

ERP Correlates of Feedback and Reward Processing in the Presence and Absence of Response Choice

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The feedback negativity is a component of the event-related brain potential that is elicited by feedback stimuli associated with unfavorable outcomes. The present research investigated whether this component reflects an evaluation of the valence of experienced outcomes or a process of learning about actions that led to those outcomes. The latter hypothesis predicts that the feedback negativity should be observed only when negative outcomes are experienced in relation to executed actions. Contrary to this prediction, feedback negativities were observed in simple monetary gambling tasks in which participants made no active choices (experiment 1) and no overt actions (experiment 2). However, the amplitude of the component was reduced in these tasks relative to a gambling task in which the outcomes appeared to be contingent upon participants' response choices. This reduction was correlated with changes in participants' subjective ratings of involvement in the tasks, suggesting that the evaluative process indexed by the feedback negativity is sensitive to the motivational significance of ongoing events.

Keywords: anterior cingulate cortex, error-related negativity, ERN, evaluation, medial frontal negativity, P300

Introduction

There is increasing interest in the neural mechanisms responsible for evaluating the reward value and motivational significance of ongoing events and for adapting behavior accordingly. Study of event-related brain potentials (ERPs) promises to provide important insights into the nature of these mechanisms, since a number of experiments have found that particular ERP components are selectively sensitive to whether encountered stimuli are associated with positive or negative outcomes. In particular, it has been reported that performance feedback elicits an ERP waveform that is characterized by a negative-going component, peaking 250–300 ms after feedback presentation, that is maximal over medial frontal scalp locations. The amplitude of this *feedback negativity* is larger following feedback stimuli associated with unfavorable outcomes, such as incorrect responses or the loss of money, than following positive feedback (Miltner *et al.*, 1997; Gehring and Willoughby, 2002; Holroyd and Coles, 2002; Nieuwenhuis *et al.*, 2004).

Source localization analyses have consistently identified anterior cingulate cortex (ACC) as the most likely generator of the feedback negativity (Miltner *et al.*, 1997; Gehring and Willoughby, 2002; Ruchow *et al.*, 2002; Luu *et al.*, 2003). The localization of the feedback negativity in ACC is further supported by several lines of converging evidence (see Holroyd *et al.*, 2004b, for a review). First, functional magnetic resonance imaging (fMRI) studies have consistently found evidence of feedback-related activity in caudal-dorsal ACC (Delgado *et al.*, 2000; Knutson *et al.*, 2000) that is enhanced following feedback indicating unfavor-

able outcomes (Monchi *et al.*, 2001; Bush *et al.*, 2002; Delgado *et al.*, 2003; Ullsperger and von Cramon, 2003; Holroyd *et al.*, 2004c). Correspondingly, single-cell recording studies in primates have shown that cells in ACC show increased activity following negative outcomes, such as the omission of expected rewards (Niki and Watanabe, 1979; Shima and Tanji, 1998; Ito *et al.*, 2003). In terms of anatomy, caudal-dorsal regions of ACC share connections with other neural systems implicated in reward processing and decision making, including the mesencephalic dopamine system (Crino *et al.*, 1993) and orbitofrontal cortex (van Hoesen *et al.*, 1993; Morecraft and van Hoesen, 1998). Finally, it has been noted that the orientation of pyramidal cells in the anterior cingulate sulcus could generate a negative frontocentral component like the feedback negativity, whereas cortical layers in the nearby cingulate gyrus and supplementary motor area (SMA) are oriented tangentially to the scalp and hence would not be expected to produce a corresponding scalp potential (Holroyd and Coles, 2002).

Thus, converging evidence suggests that caudal-dorsal ACC plays a critical role in feedback and reward processing. This region has strong anatomical (Dum and Strick, 1993; Devinsky *et al.*, 1995) and functional (Picard and Strick, 1996; Koski and Paus, 2000) connections with areas such as the pre-SMA and dorsolateral prefrontal cortex, suggesting a role in high-level motor control and action selection. Consistent with this notion, ACC has been implicated in a number of critical cognitive functions, including error detection (Miltner *et al.*, 1997), response conflict monitoring (Carter *et al.*, 1998; Botvinick *et al.*, 2001; Yeung *et al.*, 2004), evaluations of reward value or motivational significance (Gehring and Willoughby, 2002), and response selection or selection-for-action (Posner and Petersen, 1990; Paus *et al.*, 1993; Paus, 2001; Picard and Strick, 2001; Holroyd and Coles, 2002).

Investigation of the functional properties of the feedback negativity therefore promises to provide important evidence about the functional role of ACC. In particular, the high temporal resolution afforded by scalp electrophysiology should yield critical insights into the timing of activity in this region, complementing the precise spatial information provided by fMRI methods. In this regard, an important implication of previous ERP findings — which have reported that the feedback negativity peaks within just 250–300 ms of stimulus onset — is that ACC activity may reflect a very rapid evaluation of the feedback stimulus (Gehring and Willoughby, 2002; Holroyd *et al.*, 2003; Nieuwenhuis *et al.*, 2004; Yeung and Sanfey, 2004). However, the precise nature of the information conveyed by the feedback negativity remains a matter of debate. Miltner *et al.* (1997) originally proposed that the feedback negativity reflects the operation of an error-processing system. They further

suggested that the feedback negativity is functionally similar to the error-related negativity (ERN), an ERP component that is observed following error commission in choice reaction tasks even in the absence of explicit performance feedback (Falkenstein *et al.*, 1990; Gehring *et al.*, 1993). This conjecture is supported by recent evidence of error- and feedback-related activity in common regions of ACC (Holroyd *et al.*, 2004c; although see Luu *et al.*, 2003). Because of the hypothesized association with the response-related ERN, the feedback negativity is sometimes called the *feedback ERN*.

More recent theories, however, have emphasized the reward-signaling function of feedback, rather than relating the feedback negativity specifically to error monitoring. In particular, Gehring and Willoughby (2002) and Holroyd and Coles (2002) have proposed related theories that each associate the feedback negativity with processing of the reward value and motivational significance of ongoing events. These theories differ, however, in the proposed role of ACC. According to Gehring and Willoughby (2002), the feedback negativity (which they termed the *medial frontal negativity*) reflects directly the role of ACC in evaluating the motivational significance of ongoing events. In contrast, Holroyd and Coles (2002) suggest that ACC is the recipient, rather than source, of evaluative information. Specifically, they propose that the feedback negativity is generated by the arrival in ACC of reward-related information — more precisely, information about changes in reward prediction (Schultz *et al.*, 1997; Sutton and Barto, 1998) — that is carried by the mesencephalic dopamine system. According to this theory, the role of ACC is to use information about rewards and penalties to learn about the consequences of recent actions and hence to select more appropriate responses in the future.

From existing data it is therefore unclear whether ACC is involved in evaluations of the reward value or motivational significance of the experienced outcomes, or whether it is involved in processing (e.g. error monitoring) that is specifically related to the action choice that led to those outcomes. This uncertainty is perhaps a consequence of the fact that the feedback negativity has typically been studied in task contexts in which participants attempt to learn response patterns in conditions of uncertain or unpredictable outcomes, such as simple learning tasks (Miltner *et al.*, 1997; Holroyd and Coles, 2002; Nieuwenhuis *et al.*, 2002) or simple monetary gambling games (Gehring and Willoughby, 2002; Ruchow *et al.*, 2002; Holroyd *et al.*, 2003, 2004a; Nieuwenhuis *et al.*, 2004; Yeung and Sanfey, 2004). In all of these tasks, feedback stimuli serve a number of related purposes: they indicate whether the preceding response was correct or incorrect (an error-signaling function), and hence indicate whether the current response strategy should be pursued or abandoned (a reinforcement learning function). In addition, the feedback stimuli typically also indicate gains or losses of rewards (a reward-signaling function), events that have direct motivational significance.

