Van Veen & Carter, 2002). Intracerebral recording studies have reported ERN/Pe responses from neural populations in ACC tissue (Brazdil et al., 2002), and neuroimaging studies have shown increased ACC activity during error trials (Carter, Braver, Barch, Botvinick, Noll, & Cohen, 1998; Kiehl, Liddle, & Hopfinger, 2000) and during increased conflict conditions (Carter, MacDonald, et al., 2000).

Correlations between ACC activity levels and response latencies during increased conflict conditions have also been reported, implicating the ACC in the slowing of responses associated with performing a more difficult task (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999). Furthermore, Mathalon et al. (2003) showed that fMRI-determined ACC activity correlated with ERN, CRN, and N2 amplitudes from the same individual performing a response-conflict task. Sanfey, Rilling, Aronson, Nystrom, and Cohen's (2003) fMRI study suggested that affective processing of "unfairness" during decision making produced increased ACC activity. The ACC is also broadly implicated in pain-related functioning, emotion processing, motivation, and personality (Devinsky, Morrell, & Vogt, 1995; Drevets, 1998; Drevets, Ongür, & Price, 1998; Heller, & Nitschke, 1997; Phan, Wager, Taylor, & Liberzon, 2002; Taylor, Phan, Decker, & Liberzon, 2003). For example, Sowards and Sowards (2002) proposed that the ACC represents the motivational aspect of pain based on integrating input from central and peripheral structures. Potentially expressed from the same ACC cortical network, the ERN/Ne, CRN, Pe, N2, and MFN may represent the initiation of dynamic, information-driven adjustments in performance strategy to meet both cognitive and affective goals. The MFN, in particular, may signal a primarily affect-driven impetus for readjustment.

This study was carried out to determine whether negative emotion elicitation contemporaneous with but un-

related to task-response requirements modulates response-locked ERPs associated with performance monitoring. ERP components from correct-response trials on a working memory delay/Stroop task were measured in two emotion (negative vs. neutral) and cognitive conflict (congruent vs. incongruent) conditions. Highly aversive or neutral pictures were presented at the center of the task monitor immediately before each brief, laterally presented numeric Stroop stimulus. Subjects were explicitly instructed to maintain central fixation throughout the task and told that they would see a variety of pictures between task-relevant stimuli. They were asked to notice the intervening pictures as naturalistically as possible and not to ignore or avoid looking at them while doing the task. Numeric Stroop task stimuli were presented very briefly immediately after the pictures, meaning that subjects had to be looking at the pictures in order to detect and respond correctly to the task stimuli. Our hypothesis was that the pictures would induce transient (to each picture) and sustained (cumulative effect of repeated aversive pictures) negative emotional processes, which would dynamically modulate response-locked ERP components over the course of the experiment. We predicted that performance-monitoring response-locked ERPs would show increased amplitude during condi-

tions featuring maximal competition between cognitive and negative emotional processing demands in a lateralized and temporally sensitive manner.

METHOD

Subjects

Fourteen healthy volunteers (8 female, mean age: 21) were recruited from the University of California community to participate in this study. The subjects were prescreened for right-handedness, lack of past or present psychiatric or neurological disorder or injury, and absence of current prescription or nonprescription drug use. The use of human subjects was approved by the Committee for the Protection of Human Subjects at UC Berkeley, and informed consent was obtained prior to participation. The subjects earned course credit and/or an hourly honorarium for their time and effort.

EEG

EEGs (0.1–100-Hz bandwidth; 256 samples/sec) were recorded from 60 scalp electrodes located in standard 10/20 electrode positions embedded in an elastic cap recording device (ElectroCap, Inc.).

Electrooculogram (EOG)

Electrodes were placed at the outer canthi of each eye to measure horizontal eye movements. Vertical eye movements were measured from one electrode placed on the right suborbital ridge and from FP2, an electrode located just above the right eyebrow. All elec-

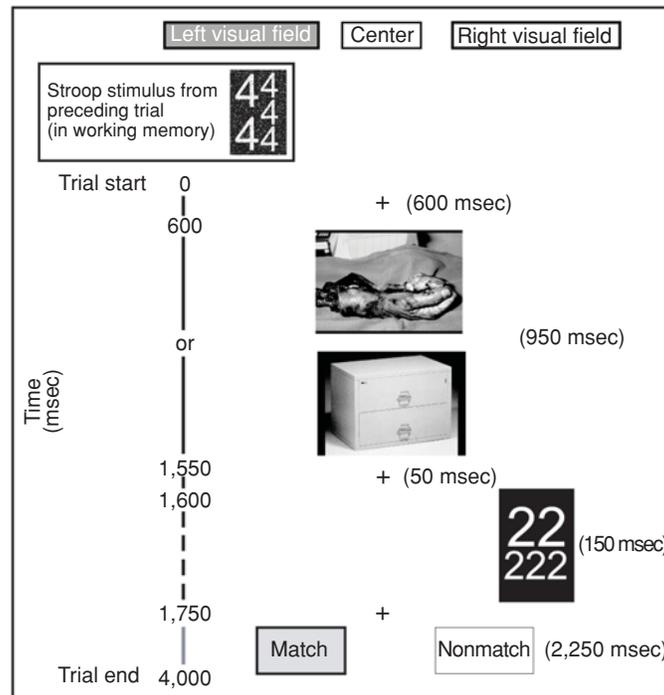


Figure 1. Task specifications for incongruent stimulus trials with either neutral or aversive pictures. A trial began with a white “+” at the center of the monitor. After 600 msec, the “+” sign was replaced by an aversive or neutral picture that lasted 950 msec. Fifty milliseconds after the picture offset, a Stroop stimulus was presented for 150 msec in the right or left visual field, followed by a 2,250-msec response window and then the onset of the “+” sign for the subsequent trial. Trials were presented in blocks of 63 trials of either congruent or incongruent stimuli.

trodes were referenced to linked mastoids. Skin impedances for reference and ground electrodes were brought to below 5 k Ω . Other electrode impedances were brought to below 20 k Ω .

Task

A 1-back working memory task that used numeric Stroop stimuli was designed for this study. The Stroop stimuli consisted of groups of numbers, each with one to five repetitions of an integer from 1 to 5. There were 10 “congruent” Stroop stimuli, where the integer used was the same as the number of instances—for example, 333—and 10 “incongruent” stimuli—for example, 444. The subjects were instructed to detect the number of integers in each stimulus, and to indicate whether this value matched the quantity of integers from the immediately preceding stimulus (see Figure 1). The subjects responded by pressing a “match” or “nonmatch” button on a button control panel with the index and middle fingers of their right hand. Between presentations of the number stimuli, one highly aversive or neutral picture from the International Affective Picture System (IAPS; Lang, 1999) was presented. The pictures used in this experiment were selected according to normative pleasantness and arousal ratings that accompanied the IAPS set. Highly aversive images had the lowest pleasantness and highest arousal ratings and included gruesome scenes. Neutral images had low arousal ratings and included ordinary people and objects. Twenty-one images of each type were used, with repetition, throughout the experiment. Pictures appeared in pseudorandom order (with repetition only after exhausting the complete set of 42 within a block and no immediate sequential repetition of the same picture) between the Stroop stimuli. Each picture was repeated no fewer than three and no more than six times during the course of a subject’s experiment.

