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Brain potentials related to self-generated and external information used for performance monitoring

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Abstract

Objective: Humans need to supervise and adjust their own behavior by means of an error detection and correction system as well as by using externally available information. The purpose of the present study was to compare the electrophysiological effects related to self-generated internal and to external (feedback) information used for performance monitoring.

Methods: Fourteen young normal subjects learned to associate each of several line-drawings with either a left-hand or right-hand response. In the experiment proper multi-channel ERPs were obtained time-locked to (a) the line-drawings, (b) the button-press, and (c) subsequent feedback stimuli. Feedback was either affirmative, negative, or equivocal. Event-related potentials were quantified and statistically evaluated using standard methodology.

Results: Response-locked ERPs showed a typical error-related negativity (ERN) for erroneous responses. ERPs to negative and equivocal feedback stimuli contained a negativity with a more posterior distribution than that of the ERN, which occurred earlier and had a higher peak amplitude in the equivocal condition. Dipole modeling suggests that this feedback-related negativity is generated by medial prefrontal and posterior cingulate cortex areas.

Conclusions: Different brain systems support the use of internal and external information necessary for performance monitoring and modification.

Significance: The flexible use of internal and external information for performance control is a core executive function. The delineation of the corresponding brain correlates will further our understanding of executive dysfunction in neurological disorders.
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Keywords: Error related negativity; Feedback; Anterior cingulate cortex; Evoked potential; Error monitoring

1. Introduction

To adapt and optimize their behavior humans (and other species) can exploit several sources of information. Firstly, using internal 'monitoring devices' they can compare their actual behavior (e.g. a motor response) with the desired outcome. Secondly, they might also use external information that gives feedback about the quality of the response.

The internal monitoring processes have been targeted by a number of electrophysiological and neuroimaging studies

during the past 10 years or so. By averaging event-related brain potentials (ERPs, see Münte et al., 2000) time-locked to erroneous and correct responses, a negative wave peaking about 80 ms after the response has been described for errors that has been termed error-related negativity (ERN, Gehring et al., 1993, 1995; Gehring and Knight, 2000; Holroyd et al., 1998; Scheffers et al., 1996) or error negativity (N_E, Falkenstein et al., 1990, 1995, 2000, 2001). The ERN has a focal midline frontocentral maximum and has been shown to likely arise from the anterior cingulate gyrus (ACG) (Dehaene et al., 1994) with additional contributions from the lateral prefrontal cortex (Luu and Tucker, 2001; van Veen and Carter, 2002). Functional magnetic resonance imaging (fMRI) studies have localized

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error processing in the anterior cingulate and lateral inferior frontal cortex extending to bilateral insular cortex (see Carter et al., 1998, 2001; Kiehl et al., 2000; Menon et al., 2001; Ullsperger et al., 2002) which converges with the previously proposed ERP models.

With regard to the functional significance of the ERN, two major proposals have to be considered (see for reviews Botvinick et al., 2001; Holroyd and Coles, 2002). First, the so-called error-detection account holds that the ERN is emitted whenever the system detects a discrepancy between the actual response and the desired response (Falkenstein et al., 1995; Gehring et al., 1993; Holroyd and Coles, 2002). The conflict monitoring account on the other hand proposes that the ERN occurs, whenever two or more conflicting response alternatives are present (Botvinick et al., 2001; Cohen et al., 2000). This explains the presence of the ERN in correct trials in certain studies (Carter et al., 1998; Luu et al., 2000; Scheffers and Coles, 2000; Vidal et al., 2000), when responses involve motor conflict (Barch et al., 2000; Gehring and Fencsik, 2001; van Veen et al., 2001) and when the on-line corrective-response is being prepared (Rodriguez-Fornells et al., 2002). While one study showed a close correlation between the amplitude of the ERN and the subjectively perceived accuracy of the response in a typical flanker task (Scheffers and Coles, 2000), another study, using an antisaccade task has found the ERN to be unrelated to subjective awareness of the error (Nieuwenhuis et al., 2001). Nieuwenhuis et al. (2002) have resolved this apparent contradiction by stating that the ERN varies as a function of error awareness, when the degree of certainty about the accuracy of the response depends on data limitations, as in Scheffers and Coles (2000) study. Conversely, the ERN is unaffected by awareness, when there is uncertainty about the actual erroneous response, as in Nieuwenhuis et al. (2001) experiment. Its exact nature notwithstanding, the ERN has been shown to reliably index the activity of the *internal monitoring* system.

1.1. Feedback (knowledge of results) and ERPs

In addition to internally generated information on performance quality, presumably reflected in the ERN, performance can also be monitored via the use of externally provided *feedback* information. It is important to note that the word feedback has two connotations: In addition to the 'cognitive' feedback provided by symbolic cues, the term feedback is also used with regard to proprioceptive information used to adjust movements (e.g. Angel, 1976). In this communication, we will use feedback in the former sense, for which the term *Knowledge of Results* has been used by some authors (e.g. Brunia et al., 2000). In line with other studies on the relation of ERN and feedback evoked potentials (Holroyd and Coles, 2002; Mars et al., 2004 among others), we will stick to the label 'feedback' in this study.

With regard to the use of *external information* in the modification of behavior, a number of studies have also recorded ERP responses time-locked to feedback stimuli (Barcelo et al., 2002; Chwilla and Brunia, 1991; De Swart et al., 1981; Johnson and Donchin, 1978; Kotani and Aihara, 1999; Kotani et al., 2001, 2003; Ruchkin et al., 1980, 1981, 1982; Warren and McDonough, 1995). In the majority of these studies feedback has been studied in relation to the P3 component, which has been interpreted as reflecting the processing of relevant information about past events that can be used to modify future behavior. In addition, using a time-estimation paradigm, Brunia and coworkers have also studied another ERP component which precedes the appearance of the feedback stimulus, the Stimulus Preceding Negativity (SPN) (Brunia and Damen, 1988; Chwilla and Brunia, 1991). The amplitude of the SPN was larger when the feedback stimuli provided relevant knowledge. The authors suggested that this component can be viewed as a sign of expectancy regarding the forthcoming feedback stimulus. Kotani et al. (2001, 2003) were able to show that the SPN-amplitude can be manipulated by the informational content of the feedback stimulus (detailed vs. less detailed information), by the reward associated with accurate performance, and by the emotional valence of the feedback stimulus.