Thus, it is currently unknown whether activity in ACC will be elicited by feedback stimuli that are not associated with a particular response choice. This issue provides a critical contrast between existing theories of processing in ACC as it is reflected in the feedback negativity: if the feedback negativity reflects a process of performance monitoring and/or learning about recently executed actions, then it should be observed only when negative outcomes are experienced in relation to active response choices, but not when negative outcomes are experienced in the absence of such choices. In contrast, if the

feedback negativity reflects an evaluation of whether ongoing events are good or bad, irrespective of whether those events are associated with executed actions, then a feedback negativity should be observed in both conditions. To contrast these predictions, we ran two experiments in which we contrasted the ERPs elicited by feedback stimuli that appeared to be contingent upon the participants' response choices against the ERPs elicited by identical stimuli that were not contingent upon a response choice (experiment 1) or any executed action (experiment 2).

Materials and Methods

Participants

There were seven male and seven female participants, ages 19–22, in experiment 1, and nine male and five female participants, ages 18–22, in experiment 2. All were undergraduates from Princeton University who received course credit and a small monetary bonus for their participation. The amount of monetary bonus depended on the outcomes and the participants' performance in the gambling tasks, as described below. All participants gave written informed consent, and the study was approved by the local research ethics committee.

Procedure

The procedure in experiment 1 was as follows: The participants were seated comfortably ~1 m in front of a computer screen in a dimly lit, electromagnetically shielded room. They performed three separate tasks — two gambling tasks and an *oddball* counting task — in the experimental session. The two gambling tasks were designed to be as similar as possible except that in one task, the *Choice task*, participants were instructed that the outcomes of the task depended upon their active choices, whereas in the second, *No-choice task*, participants did not make active choices between response alternatives, but instead simply pressed a single button that led to the computer making a random selection between alternatives. Unbeknownst to the participants, the outcomes in the two tasks were determined according to an identical pseudo-random schedule: the tasks were intended primarily as a plausible context in which participants could encounter wins and losses that appeared to be contingent upon their responses (Choice task) or independent of their actions (No-choice task). The oddball task was included as a control condition in which the participants experienced the same outcome stimuli as in the gambling tasks, but in a context in which these stimuli were not associated with monetary losses and gains. The order in which the gambling tasks were performed was counter-balanced across participants; the oddball task was always performed last.

The procedure of experiment 2 was identical to that of experiment 1 except that we replaced the No-choice task with a *No-response task* in which the participants made no response at all during the block. The aim of this experiment was to determine whether the feedback negativity can be observed in the absence of any overt actions.

Choice Task

The participants were presented on each trial with four colored circles displayed side-by-side, and were asked to imagine that these were balloons containing small monetary wins and losses. They selected one balloon by pressing one of four buttons with the index or middle finger of their left or right hand; the buttons were compatibly mapped to the locations of the balloons on the screen. Following their response, a line appeared under the selected balloon to indicate the choice. After 750 ms, a symbol appeared in the chosen balloon, either “☺” or “☹”. The participants were told that the happy face indicated that they had won 4¢, and that the sad face indicated that they had lost 2¢. The difference in the size of wins and losses ensured that participants tended to accumulate winnings steadily throughout the experiment (at an average rate of 1¢ per trial), a manipulation that was intended to increase participants' motivation and interest in the task. Feedback stimuli appeared on the screen for 1250 ms, at which time the screen cleared for a 750 ms inter-trial interval.

The participants were instructed that their task was to try to select balloons that contained the good outcomes, and that they would get to

keep any winnings at the end of the experiment. In fact, the outcome was selected pseudo-randomly on each trial such that winning and losing outcomes were equally probable. The participants were not informed of this contingency, and were simply instructed to use any strategy they could to maximize their winnings. The assignment of the four balloon colors (red, blue, green and purple) to each of the four locations was randomized across trials: we anticipated that this design would lead participants to form strategies regarding colors and locations, and that this might increase their involvement in the task.

To further ensure that the participants attended to the outcomes, they were asked to keep count of their winnings in each block. Thus, the participants were required to keep a running count of the outcomes as they performed the task, incrementing their count by 4¢ following each win, and decrementing the count by 2¢ following each loss. If they correctly reported the total at the end of the block, they won a 25¢ bonus. There were five blocks of 50 trials each. After they completed the task, the participants were given a short questionnaire in which they were asked to give subjective ratings of their interest in the task, the degree to which they paid attention to the outcomes, and how they felt when they won and lost money.

No-choice Task (Experiment 1 Only)

Participants were told that they would play a game similar to roulette. On each trial, they were presented with four colored squares positioned side-by-side. Pressing a button started 'spinning the wheel': an arrow appeared briefly under each square in turn, slowing down to settle on one of the squares after 1700–1800 ms. A further 750 ms later, a happy or sad face appeared in the selected square for 1250 ms, followed by a 750 ms inter-trial interval. Half of the participants pressed a button with the index finger of their left hand to start the random-selection 'roulette wheel'; the other half of the participants pressed with their right index finger. All other details, including the experimental contingencies, were identical to the Choice task: the happy and sad faces indicated outcomes of +4¢ and -2¢ respectively; these outcomes were selected pseudo-randomly such that wins and losses were equiprobable; the assignment of colors to locations on the screen was varied randomly across trials; and participants were given 25¢ bonuses when they successfully counted the winnings in each block so as to ensure that they attended to the outcome stimuli. There were five blocks of 50 trials each. Again, a short questionnaire was administered at the end of the task.

No-response Task (Experiment 2 Only)

This task was identical to the No-choice task except that, instead of having participants press a button to 'spin the wheel', in this task the wheel began spinning automatically 500 ms after the start of the trial. Thus, the participants' sole requirement was to attend to the outcomes in order to keep count of their winnings.

Oddball Task

In the final section of the experiment, participants were presented with a series of happy and sad faces in the center of the screen. In two blocks, they were instructed to count the happy faces and to ignore the sad faces. In one of these blocks, the probability that a given stimulus was a target happy face was 0.25; in the other block, the probability was 0.5. In two further blocks, the participants were instructed to count the sad faces, and again these targets occurred with probabilities of 0.25 and 0.5 in separate blocks. The order of the four block types was randomized across participants. In each block, 120 stimuli were presented for 300 ms each, separated by an inter-stimulus interval that varied randomly from 1500 to 1600 ms. Participants won a 25¢ bonus for each block in which they correctly counted the number of targets.

EEG Methods

We recorded the EEG using Ag-AgCl electrodes embedded in a fabric cap (Electro-Cap International, Eaton, OH), arranged according to the 10–20 system. The EEG was recorded from channels FP1, FP2, AFz, F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, T7, C3, Cz, C4, T8, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, O1, Oz, O2. Other electrodes were placed on the right mastoid, above and below the left eye, and on the outer canthi of both eyes. The electrode common was placed on the chin. All

electrode recordings were referenced to an electrode placed on the left mastoid, and electrode impedances were kept below 40 kΩ. EEG data were sampled at 250 Hz, and were amplified by a gain of 20 000 with a 12-bit processor using Sensorium (Charlotte, VT) EPA-6 electrophysiology amplifiers with 1 GΩ input impedance.

