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Error-related ERP components and individual differences in punishment and reward sensitivity☆

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ABSTRACT

Although the focus of the discussion regarding the significance of the error related negatively (ERN/Ne) has been on the cognitive factors reflected in this component, there is now a growing body of research that describes influences of motivation, affective style and other factors of personality on ERN/Ne amplitude. The present study was conducted to further evaluate the relationship between affective style, error related ERP components and their neural basis. Therefore, we had our subjects fill out the Behavioral Activation System/Behavioral Inhibition System (BIS/BAS) scales, which are based on Gray's (1987, 1989) biopsychological theory of personality. We found that subjects scoring high on the BIS scale displayed larger ERN/Ne amplitudes, while subjects scoring high on the BAS scale displayed larger error positivity (Pe) amplitudes. No correlations were found between BIS and Pe amplitude or between BAS and ERN/Ne amplitude. Results are discussed in terms of individual differences in reward and punishment sensitivity that are reflected in error related ERP components.

1. Introduction

Evaluation of current performance has a role of central importance in the regulation of cognitive processes. The discovery of the neural correlates of performance evaluation has inspired an abundance of research in recent years. In particular, event-related potential (ERP) studies have revealed a neural response to errors that has been termed the error-related negativity (ERN) or error negativity (Ne). Observed at fronto-central recording sites (Fz, FCz, Cz), the ERN/Ne consists of a large negative shift in the response-locked ERP occurring 50–100 ms after subjects have made an erroneous response (Falkenstein et al., 1990; Gehring et al., 1990). Originally, it was assumed that the ERN/Ne reflects the detection of errors, but a growing body of literature suggests that this ERP component is involved in a more general evaluation of action plans (Luu et al., 2000; Vidal et al., 2000) or the estimation of the motivational value of ongoing events (Bush et al., 2000; Pailing and Segalowitz, 2004; Hajcak et al., 2005). Localization with dipole localization algorithms has led

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most authors to conclude that the ERN/Ne is generated in the Anterior Cingulate Cortex (ACC; Dehaene et al., 1994; Wijers and Boksem, 2005), a neural structure in the medial wall of the PFC. These findings are corroborated with results from fMRI studies (Ullsperger and Von Cramon, 2003; Ridderinkhof et al., 2004) that show increased activation of the ACC during error trials, relative to correct trials.

Holroyd and Coles (2002) proposed a monitoring system located in the basal ganglia that predicts the outcome (good or bad) of an action, on the basis of information received from the external environment and an 'efference copy' of the action. When the basal ganglia find that events are better or worse than expected, they produce error signals. These error signals are coded as phasic increases and decreases, respectively, of the tonic activity of the mesencephalic dopaminergic system (Schultz, 2002). These authors propose that a phasic decrease in activity of mesencephalic dopaminergic neurons following the commission of an error, disinhibits the apical dendrites of motor neurons in the ACC, producing the ERN/Ne (Holroyd and Yeung, 2003).

Thus, it appears that dopamine is critically involved in the generation of the ERN/Ne. Corroborating this theory, De Bruijn et al. (2004) showed that administering amphetamine, which increases dopamine release, results in increased ERN/Ne amplitude. In addition, caffeine (which indirectly simulates dopamine production) elicits an increased ERN/Ne (Tieges et al., 2004), while ethanol (a sedative substance that indirectly acts on dopamine receptors) and mental fatigue (which is supposed to involve reduced dopaminergic activity) result in a reduction of ERN/Ne amplitude (Ridderinkhof et al., 2002; Boksem et al., 2006). Moreover, patients suffering from Parkinson's disease, which involves a disturbance of the mesencephalic dopaminergic system, show attenuated ERN/Ne amplitudes (Falkenstein et al., 2001, 2005; but see Holroyd et al., 2002).

Holroyd and Coles (2002) further proposed that this dopamine-mediated monitoring system is part of a system for reinforcement learning. Their theory holds that this system utilizes information obtained from rewards and punishments (or non-rewards), as well as from abstract indicators of success and failure (feedback stimuli), in order to select the appropriate responses for achieving goals. ERP studies support the theory that the ERN/Ne reflects responses to punishment or non-reward. In designs using outcome stimuli that inform subjects about gains and losses, feedback indicating a loss (punishment) results in larger 'feedback ERNs' (an ERN/Ne-like component in response to the negative feedback; Gehring and Willoughby, 2002; Holroyd et al., 2004). Consistent with the ERN/Ne reflecting an ACC-based reinforcement (punishment) learning system, there is evidence for a sensitivity of (rostral) ACC activity to reductions in reward or to punishment (Bush et al., 2002; Knutson et al., 2000).