To our knowledge, only four studies have explicitly compared the effect of real versus false feedback (Chwilla and Brunia, 1991; De Swart et al., 1981; Johnson and Donchin, 1978; Warren and McDonough, 1995). In the study of Chwilla and Brunia (1991), the veracity of the feedback stimuli was manipulated over different experimental blocks of a time-estimation task. In the *true feedback* condition, participants were informed whether their performance had been correct or if they had committed under- or over-shooting errors. In contrast, in the *false feedback* condition random information was provided not related to the real performance. A control *no-feedback* condition was also used. The SPN component, with a maximum over parietal electrodes, was significantly larger in the true feedback condition. In addition, a larger centroparietal positivity was found to the stimuli in the true feedback compared to the false feedback condition (see also Warren and McDonough, 1995). In the true feedback condition the amplitude of this positivity was larger at frontocentral locations for errors when compared to correct responses, which replicated previous findings (Haschke et al., 1985).

Further experiments have yielded completely different patterns of results. For example, a negativity peaking roughly 270 ms after the feedback stimulus to incorrect responses has been interpreted as resembling the ERN component in terms of its amplitude and topographical distribution (Miltner et al., 1997). However, to distinguish this effect from the ERN proper we will use the label FRN (for feedback related negativity) in this communication. Interestingly, the FRN was elicited independently from a response generation process in Miltner et al. (1997) study.

The authors acknowledged that the topography of the FRN was different from the typical frontocentral midline distribution of the ERN. The FRN was more widely distributed spreading well into parietal areas. Consequently, dipole modeling showed that a single dipole centered in anterior cingulate gyrus can explain only part of the variance of the FRN field (e.g. 83% in the visual condition of Miltner et al.).

A negative component was also reported in relation to feedback stimuli in a gambling task (Gehring and Willoughby, 2002). The negativity was greater in amplitude following losses than following gains and, because of its frontocentral distribution, the authors considered it to be related to the ERN component. Its amplitude appeared to be dependent on the motivational impact of the events and not related to the response or error feedback.

Holroyd and Coles (2002) assessed error- and feedback-related negativities in a probabilistic learning paradigm that required the learning of stimulus-response mappings. In each run, 6 pictures of everyday objects were presented multiple times in random order. Two of the stimuli were mapped consistently to a right or to a left response button. Subjects received true feedback on their button presses for these two stimuli (condition a). In two other stimuli of each block feedback was delivered at random and unrelated to the actual button-press of subject (condition b). For a fifth picture stimulus affirmative feedback was given, regardless of the subject's response (condition c). For the sixth stimulus the subject always received negative feedback (condition d). In the first condition, the ERN was larger than the FRN, presumably because subjects had already determined whether or not their response had been correct before the appearance of the feedback. In condition b, in which participants had no way to know if a response had been correct or not, they had to wait until the feedback signal provided the information they needed; in this condition a reduced ERN and increased FRN was found. When no relevant information was provided as in conditions (c) and (d), the ERN and the FRN showed reduced amplitudes in both cases. ERPs were thus related to the different informational value of the real response or the feedback signal. In terms of their model Holroyd and Coles (2002) expected no differences between the neural generators of the ERN and the FRN and the scalp distribution of both components were not evaluated in their study. In a further recent study participants were required to guess which of the four aces of a French card play would be presented next (Ruchsow et al., 2002). After each guess a random feedback signal was presented. An FRN component was observed following negative feedback. Two dipoles were fitted in order to explain this component, in the anterior cingulate and the inferior frontal cortex.

In conclusion, the studies discussed so far have not yet revealed the exact function underlying the FRN. Furthermore, it is unclear whether or not the FRN is similar or identical to the ERN.

1.2. Brain imaging data

Feedback processing has not been extensively studied with functional neuroimaging methods. A PET study by Brunia et al. (2000) directly investigated the effect of visual feedback stimuli (knowledge of results) in a time estimation task. These researchers contrasted a condition in which subjects either received true feedback information about their response (on time, too early, too late) with a condition in which random feedback was given. A right hemisphere network comprising BA45, the junction of the posterior insula with the temporal transverse gyrus and the posterior part of the parietal cortex was identified. This network was related to the anticipatory attention towards the feedback stimulus. In a more recent fMRI study, using a similar probabilistic learning task as Holroyd and Coles (2002) and Holroyd et al. (2004) showed that an area of the dorsal anterior cingulate cortex at the border of Brodmann areas 32 and 8 was active for both, internal and external error signals.

In addition to Brunia et al. (2000) and Holroyd et al. (2004) studies, several paradigms that require the use of external information in the modification or evaluation of one's own performance and/or states or traits have been reported. Two brain areas show consistent activation across different studies, the medial prefrontal cortex (MPFC) and the posterior cingulate cortex (PCC). These brain areas were found activated when participants had to evaluate statements with respect to themselves (e.g. "I am very generous") (Johnson et al., 2002), make judgments about trait adjectives describing themselves (Kelley et al., 2002), make moral judgments (Greene et al., 2001), introspective judgments about affective pictures (Gusnard et al., 2001), or evaluative judgments in general (Zysset et al., 2002) (see Table 1). Further studies, based on the 'theory of mind' concept, which describes the ability to attribute mental states to oneself or others in order to explain behavior, pointed to the MPFC as the crucial area (see Castelli et al., 2000; Fletcher et al., 1995; Gallagher et al., 2000; Lane et al., 1997; see also Table 1). As feedback, especially equivocal feedback (see below) requires the evaluation and comparison of external and internal information; we predicted that these areas should contribute also to the electrophysiological effects to feedback stimuli.

