The feedback correct-related positivity: Sensitivity of the event-related brain potential to unexpected positive feedback

CLAY B. HOLROYD,[a] KAIVON L. PAKZAD-VAEZI,[b] AND OLAVE E. KRIGOLSON[a]

[a]Department of Psychology, University of Victoria, Victoria, British Columbia, Canada
[b]Faculty of Medicine, University of British Columbia, Vancouver, British Columbia, Canada

Abstract

The N200 and the feedback error-related negativity (fERN) are two components of the event-related brain potential (ERP) that share similar scalp distributions, time courses, morphologies, and functional dependencies, which raises the question as to whether they are actually the same phenomenon. To investigate this issue, we recorded the ERP from participants engaged in two tasks that independently elicited the N200 and fERN. Our results indicate that they are, in fact, the same ERP component and further suggest that positive feedback elicits a positive-going deflection in the time range of the fERN. Taken together, these results indicate that negative feedback elicits a common N200 and that modulation of fERN amplitude results from the superposition on correct trials of a positive-going deflection that we term the feedback correct-related positivity.

Descriptors: Feedback error-related negativity, N200, Oddball task, Correct-related positivity, Reinforcement learning, Anterior cingulate cortex

The N200 and the feedback error-related negativity (fERN) are two components of the event-related brain potential (ERP) that share many similar characteristics but are normally assumed to reflect different underlying neurocognitive processes. Both are frontal-centrally distributed, negative-going deflections that peak about 250 ms following stimulus onset, and both are thought to be generated in dorsal anterior cingulate cortex (dACC; Gehring & Willoughby, 2002; Holroyd, 2004; Miltner, Braun, & Coles, 1997; Towey, Rist, Hakerem, Ruchkin, & Sutton, 1980; Yeung, Botvinick, & Cohen, 2004; but see Nieuwenhuis, Slagter, von Geusau, Heslenfeld, & Holroyd, 2005). Several varieties of the N200 have been reported in the literature (for reviews, see Folstein & van Petten, 2008; Pritchard, Shappell, & Brandt, 1991); we refer here to the negative deflection that is seen in so-called oddball tasks (e.g., Towey et al., 1980), usually in tandem with the P300 (Donchin & Coles, 1988). Importantly, the amplitude of the N200 increases in proportion to the unexpectedness of the event, being larger for in-

frequently occurring task-relevant stimuli. Similarly, in trial-and-error learning tasks, the fERN is elicited by unexpected negative feedback stimuli, but not by unexpected positive feedback stimuli (e.g., Holroyd & Krigolson, 2007; Miltner et al., 1997; for reviews, see Holroyd, Nieuwenhuis, Mars, & Coles, 2004; Nieuwenhuis, Holroyd, Mol, & Coles, 2004). The striking resemblance between these ERP components raises a number of important questions, namely, are the N200 and fERN actually the same phenomenon (Folstein & van Petten, 2008; Holroyd, 2004)? And if they are the same, then why does positive feedback not elicit an N200? Alternatively, if the two ERP components constitute different phenomena, then why is the N200 elicited by task-relevant stimuli in general, but not by feedback stimuli specifically? What makes feedback the exception?

We addressed these questions by directly comparing the fERN with the N200 in the same participants. In a previous experiment, we found that infrequent error feedback stimuli in a guessing task and infrequent target stimuli in an oddball task both elicited negative-going, frontal-centrally distributed ERP components with comparable latencies and amplitudes (Holroyd, Krigolson, & Pakzad-Vaezi, 2006). This result suggested that the fERN and the N200 may, in fact, be the same ERP component, and further, that variation in fERN amplitude may be driven more by neural activity on correct trials than on error trials. In the present experiment, we replicated and extended this finding by comparing the neural response to infrequent stimuli in an oddball task to that of both unexpected error feedback and unexpected correct feedback in a reinforcement learning task

(Pakzad–Vaezi, Krigolson, & Holroyd, 2006). Specifically, we recorded the N200 and fERN from participants engaged in, respectively, a standard oddball task (e.g., Towey et al., 1980) and a modified time-estimation task (Holroyd & Krigolson, 2007). Given our previous findings, we predicted that unexpected negative feedback, but not unexpected positive feedback, would elicit a fERN, and that the latency and scalp distribution of the fERN would be comparable to that of the N200, suggesting that the ERP components are, in fact, the same phenomenon. Further, we predicted that our results would point toward an entirely different ERP component as the source of the apparent variance in fERN amplitude.

We addressed this latter issue as follows. Even though it is often assumed that the fERN is elicited by a neural process that is sensitive to error feedback (e.g., Miltner et al., 1997), appearances notwithstanding, the positive and negative deflections observed in the ERP may only loosely correspond to individual neural processes (Luck, 2005). Thus it is equally possible that the difference between the ERPs on correct and incorrect trials arises from a process associated with correct trials rather than with error trials (Holroyd, 2004). For this reason, in previous studies we measured fERN amplitude using a difference wave approach where possible. The difference wave method isolates variance in the ERP associated with feedback valence irrespective of whether the source of that variance stems from a neural process occurring on error trials or on correct trials (e.g., Holroyd & Krigolson, 2007). By contrast, here we asked whether variance in fERN amplitude in fact results mainly from error trials or from correct trials. To do so, we relied on simple additive-factors logic: If, as predicted, the fERN and the N200 are the same ERP component and if the variance in fERN amplitude is due mainly to neural activity on correct trials, then the difference between the ERP on correct trials and the N200 should be larger than the difference between the fERN and the N200. For heuristic purposes, we call the ERP component isolated by this approach the "feedback correct-related positivity" (fCRP).

Methods

Participants

Twelve people (6 men, 26.7 ± 10.5 years old) were recruited by poster advertising on campus. All of the participants were paid $20 CAN plus a small monetary bonus that depended on their performance in the time estimation task (about $7.45 CAN; see below). They provided written, informed consent. The study was conducted in accordance with the ethical standards prescribed in the Declaration of Helsinki and was approved by the human subjects review board at the University of Victoria.

Apparatus and Procedure

Participants were seated comfortably in front of a computer monitor in an electromagnetically shielded booth and engaged in both an oddball task and a modified time estimation task, the order of which was counterbalanced across participants. Visual stimuli consisted of four color images of fruit (apple, orange, banana, pineapple; 3° of visual angle) presented against a black background on the computer monitor. For each participant, two images were designated as the target and nontarget stimuli in the oddball task, and the remaining two images were designated as positive and negative feedback in the time estimation task (see

below); the mappings between the images and the conditions were counterbalanced across participants.

Oddball task. Participants completed two blocks of 200 trials each. On each trial, a fixation cross (1° of visual angle) was presented at the center of the computer monitor for 1.0 s, followed by one of two visual images of fruit (see above) for 500 ms. The type of fruit was selected randomly (without replacement) on each trial, such that a target image appeared on 12.5% of trials and a nontarget image on the remainder. Participants were asked to count silently the target image while ignoring the nontarget image. Between the first and second blocks they relaxed during a self-paced rest period.

Time estimation task. Participants performed a modified time estimation task (Holroyd & Krigolson, 2007) in which they were required to estimate the duration of 1 s (cf. Miltner et al., 1997). Each trial began with an auditory cue (1500 Hz, 65 dB) that lasted for 50 ms. Participants pressed the left button on a mouse pad when they thought that 1 s had elapsed following the cue, and received feedback indicating the accuracy of their estimate 600 ms later. A trial was considered on time if the participant's response occurred within a window of time centered around 1 s (see below) and was considered not on time otherwise. The feedback stimuli consisted of two images of fruit (see above), one that indicated that the response was on time (correct feedback) and the other that indicated that the response was not on time (error feedback). Following the offset of the feedback stimulus a blank screen was presented for either 1400, 1500, or 1600 ms (equivalent probability of each).