For data from each gambling task, EEG epochs of 1000 ms (200 ms baseline) were extracted off-line for each feedback stimulus indicating the outcome of the trial. Corresponding epochs were extracted off-line from the oddball task data, time-locked to the occurrence of target stimuli. EEG epochs from each channel were baseline corrected by subtracting the average activity of that channel during the baseline period. Epochs were then re-referenced to linked-mastoid electrodes by subtracting half of the activity recorded at the right mastoid across the epoch from the activity recorded at each channel. Ocular artifacts were corrected with an eye-movement correction algorithm (Gratton *et al.*, 1983).

To quantify the feedback negativity, we calculated the average amplitude of the waveform in a window from 248–296 ms following the presentation of the outcome stimulus, separately for the two outcome stimuli. This window was chosen because previous research has found the feedback negativity to peak during this period (Miltner *et al.*, 1997; Gehring and Willoughby, 2002; Holroyd and Coles, 2002). The data from five midline electrodes were subjected to an analysis of variance (ANOVA) using within-subjects factors of outcome (win/loss), task (Choice/No-choice), and anterior-posterior location (Fz, FCz, Cz, CPz, and Pz), and a between-subjects factor of task order (Choice task performed first, No-choice/No-response second, and vice versa). Since there were no significant effects of task order on the behavioral and ERP results, we do not discuss this factor further.

We also measured the P300 (Donchin and Coles, 1988), the slow-wave positivity upon which the feedback negativity is typically superimposed (Yeung and Sanfey, 2004). The P300 was measured in individual EEG epochs that were first 2 Hz lowpass filtered to remove high-frequency noise (Kutas *et al.*, 1977). P300 amplitude was calculated as the most positive peak in the waveform in a window from 200 to 800 ms post-stimulus relative to a 200 ms pre-stimulus baseline. P300 latency was scored as the timing of this peak relative to stimulus onset. The P300 data were analyzed as for the feedback negativity data, except that only electrode location Pz was included in the analysis. In all analyses, the Greenhouse-Geisser correction for non-sphericity was applied where appropriate.

In a further analysis, not reported in detail here, we applied a principal components analysis (PCA) to the ERP data from each experiment. Each PCA was conducted on averaged ERP waveforms from five midline electrodes (Fz, FCz, Cz, CPz, Pz), with separate waveforms for each participant for gain and loss outcomes of each gambling task (a total of 280 waveforms per experiment). For the data of each experiment, the PCA successfully identified a component corresponding to the feedback negativity — a sharp deflection in the ERP waveform between 250 and 350 ms post-stimulus, peaking at ~300 ms — that was independent of the P300 on which this component is superimposed. This analysis therefore provides an important control that our results are not an artifact of differential overlap with the P300 across conditions. Moreover, because the component identified by the PCA covered the entire latency range of the feedback negativity (250–350 ms post-stimulus), the analysis enabled us to determine whether our results were materially affected by our choice of an early window (248–296 ms). Critically, the analysis of the amplitude variation in this component across tasks and conditions produced essentially identical results to the analysis of the feedback negativity quantified as the average voltage in the 248–296 ms window. Thus, these PCA results confirmed that the findings described below are not an artifact of the simpler average-window analysis method we used to quantify the feedback negativity.

Results

Behavioral Results

As described above, we had participants count their winnings in each block to ensure that they would pay attention to the outcome of each trial even when this outcome was not

contingent upon their response choice. Actual winnings in each block were quite variable. In experiment 1, block totals, excluding 25¢ bonuses for correct counting performance, varied between 8¢ and 116¢ (SD = 21¢, mean = 52¢); in experiment 2, block totals varied between 2¢ and 104¢ (SD = 20¢, mean = 51¢). Thus, accurate counting performance depended upon paying close attention to the outcome on each trial. The behavioral results suggest that participants did so effectively. In experiment 1, mean absolute counting error was 4.1¢ per block in the Choice task and 1.7¢ per block in the No-choice task, a reliable difference [$F(1,12) = 13.3, P < 0.01$]. In experiment 2, mean counting error was 2.0¢ per block in the Choice task and 1.5¢ per block in the No-response task, a non-significant difference ($F < 1$). Thus, participants attended to the task outcomes, and tended to keep count more effectively in the No-choice/No-response tasks than in the Choice task.

A subsequent analysis revealed that the difference in Choice task counting errors between experiments was reliable [$t(13) = 2.55, P < 0.05$]. This difference was unexpected, and perhaps reflects subtle effects of experimental context. In experiment 2, the Choice task was paired with a No-response task in which the participants' only requirement was to count the outcomes. It is possible that this context induced the participants to treat the Choice task as primarily a counting task, with consequent reductions in counting errors.

ERP Results: Experiment 1

Figure 1 presents grand-average waveforms at Cz for the two gambling tasks and the oddball task of experiment 1. For simplicity, data from the oddball task are shown only for target stimuli, and only for blocks in which targets occurred with probability 0.5, matching the probabilities of outcomes in the gambling tasks. The lower panel of Figure 1 plots, for each task, the difference wave for the contrast between the sad and happy face stimuli. These stimuli correspond to losses and gains, respectively, in the gambling tasks, and are referred to as negative and positive stimuli, respectively, in the oddball task (though they did not correspond to any differential outcomes in this task).

Gambling Tasks

As shown in Figure 1 (upper panels), the feedback negativity was superimposed on the slow-wave P300 component. Because of this overlap with the P300, no clear negative peak can be seen in the ERP waveform during the window of analysis for loss trials in the Choice condition. A small negative peak is apparent in the No-choice condition, in which the amplitude of the P300 was greatly reduced. Nevertheless, the feedback negativity is clearly evident as a sharp negative deflection peaking 292 ms after feedback onset in the difference wave calculated by subtracting the ERP waveform on gain trials from the waveform on loss trials (Figure 1, bottom panel). This difference between loss and gain trials, i.e. the feedback negativity, was significant in the period from 248–296 ms post-stimulus [$F(1,12) = 27.0, P < 0.01$], and was larger at electrode location Cz than at other electrode locations (Figure 2), although the interaction between gain/loss outcomes and anterior–posterior location was only marginally reliable [$F(4,48) = 3.08, \epsilon = 0.43, P = 0.07$]. As shown in Figure 1 (bottom panel), the difference between loss and gain trials — i.e. the amplitude of the feedback negativity — was greater in the Choice task than in the No-choice task, reflected in a reliable interaction between outcome (gain/loss) and task (Choice/No-