1.3. Objective of the present study

To gain more information about the nature of the FRN a third feedback condition was introduced in addition to the usual affirmative and negative feedback conditions. In real-life situations individuals are often faced with situations in which ambiguous or insufficient information is available about the quality of their own performance. This situation was mimicked by providing 'equivocal' feedback in a portion of the trials, i.e. subjects were told that the computer sometimes was unable to determine, whether

Table 1
Coordinates of peak activation (given in Talairach space) in different imaging studies related to external monitoring and evaluation judgments

Study	Task	Area	X	Y	Z
Fletcher et al. (1995)	Mental state attribution in story comprehension	MPFC	−12	36	36
		PCC	6	−56	16
Lane et al. (1997)	Monitoring own mental emotional states	MPFC	0	50	16
Gallagher et al. (2000)	Mental state attribution in stories and cartoon comprehension	MPFC	10	50	30
Gusnard et al. (2001)	Introspective judgments about affective pictures	MPFC	−4	38	37
Kelley et al. (2002)	Self-relevance vs. other. Trait adjective judgments.	MPFC	10	52	2
		PCC	12	−48	50
Mitchell et al. (2002)	Person vs. inanimate objects. Semantic judgments	dMPFC	0	54	21
		vMPFC	3	59	0
Zysset et al. (2002)	Evaluative judgments	MPFC	−6	55	13
Greene et al. (2001)	Moral judgments	MPFC	1	52	17
		PCC	−4	−54	35
Johnson et al. (2002)	Self-reflection about subject's own attributes	MPFC	0	54	5
		PCC	−2	−61	32

MPFC, medial prefrontal cortex; PCC, posterior cingulate cortex; d, dorsal; v, ventral.

a given response was correct or not. It was expected that such a situation should engage the same evaluation systems as informative feedback but probably to a greater extent, as the subject has to reexamine her/his response.

We therefore hypothesized to obtain an FRN to the equivocal feedback stimuli as well as to the negative feedback stimuli and were expecting larger amplitude for the former.

In the current learning experiment the feedback stimuli can be used by the subject to continuously improve his or her performance even during the main phase of the experiment. Thus, we would expect a decrease of the number of errors over the course of an experimental block. We further hypothesized that the FRN to negative feedback stimuli should decrease in amplitude over the course of the block, as the subjects would rely less on external information for performance monitoring towards the end of a block. Likewise, as the quality of the internally generated information was expected to improve over the course of a block, an increase of the ERN amplitude was predicted towards the end of a block.

2. Methods

2.1. Subjects

Fourteen healthy volunteers (12 women, 1 left-handed, age-range 21–27 years) were recruited from the student population of the University of Magdeburg. None of the subjects had a history of neurological or psychiatric disorders or received any centrally acting medication.

One subject was lost for analyses because of technical artifacts.

2.2. General procedure

Each session comprised 4 blocks. A new set of eighteen different line-drawings of common objects or animals was used for each of these blocks. A block began with a *instruction phase* during which each of the 18 pictures was shown twice in the middle of a computer monitor (duration 8 s per picture) together with the instruction, whether the given picture had to be responded to by a left or right button press during the subsequent main phase of the experiment. During this instruction phase no button press was required. Nine of the pictures were associated with the right button of a computer mouse, while the other 9 pictures were to be responded to with the left button.

During the *main phase* of a block, each of the 18 pictures was presented 12 times in random order in black against a white background in the middle of a video-screen for a duration of 500 ms. At the viewing distance of 100 cm, the pictures subtended between 1.5 and 4.3 degrees of visual angle in width and between 0.9 and 3.7 degrees in height.

The subject was required to make a speeded button press according to the stimulus–response associations acquired during the instruction phase. On 10 of the 12 occurrences of a given stimulus a veridical feedback was given with regard to the picture/response button association 1100 ms after the onset of the picture by presenting either a blue X ('correct', positive) or a red X ('error', negative). In the remaining 2 trials a?? was shown that provided the 'equivocal' feedback, i.e. the response could have been either correct or incorrect.

Finally, on those trials in which the subjects failed to respond within 600 ms after the onset of the picture a turquoise 0 was shown, that signaled that the response had been too slow. The 'too slow' feedback had priority over the other types of feedback stimuli. This response deadline was imposed on the subjects, as time-pressure is known to increase the rate of erroneous responses (e.g. Rodriguez-Fornells et al., 2002), a feature desired in ERN studies.

Of the total of 864 trials (216 trials–4 blocks) per session 144 trials were associated with equivocal feedback (16.6%). A fixed SOA of 2100 ms was used between the critical picture stimuli. During the entire block a fixation cross was presented in the middle of the screen.

2.3. EEG recording

The Electroencephalogram (EEG) was recorded from the scalp using tin electrodes mounted in an elastic cap located at 28 positions (Fp1/2, F3/4, C3/4, P3/4, O1/2, F7/8, T7/8, P7/8, FC1/2, FC5/6, PO1/2, PO5/6, Fz, FCz, Cz, Pz) with an electrode positioned on the left mastoid serving as online reference. The horizontal and vertical electrooculograms (EOG) were recorded using a bipolar montage to allow off-line rejection of ocular artifacts. All channels were amplified using a bandpass 0.1–70 Hz. The EEG was digitized on-line with 4 ms resolution and stored for further processing on hard disk. After artifact rejection for eye-blinks and amplifier blocking by a special purpose program, three sets of ERPs were calculated: (1) time-locked to the onset of the pictures, (2) time-locked to the onset of the button-presses, and (3) time-locked to the feedback-stimuli. Of the four feedback-stimuli, ERPs were only computed for positive, negative, and equivocal feedback stimuli. The number of trials available for the 'too slow' feedback was insufficient to warrant evaluation. Epochs were 1024 ms long and included a 200 ms baseline. Trials in which the amplitude in the EOG and frontal channels exceeded 75 μV were rejected by a computer routine. Grand-average wave-forms resulted from collapsing the individual subjects' waveforms and were calculated for thirteen subjects.