The performance window was initialized at 1000 ms ± 100 ms. Thus, each participant was required to respond between 900 and 1100 ms following the auditory cue to receive correct feedback on the first trial. Following each trial the size of the performance window decreased if the response landed within the window and increased otherwise. The amount of this change depended on three experimental conditions: control, easy, and hard. In the control condition the window size increased by 10 ms on error trials and decreased by 10 ms on correct trials. In the easy condition the window size increased by 12 ms on error trials and decreased by 3 ms on correct trials. In the hard condition the window size increased by 3 ms on error trials and decreased by 12 ms on correct trials. Participants were informed at the start of the task that each correct response would earn them 3 cents (CAD), that error responses would not, and that the total bonus would be given to them at the end of the experiment.

Participants completed five blocks of 100 trials. First, they completed one block of trials in the control condition. The control condition was followed by two blocks of trials in each of the easy and hard conditions, the order of which was counterbalanced across participants. Thus, across the three experimental conditions there were 500 trials total. The purpose of the control condition was threefold: first, to replicate the standard fERN phenomenon; second, to establish a stable performance window before participants engaged in the subsequent conditions (see below); and third, to ensure that participants practiced the task sufficiently before engaging in the hard condition. Participants were informed that some blocks would be more difficult than others, but were not told specifically which blocks were hard or easy. Importantly, the size of the performance window on each block was initialized with the value that corresponded to the end

of the previous block. Participants relaxed during self-paced rest periods between blocks.

Data Acquisition

For the oddball task, at the end of each block participants were asked to report how many target stimuli they counted. To ensure that they did not forget the stimulus mappings, at the end of the first block they were also asked to report which of the two images was the target stimulus. Likewise, at the end of each block in the time estimation task they were also asked to report which stimulus indicated correct performance. Response time (in milliseconds) and accuracy (on time vs. not on time) were recorded on each trial of the time estimation task using a standard USB mouse.

The electroencephalogram (EEG) was recorded from 41 electrode locations using Brain Vision Recorder software (Version 1.3, Brainproducts, Munich, Germany). The electrodes were mounted in a fitted cap with a standard 10–20 layout and were referenced to the average voltage across channels. The vertical and horizontal electrooculogram were recorded from electrodes placed above and below the right eye and on the outer canthi of the left and right eyes, respectively. Electrode impedances were kept below 10 kΩ. The EEG data were sampled at 250 Hz, amplified (Quick Amp, Brainproducts, Munich, Germany), and filtered through a passband of 0.017–67.5 Hz (90 dB octave roll off).

Data Analysis

To confirm that the participants remembered the task instructions, the stimulus-condition mappings reported in the oddball task and the time estimation task were evaluated for each participant. Further, for the oddball task, the mean number of targets reported following each block was calculated. For the time estimation task, mean response times, accuracies, and window sizes were calculated for each participant for each condition.

The EEG data were filtered off-line through a 0.1–20 Hz passband phase-shift-free Butterworth filter and re-referenced to linked mastoids. Ocular artifacts were removed using the algorithm described by Gratton, Coles, and Donchin (1983). Trials in which the change in voltage at any channel exceeded 35 µV per sampling point were also discarded. In total, less than 5% of the data were discarded. For the two experimental conditions in the oddball task (infrequent, frequent) and the six experimental conditions in the time estimation task (error and correct feedback in the control, easy, and hard conditions), an 800-ms epoch of data (from 200 ms before each stimulus to 600 ms after) was extracted from the continuous EEG for each trial, channel, and participant. These epochs were baseline corrected relative to the 200-ms segment preceding stimulus onset. ERPs were created by averaging the EEG data by condition for each electrode channel and participant.

ERPs associated with infrequent oddball and infrequent error trials (N200 and fERN). To compare the N200 with the fERN, we analyzed the ERP components using two alternative methods: first by examining the ERPs directly, and second by performing a spatial principal components analysis (PCA) on the ERP data. To analyze the ERP components directly, we measured the N200 elicited by the infrequent targets in the oddball task (which generate the largest N200), and the fERN elicited by infrequent error feedback in the time estimation task (which generate the largest fERN), with the base-to-peak algorithm de-

scribed by Holroyd, Nieuwenhuis, Yeung, and Cohen (2003). Note that by definition the error feedback in the easy condition constitutes infrequent error feedback whereas the error feedback in the hard condition constitutes frequent error feedback. For completeness, we also measured the positive-going deflection elicited by infrequent correct feedback in the time estimation task (i.e., by correct feedback in the hard condition) with the same base-to-peak algorithm. Then, the latencies and scalp distributions of the N200 and fERN were compared. We eschewed the traditional ANOVA-based approach for comparing scalp distributions by first normalizing the voltages (McCarthy & Wood, 1985) because of recent concerns about the validity of this method (Urbach & Kutas, 2002). Instead, we characterized the similarity of the distributions using two other methods. First, we correlated the amplitudes of the N200 and fERN across channels, which provided an indication of the overall similarity of the scalp distributions. Second, for each electrode position we computed the first derivative of the scalp distribution (using the gradplot function of EEGLab; Delorme & Makeig, 2004) and the current source density (using the del2map function of EEGLab; Delorme & Makeig, 2004). The first spatial derivative indicates the degree of curvature of the distribution and is close to zero at the critical points (Marsden & Tromba, 1981). The current source density is proportional to the second derivative of the gradient (i.e., the Laplacian of the electric potential; Nunez, 1981), the sign of which indicates whether each critical point is a maximum or a minimum. For both the infrequent error and infrequent oddball conditions, we identified the channel with the smallest first derivative that (a) did not lie along the outer ring of electrodes, where the first spatial derivative is contaminated by edge effects, and (b) was associated with positive current source density, indicating a local maximum. We then checked whether this was the global maximum by comparing the voltage at this channel with the voltages at the other channels.

To provide support for this analysis, we also compared the ERP components by conducting a spatial PCA on the ERP data (Spencer, Dien, & Donchin, 2001; analyzed using the MATLAB PCA toolbox, Dien & Frishkoff, 2005; http://people.ku.edu/ ~ jdien/downloads.html). First, spatial factor loadings were obtained by submitting to a PCA the observations for each participant and electrode, for the ERPs associated with the eight experimental conditions (frequent and infrequent in the oddball task, and error and correct in the control, easy, and hard conditions of the time estimation task; Varimax rotation, no Kaiser correction). Next, we identified the factor that exhibited loadings that were maximal at frontal-central areas of the scalp. The spatial factor scores associated with each spatial factor indicate the independent contribution of that factor to the ERP at each point in time. In the case of the frontal-central spatial factor, the factor scores can be thought of as comprising "virtual ERNs" or "virtual N200s" that indicate the time course of the factor in each condition (Holroyd & Coles, 2008; Holroyd, Krigolson, et al., 2006). Although this step is sometimes followed by application of temporal PCA to the spatial factor scores (e.g., Spencer et al., 2001), we did not use temporal PCA here because of concerns about variation in the latency of this ERP component across conditions (see Results), as temporal PCA is confounded by latency variability (Donchin & Heffley, 1978). Instead, we analyzed the virtual-ERNs using the same base-to-peak algorithm that we applied directly to the ERPs (Holroyd et al., 2003). For display purposes, the spatial factor loadings were plotted using custom Matlab scripts built on the open source EEGLAB

toolbox (spherical spline interpolation; Delorme & Makeig, 2004; http://sccn.ucsd.edu/eeglab).