Each task trial began with the appearance of a white “+” sign on a black background, presented at the center of a computer monitor for 600 msec. The subjects were instructed to fixate their gaze on this “+” sign continuously during performance of the task. A neutral or aversive picture replaced the fixation “+” sign at the end of 600 msec and remained on the monitor for 950 msec. IAPS pictures occupied up to 5.3° of visual angle on both sides of the visual midline. After the picture disappeared, the monitor showed the black background for 50 msec, and then a white congruent or incongruent numeric Stroop stimulus was presented to either the left or the right visual field for 150 msec. Stroop stimuli occupied between 5.5° and 7.5° of visual angle on either side of the visual midline. Stroop stimuli were followed by a uniform 2,250-msec response window, during which the white “+” sign was visible at the center of the monitor. At the end of each 4-sec trial, a new trial began with the reappearance of the white “+” sign uninterrupted from the response window fixation “+” sign. To increase cognitive load, after each Stroop stimulus, the subjects indicated whether the number of integers in the current trial matched the number of integers in the immediately preceding trial, in a continuously updating fashion. Congruent and incongruent stimuli were presented in separate blocks of 63 trials.

Procedure

Upon arrival, the subjects signed consent forms and completed a screening form confirming their eligibility to participate in EEG recording. If all criteria were met, they were led into a sound-attenuated experimental booth, seated approximately 52 in. in front of a monitor, and given a button control panel. The subjects were instructed to perform four blocks (two congruent and two incongruent) of a training version of the task where the pictures were omitted from each trial. Training and experimental task block order were counterbalanced across subjects and alternated between starting with congruent or incongruent stimulus types. The subjects were encouraged to respond as quickly and as accurately as possible, and the experimenter gave general performance feedback between completed training blocks.

After completing the training, the subjects were prepared for EEG recording. After the recording cap was in place, the subjects’ ongoing EEG signals were displayed on a monitor for them to observe, while the experimenters described the basic principles of EEG and encouraged them not to blink excessively, have tense facial muscles, clench their jaw, or chew during task performance. The experimenters demonstrated how each of these activities produced artifacts in each subject’s ongoing EEG signal, providing further incentive for the subjects to minimize these activities in order to generate useful data.

Prior to starting the first experimental task block, the subjects were given a Positive and Negative Affect Scale (PANAS; Watson, Clark, & Tellegen, 1988) with instructions to rate how accurately each of the terms on the scale described the way that they were feeling at that moment (e.g., distressed: 1 = *not at all*, 5 = *very much*).

The subjects were also told that they would now see pictures between presentations of the number stimuli while doing the task, and that the pictures were irrelevant to the task. The subjects then performed four alternating congruent and incongruent blocks of the task and completed an additional PANAS after every two blocks.

Data Analysis Method

Subjective ratings. Changes in positive and negative affect were assessed from the subjects’ PANAS scores. Ratings for each positive and negative term were summed within affect category to yield an overall positive and negative score from each successive administration of the PANAS. Scores were submitted to one-factor (time: before task, after two task blocks, after four task blocks, after six task blocks, after eight task blocks) within-subjects repeated measures analyses of variance (ANOVAs). Greenhouse–Geisser corrected *p* values are reported for these and all subsequent analyses to correct for violation of the sphericity assumption.

Performance. Response times (RTs) from each subject’s correct responses were divided into eight groups according to experimental conditions: Stroop (congruent vs. incongruent), picture valence (aversive vs. neutral), and field of stimulus presentation (LVF vs. RVF), then averaged within conditions across experimental blocks. RTs were submitted to a three-factor (Stroop \times valence \times field) within-subjects repeated measures ANOVA. Planned follow-up paired *t* tests were carried out to determine how individual factors contributed to main effects. Performance data were also analyzed with respect to time. RTs from early (Blocks 1 and 2) and late (Blocks 3 and 4) experimental blocks were divided by experimental condition, then submitted to a four-factor (Stroop \times valence \times field \times time) within-subjects repeated measures ANOVA.

Because the task relied on “match” and “nonmatch” responses, accuracy was assessed using *d'* values to minimize the influence of individual response bias on group means. *d'* scores were computed from correct hit and false positive rates within each block, then averaged into the same experimental condition groups as were the RT data and submitted to the same statistical analyses.

Electrophysiology. ERPs were computed from artifact-free data epochs extending from 600 msec prior to 400 msec after the button-press responses from trials in which the subjects responded correctly. The mean signal over a 200-msec window from 600 to 400 msec prior to the response was subtracted from each EEG epoch to eliminate noise related to between-trial baseline amplitude shifts. A band-pass filter (1–20 Hz) was applied to grand-average ERPs prior to visual inspection and extraction of amplitude and latency features to reduce spurious contributions from signals below and above the frequency band that encompasses response-locked ERP components related to conflict detection. Components with latency and scalp distribution features similar to those of the ERN/Ne and Pe generated from error trials obtained during this experiment were identified as the CRN and Pe on correct trials, and features of interest were extracted from each subject’s data for statistical analysis. Amplitudes were represented as the average amplitude across a time win-

show that spanned the maximal condition-related differences in the grand-average waveforms. Amplitudes were measured on a cluster of frontal-central electrodes over the medial prefrontal cortex (F1, Fz, F2, FCz, and Cz), and then averaged together prior to statistical analysis.

Response-locked EEG epochs were divided into eight groups according to experimental condition (Stroop, valence, and field) and were then averaged within group for ERP analysis. Amplitudes of CRN and Pe features were submitted to a three-factor (Stroop × valence × field) within-subjects repeated measures ANOVA. Planned follow-up paired *t* tests were carried out to explore how differences between pairs of conditions contributed to main effects. EEG epochs were further grouped according to experimental time (early blocks, Blocks 1 and 2 and late blocks, Blocks 3 and 4) and were then averaged into early and late CRN and Pe components. Amplitudes were submitted to the same three-factor analysis as above to explore how condition effects may have changed between the early and later parts of the experiment.