2.4. Data analysis

Reaction times and error rates were obtained to describe the subjects behavior. ERPs were quantified by mean and peak amplitude as well as peak latency measures relative to the 200 ms pre-stimulus/pre-response baseline. For the response-locked ERPs, a typical window of 20–120 ms was selected for the quantification of the ERN. This time-window corresponds to previous studies. For the feedback-locked ERPs, a different latency of the negative response (FRN) to the negative and equivocal feedback was noted. Therefore, a peak amplitude measure was used in a time-window of 240–400 ms to encompass both peaks. For the stimulus-locked ERPs no temporally circumscribed effect differentiating error and correct trials was found.

This is due to the smearing out of response related ERP components in the stimulus-locked waveforms. Therefore successive 100 ms time-windows were used to quantify differences between error and correct trials. The resulting data sets were analyzed statistically by repeated measures analyses of variance (ANOVA). In cases with more than 1 degree of freedom in the numerator, the Huynh-Feldt epsilon correction was applied (Huynh and Feldt, 1980). In the result section, the original degrees of freedom are reported together with the corrected p-value.

2.5. Wave-forms

2.5.1. Modeling of ERP sources

The dipolar sources of the FRN component were modeled using the brain electrical source analysis (BESA) algorithm (Scherg, 1990). The BESA algorithm estimates the location and the orientation of multiple equivalent dipolar sources by calculating the scalp distribution that would be obtained for a given dipole model (forward solution) and comparing it to the original FRN distribution. Interactive changes in the location and in the orientation in the dipole sources lead to minimization of the residual variance between the model and the observed spatio-temporal distributions. In these calculations, BESA assumed an idealized four-shell ellipsoidal head model with a radius of 85 mm, and thickness of scalp, skull, and cerebrospinal fluid of 6, 7 and 1 mm, respectively (Berg and Scherg, 1994). The final locations of each dipole in the group-average BESA models were projected on mean structural T1 MRI image of 24 individuals (Cocosco et al., 1997) and converted into Talairach coordinates in the standard Montreal brain. The general approach followed for modeling the FRN component was to initially fit a single dipole constrained in location to the middle prefrontal cortex (MPFC) but not in orientation over a time interval corresponding to the FRN component. After fitting this dipole, we introduced a new source constrained in location to the posterior cingulate cortex (PC), and not in orientation. The locations of the MPFC and PC sources were computed based on the Talairach coordinates (Talairach and Tournoux, 1990) of a number of different fMRI studies having in common that they addressed evaluative processes (see Table 1 for the studies used to compute mean dipole locations). All of these studies, except Johnson et al. (2002), reported peak activations in Talairach space. The coordinates of Johnson et al. (2002) were converted from MNI-space into Talairach space using the conversion formula given by Brett (www.mrc-cbu.cam.ac.uk/imaging/common/mnispace.shtml). Coordinates of left and right hemisphere activations were averaged together yielding a seeding coordinate of $x=0$ for the MPFC and $x=3$ for the PC. Separately averaging the activity of the left and right hemispheres would have yielded seeding coordinates for the MPFC of $x=3$ and $x=-3$. These locations are so close that the use of two symmetrical dipoles, fixed at the average locations of each hemisphere, would have led to

a solution indistinguishable from the medial source used in the present solution.

A second source modeling approach was patterned after the classical ERN studies (see Dehaene et al., 1994; Miltner et al., 1997) in which a single dipole was fitted unconstrained with a starting point near the anterior comissure. However, a single dipole solution yielded exceedingly high residual variance ($>20\%$).

3. Results

3.1. Behavioral data

Overall, subjects committed 19.9% (SD 11) of errors with no differences for left or right hand assignments (19.8 vs. 19.9%). Average reaction times were 560 ms (SD 12) for erroneous responses and 430 ms (SD 49) for correct responses ($F(1,12)=82.4$, $p<0.0001$). No main effect of response hand was obtained ($F(1,12)=0.33$, n.s.).

3.2. ERPs time-locked to the stimuli

Of the total of 864 trials, 655 (SD 93) were associated with a correct response, 171 (SD 95) with an incorrect response and 37.5 (SD 12) with either no response or a response that exceeded the time-limit of 600 ms.

The grand average ERPs (Fig. 1) are characterized by a succession of N1, P2, and N2 components that are virtually
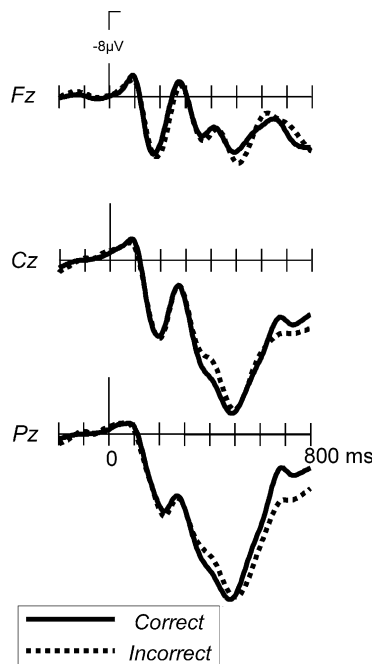

Fig. 1. Grand average ERPs time-locked to the stimuli. Stimuli associated with correct and incorrect answers gave rise to very similar ERPs. The ERPs depict the epoch from -200 to 800 ms relative to the onset of the stimulus. Tick-marks are placed every 100 ms. Stimulus onset (0 ms) is marked by a taller tick-mark.

identical for stimuli which were followed by correct and stimuli followed by incorrect answers up to about 350 ms. At this time the ERP to the incorrectly answered stimuli takes a slightly more positive course than the ERP to the correct ones. From about 500 ms onwards and especially at the central and parietal sites, the waveforms to the incorrect trials are more negative. The two waveforms were compared statistically by obtaining the mean amplitude in successive time-windows of 100 ms width starting with the 100–200 ms window (Fz, Cz, Pz sites). No main effect of response (error vs. correct) was obtained. The effects seen upon visual inspection were reflected in a significant response by electrode site interaction, however (window 300–400 ms: $F(2,24)=7.3$, $p(\mathrm{HF})<0.005$, 600–700 ms: $F(2,24)=8.5$, $p(\mathrm{HF})<0.01$, 700–800 ms: $F(2,24)=11.9$, $p(\mathrm{HF})<0.004$).