ERP associated with infrequent correct trials (fCRP). To analyze the ERP on correct trials, we first latency corrected the N200 data associated with the infrequent oddball ERPs (see Results). The latencies of the N200 associated with the infrequent oddball condition and of the fERN associated with the infrequent error condition were identified by determining, for each participant, the maximum negative value of the ERP recorded at channel FCz within a 150–350-ms window following stimulus onset. For purposes of comparison, we also determined the latencies of the positive-going deflections in the ERP that preceded and followed the N200/fERN (i.e., the P200 and the P300). These values were determined by identifying the maximum positive values within, respectively, a 100 ms to 300 ms window and a 300–500-ms window following stimulus onset. Then, we created two difference waves. First, for each subject and channel we subtracted the latency-corrected infrequent oddball ERPs from the infrequent error ERPs. Second, we subtracted the latency-corrected infrequent oddball ERPs from the infrequent correct ERPs. We then determined the maximum value of these difference waves within the period associated with the fERN (200–400 ms) and plotted their scalp distributions at that time using a spherical spline interpolation (Delorme & Makeig, 2004; http://sccn.ucsd.edu/eeglab). Further, the curvatures of these distributions were evaluated by finding polynomial functions (up to order 7) that best fit each difference wave along the midline (FPz, Fz, FCz, Cz, CPz, Pz, POz, Oz) and lateral (FT7, FC5, FC3, FC1, FCz, FC2, FC4, FC6, FT8) electrode sites (cf. Holroyd & Krigolson, 2007). We reasoned that if the fERN and the N200 are the same ERP component and if this component is absent on unexpected correct trials, then the scalp distribution of the difference wave associated with the unexpected correct ERP should be larger and more curved than that associated with the unexpected error ERP.

To confirm these findings, we also repeated the same analyses on the virtual ERNs (i.e., on the spatial factor scores associated with the frontal-central factor yielded by the spatial PCA). First, we corrected the latency of the factors scores in the infrequent oddball condition (see Results). Then, we constructed two difference waves, first from the spatial scores associated with the infrequent error and infrequent oddball conditions and second from the spatial factor scores associated with the infrequent correct and infrequent oddball conditions. The amplitudes of these difference waves were then compared with a paired *t* test.

Results

Behavioral Data

All participants remembered which stimulus was the target in the oddball task and which stimulus indicated correct feedback in the time estimation task. For the oddball task, participants reported 24.8 ± 0.5 targets per block (the correct answer was 25 for both blocks). For the time estimation task, in the control condition participants were correct on about half of the trials (48.3%), and the mean size of the performance window was 300 ms. Participants made more errors in the hard condition (75.4%) than in the easy condition (24.5%), $t(11) = -35.4$, $p < .001$, Cohen's $d = 17.5$, consistent with the mean size of the performance window, which was smaller in the hard condition (128 ms) than in the easy condition (334 ms), $t(11) = 8.5$, $p < .001$, Cohen's

$d = 2.7$. These results replicate previous findings (Holroyd & Krigolson, 2007).

Electrophysiological Data

ERPs associated with infrequent oddball and infrequent error trials (N200 and fERN). Figure 1a illustrates the ERPs elicited by the frequent and infrequent stimuli in the oddball task, and Figure 1b illustrates the ERPs elicited by infrequent error, infrequent correct, frequent error, and frequent correct ERPs in the time estimation task, all recorded at channel FCz, where these components typically reach maximum amplitude (e.g., Miltner et al., 1997; Yeung et al., 2004). Qualitatively, the infrequent oddball ERP replicates the standard N200–P300 complex seen in oddball tasks (e.g., Holroyd, 2004; Towey et al., 1980). The time estimation ERPs exhibit modulation of fERN amplitude by expectancy, as seen previously (Holroyd & Krigolson, 2007). Because the fERN in this task has already been examined extensively in this previous study, we instead focus here on the subject of interest, which is a comparison of the N200 with the fERN and with the ERP on correct trials. To do so, we considered only the infrequent conditions in which the fERN and N200 were largest (e.g., Holroyd, 2004; Holroyd & Krigolson, 2007). The ERPs recorded at channel FCz for the infrequent oddball trials, infrequent error trials (i.e., errors in the easy condition), and infrequent correct trials (i.e., corrects in the hard condition) are replotted together in Figure 2a. Figure 3a and Figure 3b show the scalp distributions of the N200 and the fERN (measured base to peak), respectively. In both cases, the distributions were maximal at channel FCz. Further, both N200 amplitude (-10.0 µV), $t(11) = 6.2$, $p < .0001$, Cohen's $d = 2.5$, and fERN amplitude (-7.4 µV), $t(11) = 3.9$, $p < .005$, Cohen's $d = 1.7$, were larger than a negative deflection recorded at this channel on correct trials (-2.3 µV), but were not significantly different from each other, $t(11) = 1.6$, $p > .10$, Cohen's $d = 0.4$.

To characterize the similarity of the scalp distributions, we correlated the amplitude of the N200 with the fERN across electrodes. This correlation was .68, indicating strong similarity between the components; by contrast, the correlation between the N200 and the small negative-going deflection on correct trials was $-.12$. Further inspection revealed that the outliers in the N200–fERN correlation were associated with the far-frontal electrode channels FP1, FPz, and FP2, which were relatively more negative for the infrequent error condition (or relatively less negative for the infrequent oddball condition). To characterize the similarity of the distributions further, we computed the first and second spatial derivatives of the infrequent error and infrequent oddball scalp distributions (see Methods). This analysis confirmed that both distributions reached a global maximum at channel FCz. Finally, we predicted that if the N200 and fERN are the same ERP component, then their amplitudes (measured at channel FCz) would be positively correlated across participants; this prediction was confirmed, Pearson $r = .55$, $p = .03$ (one tailed).

Inspection of the ERPs suggested that a positive–negative–positive sequence of deflections corresponding to the P200–N200–P300 was present in both the infrequent oddball and infrequent error ERPs, but that this sequence was slightly delayed in the oddball ERP relative to the time estimation ERP (Figure 2a). Table 1 indicates the latencies of the N200 across conditions; for comparison, the relative timings of the P200 and P300 (as measured at channel FCz) are also given; the differences in these
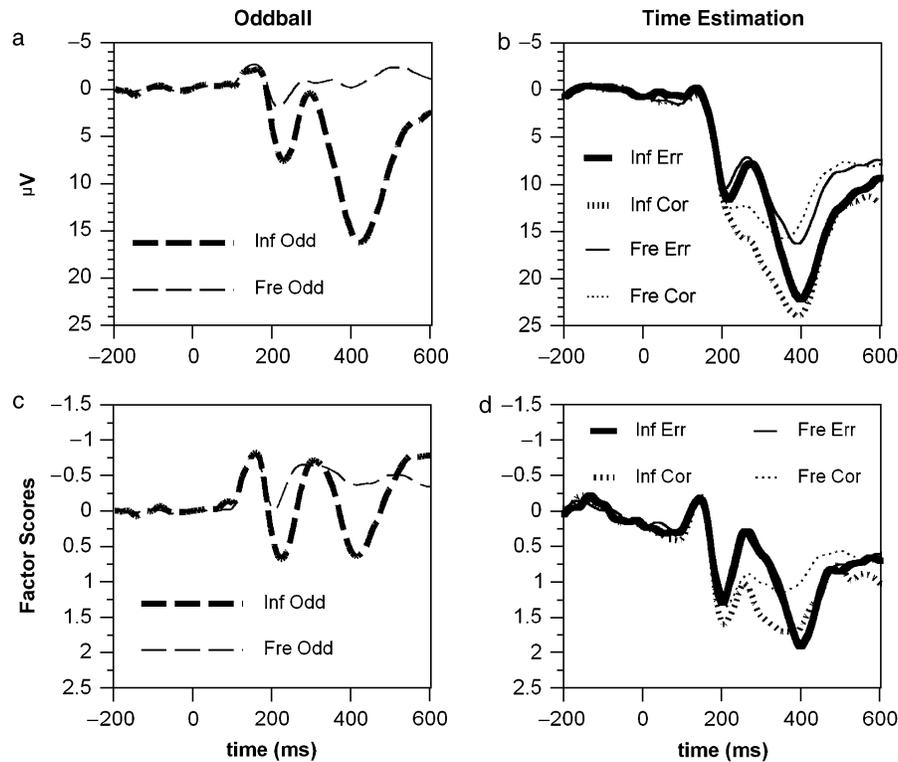
Figure 1. Event-related brain potential (ERP) data and spatial factor scores. a, b: ERP data associated with the oddball (a) and time estimation (b) tasks, recorded at channel FCz. c,d: Spatial factor scores associated with the oddball (c) and time estimation (d) tasks, for the frontal-central spatial factor. Zeros on abscissae indicate time of stimulus onset. Negative is plotted up by convention. Inf Odd: infrequent oddball condition. Fre Odd: frequent oddball condition. Inf Err: infrequent error condition. Inf Cor: infrequent correct condition. Fre Err: frequent error condition. Fre Cor: = frequent correct condition.