RESULTS

Performance

Subjective ratings. There was a main effect of time on positive PANAS scores [$F(4,52) = 9.7, p < .001$]: Subjective ratings of positive affect decreased throughout the experiment. There was also a main effect of time for negative PANAS scores [$F(4,52) = 9.4, p < .001$]: Ratings of negative affect increased between the baseline (before starting the task) and the second block of the task ($p < .005$), then gradually decreased throughout the remainder of the experiment (see Figure 2).

RTs. RTs showed a predicted main effect of Stroop [$F(1,13) = 17.6, p < .001$]: Subjects' responses were faster to congruent stimuli (CS) than to incongruent stimuli (IS; 591 ± 36 and 645 ± 46 , respectively). There were no main effects or interactions involving valence or field on RT data. There was a main effect of time [$F(1,13) = 57.5, p < .001$] due to slower RTs during early task blocks (674 ± 44 and 563 ± 40 , respectively). There was also a time × field interaction [$F(1,13) = 6.2, p < .05$]: RTs tended to be faster for stimuli presented to the LVF than for those presented to the RVF during early task blocks (662 ± 44 vs. $685 \pm 45, p = .06$), whereas there were no differences related to field in later blocks (568 ± 42 vs. $556 \pm 37, p = .3$).

Accuracy. There were no main effects of Stroop, field, or valence on *d'* scores. There was, however, a field × valence interaction [$F(1,13) = 6.4, p < .05$]. Planned follow-up comparisons showed that accuracy for LVF

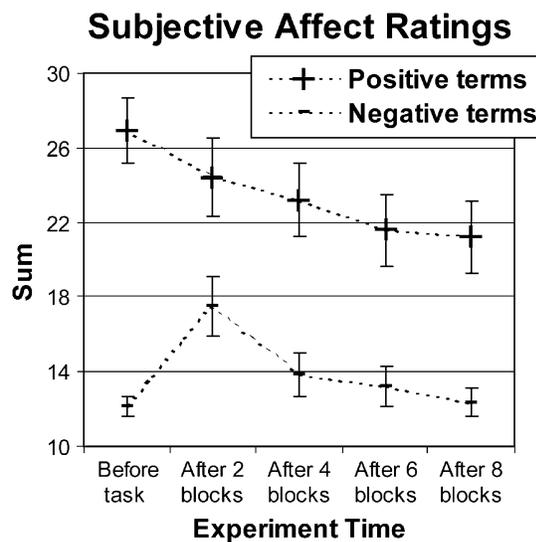


Figure 2. Subjective ratings on successive administrations of the Positive and Negative Affect Scale throughout the experiment. Positive ratings decreased and negative ratings increased after task initiation ($p < .001$ and $p < .005$, respectively), then gradually decreased until the end of the experiment.

stimuli was greater after aversive than after neutral pictures ($4.3 \pm 0.36, 3.6 \pm 0.3$, respectively, $p < .001$). For stimuli that followed aversive pictures accuracy was marginally greater for LVF than for RVF stimuli ($p = .07$), whereas for stimuli that followed neutral pictures accuracy was marginally greater for RVF than for LVF stimuli ($p = .06$; see Table 1). Further grouping of accuracy data by time revealed no additional main effects, interactions, or trends.

Electrophysiology

Response-locked ERPs. A negative ERP component similar in shape and scalp topography to the ERN computed from error-response trials was observed after correct responses, henceforth referred to as the CRN (see Figure 3). A 2 (component: ERN, CRN) × 57 (common scalp recording electrodes) ANOVA of vector normalized mean amplitudes (McCarthy & Wood, 1985; Ruchkin, Johnson, & Friedman, 1999) showed no main effects or interactions between component and electrode ($p > .5$ for both), verifying that the topographic distributions of the ERN and

Table 1
Task Performance Accuracy
Across Conditions Assessed as *d'* Scores

Visual Field	Picture Type	<i>d'</i>	SE	Comparisons	Effects
Left	(a) Aversive	4.26	0.36	a > b	$p < .001$
	(b) Neutral	3.62	0.30	a > c	$p < .07$
Right	(a) Aversive	3.71	0.33	c > d	$p < .2$
	(b) Neutral	4.10	0.33	b > d	$p < .06$

Note—Responses to LVF stimuli were more accurate after aversive relative than after neutral pictures, whereas responses to RVF stimuli were less accurate after aversive than after neutral pictures ($p < .05$).

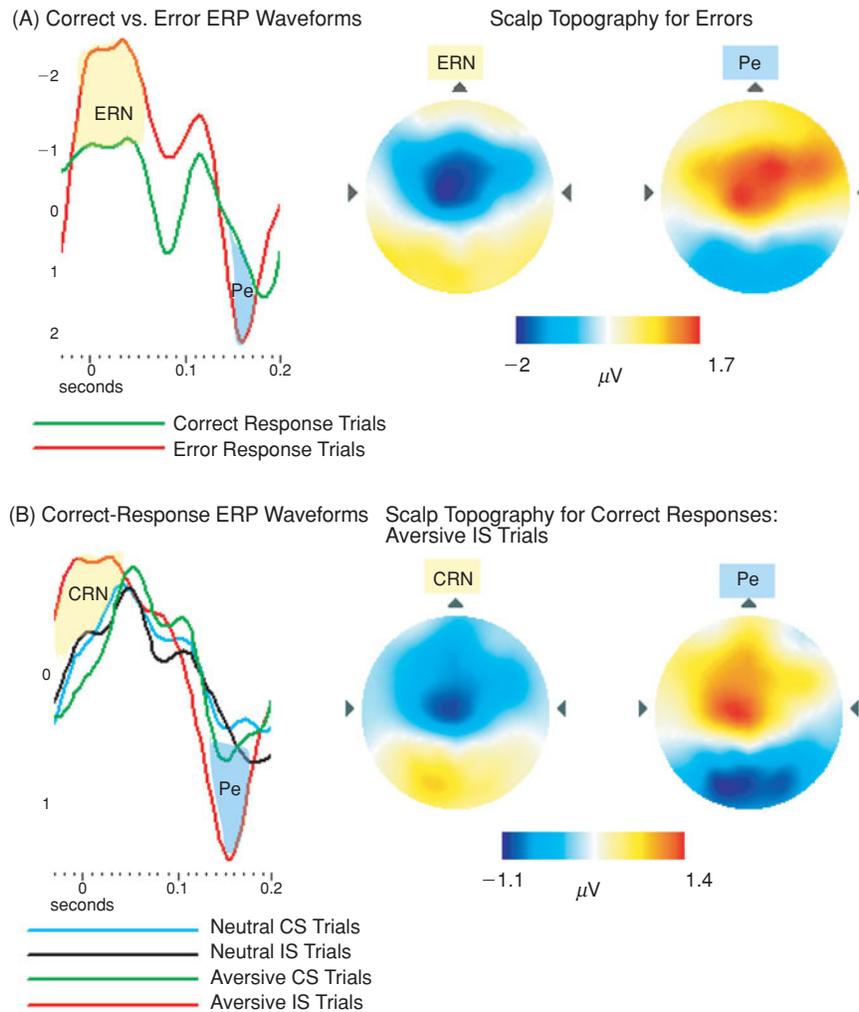


Figure 3. (A) ERN (shaded yellow) and Pe (shaded blue) components of the response-locked ERP at frontal-central electrode FCz for correct vs. error trials, and scalp topographic distribution of ERN and Pe components for error trials. (B) CRN and Pe components of the response-locked ERP at FCz for correct trials grouped by experimental condition: congruent (CS) versus incongruent (IS) and aversive versus neutral picture conditions. Scalp topographies for CRN and Pe components from correct-response, aversive-picture IS trials.