3.3. ERPs time-locked to the responses

The ERPs time-locked to the responses are shown in Fig. 2. A typical error-related negativity emerges for the error-trials. The spline-interpolated isovoltage maps show the well-known frontocentral midline maximum. The ERN was tested by a mean amplitude measure in the 20–120 ms time-window (Fz, Cz sites). The factor response (error vs. correct) yielded a highly significant main effect ($F(1,12)=18.37$, $p<0.0015$).

3.4. ERPs time-locked to the feedback stimuli

The main focus of the present study was the investigation of the ERPs to the feedback stimuli shown in Fig. 3. The waveforms to the feedback stimuli are characterized by a small initial negativity at about 120 ms (best visible for electrode site Fz) followed by a sharp positivity reaching its maximum at about 230 ms in the correct condition. Apparently superimposed upon this positivity, both negative and equivocal feedback conditions show phasic negativities. The negativity is of considerably larger amplitude in the equivocal condition and also appears to have earlier peak latency. While being smaller and later, the effect in the negative feedback condition shows a virtually identical scalp distribution (Fig. 3, right side).

Statistically, peak latencies determined on the 'negative minus positive feedback' and 'equivocal minus positive feedback' difference waves in the 240–400 ms time window (Fz, Cz sites) showed a significant difference between the conditions (equivocal 290 ms [SD 10], negative 322 ms [SD 47], F(1,12)=5.5, $p<0.04$). As suggested by visual inspection, amplitudes of the feedback negativities in the difference waves were significantly different (peak amplitude measure; Fz, Cz sites, 240–400 ms time window; equivocal -7.5 μV [SD 2.3], negative -2.4 μV [SD 2.1], F(1,12)=65.8, $p<0.0001$). The similarity of the distribution of the negativities was supported statistically: mean amplitudes were taken on the 'equivocal minus positive'
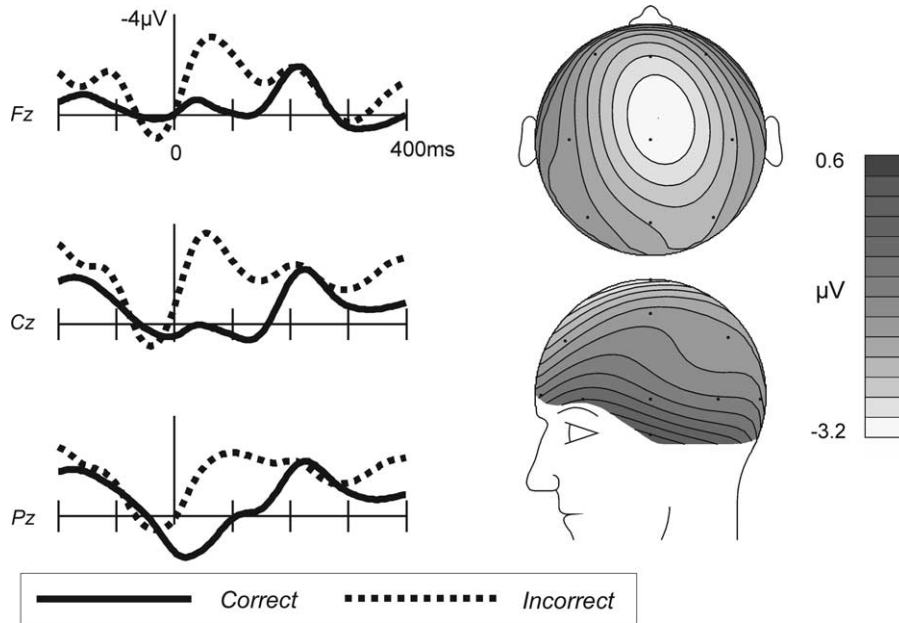
Fig. 2. Grand average ERPs time-locked to the responses. To attenuate the late positive component that was elicited by the stimuli (cf. Fig. 1), a 1.5–8 Hz bandpass filter (half amplitude cut-off) was applied to the waveforms. A clear ERN emerged for the error trials with a typical fronto-central midline maximum. The ERPs depict the epoch from −200 to 400 ms relative to the onset of the subjects' response. Tick-marks are placed every 100 ms. The time of response (0 ms) is marked by a taller tick-mark. The topography of the ERN can be derived from the isovoltage maps, which are based on the mean amplitude of the error-trials in the 20–100 ms time-window (relative to the onset of the response).
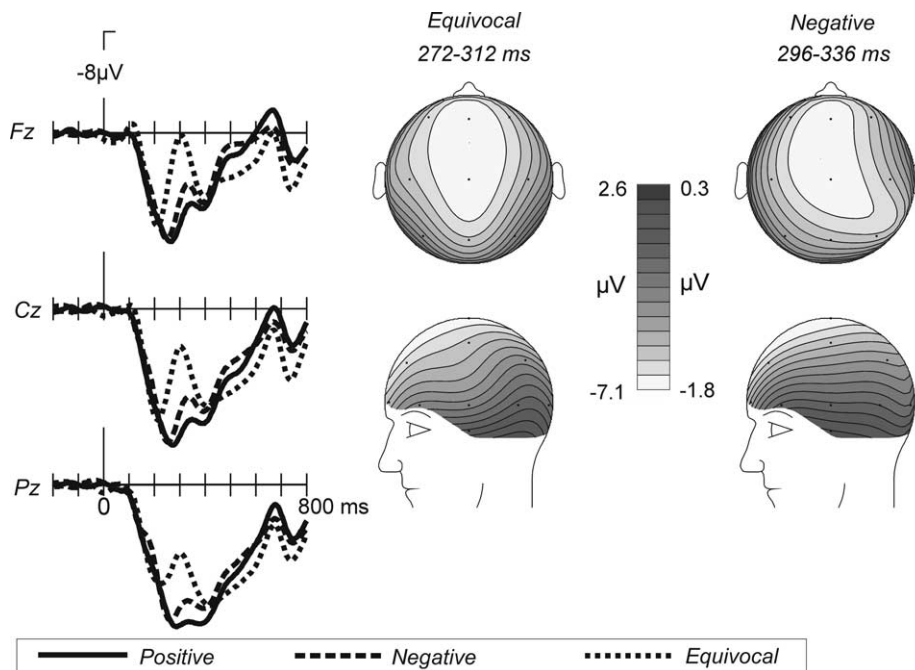