Indeed, although the focus of the discussion regarding the significance of the ERN/Ne has largely been on the cognitive factors reflected in this component, there is now a growing body of research that describes influences of motivation, affective style and other factors of personality on ERN/Ne amplitude. For example, Dikman and Allen (2000) examined the ERN/Ne in relation to punishment sensitivity (low socialization). These authors found that subjects scoring low on a socialization scale, produced smaller ERN/Nes in a task in which they were punished for incorrect responses compared to a task in which they were rewarded for correct responses, while high socialization subjects produced similar ERN/Nes in both conditions.

In addition, worry and anxiety (Hajcak et al., 2003a) have been associated with pronounced ERN/Nes, and an increase in 'feedback ERN' has been observed in subjects diagnosed with clinical depression (Tucker et al., 2003). Hajcak et al. (2004) argued that this enhancement of ERN/Ne amplitude is not a function of either anxiety or depression specifically, but relates to the underlying characteristic of high negative affect common to both syndromes (see also Tucker et al., 1999; Luu et al., 2000). Negative affect, in turn, is thought to be strongly related to punishment sensitivity (Watson et al., 1999), providing additional support for the notion that the ERN/Ne reflects the neural responses to punishment.

Compared to the ERN/Ne, the functional significance of the error positivity (Pe) is markedly less substantiated (Overbeek et al., 2005). This ERP component typically follows the ERN/Ne and consists of a slow positive going deflection that reaches its maximum between 200 and 400 ms after subjects make an error. Its distribution is quite diffuse, but appears slightly more posterior compared to the ERN/Ne (Falkenstein et al., 2000). The Pe has been proposed to reflect error awareness (Nieuwenhuis et al., 2001) or error salience (Leuthold and Sommer, 1999) and may be related to performance adjustments following an error (Nieuwenhuis et al., 2001; Hajcak et al., 2003b). Reports of relationships between Pe and affective style are scarce; however, Hajcak et al. (2004) reports that negative affect was associated with a reduced Pe.

There is a notable link between theories and data concerning the ERN/Ne and Gray's theory that the descending pathway of the prefrontal cortex–ACC-septo-hippocampal behavioral inhibition system (BIS) is an important route in bringing about behavioral inhibition in anxiety disorders (Gray, 1987, p. 338; 1989). This system comprises cholinergic projections that inhibit dopaminergic behavioral approach systems (BAS; Gray, 1989). The BIS organizes responses to conditioned signals of punishment and its main effects are inhibition of ongoing behavior by avoiding punishment with inactivity (passive avoidance) or by abandoning behaviors that do not bring reward (extinction). According to Gray, the most likely sites of interaction between the behavioral inhibition and approach systems lie in the ventral striatum (nucleus accumbens) and lateral septal area. The ventral striatum is an ideal site at which the behavioral inhibition system could inhibit striatal output destined to facilitate motor behavior aimed at the attainment of reward or non-punishment. A medial septal cholinergic projection to the hippocampal formation is followed by the subicular projection to the nucleus accumbens which may inhibit the approach system, and a projection from A10 in the ventral tegmental area to the lateral septal area, together with the projection from the lateral to the medial septal area, may mediate the reciprocal inhibitory link from the approach to the behavioral inhibition system (Gray, 1989). According to Gray, activation of the inhibitory system is guided by a 'comparator', in response to prediction errors and to aversive stimuli (i.e., punishment or non-reward).

The model of Gray seems to fit rather well with the findings that relate the ERN/Ne to errors, punishment and non-reward. However, while Holroyd and Coles (2002) suggests that a dopaminergic system is of primary importance in the generation of the ERN/Ne, Gray suggests that the first response to prediction error and punishment is mediated by a cholinergic BIS system. Since this BIS system inhibits the dopaminergic BAS system, Gray's model is consistent with the theory of Holroyd and Coles. In addition, it stresses the importance of a non-dopaminergic (BIS) system involved in response monitoring that has received hardly any attention in theories regarding the ERN/Ne (although see Luu and Tucker, 2001).