values did not differ across ERP components, $F(2,22) = 2.23$, $p > .10$, $\eta_p^2 = .17$. These results indicate that the N200 is delayed relative to the fERN by about 24 ms, but suggest that this delay results from a general increase in latency across several endogenous ERP components. Taken together, these findings indicate that the fERN and N200 share vary similar scalp distributions and peak at approximately the same time.

To confirm these findings, we conducted a spatial PCA on the oddball (frequent, infrequent) and time estimation (control error, control correct, frequent error, frequent correct, infrequent error, infrequent correct) ERPs. The analysis yielded a primary spatial factor that accounted for 50.7% of the variance with loadings that were maximal at channel Fz (0.94). The second spatial factor accounted for 39% of the variance and exhibited loadings with a posterior scalp distribution; the remaining factors each accounted for less than 3.0% of the total variance in the data. Although slightly more frontal than the frontal-central negativity, we took the first spatial factor with the frontal distribution as best representative of this ERP component (Figure 3c). The spatial factor scores associated with this factor are depicted in Figure 1c for the oddball task and Figure 1d for the time estimation task; those associated with the conditions of interest—infrequent oddball, infrequent error, and infrequent correct—are replotted together in Figure 2d. The frontal-central factor (measured base to peak) was larger in the infrequent oddball condition than in the infrequent correct condition, $t(11) = 4.0$, $p < .005$, Cohen's $d = 2.4$, and larger in the infrequent error condition than in the infrequent correct condition, $t(11) = 2.3$, $p < .05$, Cohen's $d = 1.4$, but not significantly differ-

ent between the infrequent oddball condition and the infrequent error condition, $t(11) = 2.0$, $p > .05$, Cohen's $d = 1.2$. Further, as with the ERPs, inspection of the spatial factor scores suggested that a positive–negative–positive sequence of deflections was delayed for the infrequent oddball condition relative to the infrequent error condition. We computed this latency difference from the spatial factor scores in the same way as we did from the P200, N200, and P300 (Table 1), which revealed an average difference of 21 ms in the latency of these deflections across conditions; this difference did not differ across ERP components, $F(2,22) = 0.16$, $p > .85$, $\eta_p^2 = .01$. Taken together, these results indicate that infrequent targets in an oddball task and infrequent error feedback in a time estimation task both elicit a frontal or frontal-centrally distributed, negative-going component that reaches maximum amplitude at approximately 280–310 ms.

In summary, both the direct analysis on the ERPs and a separate analysis on the spatial factor scores indicated that the N200 and fERN share similar latencies and scalp distributions. The direct ERP analysis revealed that both ERP components are distributed over frontal-central areas of the scalp and reach maximum amplitude at channel FCz. These findings were confirmed by the spatial PCA, which yielded a frontally distributed spatial factor with scores that behaved like the fERN and N200 in the time range of these components. Although the N200 occurred later than the fERN by about 24 ms, this appears to have resulted from a general slowing of endogenous ERP components in the oddball task, rather than from slowing specific to the N200. Together, these results suggest that the fERN and N200 are the same ERP component.
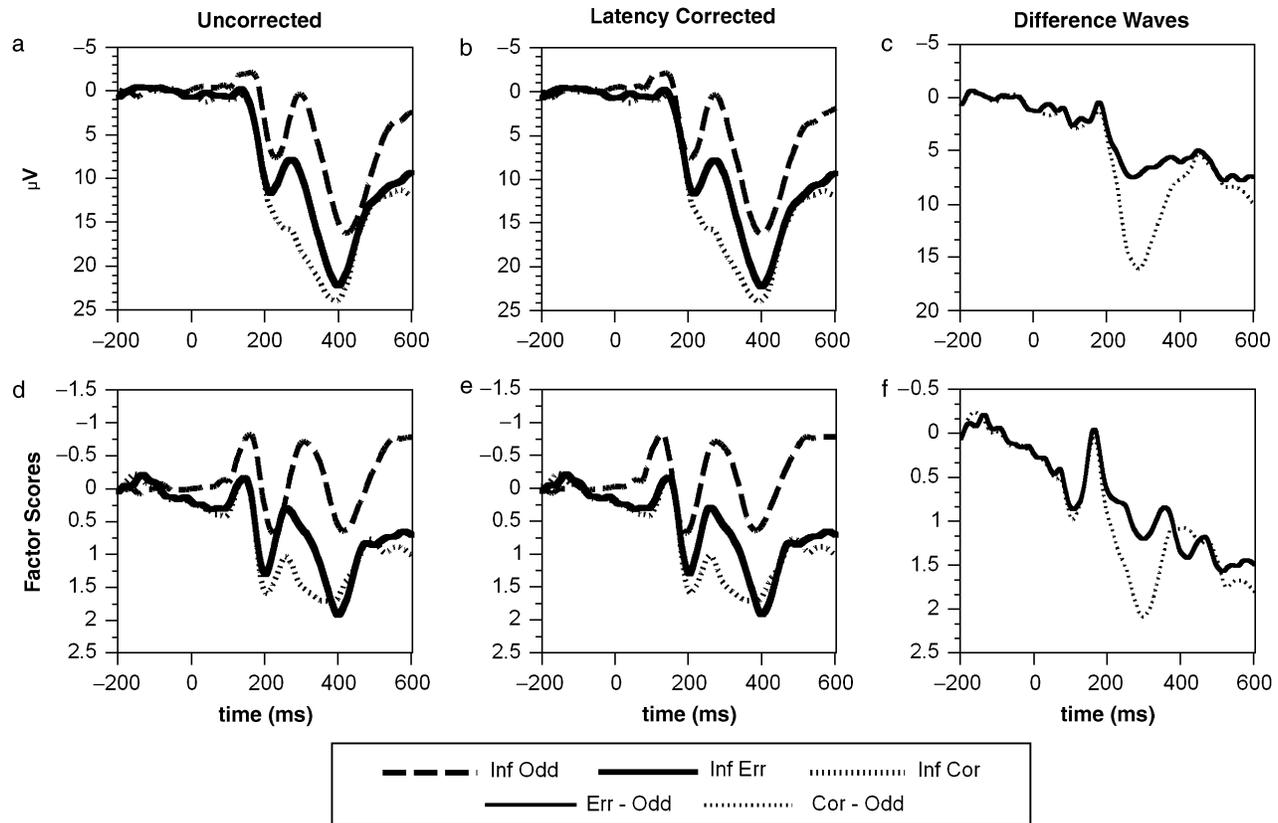
Figure 2. Event-related brain potential (ERP) data and spatial factor scores, with and without latency correction, and associated difference waves. a-c: ERP data recorded at channel FCz, uncorrected (a) and corrected (b) for differences in N200 latency, and associated difference waves (c). d-f: Spatial factor scores for the frontal-central spatial factor, uncorrected (d) and corrected (e) for differences in N200 latency, and associated difference waves (f). Zeros on abscissae indicate time of stimulus onset. Negative is plotted up by convention. Inf Odd: infrequent oddball condition. Inf Err: infrequent error condition. Inf Cor: infrequent correct condition. Err–Odd: difference wave constructed from the infrequent error condition and the latency corrected infrequent oddball condition. Cor—Odd: difference wave constructed from the infrequent correct condition and the latency corrected infrequent oddball condition.