Fig. 3. Grand average ERPs to the feedback stimuli. All feedback categories are characterized by an initial negativity followed by a sharp positivity reaching its maximum at about 230 ms in the correct condition. Relative to the positive feedback events negative feedback trials were associated with a phasic negativity superimposed upon the late positive component (feedback related negativity, FRN). For the events with equivocal feedback a similar phasic FRN with greater amplitude and earlier latency was seen. The ERPs depict the epoch from −200 to 800 ms relative to the onset of the feedback-stimulus. Tick-marks are placed every 100 ms. Feedback onset (0 ms) is marked by a taller tick-mark. To derive the isovoltage maps on the right side the (negative minus positive) and (equivocal minus positive) difference waves were obtained. The peak latency of the FRN was determined in the Cz channel. The maps are based on the mean amplitude values in the 40 ms time-window centered upon the peak latency. The distribution of the FRNs is clearly different from the distribution of the ERN (see Fig. 2).

and 'negative minus positive' difference waves in 40 ms time-windows centered upon the grand average peak-latencies and compared after vector-normalization (McCarthy and Wood, 1985). A mean amplitude measure centered upon the peak-latency of the effect was chosen because a peak amplitude measure would have provided peak amplitudes at different latencies in the different channels. The interaction between condition (equivocal/negative) and electrode site (28 channels) was not significant ($F(27,324) = 1.9$, $p(HF) = 0.21$) indicating that the distributions were not different.

3.5. Comparison of error-related and feedback-related negativities

The inspection of the distribution of the ERN (Fig. 2) and the feedback negativity (Fig. 3) suggests that at least partially different neural generators underlie the two effects. To compare the distributions more formally, the mean amplitudes of the effects were measured in 40 ms time windows centered upon their grand average peak-latencies in the difference waves (ERN: error minus correct trials, response-locked; feedback/equivocal: equivocal minus positive; feedback/negative: negative minus positive). The amplitudes were vector normalized (McCarthy and Wood, 1985) and entered into a repeated measures ANOVA with effect (ERN, feedback/equivocal, feedback/negative) and electrode-site (28 channels) as factors. A highly significant effect × electrode site interaction was obtained, indicating that indeed the ERN and feedback negativities had different distributions ($F(54,648) = 4.7$, $p(HF) < 0.0005$).

3.6. Dipole source modeling of the FRN

From the grand-averaged difference waveforms of the equivocal minus positive feedback conditions the dipolar sources of the FRN component were modeled using BESA algorithm. The Talairach coordinates of each modeled dipole were (mean values from Table 1): middle prefrontal cortex (0.7, 51.3, 15.8) and posterior cingulate cortex (3, -55, 33.3). The resulting dipole locations and the time course of the modeled activity for each dipole are represented projected onto mean MRI sagittal and axial images for illustrative purposes (see Fig. 4). Together these two dipoles accounted for 95% of the variance in the scalp distribution of the FRN component between 250 and 300 ms.

3.7. Comparison of first and second halves of the experimental blocks

To assess changes of the ERP components and behavioral measures, separate averages were obtained for the first and second halves of each block. These data were averaged across blocks and are displayed in Fig. 5.
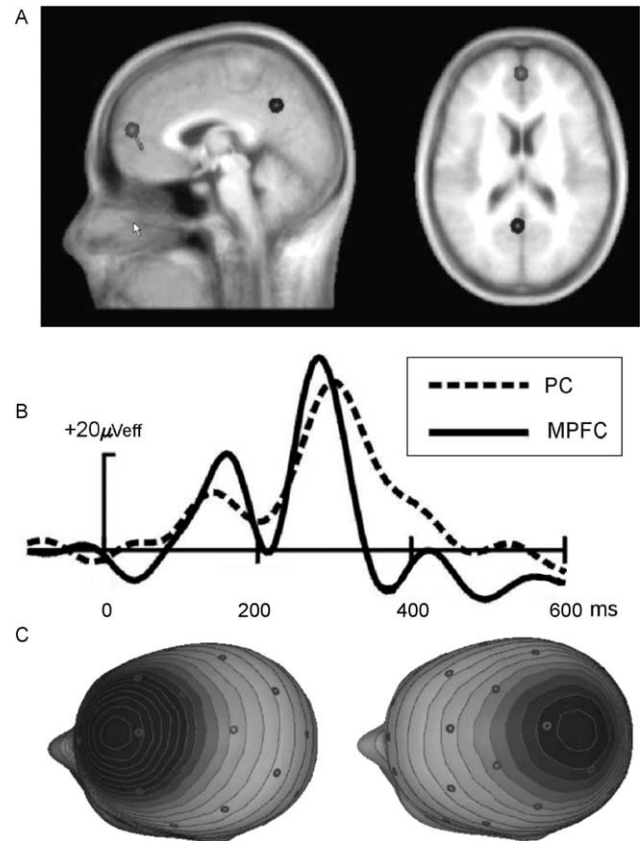

Fig. 4. Dipole model of FRN component based on the (equivocal minus positive) difference wave which afforded a better signal to noise ratio than the (negative minus positive) difference wave. (a) The locations (in Talairach coordinates) of both dipolar sources (indicated with dots) for the FRN (250–300 ms) are shown projected onto a sagittal and axial sections from a standard mean MRI image; (b) source waveforms on the right show the time course of the modeled activity for each dipole; (c) relative scalp distribution of each dipolar source, for the middle prefrontal dipole (left) and posterior cingulate gyrus dipole (right).