The present study was conducted to evaluate the respective contributions of a reward seeking system (BAS) and of punishment sensitivity (BIS) to error-related ERP components, using an individual differences approach. Therefore, we had our subjects fill out the BIS/BAS Scales (Carver and White, 1994; Franken et al., 2005), which are based on Gray's (1987, 1989) biopsychological theory of personality. The BAS scale has three subscales: fun seeking (BAS-fun), reward responsiveness (BAS-reward) and drive (BAS-drive). The BIS scale has no such subscales. In addition, we used other personality questionnaires as measures of convergence. Like BAS, extraversion is believed to reflect the responsiveness of the dopaminergic reward system (Depue and Collins, 1999; Watson et al., 1999). Similarly, in recent years much support has accumulated for an association between novelty seeking (Cloninger et al., 1994) and dopaminergic activity (see e.g. Savitz and Ramesar, 2004 for a review). Finally, measures like neuroticism (e.g. Watson et al., 1999) and Harm Avoidance (Cloninger et al., 1994), like the BIS scale, tap on punishment sensitivity.

If the error-related ERP components are related to the responsiveness of a dopaminergic reward system, we would expect a relationship between these components and individual differences in BAS scores. Conversely, if these error-related components are related to an inhibitory punishment system, we would expect a relationship between these components and BIS scores, making a primary relationship with dopamine transmission less plausible. Finding one of these two relationships would provide us with a better understanding of the neural basis of error processing and its relationship with individual differences.

2. Results

In Table 1, relevant correlations are presented between ERN/Ne, Pe, self-reported measures and behavior. All other correlations of interest were found to be non-significant and will not be reported here.

2.1. Questionnaires

Gray (1987) conceptualized the BIS and BAS sensitivities to be orthogonal. Indeed, we found BIS and BAS-tot to be unrelated. However, examination of the correlations between BIS and subscales of the BAS revealed that BAS-reward and BAS-drive tended to be positively related to BIS (n.s.), while only BAS-fun correlated negatively with BIS, although this failed to reach

Table 1 – Correlations between self-reported personality measures and error-related ERP components

	BIS	BAS-tot	BAS-fun	BAS-rew	BAS-drive	Extra version	Neuroticism	Novelty seeking	Harm avoidance	ERN/Ne	Pe	RT	Errors	Error slowing
BIS		−0.04	−0.38[a]	0.22	0.28	−0.36[a]	0.54[b]	−0.42[c]	0.57[b]	0.56[b]	−0.18	−0.06	−0.31	0.15
BAS-tot	−0.04		0.80[b]	0.70[b]	0.59[b]	0.42[b]	−0.01	0.61[b]	−0.43[c]	0.01	0.43[c]	−0.40[a]	0.09	0.06
BAS-fun	−0.38[a]	0.80[b]		0.39[a]	0.09	0.58[b]	−0.34	0.74[b]	−0.55[b]	−0.30	0.57[b]	−0.18	0.15	0.09
BAS-rew	0.22	0.70[b]	0.39[a]		0.26	0.35	0.16	0.17	−0.24	0.17	0.19	−0.36[a]	−0.02	−0.04
BAS-drive	0.28	0.59[b]	0.09	0.26		−0.13	0.32	0.20	−0.02	0.28	0.03	−0.36[a]	0.01	0.02
Extraversion	−0.36[a]	0.42[b]	0.58[b]	0.35	−0.13		−0.39[a]	0.56[b]	−0.73[b]	−0.36[a]	0.39[a]	−0.12	0.06	−0.12
Neuroticism	0.54[b]	−0.01	−0.34	0.16	0.32	−0.39[a]		−0.18	0.62[b]	0.62[b]	−0.28	0.06	0.18	−0.16
Novelty Seeking	−0.42[c]	0.61[b]	0.74[b]	0.17	0.20	0.56[b]	−0.18		−0.62[b]	0.23	0.37[a]	−0.02	0.05	0.18
Harm Avoidance	0.57[b]	−0.43[c]	−0.55[b]	−0.24	−0.02	−0.73[b]	0.62[b]	−0.62[b]		0.39[a]	−0.39[a]	0.19	0.17	−0.06
ERN/Ne	0.56[b]	0.01	−0.30	0.17	0.28	−0.36[a]	0.62[b]	0.23	0.39[a]		−0.53[b]	0.11	−0.28	−0.24
Pe	−0.18	0.43[c]	0.57[b]	0.19	0.03	0.39[a]	−0.28	0.37[a]	−0.39[a]	−0.53[b]		−0.31	−0.01	0.44[c]
RT	−0.06	−0.40[a]	−0.18	−0.36[a]	−0.36[a]	−0.12	0.06	−0.02	0.19	0.11	−0.31		−0.24	−0.29
Errors	−0.31	0.09	0.15	−0.02	0.01	0.06	0.18	0.05	0.17	−0.28	−0.01	−0.24		0.09
Error slowing	0.15	0.06	0.09	−0.04	0.02	−0.12	−0.16	0.18	−0.06	−0.24	0.44[c]	−0.29	0.09	

Note: For all correlations: $n = 24$. Correlations with absolute ERN/Ne amplitudes are presented.