ERPs associated with infrequent correct trials (fCRP). If the fERN and N200 are indeed the same phenomenon, as suggested by the above evidence, then the question arises as to what causes the absence of the fERN/N200 on correct trials. To answer this question, we subtracted the ERP associated with the infrequent oddball condition from both the infrequent error condition and the infrequent correct condition. We reasoned that, to the extent the N200 and the fERN are identical and the N200 and the ERP on correct trials are not identical, then the error–oddball difference should be smaller than the correct–oddball difference. Given the shift in ERP component latency across conditions (see above and Table 1), we first shifted the ERPs in the infrequent oddball condition for each participant by -24 ms; the latency-corrected ERPs are shown in Figure 2b. We then subtracted the latency-corrected infrequent oddball ERPs from both the infrequent error ERPs and the infrequent correct ERPs.[1]

The resulting difference waves, plotted in Figure 2c, revealed a slow, positive-going deflection associated with both error and correct trials. In addition, the infrequent correct difference wave

revealed a relatively large phasic positivity in the time range of the fERN. A peak analysis indicated that this positive deflection was maximal at channel FCz for both the error and correct difference waves (error: 11.4 μV, 297 ms; correct: 19.1 μV, 298 ms); polynomial fits of the maximum amplitudes of the difference waves along the midline indicated that the scalp distributions were significantly curved (Figure 3d; Table 2). Further, the difference was larger (i.e., more positive) for the difference wave associated with correct trials than with error trials, $t(11) = 4.5$, $p < .001$, Cohen's $d = 2.7$. Thus, relative to infrequently presented oddball stimuli, the ERP in the time range of the fERN was significantly more positive on correct trials than on error trials, and this positivity exhibited a frontal central distribution that is characteristic of the fERN.

To confirm these results, we also latency corrected the factor scores associated with the infrequent oddball condition by shifting them by -24 ms (Table 1); the result is plotted in Figure 2e against the factor scores associated with the infrequent error and infrequent correct conditions. As with the direct ERP analysis, we computed the difference between the factor scores associated with the infrequent oddball condition and the factor scores associated with both the infrequent error and infrequent correct conditions (Figure 2f). As can be seen, both difference waves were characterized by positive-going deflections that increased

---

[1]Note that the results of interest are not materially affected by the latency correction and are statistically significant even without it. However, the shift improves the clarity of the analysis, especially as illustrated by the figures.
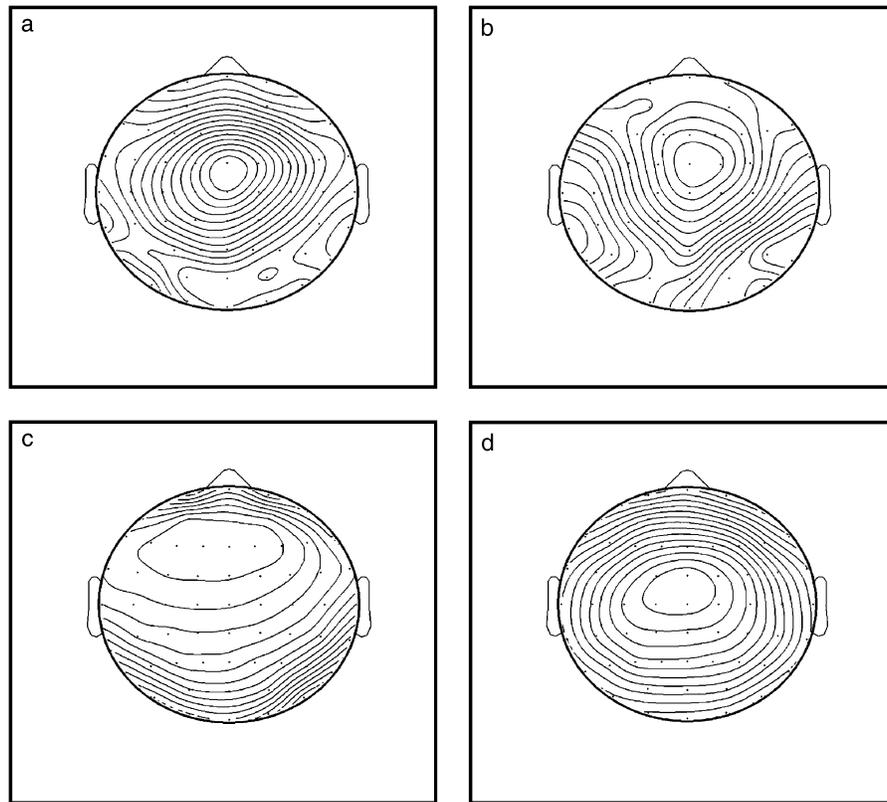
Figure 3. Scalp distributions. a: Scalp distribution associated with the oddball N200; the change in potential between adjacent contours is 0.50 μV. b: Scalp distribution associated with the feedback error-related negativity; the change in potential between adjacent contours is 0.42 μV. c: Factor loadings associated with the frontal-central spatial factor; the change in value between adjacent contours is 0.07. d: scalp distribution associated with the infrequent oddball—infrequent correct difference wave; the change in potential between adjacent contours is 1.34 μV.

across the trial, but the infrequent correct difference wave was characterized by an additional phasic positivity in the time range of the fERN that was small or absent in the infrequent error difference wave, $t(11) = 3.3$, $p < .01$, Cohen's $d = 2.0$. Taken together, these results indicate that the N200 on oddball trials is more similar to the fERN on error trials than to the ERP during this time range on correct trials, and therefore that the essential difference between conditions is associated with neural activity on correct trials rather than neural activity on error trials.

DISCUSSION

The fERN is commonly understood to be a negative deflection in the ERP that is elicited by error feedback stimuli but not by

correct feedback stimuli (e.g., Miltner et al., 1997). From this position, it follows that the difference between the error and correct ERPs results from a neurocognitive process activated only on error trials and not on correct trials. However, appearances can be deceiving: The difference between the ERPs associated with any two conditions can, in fact, be caused by neural activity associated with either condition (Luck, 2005). For this reason, it is also possible that variance in fERN amplitude results primarily from neural activity on correct trials rather than on error trials (Holroyd, 2004). Our results are consistent with this latter possibility: The present findings indicate that, rather than evoking an ERP component that is unique to error trials, error feedback simply elicits a specific instance of a more common phenomenon, the N200, which is elicited by task-relevant events

Table 1. *ERP Component Latencies*

Analysis	Type	P200	N200/FERN	P300
ERP	Infr. oddball	234 ± 22 ms	303 ± 26 ms	416 ± 29 ms
	Infr. error	224 ± 15 ms	279 ± 26 ms	395 ± 19 ms
	Difference	10 ms	24 ms	21 ms
PCA	Infr. oddball	229 ± 24 ms	310 ± 29 ms	413 ± 27 ms
	Infr. error	212 ± 14 ms	289 ± 33 ms	391 ± 20 ms
	Difference	17 ms	21 ms	22 ms

Note. ERP: event-related brain potential; PCA: principal components analysis; Infr.: Infrequent. For the purpose of this analysis, all ERP latencies were evaluated at channel FCz.