CRN overlapped. A subsequent positive component was also observed during correct-response trials and showed no differences in distribution from the error-trial Pe. Finally, an ANOVA comparing topographic distributions of correct-trial components (CRN, correct-trial Pe) revealed no main effects of component or interactions, suggesting that the distributions of the CRN and the correct-trial Pe also overlap at the scalp.

The CRN computed from this data had two distinguishable peaks. There was an earlier peak maximal between -30 and 10 msec around the buttonpress response and a slower peak between 20 and 60 msec after the buttonpress response. A broad measure of CRN amplitude across both peaks (-30 to 60 msec) showed no main effects of valence, Stroop, or field. There was,

however, a valence \times Stroop interaction [$F(1,13) = 6.1$, $p < .05$]. CRN amplitude was selectively enhanced for responses to IS that followed aversive pictures. Planned comparisons showed that the CRN was greater for IS that followed aversive pictures than for CS that followed aversive pictures or for IS that followed neutral pictures ($p < .05$ for both).

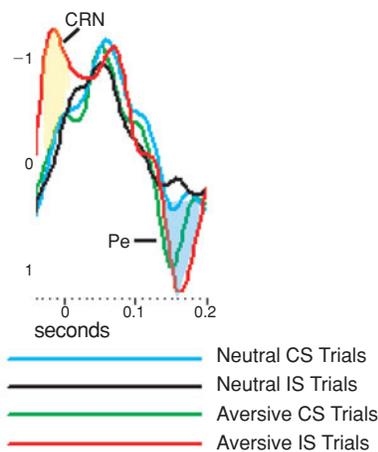
When grouped by time into early versus late experimental blocks, the early-block CRN peak overlapped with the faster peak observed in the CRN from all blocks, whereas the late-block CRN overlapped with the slower peak observed in the CRN from all blocks. A time-to-peak latency comparison between early- and late-block CRNs did not reveal a significant effect of time on latency. However, there were unique condition-related dif-

ferences in early- versus late-block CRN amplitudes. Between -30 and 10 msec on the early-block CRN, amplitudes showed a near-significant valence effect ($p = .07$). Follow-up planned comparison of CRNs for IS revealed a main effect of valence [$F(1,13) = 6.6, p < .05$]: CRNs for IS were greater following aversive pictures (see Figure 4A). For the slower, 20- to 60-msec, window, late-block CRN amplitudes showed a valence \times field interaction [$F(1,13) = 5.5, p < .05$]. Planned comparisons showed that the CRN for RVF stimuli that followed aversive pictures was greater than that for RVF stimuli

that followed neutral pictures and greater than the CRN for LVF stimuli that followed aversive pictures ($p < .05$ for both) (see Figure 4B). The slower CRN was not affected by the congruency of the stimuli.

The Pe component was maximal between 130 and 180 msec after correct buttonpress responses. Over all blocks, Pe amplitude showed a main effect of valence, being greater for stimuli that followed aversive pictures [$F(1,13) = 8.8, p < .05$]. Pe also showed a valence \times Stroop interaction [$F(1,13) = 7.2, p < .05$]. Like the CRN, Pe amplitude showed greater enhancement for re-

(A) Correct-Response ERP Waveforms:
Early Task Blocks



(B) Correct-Response ERP Waveforms:
Late Task Blocks

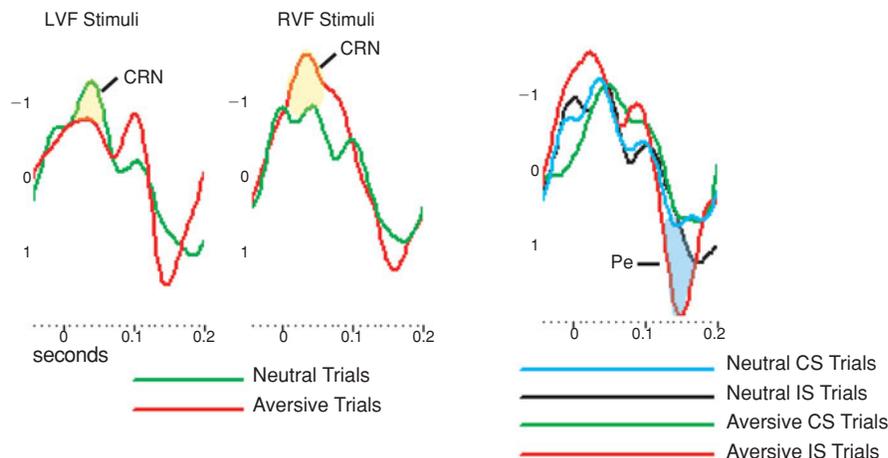


Figure 4. (A) The CRN (shaded yellow) and Pe (shaded blue) components of the response-locked ERP during early task blocks at frontal-central electrode FCz. The CRN peak occurred earlier and was increased for responses to incongruent stimuli that followed aversive pictures ($p < .05$), and the Pe was increased for all stimuli that followed aversive pictures ($p < .05$). (B) The CRN and Pe components of the response-locked ERP during late task blocks at frontal central electrode FCz. The CRN peak occurred later and was increased for conditions that corresponded to increased error rates (LVF after neutral pictures, RVF after aversive pictures; $p < .05$). The Pe from later experimental blocks was increased only for incongruent stimuli that followed aversive pictures ($p < .05$).

sponses to IS that followed aversive pictures (see Figure 4A). Planned comparisons showed that error positivity values were greater for IS following aversive pictures than for CS following aversive, or than for IS following neutral pictures ($p < .05$ for both).