[a] $P < 0.10$.

[b] $P < 0.01$.

[c] $P < 0.05$.

significance ($P = 0.07$). This suggests that BAS-fun may provide the best contrast with the BIS. In addition, BAS-tot and BAS-fun were positively related to extraversion and novelty seeking, while BIS was positively related to neuroticism and harm avoidance.

2.2. Performance

To investigate task-related performance differences, reaction times and number of errors were calculated for the two trial types (congruent and incongruent) separately. For reaction times, repeated-measures ANOVA indicated a significant main effect for trial type, $F(1,23) = 241.55$, $P < 0.001$: subjects responded slower on incongruent trials (515 ms) compared to congruent trials (458 ms). The same analyses also revealed a main effect of trial type for the number of errors, $F(1,23) = 53.85$, $P < 0.001$: the number of errors made on incongruent trials (12.7%) was substantially larger than the number of errors committed on congruent trials (3.9%). These effects on performance were unrelated to BIS or BAS scores, although subjects scoring high on BAS tended to have shorter reaction times ($r = -0.40$, $P = 0.10$). This effect, however, failed to reach significance and was not different for congruent and incongruent trials.

2.3. Correlations between ERPs, personality and behavior

Subjects scoring high on the BIS, displayed larger ERN/Ne amplitudes compared to subjects with lower BIS scores (Fig. 1), while BAS scores were unrelated to ERN/Ne amplitude. Conversely, subjects with high BAS scores displayed larger Pe amplitudes compared to subjects that had lower scores on the BAS (Fig. 2). Of the BAS subscales, only BAS-fun showed this correlation with Pe amplitude; BAS-reward and BAS-drive appeared to be unrelated to Pe amplitude. Partial correlations support these findings. When controlling for BAS and Pe, BIS remained positively correlated with ERN/Ne amplitude ($r = 0.59$, $P < 0.001$), while BAS remained positively related to Pe amplitude when controlling for BIS and ERN/Ne amplitude ($r = 0.54$, $P < 0.01$).

Like the BIS, neuroticism was positively related with ERN/Ne amplitude, while extraversion appeared to be related to Pe amplitude, although this effect was only marginally significant ($P = 0.06$). Similarly, we found a trend of harm avoidance being related to ERN/Ne amplitude ($P = 0.08$) and novelty seeking being related to Pe amplitude ($P = 0.08$). In addition, Pe amplitude showed a positive correlation with post error slowing. No such relationship between BAS and post error slowing was observed; however, BAS (all except BAS-fun)