Table 2. *Polynomial Fits to Medial and Lateral Dimensions of Difference Wave Scalp Distributions*

Type	Dimension	Best fit	F
Error	medial	quadratic	36.4*
	lateral	quadratic	30.0*
Correct	medial	quadratic	90.5*
	lateral	quadratic	109.4*

Note. Error: infrequent error–infrequent oddball difference wave; Correct: infrequent correct–infrequent oddball difference wave. For all fits, $df = (1,11)$. *$p < .001$.

in general (e.g., Towey et al., 1980). This conclusion follows from the fact that both ERP components are negative going and exhibit very similar—if not identical—scalp distributions and latencies, satisfying the criteria by which ERP components are defined and identified (Coles & Rugg, 1995; Donchin, Ritter, & McCallum, 1978). We believe that this interpretation is more parsimonious than the alternative, which is that task-relevant events generally elicit an N200, except for events that are associated with feedback stimuli, which in the case of error feedback elicit a negative-going ERP component that is nearly identical to the N200 but that is not, in fact, an N200.

Thus, rather than error trials eliciting a novel ERP component, most of the action appears to occur on correct trials when the N200 is absent. This inference is based on the straightforward observation that the ERP elicited by infrequent oddball stimuli was more similar to the ERP elicited by error feedback stimuli than to the ERP elicited by correct feedback stimuli. The reduction in N200 amplitude on correct trials could have resulted from inhibition of the process that produces the N200 or from superposition of a frontal-central, positive-going deflection that cancels out the N200.[2] Although our data cannot decide between these two possibilities, for heuristic purposes we have elected to call this ERP component the feedback correct-related positivity, because this term clearly distinguishes it from the N200/fERN. Stated plainly, the fCRP is an electrophysiological index of a neural process elicited by correct feedback that reduces the amplitude of the N200.

Our conclusions are based on the assumption that the N200 was delayed by about 24 ms on infrequent oddball trials relative to infrequent error trials. We assume this with some confidence, as not just the N200, but the entire P200–N200–P300 complex was delayed by about this amount, suggesting that the stimulus evaluation process was generally slower in the oddball task relative to the time estimation task. Further, the amplitude of these ERP components was smaller in the oddball task relative to the time estimation task, as can be observed by the positive-going difference between the infrequent error and infrequent oddball ERPs (Figure 2c). We suggest that participants were more engaged by the time estimation task than by the oddball task, as the former was more demanding than the latter and provided a monetary incentive that depended on performance. For these reasons, participants may have paid more attention to the stimuli in the time estimation task than in the oddball task, leading to a relative decrease in the latencies and increase in the amplitudes of these ERP components.

The "reinforcement learning theory of the error-related negativity" (RL-ERN theory) holds that the fERN is elicited by the impact of "reward prediction error signals" carried by the midbrain dopamine system on dACC (Holroyd & Coles, 2002). This theory is motivated by evidence that the activity of the midbrain dopamine system briefly increases and decreases when ongoing events are determined to be, respectively, better and worse than expected, and that these signals are utilized by the targets of the dopamine system for the purpose of reinforcement learning (Montague, Hyman, & Cohen, 2004; Schultz, 2002). According to the theory, negative reward prediction error signals that indicate that events are worse than expected, seen as phasic de-creases in dopamine neuron activity, are carried by the midbrain dopamine system to dACC, where they elicit the fERN by disinhibiting the apical dendrites of motor neurons there (Holroyd & Coles, 2002). Conversely, positive reward prediction error signals that indicate that events are better than expected, seen as phasic increases in dopamine neuron activity, are carried by the midbrain dopamine system to dACC, where they reduce the amplitude of the fERN by inhibiting the apical dendrites of motor neurons there (Holroyd, 2004). Because both positive and negative reward prediction error signals could, in principle, affect fERN amplitude, in practice our method of choice for analyzing fERN data has depended on creating difference waves from the ERPs associated with correct and error feedback. This approach preserves the variance in the ERP associated with the evaluative process irrespective of the source of variance (whether from correct or error feedback; e.g., Holroyd & Krigolson, 2007). The present findings suggest that the variance in fERN amplitude across conditions results more from the effect of unpredicted positive feedback than from unpredicted negative feedback. This inference seems consistent with the observation that the phasic changes in dopamine activity associated with unpredicted stimuli are generally larger for positive than for negative events (Schultz, 2002), and thus that the impact of these signals on the neural targets of the dopamine system may be concomitantly stronger for the former than for the latter (Bayer & Glimcher, 2005). The result also dovetails with a growing body of evidence suggesting greater modulation of fERN amplitude by correct feedback than by error feedback (Eppinger, Kray, Mock, & Mecklinger, 2008; Hewig et al., 2008; Holroyd & Coles, 2008; Potts, Martin, Burton, & Montague, 2006).[3]

Across a series of experiments, it has also been found that neutral stimuli elicit an fERN-like component that is as large or larger than the fERN. These results have suggested that the system that produces the fERN categorizes outcomes in a binary manner: as events that either do, or do not, indicate that the task goal has been achieved (Hajcak, Moser, Holroyd, & Simons, 2006; Holroyd, Hajcak, & Larsen, 2006; Toyomaki & Murohashi, 2005; Yeung & Sanfey, 2004). Understood in the present context, these findings suggest that events that fail to indicate that a task goal has been achieved (including the occurrence of both neutral and error feedback stimuli) elicit the N200, whereas events that do indicate that a task goal has been achieved elicit the fCRP. However, it should be noted that these studies uniformly measured fERN amplitude using a base-to-peak approach, rather than a difference wave approach, and thus may have overlooked variance in the amplitude of the fCRP (Holroyd & Krigolson, 2007). In fact, a recent study revealed small fluctuations in fCRP amplitude in a task where response correctness was highly ambiguous and required participants to infer the appropriate behavioral strategy by ongoing trial and error (Holroyd & Coles, 2008).

If the fERN and the N200 are the same component, then they should both be generated in the same brain region. In fact, source

---

[2]Note that the fCRP did not result from overlap of the P300 with the N200, as the fCRP was distributed over frontal-central areas of the scalp whereas the P300 is distributed posteriorly (see Holroyd, 2004, and Holroyd and Krigolson, 2007, for discussions of this issue).

[3] Cohen, Elger, and Ranganath (2007) have also reported that the ERP on correct trials is more sensitive than the ERP on error trials to reward probability. This conclusion was based on an examination of the ERPs elicited by reward and punishment across three task conditions in which the probability of reward was said to be systematically varied by 75%, 50%, and 25%. However, it seems that participants probability matched in this task, such that the actual probability of reward was actually about 63%, 50%, and 63% for these three conditions, respectively, and hence not systematically varied as described.

localization studies have suggested that both ERP components are generated in dACC (e.g., Gehring & Willoughby, 2002; Miltner et al., 1997; Yeung et al., 2004). Due to the inverse problem, this conclusion must be evaluated with caution, but it has been supported by the results of fMRI studies involving human participants (e.g., Botvinick, Braver, Barch, Carter, & Cohen, 2001; Holroyd, Nieuwenhuis, Yeung et al., 2004; Huettel & McCarthy, 2004; Kiehl, Laurens, Duty, Forster, & Liddle, 2001; Linden et al., 1999; Mars et al., 2005; Ullsperger & von Cramon, 2003) and intracranial studies involving monkeys (Amiez, Joseph, & Procyk, 2005; Emeric et al., 2008; Ito, Stuphorn, Brown, & Schall, 2003; Matsumoto, Matsumoto, Abe, & Tanaka, 2007; Niki & Watanabe, 1979) and humans (Halgren, Boujon, Clarke, Wang, & Chauvel, 2002; Wang, Ulbert, Schomer, Marinkovic, & Halgren, 2005). Nevertheless, some findings have been equivocal (e.g., Nieuwenhuis et al., 2005; Van Veen, Holroyd, Cohen, Stenger, & Carter, 2004), so the question has not yet been answered definitively.