Measured from early block ERPs, the Pe showed a main effect of valence [$F(1,13) = 6.7, p < .05$]; its amplitude was greater for responses to stimuli that followed aversive pictures. Error positivity values from later blocks, however, showed more complex main effects of valence [$F(1,13) = 5.7, p < .05$] and Stroop [$F(1,13) = 5.6, p < .05$] and a valence \times Stroop interaction [$F(1,13) = 7.7, p < .05$]. During later experimental blocks, Pe amplitude was increased for all stimuli that followed aversive pictures, all IS, and most prominently for responses to IS that followed aversive pictures (see Figure 4B). Planned comparisons revealed that this effect was weighted by significantly increased Pe amplitude for responses to IS after aversive pictures versus after neutral pictures and versus CS after aversive pictures ($p < .01$ for both).

DISCUSSION

This study explored the influence of negative emotion on behavior and response-locked ERPs associated with performance monitoring. EEG was acquired from subjects performing a working memory delay task that used numeric Stroop stimuli interspersed with neutral and aversive pictures from the IAPS (Lang, 1999). Subjective measures revealed that subjects felt more negative, and task behavior showed that they performed the task differently as a result of viewing the aversive pictures. Early in the experiment, when self-ratings of negative feeling were the highest, RTs were faster for stimuli presented to the right hemisphere (LVF) than to the left hemisphere (RVF). Throughout the experiment, responses were more accurate for stimuli presented to the right hemisphere (LVF) and less accurate for stimuli presented to the left hemisphere (RVF) following aversive pictures. Correct-trial response-locked ERPs revealed CRN and Pe components that were dynamically sensitive to stimulus visual field (i.e., initial processing hemisphere), Stroop interference, and picture valence.

Self-ratings on the PANAS showed that subjects felt emotionally affected as a consequence of viewing the aversive IAPS pictures (Codispoti, Bradley, & Lang, 2001; Sutton, Davidson, Donzella, Irwin, & Dottl, 1997). After performing two blocks of the task (one congruent and one incongruent), subjects associated their current feeling significantly more with negative terms and less with positive terms. With further repetition, successive negative affect ratings gradually decreased, suggesting that subjects' feelings and underlying emotional responses were habituating to the repeated presentation of aversive pictures (Carretié, Hinojosa, & Mercado, 2003; Feinstein, Goldin, Stein, Brown, & Paulus, 2002; Fischer et al., 2003). Ratings of positive affect continued to decrease, albeit less precipitously, throughout the experiment.

The PANAS ratings provided a useful measure of the sustained, tonic effects that viewing aversive pictures had on subjects' emotional states. Phasic, individual picture-related effects on subjective emotion were not explicitly measured in this study. Several studies have reported similar affective responses to IAPS pictures presented for brief trial intervals and for runs of longer series, suggesting that brief and sustained affective responses were elicited with repeated picture presentation in this study (Bradley, Cuthbert, & Lang, 1996; Codispoti et al., 2001).

Subjects' RTs during incongruent stimulus blocks were slower than their RTs during congruent stimulus blocks, confirming that the incongruent condition was more demanding than the congruent condition. However, since congruent and incongruent stimuli were presented separately in blocks, the difficulty of the incongruent condition cannot be directly attributed to traditional Stroop interference—that is, increased conflict between prepotent and task-instructed processing of and responding to the number of stimuli (Stroop, 1935). Subjects may have developed a rule-based cognitive strategy for responding during the incongruent block condition, responding without necessarily choosing or switching between the prepotent and task-relevant options, since the task-relevant option was always the appropriate one within each block. RTs were slower during earlier experimental blocks, suggesting that subjects' performance improved with task repetition. There was also an interaction between experiment time and field of stimulus presentation: During earlier task blocks, RTs to LVF (right-hemisphere) stimuli were faster than those to RVF (left-hemisphere) stimuli, whereas RTs were not significantly different across fields later in the experiment. Faster RTs to LVF stimuli suggests that there was a right-hemisphere advantage during the early blocks of the task. This laterality difference was not observed during the four practice trials that excluded picture stimuli ($p = .58$), indicating that the cognitive demands of the task did not afford an intrinsic right-hemisphere advantage. Therefore, the RT differences suggest that the early right-hemisphere RT advantage was driven by the tonic or sustained aversive emotional state invoked by the repeated negative pictures. In further support of this claim, the right-hemisphere RT advantage diminished as negative-emotion subjective ratings decreased later in the experiment. This early right-hemisphere advantage may reflect a tonic facilitation of right-hemisphere processing induced by subjects' shift toward a more negative emotional state. In agreement with the valence hypothesis, which purports that there is a right-hemisphere dominance in processing withdrawal-related emotions (Davidson, 1998; Davidson, & Irwin, 1999) including fear and disgust, the aversive pictures may have initiated a fear/avoidance-oriented emotional state early in the experiment that selectively cued the right hemisphere to orient attention, detect, and respond faster to task stimuli (Posner & Petersen, 1990; Stormark, Nordby, & Hugdahl, 1995).

Task accuracy showed an enduring and distinct hemispheric influence of negative emotion on cognitive performance. Subjects responded more accurately to LVF (right-hemisphere) stimuli than to RVF (left-hemisphere) stimuli when they followed aversive images throughout the experiment. Together, the RT and accuracy data suggest that subjects' emotional responses to the pictures enhanced or primed the right hemisphere, which benefited subsequent stimulus processing. This agrees with several other studies that show improved right-hemisphere function in emotion-cognition paradigms (Van Strien & Heijt, 1995; Van Strien & Luipen, 1999; Van Strien & Morpurgo, 1992).

There are, however, reports of findings that are inconsistent with the negative-emotion right-hemisphere facilitation hypothesis. Hartikainen et al. (2000) proposed, having observed *slower* RTs to LVF (right-hemisphere) than to RVF (left-hemisphere) targets after aversive pictures in their study, that processing of aversive pictures selectively distracted the right hemisphere and interfered with cognitive task target processing. Although not resolved, several hypotheses may explain the apparent inconsistency between these two findings. First, the effects of emotion on cognition may be modulated by task parameters such as task cognitive load or interstimulus intervals between emotion-eliciting and cognitive task-related stimuli. The cognitive task in the Hartikainen study was a very simple target-detection task, whereas this study involved complex higher executive control. Negative-emotion elicitation may affect these two levels of cognitive processes uniquely. Second, depending on the time elapsed between the onset of an emotion elicitor and a cognitive stimulus, the emotional pictures can serve as cues to orient attention (longer time) or distractors that interfere with or impair attention shifting (shorter time) (Dolan, 2002). In the Hartikainen study, task-related stimuli appeared 350 msec after the onset of the emotion-eliciting pictures. In the present study, the task stimuli appeared 1 sec after the onset of the emotion elicitors. Shorter intervals between emotion elicitation and the task-related stimuli may result in interference between the emotional and cognitive processes, whereas longer intervals may allow for integration between the two (Codiopoti et al., 2001). Related to this, Stormark et al. showed that emotional stimuli improve attention orienting as well as impair attention shifting, depending on the duration of the emotion stimulus (Stormark, Field, Hugdahl, & Horowitz, 1997).