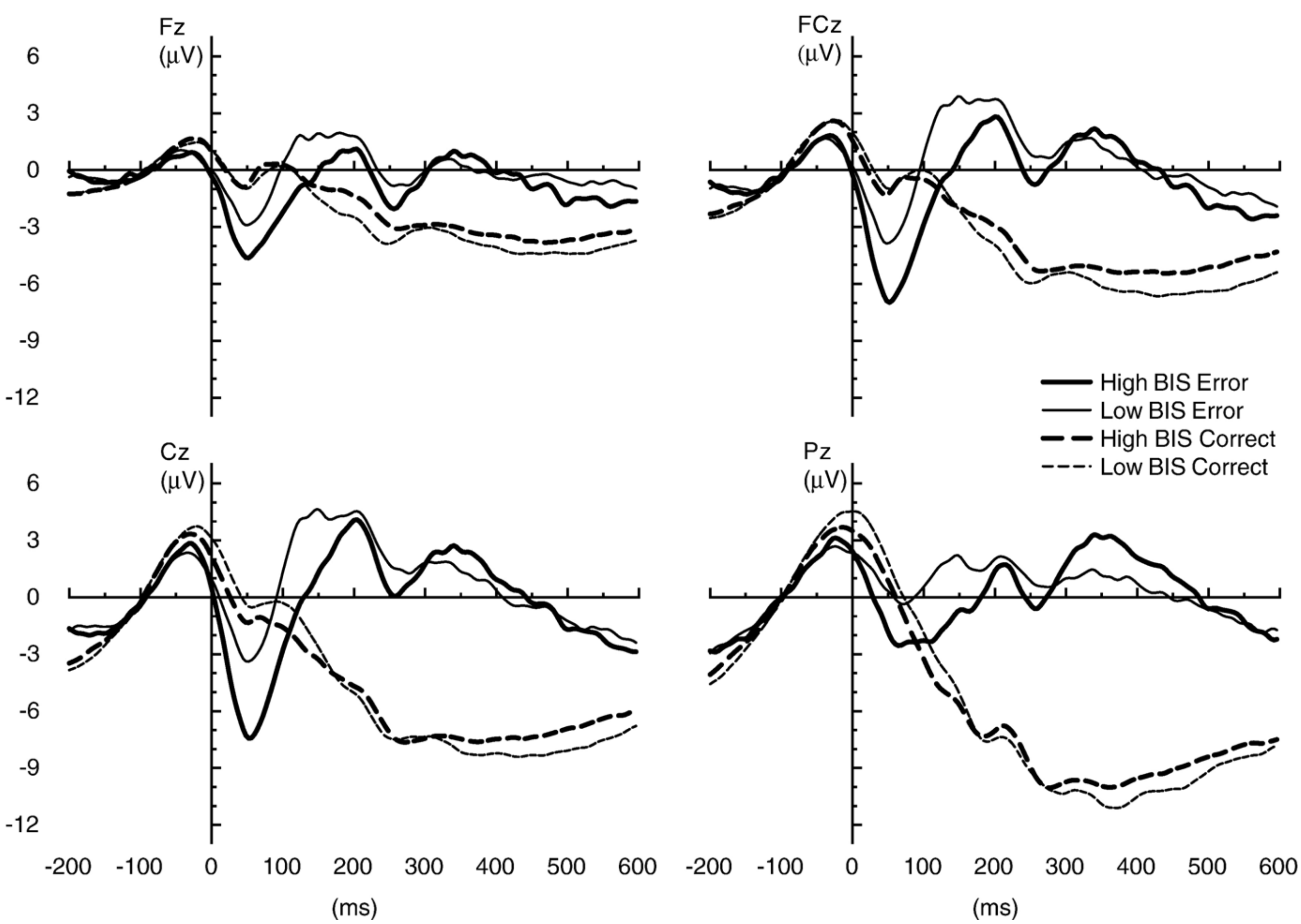

Fig. 1 – Grand-averaged response-locked ERPs at the Fz, Fcz, Cz and Pz recording sites, for high BIS ($n = 13$) and low BIS ($n = 11$) subjects. Groups were formed using a median split procedure (only for illustrative purposes). BIS scores were positively related to ERN/Ne amplitude.