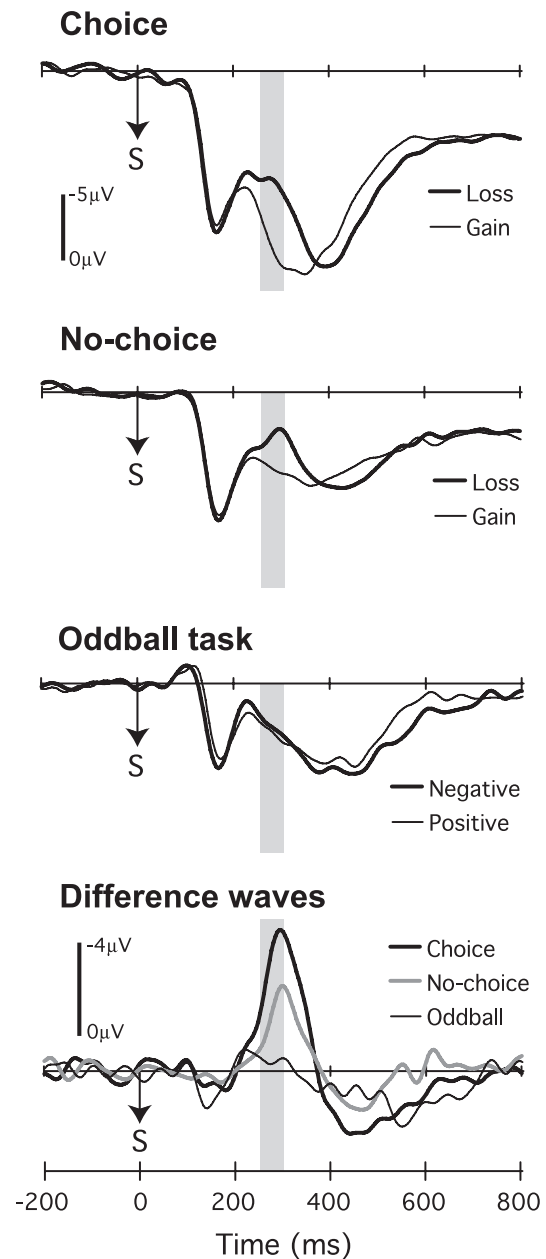


Figure 1. Grand-average ERP waveforms at Cz in experiment 1, separately for gain and loss trials in the Choice task (top panel) and No-choice task (upper middle panel), and for happy (positive) and sad (negative) face target stimuli in the oddball counting task (lower middle panel). The lower panel plots the difference between grand-average ERP waveforms for negative and positive stimuli in each condition. 'S' indicates the time of feedback stimulus onset. The gray shaded areas indicate the 248–296 ms analysis window in which the feedback negativity was quantified.

choice) [$F(1,12) = 4.82, P < 0.05$]. However, pairwise comparisons revealed significant differences between loss and gain trials during the 248–296 ms window for the No-choice task ($P < 0.01$) as well as for the Choice task ($P < 0.01$). Thus, a robust feedback negativity was apparent even in the No-choice task, in which outcomes were not perceived by the participants to be contingent upon their actions.

As mentioned above, P300 amplitude was greater in the Choice task (22.9 µV) than in the No-choice task (17.0 µV) [$F(1,12) = 20.0, P < 0.01$], but the latency of the P300 did not vary significantly across tasks ($F < 1$). P300 amplitude was also

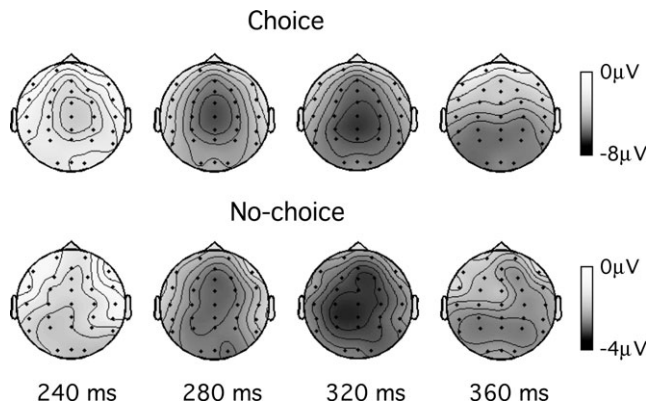


Figure 2. Scalp topography of the voltage differences between negative and positive outcomes in the Choice and No-choice tasks of experiment 1. Timings are given relative to the onset of the outcome stimulus.

slightly larger on gain trials (20.4 μV) than on loss trials (19.6 μV) [$F(1,12) = 3.06, P = 0.11$]. In addition, the latency of the P300 was significantly greater on loss trials than on gain trials [$F(1, 12) = 9.72, P < 0.01$], resulting in amplitude differences between loss and gain trial waveforms in particular time-windows: at the time of the P300 peak on gain trials (348 ms after stimulus onset), the waveform on loss trials was less positive (more negative) than the waveform on gain trials; conversely, at the time of the P300 peak on loss trials (392 ms after stimulus onset), the waveform on loss trials was more positive than the waveform on gain trials. It is worth noting that these amplitude differences cannot explain the feedback negativity observed 248–296 ms after stimulus onset: to the extent that between-condition differences reflect changes in P300 amplitude, they should be maximal at posterior electrode locations where the P300 is maximal. However, as noted above, the amplitude of the feedback negativity was largest over Cz. Instead, amplitude differences resulting from the delayed P300 peak on loss trials were evident as a negativity, centered over posterior electrodes, occurring after the feedback negativity, 320–360 ms after stimulus onset (as can be seen in Figure 2).

Oddball Task

As described above, the oddball task provided a control condition in which we could measure the ERPs elicited by happy and sad face stimuli in a context in which they were not associated with monetary wins and losses. As shown in the lower panels of Figure 1, the ERP waveforms elicited by sad face (negative) and happy face (positive) stimuli in the oddball task did not differ in the latency range of the feedback negativity [$F(1,12) = 1.23, P = 0.29$]. This finding demonstrates that the feedback negativity observed in the gambling tasks is not attributable to the particular stimuli used: the sad face icon only elicited a feedback negativity when it was associated with a loss of money. There was a trend for sad face targets to elicit a larger P300 component than happy faces, but the difference was not statistically reliable [$F(1,13) = 1.37, P = 0.26$].

ERP Results: Experiment 2

Grand-average ERP waveforms from electrode Cz are presented in Figure 3, separately for the two outcome/target stimuli in each task. The lower panel shows difference waves for the contrast between the sad and happy face stimuli. Once again, these stimuli correspond to losses and gains, respectively, in the

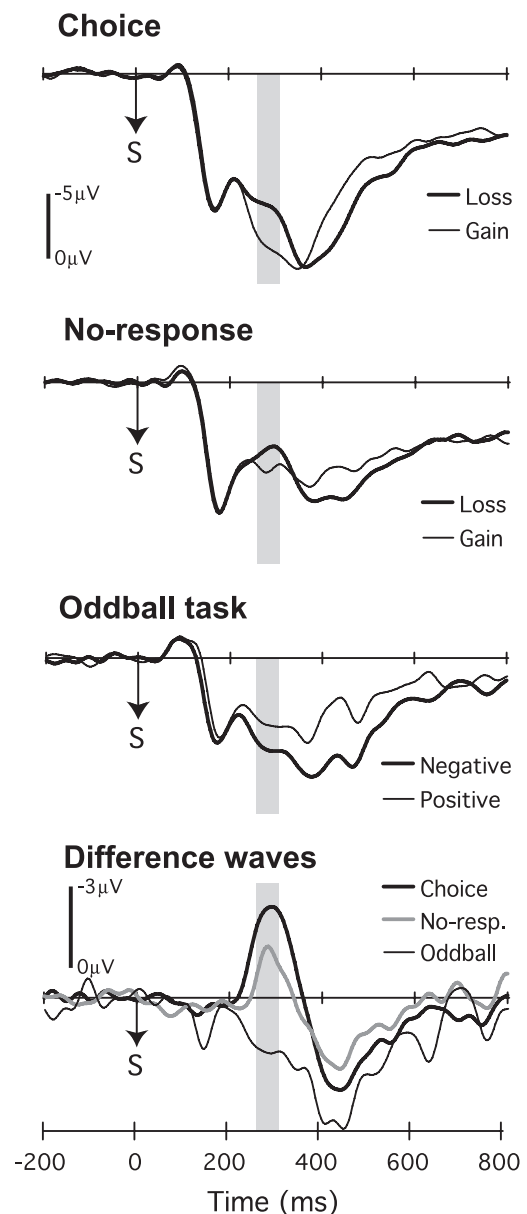


Figure 3. Grand-average ERP waveforms at Cz in experiment 2, separately for gain and loss trials in the Choice task (top panel) and No-response task (upper middle panel), and for happy (positive) and sad (negative) face target stimuli in the oddball counting task (lower middle panel). The lower panel plots the difference between grand-average ERP waveforms for negative and positive stimuli in each condition. 'S' indicates the time of feedback stimulus onset. The gray shaded areas indicate the 248–296 ms analysis window in which the feedback negativity was quantified.

gambling tasks, and are referred to as negative and positive stimuli, respectively, in the oddball task.