Valence, brain hemisphere, and Stroop interference related influences on the CRN and Pe components indicate that emotional processes and cognitive goal-oriented processes concurrently and dynamically modulate performance-monitoring signals. The CRN component increased with incongruent stimuli preceded by aversive pictures; this condition featured the greatest degree of competition between cognitive processing and negative emotional processing. Several studies have established a reliable CRN response during conditions of increased re-

sponse conflict, albeit primarily between cognitive response options, and have proposed that the CRN may be generated by the anterior cingulate cortex (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick et al., 1999; Carter et al., 2000; Fan, Flombaum, McCandliss, Thomas, & Posner, 2003; Gehring et al., 2001; Mathalon, Whitfield, & Ford, 2003; Nieuwenhuis, Yeung, van den Wildenberg, & Ridderinkhof, 2003; Van Veen & Carter, 2002; Van Veen, Cohen, Botvinick, Stenger, & Carter, 2001). Such cognitive neuroscience-based theories of anterior cingulate function characterize it as the essential structure in a cognitive conflict-monitoring system. Our findings suggest that the conflict-related signals of the anterior cingulate are mediated by fluctuations in both cognitive and affective demand and salience. This conclusion is parsimonious with the anatomical connectivity and positioning of the anterior cingulate with respect to putative higher cognitive and emotion processing regions of the cerebral cortex (Bush, Luu, & Posner, 2000; Koski & Paus, 2000).

Detailed analysis of the CRN generated in this study revealed an earlier and a later subcomponent, differentially sensitive to conflict, affect, and error likelihood. The earlier latency subcomponent of the CRN was increased in the initial blocks of the experiment (when negative emotional ratings were highest) for responses to stimuli that followed aversive pictures and to a greater extent if they were incongruent. Several researchers have described response and task feedback related ERP components that increase with negative affect associated with error commission or the detection of loss (Falkenstein et al., 2000; Gehring et al., 2002; Holroyd, Coles, & Nieuwenhuis, 2002; Holroyd, Nieuwenhuis, Yeung, & Cohen, 2003; Luu, Flaisch, & Tucker, 2000; Luu, Tucker, & Collins, 2000; Luu et al., 2003; Stemmer et al., 2001). The later latency CRN subcomponent was selectively increased for RVF stimuli following aversive pictures during later experimental trials, when negative emotional reactions to the repeated aversive pictures were attenuated. Behaviorally, error rates were highest for RVF stimuli that followed aversive pictures. The increased CRN for RVF stimuli after aversive pictures may reveal some incidental conflict between left-hemisphere initiated task processing and concurrent sustained negative emotional processing, or the emergence of heightened conflict or ERP signal in the condition that had been showing the greatest frequency of errors.

The dynamic sensitivity of the CRN described here suggests that it confers dynamic contextual salience with cognitive and emotional input. In earlier experimental blocks, the influence of the disturbing pictures was more salient, whereas in later experimental blocks, cognitive demand related to task performance goals was more influential. Across the whole experiment, the CRN showed a more complex interaction between conditions that probably reflected summated responses to temporally fluctuating processing of negative emotional and cognitive demands.

The Pe, a less studied electrophysiological index of error or conflict detection, showed a systematic, temporally constrained, and reliable pattern of sensitivity to the fluctuating combination of cognitive demand and negative affect. Over all blocks, the Pe, like the CRN, showed increased amplitude for responses to incongruent (increased-demand/conflict) stimuli that followed aversive pictures. However, the Pe from earlier task blocks showed a general increase for responses to stimuli that followed aversive pictures. In later blocks, the Pe showed a more selective increase with incongruent stimuli that followed aversive pictures, echoing the shift from affective-salience-driven modulation to cognitive-demand/conflict-driven modulation exhibited in the CRN.

Taken together, the results support the notion that the CRN and Pe represent online detection of the need for reallocation of neural resources in the interest of (1) responding to circumstances that elicit negative emotional states and (2) solving a cognitive or goal-oriented problem that entails greater demand.

The hemispheric effects of aversive pictures on performance measures interacted with response-locked ERP modulation only in some conditions (the slower CRN subcomponent). Stroop stimulus-locked ERP components, however, showed comparable patterns of negative affect based hemispheric influence on components related to attention and early cognitive processing (Simon-Thomas et al., 2005). There are several reasons why effects of stimulus presentation side would be less prominent in the buttonpress response-locked ERPs examined in this study. First, in the time lapsed between the appearance of the Stroop stimulus and the executed response, hemispheres that may have initially had different levels of involvement in visual feature analysis are likely to have transferred and integrated information back and forth. Second, subjects' buttonpress responses were always carried out by fingers on the right hand, meaning that response-related processing had to be integrated into the left motor cortex for all responses.

In summary, the data show that the CRN and Pe components of response-locked ERPs interact dynamically with increased conflict related to cognitive demand and negative affect, even when responses are correct.