The time-windows and electrodes for ERP measurements are given in the figure legends.

Error rates were significantly lower in the second half of each block ($t(12) = 3.48$, $p < 0.005$) as were reaction times for both, correct ($t(12) = 17.73$, $p < 0.001$) and error ($t(12) = 21.4$, $p < 0.001$) trials. The FRN for negative feedback was smaller during the second block of the experiment, which was reflected by a statistical trend ($t(12) = 2.08$, $p = 0.06$). No significant difference was seen for the FRN to equivocal feedback ($t(12) = 1.2$). The ERN to error trials was found to be slightly larger during the second half of each block ($t(12) = 2.32$, $p < 0.04$).

4. Discussion

The main purpose of the present experiment was to investigate the differences between the brain responses to self-generated and externally provided information on performance quality. In line with a great number of
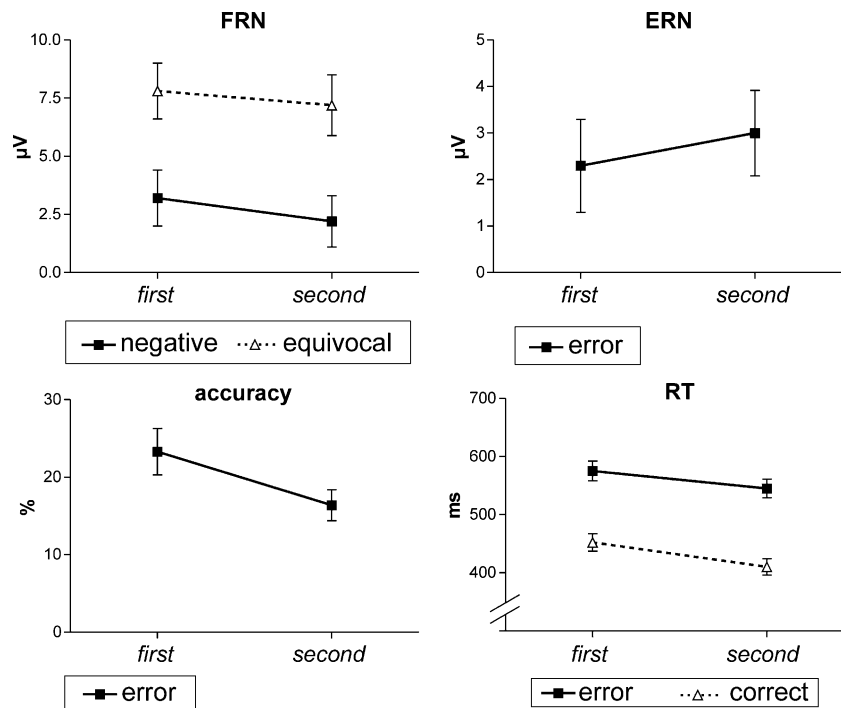
Fig. 5. Comparison of data from the first and second halves of each block. Upper left: the amplitude of the FRN was determined as the peak amplitude in 240–400 ms time window in the (negative minus positive feedback) and (equivocal minus positive feedback) difference waves. The FRN amplitude tended to be smaller in the second half of the blocks. Upper right: the amplitude of the ERN was determined as mean amplitude in the 20–120 ms time-window (relative to the response) on the original waveforms (bandpass filter 1.5–8 Hz applied). Lower left: The percentage of error trials was smaller in the second half of the blocks. Lower right: the reaction times were somewhat faster in the second half of the blocks.

electrophysiological studies, response-locked ERPs to erroneous responses elicited an error-related negativity (ERN) with a peak latency of about 80 ms in the present experiment and a typical frontocentral midline distribution. The ERN can be taken as an index of an internal monitoring system, with previous source modeling (Dehaene et al., 1994; Luu and Tucker, 2001; van Veen and Carter, 2002) and brain imaging (Carter et al., 1998, 2001; Kiehl et al., 2000; Menon et al., 2001; Ullsperger et al., 2002) studies suggesting neural generators in the anterior cingulate gyrus and the lateral prefrontal cortex (see also Gehring and Knight, 2000; Ullsperger et al., 2002).

With regard to external information, a negativity peaking approximately 300 ms after the feedback stimulus, the 'FRN', was found. Relative to the ERPs to positive feedback stimuli, both, negative and equivocal conditions, were associated with a phasic negative component.[1] When subjects received feedback that was equivocal with regard to the accuracy of their button response, the amplitude of the FRN

was increased by a factor of 3 in the equivocal relative to the negative FRN, while the morphology and distribution of the effect in the two conditions was virtually identical.