Gambling Tasks

As in experiment 1, the feedback negativity was small relative to the P300 component upon which it was superimposed. Nevertheless, the feedback negativity is clearly evident in difference waves created by subtracting gain trial waveforms from loss trial waveforms (Fig. 3, lower panel). This feedback negativity was significant in the period from 248–296 ms after stimulus onset [$F(1,12) = 23.0, P < 0.01$], and tended to be larger at Cz than at other midline electrodes [$F(1,12) = 2.95, \epsilon = 0.40, P = 0.09$; see

Fig. 4). The feedback negativity was reliably larger in the Choice task than in the No-response task, reflected in a reliable interaction between outcome (gain/loss) and task (Choice/No-response) [$F(1,12) = 5.06, P < 0.05$; see Fig. 3, bottom panel]. Nevertheless, pairwise comparisons revealed that a significant difference between loss and gain trials was present at Cz in the No-response task ($P < 0.01$) as well as in the Choice task ($P < 0.01$), evidence that the feedback negativity may be observed even in the absence of an executed response.

Figure 4 shows the scalp topography of voltage differences between loss trials and gain trials. Once again, the feedback negativity was evident over central midline electrodes in the period 248–296 ms after stimulus onset. At later time points, a negativity was observed over more posterior scalp regions, reflecting a delay in the P300 on loss trials (511 ms) compared with gain trials (492 ms) [$F(1,12) = 8.32, P < 0.05$]. Also replicating the results of experiment 1, P300 amplitude was larger in the Choice task (21.9 μV) than in the No-response task (17.9 μV) [$F(1,12) = 7.34, P < 0.05$], but did not differ for loss and gain trials ($F < 1$).

Oddball Task

As in experiment 1, there was no hint of a feedback negativity to the sad faces when these stimuli were simply counted in the oddball task: on the contrary, there was a trend in the opposite direction [$F(1,13) = 3.05, P = 0.11$], with a more positive waveform on trials with sad faces than happy faces during the 248–296 ms window. This difference appears to reflect an increase in P300 amplitude observed following sad faces relative to happy faces [$F(1,13) = 6.92, P < 0.05$; see Fig. 3].

The Feedback Negativity and Subjective Ratings

The preceding analyses have demonstrated that the feedback negativity may be observed even following outcomes that are not perceived by participants to be contingent upon their actions. Nevertheless, in both experiments we found that the amplitude of the feedback negativity was significantly greater in the Choice task than in the No-choice/No-response tasks in which the participants made no active choices. To provide insight into the cause of this amplitude difference across tasks, we analyzed the questionnaire data that were collected at the end of each gambling task. In this questionnaire, the participants were asked to rate how interesting they found the task (1 = ‘very boring’; 7 = ‘very interesting’), how much attention they paid to the outcome of each gamble (1 = ‘ignored outcomes’; 7 = ‘paid close

attention’), how they felt when they won 4¢ (1 = ‘very unhappy’; 7 = ‘very happy’), and how they felt when they lost 2¢ (1 = ‘very unhappy’; 7 = ‘very happy’). Because there were few differences between how participants responded to the No-choice and No-response tasks, for simplicity we present the results of analyses that pooled the data from these tasks and compared them with data pooled across the Choice tasks of experiments 1 and 2.

The participants rated the Choice task as more interesting (mean = 4.4, SD = 1.4) than the No-choice/No-response tasks (mean = 2.5, SD = 1.4) [$F(1,24) = 48.0, P < 0.01$]. They nonetheless paid close attention to outcomes in both tasks, reflected in their accurate counting performance (as described above) and in their subjective rating of how much attention they paid to the outcomes: the rating was high in both tasks (Choice task: mean = 6.0, SD = 0.9; No-choice/No-response tasks: mean = 5.5, SD = 1.3) and did not reliably differ between them [$F(1,24) = 3.67, P = 0.07$]. As one would expect, participants felt happier after winning money (mean = 5.5, SD = 0.8) than after losing money (mean = 2.8, SD = 0.9) [$F(1,24) = 167.8, P < 0.01$]. More interestingly, the difference in affective rating between wins and losses was greater in the Choice task than in the No-choice/No-response tasks [$F(1,24) = 12.8, P < 0.01$]: it seems that participants cared more about losses and gains when these outcomes appeared to be contingent upon their actions.

The subjective rating data indicate important differences between participants’ degree of subjective involvement in the different tasks: they found the Choice task more interesting than the No-choice/No-response tasks, and had greater affective responses to the outcomes of this task. To assess whether these differences might explain the disparity in the amplitude of the feedback negativity across tasks, we ran a multiple linear regression analysis with four predictors: Affect, Interest, Attention and P300 amplitude. Each variable was calculated as a between-task difference measure (Choice minus No-choice/No-response), separately for each participant (see Table 1 for an example). These difference scores indicate the extent to which participants found the Choice task more interesting, more affectively involving and more worthy of attention than the No-choice/No-response tasks. The critical question was whether these difference scores would correlate with between-task differences in feedback negativity amplitude. P300 amplitude was included as a predictor in case variability in this component contributed to the between-condition differences in the 248–296 ms window in which we measured the feedback negativity.

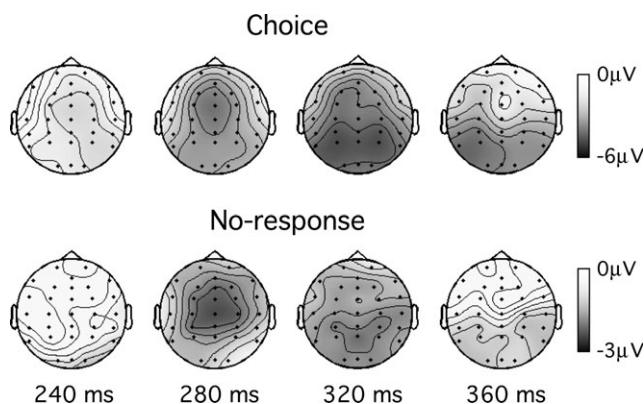


Figure 4. Scalp topography of the voltage differences between negative and positive outcomes in the Choice and No-response tasks of experiment 2.

Table 1

Calculation of variables entered into the multiple linear regression analysis, giving an example of the data from one participant of experiment 1

Factor	Measure	Choice task		No-choice task		Formula	Score
		Loss	Win	Loss	Win		
Feedback negativity	Mean voltage at Cz 248–296 ms	10.2 _A	16.8 _B	8.9 _C	11.6 _D	(A – B) – (C – D)	–3.9
	Peak voltage at Pz 200–800 ms	17.4 _A	19.6 _B	15.5 _C	15.1 _D	(A – B) – (C – D)	–2.7
Affect	Affective ratings of outcomes	3 _A	6 _B	3 _C	5 _D	(B – A) – (D – C)	1
Interest	Rating of interest in the task	3 _A		1 _B		A – B	2
Attention	Rating of attention to outcomes	6 _A		4 _B		A – B	2

Annotation: the subscripted letters in the data columns correspond to the variables in the formula column.