REFERENCES

- BOTVINICK, M. M., BRAVER, T. S., BARCH, D. M., CARTER, C. S., & COHEN, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review*, **108**, 624-652.
- BOTVINICK, M. M., NYSTROM, L. E., FISSELL, K., CARTER, C. S., & COHEN, J. D. (1999). Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature*, **402**, 179-181.
- BRADLEY, M. M., CUTHBERT, B. N., & LANG, P. J. (1996). Picture media and emotion: Effects of a sustained affective context. *Psychophysiology*, **33**, 662-670.
- BRAZDIL, M., ROMAN, R., FALKENSTEIN, M., DANIEL, P., JURAK, P., & REKTOR, I. (2002). Error processing—evidence from intracerebral ERP recordings. *Experimental Brain Research*, **146**, 460-466.
- BUSH, G., LUU, P., & POSNER, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences*, **4**, 215-222.
- CARRETIÉ, L., HINOJOSA, J. A., & MERCADO, F. (2003). Cerebral patterns of attentional habituation to emotional visual stimuli. *Psychophysiology*, **40**, 381-388.
- CARTER, C. S., BRAVER, T. S., BARCH, D. M., BOTVINICK, M. M., NOLL, D., & COHEN, J. D. (1998). Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science*, **280**, 747-749.
- CARTER, C. S., MACDONALD, A. M., BOTVINICK, M. M., ROSS, L. L., STENGER, V. A., NOLL, D., & COHEN, J. D. (2000). Parsing executive processes: Strategic vs. evaluative functions of the anterior cingulate cortex. *Proceedings of the National Academy of Sciences*, **97**, 1944-1948.
- CODISPOTI, M., BRADLEY, M. M., & LANG, P. J. (2001). Affective reactions to briefly presented pictures. *Psychophysiology*, **38**, 474-478.
- DAVIDSON, R. J. (1998). Anterior electrophysiological asymmetries, emotion, and depression: Conceptual and methodological conundrums. *Psychophysiology*, **35**, 607-614.
- DAVIDSON, R. J., & IRWIN, W. (1999). The functional neuroanatomy of emotion and affective style. *Trends in Cognitive Neurosciences*, **3**, 11-21.
- DERRYBERRY, D. (1990). Right hemisphere sensitivity to feedback. *Neuropsychologia*, **28**, 1261-1271.
- DEVINSKY, O., MORRELL, M. J., & VOGT, B. A. (1995). Contributions of anterior cingulate cortex to behaviour. *Brain*, **118**, 279-306.
- DOLAN, R. J. (2002). Emotion, cognition, and behavior. *Science*, **298**, 1191-1194.
- DREVETS, W. C. (1998). Functional neuroimaging studies of depression: The anatomy of melancholia. *Annual Review of Medicine*, **49**, 349-361.
- DREVETS, W. C., ONGÜR, D., & PRICE, J. L. (1998). Neuroimaging abnormalities in the subgenual prefrontal cortex: Implications for the pathophysiology of familial mood disorders. *Molecular Psychiatry*, **3**, 220-6, 190-1.
- FALKENSTEIN, M., HOORMANN, J., CHRIST, S., & HOHNSBEIN, J. (2000). ERP components on reaction errors and their functional significance: A tutorial. *Biological Psychology*, **51**, 87-107.
- FAN, J., FLOMBAUM, J. I., MCCANDLISS, B. D., THOMAS, K. M., & POSNER, M. I. (2003). Cognitive and brain consequences of conflict. *NeuroImage*, **18**, 42-57.
- FEINSTEIN, J. S., GOLDIN, P. R., STEIN, M. B., BROWN, G. G., & PAULUS, M. P. (2002). Habituation of attentional networks during emotion processing. *NeuroReport*, **13**, 1255-1258.
- FISCHER, H., WRIGHT, C. I., WHALEN, P. J., MCINERNEY, S. C., SHIN, L. M., & RAUCH, S. L. (2003). Brain habituation during repeated exposure to fearful and neutral faces: A functional MRI study. *Brain Research Bulletin*, **59**, 387-392.
- GEHRING, W. J., & FENCSEK, D. E. (2001). Functions of the medial frontal cortex in the processing of conflict and errors. *Journal of Neuroscience*, **21**, 9430-9437.
- GEHRING, W. J., & WILLOUGHBY, A. R. (2002). The medial frontal cortex and the rapid processing of monetary gains and losses. *Science*, **295**, 2279-2282.
- HAJCAK, G., McDONALD, N., & SIMONS, R. F. (2003). To err is automatic: Error-related brain potentials, ANS activity, and post-error compensatory behavior. *Psychophysiology*, **40**, 895-903.
- HARTIKAINEN, K. M., OGAWA, K. H., & KNIGHT, R. T. (2000). Transient interference of right hemispheric function due to automatic emotional processing. *Neuropsychologia*, **38**, 1576-1580.
- HELLER, W., & NITSCHKE, J. B. (1997). Regional brain activity in emotion: A framework for understanding cognition in depression. *Cognition & Emotion*, **11**, 637-661.
- HOLROYD, C. B., COLES, M. G., & NIEUWENHUIS, S. (2002). Medial prefrontal cortex and error potentials. *Science*, **296**, 1610-1611.
- HOLROYD, C. B., NIEUWENHUIS, S., YEUNG, N., & COHEN, J. D. (2003). Errors in reward prediction are reflected in the event-related brain potential. *NeuroReport*, **14**, 2481-2484.
- IACOBONI, M., RAYMAN, J., & ZAIDEL, E. (1997). Does the previous trial affect lateralized lexical decision? *Neuropsychologia*, **35**, 81-88.
- KAPLAN, J. T., & ZAIDEL, E. (2001). Error monitoring in the hemispheres: The effect of lateralized feedback on lexical decision. *Cognition*, **82**, 157-178.