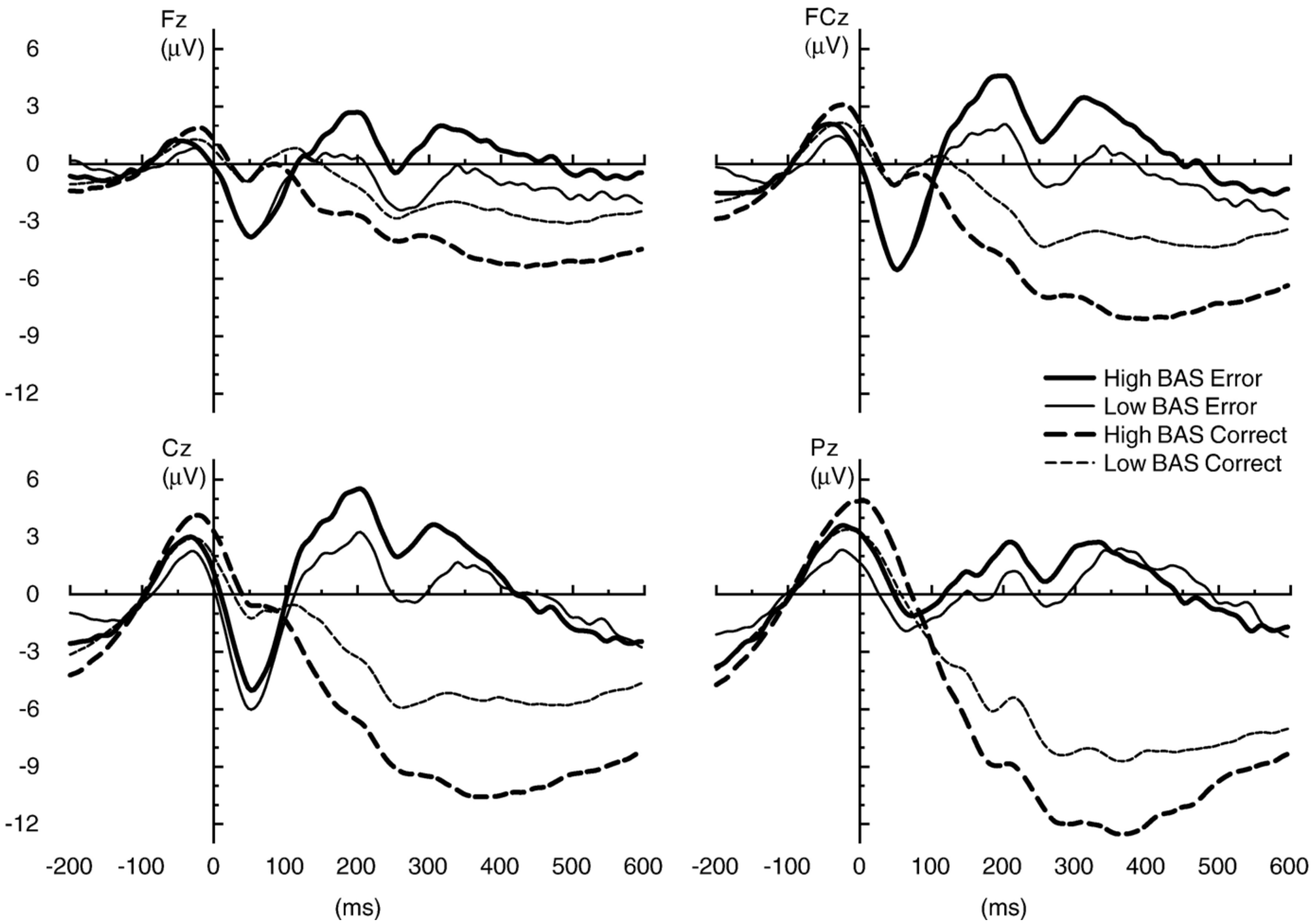

Fig. 2 – Grand-averaged response-locked ERPs at the Fz, Fcz, Cz and Pz recording sites, for high BAS (*n* = 11) and low BAS (*n* = 13) subjects. Groups were formed using a median split procedure (only for illustrative purposes). BAS scores were positively related to Pe amplitude.

tended to be related to shorter RTs, although this effect failed to reach significance ($0.05 < P < 0.10$).

All correlations between response-locked ERPs and personality or behavioral measures were specific for error trials: no relations were found between response-locked ERPs on correct trials and any of these measures.

The stimulus-locked P3 was positively correlated with the Pe ($r = 0.51$, $P < 0.05$), but was unrelated to other measures. The stimulus-locked N2, although larger for incompatible trials compared to compatible trials, $F(1,21) = 49.76$, $P < 0.001$, showed no relation with any measure of performance or personality (Fig. 3).

3. Discussion

The goal of the present study was to further investigate the relation between error-related ERP components and individual differences in reward and punishment sensitivity. We found that subjects scoring high on the BIS scale displayed larger ERN/Ne amplitudes, while subjects scoring high on the BAS scale (especially on fun seeking) displayed larger Pe amplitudes. No correlations were found between BIS and Pe amplitude or between BAS and ERN/Ne amplitude. Moreover, BIS was shown to be positively related to neuroticism and harm avoidance, and BAS was found to be positively related to extraversion and novelty seeking. Importantly, all the personality traits associated with punishment sensitivity (BIS, neuroticism and harm avoidance) and those associated with reward seeking (BAS fun seeking, extraversion and novelty seeking) were related in the same way to ERN/Ne and Pe amplitudes, respectively. These results are consistent with a number of previous studies demonstrating a relationship between negative affectivity/punishment sensitivity (e.g. neuroticism) and ERN/Ne amplitude (Tucker et al., 1999; Luu et al., 2000; Gehring et al., 2000; Hajcak and Simons, 2002; Hajcak et al., 2003a, 2004; Pailing and Segalowitz, 2004). However, to our knowledge, we are the first to demonstrate a relationship between BAS/reward seeking and Pe amplitude.