Figure 5 presents partial regression plots for each of the four predictors, showing the extent to which between-task differences in the amplitude of the feedback negativity correlate with between-task differences in each of the variables. Reliable correlations were observed for the Interest and P300 predictors, but not for the Affect or Attention variables. The reliable negative correlation involving the Interest variable indicates that the amplitude of the feedback negativity was reduced in the No-choice/No-response tasks to the extent that participants found these tasks less interesting than the Choice task. Indeed, when the effect of Interest was partialled out, we found no significant difference in the amplitude of the feedback negativity between the Choice and No-choice/No-response tasks [$t(27) = 1.41, P = 0.17$], although a small difference ($-0.7 \mu\text{V}$) remained. In contrast, although the P300 variable was likewise a reliable predictor of between-task differences in the feedback negativity, the feedback negativity remained reliably larger in the Choice task (by $-1.9 \mu\text{V}$) even when effects of P300 amplitude were partialled out [$t(27) = 4.24, P < 0.01$]. Thus, although variability in P300 amplitude may have had some influence on scalp voltage in the 248–296 ms window in which we measured the feedback negativity, this variability did not fully account for the observed differences between the Choice and No-choice/No-response tasks.

Neither Affect nor Attention was significantly correlated with the amplitude of the feedback negativity. In subsequent analyses, not reported in detail here, we also measured within-task (rather than between-task) correlations between affective ratings for wins and losses and feedback negativity amplitude. Again, we found no significant correlations. However, these null correlations do not establish that the feedback negativity is insensitive to affective or attentional variables. It could equally be

that our subjective rating measures — in which participants made simple numerical ratings at the end of each task — provide a relatively insensitive measure of participants' affective and attentional states as they varied during task performance. Thus, the relation between the feedback negativity and affective or attentional variables remains an important area of investigation for future research.

In a final analysis, we investigated whether subjective ratings of involvement were related to observed between-task differences in P300 amplitude (recall that greater P300 amplitude was observed in the Choice task than in the No-choice and No-response tasks). To this end, we calculated for each subject the difference in P300 amplitude between tasks, now averaging across positive and negative outcomes (rather than focusing on the difference between them). We then correlated this measure with our measures of between-task differences in Interest, Affect and Attention. This analysis revealed a reliable positive correlation between P300 amplitude and Interest [$r(27) = 0.38, P < 0.05$], a marginally reliable positive correlation between P300 amplitude and Affect [$r(27) = 0.32, P < 0.1$], but no relationship between P300 amplitude and Attention [$r(27) = -0.1, P = 0.61$]. These findings indicate that P300 amplitude was reduced in the No-choice/No-response tasks to the extent that participants found these tasks less interesting, and less affectively engaging, than the Choice task.

Discussion

The principal findings of the present research may be summarized as follows. First, a feedback negativity was observed following unfavorable outcomes even in task contexts in which these outcomes did not follow an overt response choice (experiment 1) or any executed action (experiment 2).

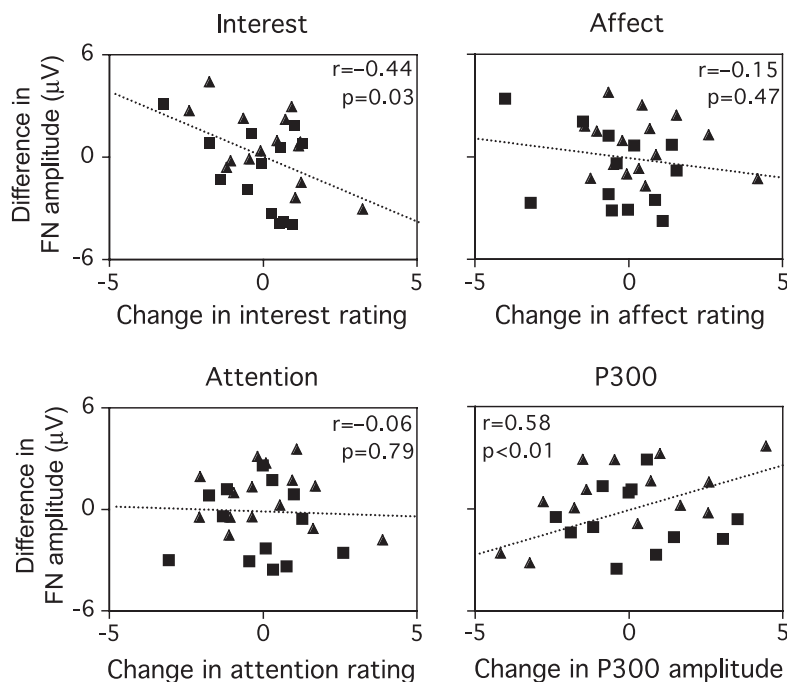


Figure 5. Partial regression plots from a multiple linear regression analysis designed to investigate whether between-task differences in the amplitude of the feedback negativity (FN) correlate with between-task changes in subjective ratings of Interest, Affect, and Attention, and P300 amplitude. The data from experiments 1 and 2 were pooled together in the regression analysis to ensure a sufficient sample size, but are indicated separately in each panel as squares and triangles respectively. Along the ordinate of each panel, more negative values indicate increases in the amplitude of the feedback negativity in the Choice task relative to the No-choice/No-response tasks. Along the abscissa of the panels, more positive values indicate increases in P300 amplitude and in subjective ratings of Interest, Affect, Attention in the Choice task relative to the No-choice/No-response tasks.

However, the amplitude of the feedback negativity was modestly, but reliably, smaller in the No-choice/No-response tasks than in a task in which the outcomes appeared to be contingent upon participants' response choices. This difference did not appear to reflect a difference in the extent to which participants attended to outcome stimuli: the participants' behavioral performance and subjective reports indicated that they paid close attention to outcome stimuli in both tasks. Instead, the reduction in feedback negativity amplitude in the No-choice/No-response tasks was correlated with reduced ratings of subjective involvement in these tasks compared with the Choice task. Indeed, when the effects of subjective involvement were partialled out, we found no difference in the amplitude of the feedback negativity between tasks.

The present findings cannot be explained in terms of confounding effects of between-condition differences in P300 amplitude that might have contaminated our measure of the feedback negativity. First, changes in P300 amplitude should result in between-condition differences that are maximal over posterior scalp locations, whereas the peak of the feedback negativity was observed over central and frontocentral sites. Second, the results of our PCA and correlational analysis, each of which provides a method for factoring out the contribution of the P300, both provided evidence that our findings reflect specific, significant changes in the feedback negativity. Our findings are also unlikely to reflect the requirement that participants had to keep a running count of the outcomes experienced in each block (something that has not been required in most previous studies of the feedback negativity). The latency and morphology of the feedback negativity that we observe is very similar to the latency and morphology of the feedback negativity observed in experiments that did not require concurrent counting of outcomes (Gehring and Willoughby, 2002; Ruchow *et al.*, 2002; Holroyd *et al.*, 2003, 2004a; Nieuwenhuis *et al.*, 2004; Yeung and Sanfey, 2004). Moreover, as demonstrated by the data from the oddball task, counting outcomes in the absence of monetary wins and losses does not result in a feedback negativity.

Overall, therefore, the present results provide important new insights into neural activity in ACC as it is reflected in the feedback negativity. This component has previously been studied using tasks in which participants experience unpredictable outcomes in the context of uncertain response choices (Miltner *et al.*, 1997; Holroyd and Coles, 2002; Ruchow *et al.*, 2002; Holroyd *et al.*, 2003, 2004a; Nieuwenhuis *et al.*, 2004; Yeung and Sanfey, 2004). In these tasks, negative feedback is used to indicate that the preceding response was incorrect in some way. Thus, one interpretation of the feedback negativity has been that it reflects the operation of a neural system of error detection implemented in ACC (Miltner *et al.*, 1997). However, in our experiments the feedback negativity was observed in the absence of response choices, and hence in the absence of incorrect responses. Thus, if an error is defined as an incorrect response within the context of the experimental task, then our findings are difficult to reconcile with the hypothesis that the feedback negativity indexes an error-detection process. Instead, our findings seem to be more consistent with theories proposing that ACC is involved in evaluating the reward value (Holroyd and Coles, 2002) or motivational impact (Gehring and Willoughby, 2002) of experienced events.