Another important issue for future research concerns the relationship between the fCRP and the N200. The RL-ERN theory holds that activity of the midbrain dopamine system modulates activity of the dACC, variously disinhibiting and inhibiting it following unpredicted error and correct events, respectively (Holroyd, 2004). However, the theory leaves unspecified the nature of the dACC activity that is being modulated by dopamine, beyond the broad statement that it must be related to cognitive control over motor behavior (Holroyd & Coles, 2002). Interestingly, a prominent theory of dACC suggests that it is sensitive to response conflict (Botvinick et al., 2001), and that response conflict is manifested in the ERP as the N200 (Yeung et al., 2004). Considering this, one possibility is that the phasic increases in dopamine activity elicited by unpredicted positive feedback could inhibit the conflict-related process mediated by dACC and consequently reduce the amplitude of the N200 (Holroyd, 2004; see also Botvinick, Cohen, & Carter, 2004; Holroyd, Nieuwenhuis, Yeung et al., 2004; Holroyd, Yeung, Coles, & Cohen, 2005). By this view, the dopamine signals would train dACC to execute behavior in a manner that minimizes response conflict.

Finally, the RL-ERN theory holds that the difference between correct and error ERPs should be manifest by the first indication that events are better or worse than expected. Thus, if the system can predict the outcome of the trial at the time of the response, then the difference between the ERPs occurs at that time (a response-related difference); but if the system cannot determine the outcome beforehand, then the difference between the ERPs follows the feedback (a feedback-related difference). In previous trial-and-error learning studies, it has been shown that the error-related negativity "propagates back in time" as participants learn the stimulus–response mappings, from the time of the feedback (where it is seen as the fERN) to the time of the response (where it is seen as the "response error-related negativity"; Holroyd & Coles, 2002; see also Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990; Gehring, Goss, Coles, Meyer, & Donchin, 1993). If our present conclusions are correct, then the fCRP should propagate in like fashion from the time of feedback delivery to the time of response generation. Suggestively, a "correct-preceding positivity" has been observed following correct responses that immediately precede error trials (Hajcak, Nieuwenhuis, Ridderinkhof, & Simons, 2005; Ridderinkhof, Nieuwenhuis, & Bashore, 2003; see also Allain, Carbonnell, Falkenstein, Burle, & Vidal, 2004). We speculate that this ERP component constitutes another instance of the correct-related positivity, one that follows the response rather than the feedback stimulus. This question is ripe for investigation.

REFERENCES

Allain, S., Carbonnell, L., Falkenstein, M., Burle, B., & Vidal, F. (2004). The modulation of the Ne-like wave on correct responses foreshadows errors. *Neuroscience Letters*, *372*, 161–166.

Amiez, C., Joseph, J.-P., & Procyk, E. (2005). Anterior cingulate error-related activity is modulated by predicted reward. *European Journal of Neuroscience*, *21*, 3447–3452.

Bayer, H. M., & Glimcher, P. W. (2005). Midbrain dopamine neurons encode a quantitative reward prediction error signal. *Neuron*, *47*, 129–141.

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., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: An update. *Trends in Cognitive Sciences*, *8*, 539–546.

Cohen, M. X., Elger, C. E., & Ranganath, C. (2007). Reward expectation modulates feedback-related negativity and EEG spectra. *NeuroImage*, *35*, 968–978.

Coles, M. G. H., & Rugg, M. D. (1995). Event–related brain potentials: An introduction. In M. D. Rugg & M. G. H. Coles (Eds.), *Electrophysiology of mind* (pp. 1–26). Oxford: Oxford University Press.

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*, 9–21.

Dien, J., & Frishkoff, G. A. (2005). Principal components analysis of ERP data. In T. C. Handy (Ed.), *Event-related potentials: A methods handbook* (pp. 189–207). Cambridge, MA: The MIT Press.

Donchin, E., & Coles, M. G. H. (1988). Is the P300 component a manifestation of context updating? *Behavioral and Brain Sciences*, *11*, 355–372.

Donchin, E., & Heffley, E. F., III. (1978). Multivariate analysis of event-related potential data: A tutorial review. In D. Otto (Ed.), *Multidisciplinary perspectives in event-related potential research* (pp. 555–572). Washington, DC: U.S. Government Printing Office.

Donchin, E., Ritter, W., & McCallum, W. C. (1978). Cognitive psychophysiology: The endogenous components of the ERP. In E. Callaway, P. Tueting, & S. Koslow (Eds.), *Event-related brain potentials in man* (pp. 349–411). New York: Academic Press.

Emeric, E. E., Brown, J. W., Leslie, M., Pouget, P., Stuphorn, V., & Schall, J. D. (2008). Performance monitoring local field potentials in the medial frontal cortex of primates: Anterior cingulate cortex. *Journal of Neurophysiology*, *99*, 759–772.

Eppinger, B., Kray, J., Mock, B., & Mecklinger, A. (2008). Better or worse than expected? Aging, learning and the ERN. *Neuropsychologia*, *46*, 521–539.

Falkenstein, M., Hohnsbein, J., Hoormann, J., & Blanke, L. (1990). Effects of errors in choice reaction tasks on the ERP under focused and divided attention. In C. Brunia, A. Gaillard, & A. Kok (Eds.), *Psychophysiological brain research* (pp. 192–195). Tilburg, The Netherlands: Tilburg University Press.

Folstein, J. R., & van Petten, C. (2008). Influence of cognitive control and mismatch on the N2 component of the ERP: A review. *Psychophysiology*, *45*, 152–170.

Gehring, W. J., Goss, B., Coles, M. G. H., Meyer, D. E., & Donchin, E. (1993). A neural system for error detection and compensation. *Psychological Science*, *4*, 385–390.

Gehring, W. J., & Willoughby, A. R. (2002). The medial frontal cortex and the rapid processing of monetary gains and losses. *Science*, *295*, 2279–2282.

Gratton, G., Coles, M. G. H., & Donchin, E. (1983). A new method for off–line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, *55*, 468–484.

Hajcak, G., Moser, J., Holroyd, C. B., & Simons, R. F. (2006). The feedback–related negativity reflects the binary evaluation of good versus bad outcomes. *Biological Psychology*, *71*, 148–154.

Hajcak, G., Nieuwenhuis, S., Ridderinkhof, K. R., & Simons, R. F. (2005). Error-preceding brain activity: Robustness, temporal dynamics, and boundary conditions. *Biological Psychology*, *70*, 67–78.

Halgren, E., Boujon, C., Clarke, J., Wang, C., & Chauvel, P. (2002). Rapid distributed fronto-parieto-occipital processing stages during working memory in humans. *Cerebral Cortex*, *12*, 710–728.

Hewig, J., Trippe, R. H., Hecht, H., Coles, M. G. H., Holroyd, C. B., & Miltner, W. H. R. (2008). An electrophysiological analysis of coaching in blackjack. *Cortex*.

Holroyd, C. B. (2004). A note on the Oddball N200 and the feedback ERN. In M. Ullsperger & M. Falkenstein (Eds.), *Errors, Conflicts, and the Brain. Current Opinions on Performance Monitoring* (pp. 211–218). Leipzig: MPI of Cognitive Neuroscience.