In a recent study (Amodio et al., 2005), BIS scores were shown to be correlated with larger No-go N2 amplitudes. This stimulus-locked ERP component is associated with pre-response conflict monitoring and response inhibition. As the detection of conflict signals increased probability of committing errors (errors are more frequent on high conflict trials) and the N2 and ERN/Ne are generated in both overlapping and distinct ACC regions (Mathalon et al., 2003), this result is consistent with the present results and the conception of BIS

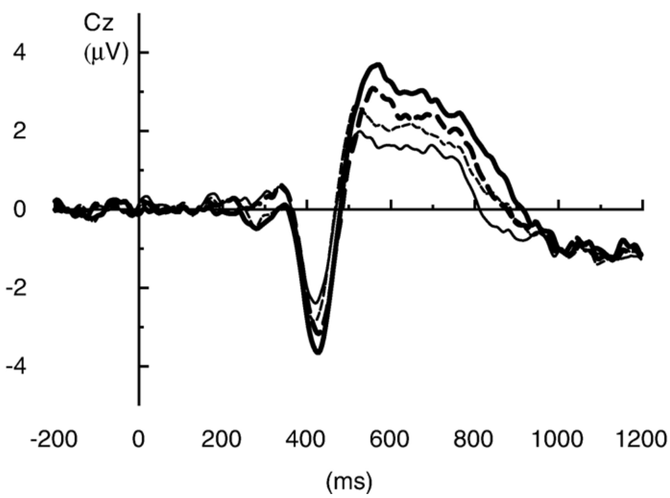

Fig. 3 – Difference waves (incongruent–congruent) of grand-averaged stimulus-locked ERPs at the Cz and Pz recording sites, for high BAS (*n* = 11), low BAS (*n* = 13), high BIS (*n* = 13) and low BIS (*n* = 11) subjects. Groups were formed using a median split procedure (only for illustrative purposes). There was no correlation between BIS/BAS scores and N2 or P3 amplitude.

as important for detecting and processing threat (the impending risk of making errors) and punishment (committing errors). However, in the present study using a flanker task, we did not find an association between BIS scores and N2 amplitudes.

Another stimulus-locked ERP component, the P3, correlated with the Pe, but not with BAS scores or post-error slowing. It has been suggested that the Pe may constitute a P3 associated with the motivational significance of the error (Leuthold and Sommer, 1999). Here, we show that, although Pe amplitude was related to P3 amplitude, the correlation between Pe and BAS and the correlation between Pe and post-error slowing do not result from a correlation between P3 amplitude and these measures.

Interestingly, Gray and Braver (2002) found in an fMRI study that high BIS individuals tended to show greater caudal ACC activity, while high BAS individuals tended to show low caudal ACC activity. In addition, they also observed that, in the rostral/ventral part of the ACC, activation was significantly related to BIS/BAS personality. These authors interpret the activity in the caudal part of the ACC (which is part of the cognitive subdivision of the ACC; Bush et al., 2000) in terms of high BIS individuals showing a bias towards 'reactive control', while the activation in the rostral part of the ACC (the emotional subdivision of the ACC) is interpreted in terms of high BIS individuals being more sensitive to negative outcomes/punishment, which may contribute to their greater tendency towards worry and anxiety. Conversely, these authors propose that the BAS trait is correlated with a bias towards 'proactive control' (Braver et al., in press). The difference between reactive and proactive control is that proactive control involves actively preparing the cognitive system to respond efficiently to external events by biasing processing in accordance with current goals, while reactive control involves a more passive strategy of engaging control only when an imperative event has already occurred and has to be acted upon (Braver et al., in press). Proactive control, as described by Braver and colleagues, seems similar to the concept of approach motivation that the BAS scale intends to measure. Because of the involvement of the ACC in the evaluation of performance and the generation of the ERN/Ne, one would expect larger ERN/Ne amplitudes when reactive control is dominant. Consistent with this, we observed a larger ERN/Ne in high BIS individuals.

Although an interpretation of the Pe amplitude in terms of proactive control is less straightforward, our finding that subjects scoring high on BAS displayed larger Pe amplitudes and that the Pe amplitude was positively correlated with post-error slowing (see also Nieuwenhuis et al., 2001; Hajcak et al., 2003b) does suggest that the Pe is related to proactive behavior. While the ERN/Ne may reflect a motivation towards punishment avoidance (as measured by the BIS), the Pe may reflect a post-error process of engaging in proactive control to prevent future errors and maximize future rewards (i.e. approach motivation/reward seeking, as measured by the BAS). See Mathewson et al. (2005) for a similar conclusion regarding the interpretation of ERN/Ne and Pe amplitudes. Interestingly, Hermann et al. (2004) localized the Pe to Brodman area 24 within the ACC, an area that is part of a neural system associated with reward processing (Bush et al., 2002; Knutson et al., 2000).