According to the theory proposed by Holroyd and Coles (2002), the feedback negativity reflects the arrival in ACC of a reward signal conveyed by the mesencephalic dopamine system.

The theory proposes further that these reward signals are used to guide action selection mediated by cingulate motor areas, through the reinforcement of actions associated with positive reward and the punishment of actions associated with penalty. This theory thus integrates a range of findings regarding ACC: its involvement in high-level action selection (Dum and Strick, 1993; Picard and Strick, 1996; Paus, 2001), its sensitivity to information about reward and punishment (Niki and Watanabe, 1979; Shima and Tanji, 1998; Bush *et al.*, 2002; Delgado *et al.*, 2003; Ito *et al.*, 2003), its sensitivity to information about response accuracy (Monchi *et al.*, 2001; Ullsperger and von Cramon, 2003; Holroyd *et al.*, 2004c), and its anatomical connectivity with neural systems implicated in reward processing (Crino *et al.*, 1993; van Hoesen *et al.*, 1993; Morecraft and van Hoesen, 1998). However, from previous research it has been unclear whether the feedback negativity reflects the arrival of the reward signal in ACC, or whether it reflects the use of reward information to reinforce or punish recently produced responses. In the first case, the feedback negativity should be associated with feedback stimuli in general, whereas in the latter case the feedback negativity should occur only when the feedback is provided in relation to a specific executed response. The present findings are consistent with the former prediction. Therefore, in terms of the reinforcement learning theory, our results suggest that the feedback negativity reflects the reward signal alone, not its use in reinforcing or punishing a recent response, a conclusion that contrasts with the original speculation of Holroyd and Coles (2002).

This conclusion prompts the question of why ACC is activated by an evaluative reward signal in the absence of an immediately preceding action, given that this region is thought to play a critical role in action selection (Posner and Petersen, 1990; Paus *et al.*, 1993; Paus, 2001; Picard and Strick, 2001; Holroyd and Coles, 2002). One possibility is that ACC does not only use reward signals to reinforce representations of actions (i.e. instrumental conditioning), but also uses them to learn about contingencies in the external environment (i.e. classical conditioning). For example, in the present No-choice and No-response tasks, a reinforcement learning signal might affect participants' expectations of rewards associated with particular stimulus colors or locations (even though, in fact, these features did not predict actual rewards). On this view, expectations about environmental contingencies can be considered to be covert responses that may be reinforced or punished, so that the predictive validity of these expectations tends to improve with experience. Alternatively, it could be that the reward signal does not only affect representations of actions with active eligibility traces, but is also used by ACC to evaluate more distal events and more general action plans that are not directly task-related (e.g., evaluating the overall decision to attend the experiment), or to learn about how and where to deploy attention (Holroyd *et al.*, 2004b). In this way, the present findings suggest that the reinforcement learning framework of Holroyd and Coles (2002) might need to be extended in future research to include learning that is not specifically related to recently executed actions.

Our findings are also relevant to Gehring and Willoughby's (2002) suggestion that the feedback negativity reflects an evaluation of the motivational impact of outcome events. The correlation we observed between the amplitude of the feedback negativity and subjective ratings of involvement in the experimental task is perhaps the first direct evidence that motivational

factors influence processing in ACC. Thus, the present findings are broadly consistent with the hypothesis that this region performs a critical role in integrating cognitive and affective information in the control of action (Bush *et al.*, 2000; Botvinick *et al.*, 2001; Paus, 2001). However, the nature of the influence of motivational factors on processing in ACC remains to be determined. One important question is the direction of causality in the effects we observed, i.e. whether increases in motivation and interest result in a more active evaluative system in ACC, or whether some people feel more motivated because their evaluative system is more active. A second question is whether the present findings reflect a direct effect of motivation on processing in ACC, or whether the effects we observe are mediated by a further variable — e.g. perceived reward differential between gains and losses in the two tasks — that correlates both with subjectively experienced interest and with activity in this brain region. More generally, an important challenge for future research will be to develop theories that explain how the motivational significance of events is assessed, with the aim of identifying the features that make events motivationally significant, providing an account of how these features are detected in the environment and represented in the brain, and making explicit the proposed functional consequences of these evaluations in the adaptation of behavior (Yeung, 2004).

Finally, although the P300 was not the focus of the present research, our results relate in interesting ways to previous findings regarding this component. We found that the amplitude of the P300, like that of the feedback negativity, varied with participants' involvement in the tasks (being greater in the Choice task than in the No-choice/No-response tasks), but was insensitive to the valence (positive or negative) of feedback information. The finding that P300 amplitude is insensitive to reward valence is consistent with our previous findings (Yeung and Sanfey, 2004), but initially seems inconsistent with a previous report that a larger P300 is elicited by negative images than by positive images that are matched according to subjective ratings of valence and arousal (Ito *et al.*, 1998). In this context, it is relevant that in the gambling tasks the sad face stimuli were associated with smaller monetary amounts (-2¢) than were the happy face stimuli ($+4\text{¢}$). It is possible that this difference in reward magnitude — which would tend to increase P300 amplitude on gain trials (Yeung and Sanfey, 2004) — counteracted an increase in P300 amplitude associated with sad face stimuli, so that P300 amplitude was similar for both stimulus types in the gambling tasks. Consistent with this interpretation, we observed a larger P300 following sad face targets than following happy face targets in our oddball counting task, where these stimuli were not associated with (differential) monetary outcomes. This explanation notwithstanding, it remains an open question why negative images tend to elicit a larger amplitude P300 than do positive images (Ito *et al.*, 1998), whereas monetary losses do not elicit a larger amplitude P300 than do monetary gains of equivalent magnitude (Yeung and Sanfey, 2004).

Conclusion

Many current theories view anterior cingulate cortex as a critical interface between cognitive and motivational influences in the control of behavior (Bush *et al.*, 2000; Botvinick *et al.*, 2001; Paus, 2001). The present findings on the feedback negativity, an ERP component generated by activity in anterior cingulate

cortex, provide further evidence for this view. We found that the feedback negativity can be elicited by outcomes that are not contingent upon recent actions. This result suggests that anterior cingulate cortex is not only involved in learning about the consequences of recent, task-relevant actions, but is involved more generally in processing motivationally significant information concerning rewards and punishments. Our findings demonstrate further that the neural response to stimuli associated with reward and penalty varies with subjective ratings of involvement in the task at hand. An important goal for future research will be to understand the mechanisms by which factors related to motivational state, such as interest, involvement and affective reactions, influence the evaluative process indexed by the feedback negativity.