While previous investigations have suggested that the FRN is similar or identical to the ERN obtained for erroneous responses (Gehring and Willoughby, 2002; Holroyd and Coles, 2002; Miltner et al., 1997), the scalp distribution of this effect (see Figs. 2 and 3) suggests that this might not be the case. Indeed, upon statistical comparison the distributions of response-locked ERN and the FRN were found to be different and the source model obtained with the BESA method again suggested different generators than either the anterior cingulate component solution (Dehaene et al., 1994) or the more recent multi-dipole solution (Luu and Tucker, 2001) for the ERN. In fact, when we tried to model the FRN with a single dipole seeded in the anterior cingulate gyrus, the residual variance was in excess of 20%, indicating that a single-dipole solution is not adequate for the present data set. Considering the high residual variances reported for their source models, this might have also been the case in the study of Miltner et al. (1997). In addition, because of the widespread scalp distribution of the FRN, single dipole solutions yield unphysiological locations far away from the cortical surface. We therefore followed an anatomically constrained approach to seed the possible neural sources. Based on the results obtained in relevant functional neuroimaging studies (see Table 1), we tested a forward model based on the peak activations observed in the medial

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[1] Negative ERP effects have also been reported for deviant visual stimuli in visual classification tasks (Breton et al., 1988; Heinze et al., 1992; Renault et al., 1982; Luck and Hillyard, 1994). The question therefore arises, whether the negativities found for negative and equivocal feedback simply reflect the deviance of these feedback stimuli with regard to the more common positive feedback stimuli. The N2-components in those earlier papers showed a broader peak, however, suggesting that the FRN and stimulus-deviant N2 are separate phenomena. This should be tested in further experiments.

prefrontal cortex (MPFC) and the posterior cingulate (PCC).[2] With this anatomically constrained approach, a reasonable amount of variance (95%) in the FRN time-range could be explained. Thus, the present investigation strongly suggest that different neuronal populations are involved in the use of internal and external information to monitor performance. With regard to the differences of the current FRN to the feedback-related component described by Miltner et al. (1997) it is also worth pointing out, that the current experiment is a learning task that required the learning of 18 different stimulus–response mappings per block. While errors in the usual ERN paradigms, such as the Eriksen task (Eriksen and Eriksen, 1974), are associated with faster reactions than correct responses and therefore can be classified as fast guesses, this is not the case in the present experiment. This suggests that participants in this learning task are not sure about the nature of the stimulus-response mapping in the error trials. In this regard, the feedback in the current experiment serves as a continuous aid to the improvement of performance and not just as a further proof that something has been wrong or right.

The FRN component in the present experiment is also clearly different from the medial frontal negativity reported by Gehring and Willoughby (2002) in their gambling task. In fact, their effect that was larger for monetary losses was similar to the distribution of the ERN. Gehring and Willoughby suggested, that their feedback component might be sensitive to the motivational/emotional valence of the feedback rather than to the correctness status of their previous performance. Thus, it appears that feedback related negativities vary as a function of the task and the information conveyed by the stimulus.

A novel feature of the present experiment was the introduction of ambiguous feedback that leaves the subjects in doubt about their performance and therefore requires them to reevaluate their own performance and to discard the external information. The subjects' task is thus similar to those of a number of recent imaging experiments (see also Table 1) that required the evaluation of external information which related to the subject's own behavior, or self-concept (Greene et al., 2001; Gusnard et al., 2001; Johnson et al., 2002; Kelley et al., 2002; Mitchell et al., 2002; Zysset et al., 2002). In all of these studies medial prefrontal cortex and posterior cingulate cortex were found active. It is therefore not surprising that dipoles seeded in these areas explain the feedback related activity in the present experiment.

With regard to the behavior of the ERN and FRN over the course of the block, specific predictions were made taking into account that the subjects could use the feedback information to improve their behavior over the course of a block. We expected the amplitude of the FRN to negative feedback stimuli to decline over the course of a block, reflecting the decreased need of the subjects for external information for performance evaluation, while the ERN was expected to increase, indicating the increased reliance of subjects on internal information. These predictions were fulfilled (see Fig. 5) thus indicating the flexible use of internal and external information by our subjects. At the same time, the FRN to equivocal feedback remained unchanged. In the case of equivocal feedback, there is a mismatch between the subject's internal information and the feedback information, which does not change from the first to the second half of the experimental block. This can explain the constantly high amplitude of the FRN.

At first glance, a puzzling result with regard to feedback related potentials is that some studies (Gehring and Willoughby, 2002; Holroyd and Coles, 2002; Miltner et al., 1997) including the present one do not show an effect on the P300 component, which has previously been related to feedback processing (see review in Johnson, 1986, 1988). For example, a larger P300 has been found for correct compared to false or untrue feedback (Chwilla and Brunia, 1991; De Swart et al., 1981; Haschke et al., 1985; Johnson and Donchin, 1978; Warren and McDonough, 1995). The lack of an effect on the positivity for feedback stimuli in the present experiment echoes previous results of Karis et al. (1983) and Kotchoubey et al. (1997) (see also Kotchoubey, 2002). In the informed guessing paradigm of Kotchoubey et al. (1997), the P3 amplitude was not related to the subjective expectancy but to the 'information objectively presented in the environment' (Kotchoubey, 2002).

Although feedback related components have to be further studied, it is clear that a number of different neural sources are responsible for the processing of information carried by the feedback stimulus. The present results point to the medial prefrontal and posterior cingulate cortex. In light of the rich imaging literature summarized in Table 1 these regions these likely support different but complementary cognitive processes. The posterior cingulate cortex has been implicated in the processing of the valence of emotionally pleasant and unpleasant words compared to neutral words for example (Maddock et al., 2003) and has been proposed to be is the brain area most consistently activated by emotionally salient compared to matched neutral stimuli (Maddock, 1999).[3] The role of the MPFC on the other hand appears to be the implementation of the evaluation process.

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[2] While other regions in addition to the MPFC and posterior cingulate gyrus have been shown to play a role in feedback processing (e.g. O'Doherty et al., 2003), we have used only the two seeding regions obtained from the studies given in Table 1. The frontocentral distribution of the FRN made it impossible to obtain a stable solution by introducing a third regional source into the Besa solution. This was due to the fact that the MPFC dipole explained the field in the prefrontal region very well (see the scalp distribution of the MPFC in Fig. 4).

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[3] Another view (Vogt et al., 1992) stresses the evaluative functions of the posterior cingulate cortex, which are thought to included the monitoring of sensory events and of the organism's own behavior in the service of spatial orientation and memory.

Acknowledgements

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