- KIEHL, K. A., LIDDLE, P. F., & HOPFINGER, J. B. (2000). Error processing and the rostral anterior cingulate: An event-related fMRI study. *Psychophysiology*, *37*, 216-223.
- KOSKI, L., & PAUS, T. (2000). Functional connectivity of the anterior cingulate cortex within the human frontal lobe: A brain-mapping meta-analysis. *Experimental Brain Research*, *133*, 55-65.
- LANG, P. J. (1999). *The International Affective Picture System*. Gainesville, FL: NIMH Center for the Study of Emotion and Attention, University of Florida.
- LUU, P., FLAISCH, T., & TUCKER, D. M. (2000). Medial frontal cortex in action monitoring. *Journal of Neuroscience*, *20*, 464-469.
- LUU, P., TUCKER, D. M., & COLLINS, P. (2000). Mood, personality, and self-monitoring: Negative affect and emotionality in relation to frontal lobe mechanisms of error monitoring. *Journal of Experimental Psychology*, *129*, 43-60.
- LUU, P., TUCKER, D. M., DERRYBERRY, D., REED, M., & POULSEN, C. (2003). Electrophysiological responses to errors and feedback in the process of action regulation. *Psychological Science*, *14*, 47-53.
- MATHALON, D. H., WHITFIELD, S. L., & FORD, J. M. (2003). Anatomy of an error: ERP and fMRI. *Biological Psychology*, *64*, 119-141.
- MCCARTHY, G., & WOOD, C. C. (1985). Scalp distributions of event-related potentials: An aid in the topographic analysis of brain electrical activity. *Electroencephalography and Clinical Neurophysiology*, *62*, 203-208.
- MÜLLER, M. M., KEIL, A., GRUBER, T., & ELBERT, T. (1999). Processing of affective pictures modulates right-hemispheric gamma band EEG activity. *Clinical Neurophysiology*, *110*, 1913-1920.
- NIEUWENHUIS, S., RIDDERINKHOF, K. R., BLOM, J., BAND, G. P., & KOK, A. (2001). Error-related brain potentials are differentially related to awareness of response errors: Evidence from an antisaccade task. *Psychophysiology*, *38*, 752-760.
- NIEUWENHUIS, S., YEUNG, N., HOLROYD, C. B., SCHURGER, A., & COHEN, J. D. (2004). Sensitivity of electrophysiological activity from medial frontal cortex to utilitarian and performance feedback. *Cerebral Cortex*, *14*, 741-747.
- NIEUWENHUIS, S., YEUNG, N., VAN DEN WILDENBERG, W., & RIDDERINKHOF, K. R. (2003). Electrophysiological correlates of anterior cingulate function in a go/no-go task: Effects of response conflict and trial type frequency. *Cognitive, Affective, & Behavioral Neuroscience*, *3*, 17-26.
- PAILING, P. E., & SEGALOWITZ, S. J. (2004). The error-related negativity as a state and trait measure: Motivation, personality, and ERPs in response to errors. *Psychophysiology*, *41*, 84-95.
- PAILING, P. E., SEGALOWITZ, S. J., DYWAN, J., & DAVIES, P. L. (2002). Error negativity and response control. *Psychophysiology*, *39*, 198-206.
- PHAN, K. L., LIBERZON, I., WELSH, R. C., BRITTON, J. C., & TAYLOR, S. F. (2003). Habituation of rostral anterior cingulate cortex to repeated emotionally salient pictures. *Neuropsychopharmacology*, *28*, 1344-1350.
- PHAN, K. L., WAGER, T. D., TAYLOR, S. F., & LIBERZON, I. (2002). Functional neuroanatomy of emotion: A meta-analysis of emotion activation studies in PET and fMRI. *NeuroImage*, *16*, 331-348.
- PIZZAGALLI, D., REGARD, M., & LEHMANN, D. (1999). Rapid emotional face processing in the human right and left brain hemispheres: An ERP study. *NeuroReport*, *10*, 2691-2698.
- POSNER, M. I., & PETERSEN, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25-42.
- RABBITT, P. M. A., & VYAS, S. M. (1970). An elementary preliminary taxonomy for some errors in laboratory choice RT tasks. *Acta Psychologica*, *33*, 56-76.
- RUCHKIN, D. S., JOHNSON, R., JR., & FRIEDMAN, D. (1999). Scaling is necessary when making comparisons between shapes of event-related potential topographies: A reply to Haig et al. *Psychophysiology*, *36*, 832-834.
- RUCHSOW, M., GROTHE, J., SPITZER, M., & KIEFER, M. (2002). Human anterior cingulate cortex is activated by negative feedback: Evidence from event-related potentials in a guessing task. *Neuroscience Letters*, *325*, 203-206.
- SANFELY, A. G., RILLING, J. K., ARONSON, J. A., NYSTROM, L. E., & COHEN, J. D. (2003). The neural basis of economic decision-making in the Ultimatum Game. *Science*, *300*, 1755-1758.
- SCHIEFFERS, M. K., & COLES, M. G. (2000). Performance monitoring in a confusing world: Error-related brain activity, judgments of response accuracy, and types of errors. *Journal of Experimental Psychology: Human Perception Performance*, *26*, 141-151.
- SCHUTTER, D. J. L. G., VAN HONK, J., D'ALFONSO, A. A. L., POSTMA, A., & DE HAAN, E. H. F. (2001). Effects of slow rTMS at the right dorsolateral prefrontal cortex on EEG asymmetry and mood. *NeuroReport*, *12*, 445-452.
- SCHWARTZ, G. E., DAVIDSON, R. J., & MAER, F. (1975). Right hemisphere lateralization for emotion in the human brain: Interactions with cognition. *Science*, *190*, 286-288.
- SEWARDS, T. V., & SEWARDS, M. A. (2002). The medial pain system: Neural representations of the motivational aspect of pain. *Brain Research Bulletin*, *59*, 163-180.
- SIMON-THOMAS, E. R., ROLE, K. O., & KNIGHT, R. T. (2005). Behavioral and electrophysiological evidence of a right hemisphere bias for the influence of negative emotion on higher cognition. *Journal of Cognitive Neuroscience*, *17*, 518-529.
- STEMMER, B., WITZKE, W., & SCHÖNLE, P. W. (2001). Losing the error related negativity in the EEG of human subjects: An indicator for willed action. *Neuroscience Letters*, *308*, 60-62.
- STORMARK, K. M., FIELD, N. P., HUGDAHL, K., & HOROWITZ, M. (1997). Selective processing of visual alcohol cues in abstinent alcoholics: An approach-avoidance conflict? *Addictive Behaviors*, *22*, 509-519.
- STORMARK, K. M., NORDBY, H., & HUGDAHL, K. (1995). Attentional shifts to emotionally charged cues: Behavioral and ERP data. *Cognition & Emotion*, *9*, 507-523.
- STROOP, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, *18*, 643-662.
- SUTTON, S. K., DAVIDSON, R. J., DONZELLA, B., IRWIN, W., & DOTTL, D. (1997). Manipulating affective state using extended picture presentations. *Psychophysiology*, *34*, 217-226.
- TAYLOR, S. F., PHAN, K. L., DECKER, L. R., & LIBERZON, I. (2003). Subjective rating of emotionally salient stimuli modulates neural activity. *NeuroImage*, *18*, 650-659.
- TUCKER, D. M., HARTRY-SPEISER, A., MCDUGAL, L., LUU, P., & DEGRANDPRE, D. (1999). Mood and spatial memory: Emotion and right hemisphere contribution to spatial cognition. *Biological Psychology*, *50*, 103-125.
- VAN STRIEN, J. W., & HEIJT, R. (1995). Altered visual field asymmetries for letter naming and letter matching as a result of concurrent presentation of threatening and nonthreatening words. *Brain & Cognition*, *29*, 187-203.
- VAN STRIEN, J. W., & LUIPEN, M. W. (1999). Hemispheric facilitation as a result of threatening and nonthreatening words: Blocked vs. mixed presentation effects and order effects. *Neuropsychologia*, *37*, 617-621.
- VAN STRIEN, J. W., & MORPURGO, M. (1992). Opposite hemispheric activations as a result of emotionally threatening and non-threatening words. *Neuropsychologia*, *30*, 845-848.
- VAN VEEN, V., & CARTER, C. S. (2002). The anterior cingulate as a conflict monitor: fMRI and ERP studies. *Physiology & Behavior*, *77*, 477-482.
- VAN VEEN, V., COHEN, J. D., BOTVINICK, M. M., STENGER, V. A., & CARTER, C. S. (2001). Anterior cingulate cortex, conflict monitoring, and levels of processing. *NeuroImage*, *14*, 1302-1308.
- VIDAL, F., HASBROUCQ, T., GRAPPERON, J., & BONNET, M. (2000). Is the "error negativity" specific to errors? *Biological Psychology*, *51*, 109-128.
- WATSON, D., CLARK, L. A., & TELLEGEN, A. (1988). Development and validation of brief measures of positive and negative affect: The PANAS scales. *Journal of Personality & Social Psychology*, *54*, 1063-1070.