Notes

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References

- Botvinick MM, Braver TS, Carter CS, Barch DM, Cohen JD (2001) Evaluating the demand for control: anterior cingulate cortex and crosstalk monitoring. *Psychol Rev* 108:624-652.
- Bush G, Luu P, Posner MI (2000) Cognitive and emotional influences in anterior cingulate cortex. *Trends Cogn Sci* 4:215-222.
- Bush G, Vogt BA, Holmes J, Dale AM, Greve D, Jenike MA, Rosen BR (2002) Dorsal anterior cingulate cortex: a role in reward-based decision making. *Proc Natl Acad Sci USA* 99:523-528.
- Carter CS, Braver TS, Barch DM, Botvinick MM, Noll D, Cohen JD (1998) Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science* 280:747-749.
- Crino PB, Morrison JH, Hof PR (1993) Monoaminergic innervation of cingulate cortex. In: *Neurobiology of cingulate cortex and limbic thalamus: a comprehensive handbook* (Vogt BA, Gabriel M, eds), pp. 285-310. Boston, MA: Birkhauser.
- Delgado MR, Nystrom LE, Fissell K, Noll DC, Fiez JA (2000) Tracking the hemodynamic responses to reward and punishment in the striatum. *J Neurophysiol* 84:3072-3077.
- Delgado MR, Locke HM, Stenger VA, Fiez JA (2003). Dorsal striatum responses to reward and punishment: effects of valence and magnitude manipulations. *Cogn Affect Behav Neurosci* 3:27-38.
- Devinsky O, Morrell MJ, Vogt BA (1995) Contributions of anterior cingulate cortex to behaviour. *Brain* 118:279-306.
- Donchin E, Coles MGH (1988) Is the P300 component a manifestation of context updating? *Behav Brain Sci* 11:355-372.
- Dum RP, Strick PL (1993) Cingulate motor areas. In: *Neurobiology of cingulate cortex and limbic thalamus: a comprehensive handbook* (Vogt BA, Gabriel M, eds), pp. 415-441. Boston, MA: Birkhauser.
- Falkenstein M, Hohnsbein J, Hoorman J, Blanke I (1990) Effects of errors in choice reaction tasks on the ERP under focused and divided attention. In: *Psychophysiological brain research* (Brunia CHM, Gaillard AWK, Kok A, eds), pp. 192-195. Tilburg: Tilburg University Press.
- Gehring WJ, Willoughby AR (2002) The medial frontal cortex and the rapid processing of monetary gains and losses. *Science* 295:2279-2282.
- Gehring WJ, Goss B, Coles MGH, Meyer DE, Donchin E (1993) A neural system for error detection and compensation. *Psychol Sci* 4:385-390.

- Gratton G, Coles MGH, Donchin E (1983) A new method for off-line removal of ocular artifact. *Electroencephalogr Clin Neurophysiol* 55:468-484.
- Holroyd CB, Coles MGH (2002) The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity. *Psychol Rev* 109:679-709.
- Holroyd CB, Nieuwenhuis S, Yeung N, Cohen JD (2003) Errors in reward prediction are reflected in the event-related brain potential. *Neuroreport* 14:2481-2484.
- Holroyd CB, Larsen JT, Cohen JD (2004a) Context dependence of the event-related brain potential associated with reward and punishment. *Psychophysiology* 41:245-253.
- Holroyd CB, Nieuwenhuis S, Mars RB, Coles MGH (2004b) Anterior cingulate cortex, selection for action, and error processing. In: *The cognitive neuroscience of attention* (Posner MI, ed.), pp. 219-231. New York: Guilford.
- Holroyd CB, Nieuwenhuis S, Yeung N, Nystrom LE, Mars RB, Coles MGH, Cohen JD (2004c) Dorsal anterior cingulate cortex shows fMRI response to internal and external error signals. *Nat Neurosci* 7:497-498.
- Ito T, Larsen JT, Smith NK, Cacioppo JT (1998) Negative information weighs more heavily on the brain: the negativity bias in evaluative categorizations. *J Pers Soc Psychol* 75:887-900.
- Ito S, Stuphorn V, Brown JW, Schall JD (2003) Performance monitoring by anterior cingulate cortex: comparison not conflict during countermanding. *Science* 302:120-122.
- Knutson B, Westdorp A, Kaiser E, Hommer D (2000) fMRI visualization of brain activity during a monetary incentive delay task. *Neuroimage* 12:20-27.
- Koski L, Paus T (2000) Functional connectivity of the anterior cingulate cortex within the human frontal lobe: a brain-mapping meta-analysis. *Exp Brain Res* 133:55-65.
- Kutas M, McCarthy G, Donchin E (1977) Augmenting mental chronometry: the P300 as a measure of stimulus evaluation time. *Science* 197:792-795.
- Luu P, Tucker DM, Derryberry D, Reed M, Poulsen C (2003) Electrophysiologic responses to errors and feedback in the process of action regulation. *Psychol Sci* 14:47-53.
- Miltner WHR, Braun CH, Coles MGH (1997) Event-related potentials following incorrect feedback in a time-estimation task: evidence for a 'generic' neural system for error detection. *J Cogn Neurosci* 9:788-798.
- Monchi O, Petrides M, Petre V, Worsley K, Dagher A (2001) Wisconsin card sorting revisited: distinct neural circuits participating in different stages of the task identified by event-related functional magnetic resonance imaging. *J Neurosci* 21:7733-7741.
- Morecraft RJ, van Hoesen GW (1998) Convergence of limbic input to the cingulate motor cortex in the rhesus monkey. *Brain Res Bull* 45:209-232.
- Nieuwenhuis S, Ridderinkhof KR, Talsma D, Coles MGH, Holroyd CB, Kok A, van der Molen MW (2002) A computational account of altered error processing in older age: dopamine and the error-related negativity. *Cogn Affect Behav Neurosci* 2:19-36.
- Nieuwenhuis S, Yeung N, Holroyd CB, Schurger A, Cohen JD (2004) Sensitivity of electrophysiological activity from medial frontal cortex to utilitarian and performance feedback. *Cereb Cortex* 14:741-747.
- Niki H, Watanabe M (1979) Prefrontal and cingulate unit activity during timing behavior in the monkey. *Brain Res* 171:213-224.
- Paus T (2001) Primate anterior cingulate cortex: where motor control, drive and cognition interface. *Nat Rev Neurosci* 2:417-424.
- Paus T, Petrides M, Evans AC, Meyer E (1993) Role of human anterior cingulate cortex in the control of oculomotor, manual, and speech responses: a positron emission tomography study. *J Neurophysiol* 20:453-469.
- Picard N, Strick PL (1996) Motor areas of the medial wall: a review of their location and functional activation. *Cereb Cortex* 6:342-353.
- Picard N, Strick PL (2001) Imaging the premotor areas. *Curr Opin Neurobiol* 11:663-672.
- Posner MI, Petersen SE (1990) The attention system of the human brain. *Annu Rev Neurosci* 13:25-42.
- 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. *Neurosci Lett* 325:203-206.
- Schultz W, Dayan P, Montague PR (1997) A neural substrate of prediction and reward. *Science* 275:1593-1599.
- Shima K, Tanji J (1998) Role for cingulate motor area cells in voluntary movement selection based on reward. *Science* 282:1335-1338.
- Sutton RS, Barto AG (1998) *Reinforcement learning: an introduction*. Cambridge, MA: MIT press.
- Ullsperger M, von Cramon DY (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. *J Neurosci* 23:4308-4314.
- van Hoesen GW, Morecraft RJ, Vogt BA (1993) Connections of the monkey cingulate cortex. In: *Neurobiology of cingulate cortex and limbic thalamus: a comprehensive handbook* (Vogt BA, Gabriel M, eds), pp. 249-284. Boston, MA: Birkhauser.
- Yeung N (2004) Relating cognitive and affective theories of the error-related negativity. In: *Errors, conflicts, and the brain. Current opinions on performance monitoring* (Ullsperger M, Falkenstein M, eds), pp. 63-70. Leipzig: MPI of Cognitive Neuroscience.
- Yeung N, Sanfey AG (2004) Independent coding of reward magnitude and valence in the human brain. *J Neurosci* 24:6258-6264.
- Yeung N, Botvinick MM, Cohen JD (2004) The neural basis of error detection: conflict monitoring and the error-related negativity. *Psychol Rev*, in press.