Holroyd, C. B., & Coles, M. G. H. (2002). The neural basis of human error processing: Reinforcement learning, dopamine, and the error-related negativity. *Psychological Review*, *109*, 679–709.

Holroyd, C. B., & Coles, M. G. H. (2008). Dorsal anterior cingulate cortex integrates reinforcement history to guide voluntary behavior. *Cortex*, *44*, 548–559.

Holroyd, C. B., Hajcak, G., & Larsen, J. T. (2006). The good, the bad and the neutral: Electrophysiological responses to feedback stimuli. *Brain Research*, *1105*, 93–101.

Holroyd, C. B., & Krigolson, O. E. (2007). Reward prediction error signals associated with a modified time estimation task. *Psychophysiology*, *44*, 913–917.

Holroyd, C. B., Krigolson, O. E., & Pakzad-Vaezi, K. (2006). Why we rotate: Questioning assumptions underlying spatial-temporal PCA. *Psychophysiology*, *43*, S9.

Holroyd, C. B., Nieuwenhuis, S., Mars, R., & Coles, M. G. H. (2004). Anterior cingulate cortex, selection for action, and error processing. In M. Posner (Ed.), *Cognitive neuroscience of attention* (pp. 219–231). New York: Guilford Publishing.

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.

Holroyd, C. B., Nieuwenhuis, S., Yeung, N., Nystrom, L., Mars, R., Coles, M. G. H., et al. (2004). Dorsal anterior cingulate cortex shows fMRI response to internal and external error signals. *Nature Neuroscience*, *7*, 497–498.

Holroyd, C. B., Yeung, N., Coles, M. G. H., & Cohen, J. D. (2005). A mechanism for error detection in speeded response time tasks. *Journal of Experimental Psychology: General*, *134*, 163–191.

Huettel, S. A., & McCarthy, G. (2004). What is odd in the oddball task? Prefrontal cortex is activated by dynamic changes in response strategy. *Neuropsychologia*, *42*, 379–386.

Ito, S., Stuphorn, V., Brown, J. W., & Schall, J. D. (2003). Performance monitoring by the anterior cingulate cortex during saccade countermanding. *Science*, *302*, 120–122.

Kiehl, K. A., Laurens, K. R., Duty, T. L., Forster, B. B., & Liddle, P. F. (2001). Neural sources involved in auditory target detection and novelty processing: An event-related fMRI study. *Psychophysiology*, *38*, 133–142.

Linden, D. E. J., Prvulovic, D., Formisano, E., Vollinger, M., Zanella, F. E., Goebel, R., et al. (1999). The functional neuroanatomy of target detection: An fMRI study of visual and auditory oddball tasks. *Cerebral Cortex*, *9*, 815–823.

Luck, S. (2005). *The event-related potential technique* (pp. 51–98). Cambridge, MA: MIT Press.

Mars, R. B., Coles, M. G. H., Grol, M. J., Holroyd, C. B., Nieuwenhuis, S., Hulstijn, W., et al. (2005). Neural dynamics of error processing in medial frontal cortex. *NeuroImage*, *28*, 1007–1013.

Marsden, J. E., & Tromba, A. J. (1981). *Vector calculus*. New York: W. H. Freeman.

Matsumoto, M., Matsumoto, K., Abe, H., & Tanaka, K. (2007). Medial prefrontal cell activity signaling prediction errors of action values. *Nature Neuroscience*, *10*, 647–656.

McCarthy, G., & Wood, C. C. (1985). Scalp distributions of event-related potentials: An ambiguity associated with analysis of variance models. *Electroencephalography and Clinical Neurophysiology*, *62*, 203–208.

Miltner, W. H. R., Braun, C. H., & Coles, M. G. H. (1997). Event-related brain potentials following incorrect feedback in a time-estimation task: Evidence for a "generic" neural system for error detection. *Journal of Cognitive Neuroscience*, *9*, 788–798.

Montague, P. R., Hyman, S. E., & Cohen, J. D. (2004). Computational roles for dopamine in behavioural control. *Nature*, *431*, 760–767.

Nieuwenhuis, S., Holroyd C. B., Mol, N., & Coles, M. G. H. (2004). Reinforcement–related brain potentials from medial frontal cortex: Origins and functional significance. *Neuroscience & Biobehavioral Reviews*, *28*, 441–448.

Nieuwenhuis, S., Slagter, H. A., von Geusau, N. J. A., Heslenfeld, D., & Holroyd, C. B. (2005). Knowing good from bad: Differential activation of human cortical areas by positive and negative outcomes. *European Journal of Neuroscience*, *21*, 3161–3168.

Niki, H., & Watanabe, M. (1979). Prefrontal and cingulate unit activity during timing behavior in the monkey. *Brain Research*, *171*, 213–224.

Nunez, P. L. (1981). *Electric fields of the brain*. Oxford: Oxford University Press.

Pakzad–Vaezi, K., Krigolson, O. E., & Holroyd, C. B. (2006). Underlying unity: The relationship between the N200 and the feedback ERN. *Psychophysiology*, *43*, S75.

Potts, G. F., Martin, L.E, Burton, P., & Montague, P. R. (2006). When things are better or worse than expected: The medial frontal cortex and the allocation of processing resources. *Journal of Cognitive Neuroscience*, *18*, 1112–1119.

Pritchard, W. S., Shappell, S. A., & Brandt, M. E. (1991). Psychophysiology of N200/N400: A review and classification scheme. *Advances in Psychophysiology*, *4*, 43–106.

Ridderinkhof, K. R., Nieuwenhuis, S., & Bashore, T. R. (2003). Errors are foreshadowed in brain potentials associated with action monitoring in cingulate cortex in humans. *Neuroscience Letters*, *348*, 1–4.

Schultz, W. (2002). Getting formal with dopamine and reward. *Neuron*, *36*, 241–263.

Spencer, K. M., Dien, J., & Donchin, E. (2001). Spatiotemporal analysis of the late ERP responses to deviant stimuli. *Psychophysiology*, *38*, 343–358.

Towey, J., Rist, F., Hakerem, G., Ruchkin, D. S., & Sutton, S. (1980). N250 latency and decision time. *Bulletin of the Psychonomic Society*, *15*, 365–368.

Toyomaki, A., & Murohashi, H. (2005). Discrepancy between feedback negativity and subjective evaluation in gambling. *NeuroReport*, *16*, 1865–1868.

Ullsperger, M., & von Cramon, Y. (2003). Error monitoring using external feedback: Specific roles of the habenular complex, the reward system, and the cingulate motor area revealed by functional magnetic resonance imaging. *Journal of Neuroscience*, *23*, 4308–4314.

Urbach, T. S., & Kutas, M. (2002). The intractability of scaling scalp distributions to infer neuroelectric sources. *Psychophysiology*, *39*, 791–808.

Van Veen, V., Holroyd, C. B., Cohen, J. D., Stenger, V. A., & Carter, C. S. (2004). Errors without conflict: Implication for performance monitoring theories of anterior cingulate cortex. *Brain and Cognition*, *56*, 267–276.

Wang, C., Ulbert, I., Schomer, D. L., Marinkovic, K., & Halgren, E. (2005). Responses of human anterior cingulate cortex microdomains to error detection, conflict monitoring, stimulus-response mapping, familiarity, and orienting. *Journal of Neuroscience*, *25*, 604–613.

Yeung, N., Botvinick, M., & Cohen, J. D. (2004). The neural basis of error detection: Conflict monitoring and the error–related negativity. *Psychological Review*, *111*, 931–959.

Yeung, N., & Sanfey, A. G. (2004). Independent coding of reward magnitude and valence in the human brain. *Journal of Neuroscience*, *24*, 6258–6264.