Gray (1987, 1989) suggests that the first response to prediction error and punishment is mediated by a cholinergic BIS system. Since this system then inhibits the dopaminergic BAS system, this model is consistent with the reinforcement learning theory of the ERN/Ne by Holroyd and Coles (2002). These authors propose that a phasic decrease in activity of mesencephalic dopaminergic neurons following the commission of an error disinhibits the apical dendrites of motor neurons in the ACC, producing the ERN/Ne (Holroyd and Yeung, 2003). However, in line with Gray, our results stress the importance of a non-dopaminergic (BIS) system that so far has received hardly any attention in theories on the ERN/Ne (for an exception see Luu and Tucker, 2001). At the level of the nucleus accumbens, which provides dopaminergic input to the ACC, high synaptic acetylcholine and low dopamine are correlated with an aversive state, i.e. punishment, and inhibition of behavior (Mark et al., 1995). For a discussion of similar findings, see Hoebel et al. (1999).

Scores on BAS fun seeking correlated negatively with harm avoidance, and also tended to correlate negatively with BIS scores. Furthermore, in contrast to BIS and neuroticism, harm avoidance tended to relate to smaller Pe amplitudes. It seems that compared to BIS, neuroticism and BAS fun seeking, harm avoidance may be a slightly rotated construct that may partly measure individual differences in inhibition of the BAS by the BIS. Different sensitivities of different measures and slight rotations of different constructs may explain on the one hand findings like the negative association of trait negative affectivity with Pe amplitude in a study by Hajcak et al. (2004) and our similar finding with harm avoidance, and on the other hand the absence of such a relationship of BIS and neuroticism with Pe in the present study. It is important to notice that the only measure tapping on punishment sensitivity that correlated with Pe amplitude is the one that correlated significantly negatively with BAS fun seeking.

Elsewhere, we argue and present evidence that ERN/Ne amplitude does not relate to negative affectivity per se, but rather to task engagement (Tops et al., in press). We argued that concerns over social evaluation increase task engagement and hence relate to larger ERN/Ne amplitudes. Because of the heightened concern over evaluation that is typical for subjects scoring high on negative affectivity (i.e., higher punishment sensitivity), committing errors is highly aversive for these subjects. The increased ERN/Ne displayed by these subjects may reflect the increased 'value' of errors for these subjects (see Hajcak et al., 2005 for a similar reasoning), which would result in higher task engagement.

The present findings are consistent with this suggestion: measures of negative affectivity and punishment sensitivity relate to concerns over negative social evaluation. In fact, in modern life, the most prevalent and salient forms of punishment and non-reward are probably of a social nature, and negative social evaluation is probably one of the most potent ones (e.g. leading to high cortisol responses; Dickerson and Kemeny, 2004). Indeed, several items of the BIS measure concerns about negative social evaluation. In terms of engagement, BIS and ERN/Ne amplitude may relate to negatively motivated, reactive engagement: vigilance and avoidance of punishment; BAS and Pe amplitude may relate to positively motivated, proactive engagement: reward and effort allocation, thought to be related to dopaminergic activity at the level of the ACC (Walton et al., 2003). We suggest that these differently motivated forms of engagement enlist ACC attentional systems at different points in time within a trial during task performance.

4. Experimental procedures

4.1. Subjects

Twenty-four healthy participants (all females), between 18 and 26 (M = 20, SD = 3.4) years of age, were recruited from the university population. They were paid for their participation and had normal or corrected-to-normal vision. Three participants described themselves as being left handed. None of the subjects used prescription medication. Written informed consent was obtained prior to the study.

4.2. Measures

4.2.1. Questionnaires

The participants completed the following questionnaires:

BIS/BAS-scale. Gray (1987, 1989) proposed that two general motivational systems underlie behavior and affect: a behavioral inhibition system (BIS) and a behavioral activation system (BAS). We used the 24-item BIS/BAS-scale created by Carver and White (1994) to assess dispositional BIS and BAS sensitivities. The BAS dimension (BAS-tot) contains the following subscales: BAS reward responsiveness (BAS-rew), BAS-drive, and BAS fun seeking (BAS-fun; Carver and White, 1994; Franken et al., 2005).

Five Factor Personality Inventory (FFPI). We used the 100-item FFPI to assess Extraversion, Agreeableness, Conscientiousness, Neuroticism and Autonomy (Hendriks et al., 1999).

Temperament and Character Inventory (TCI). This questionnaire measures four temperament and three character dimensions of Cloninger's psychological model of personality. We used only the four temperament dimensions of the TCI, which have been related to activity of specific neurotransmitter systems. The dimensions of temperament consist of a total of 60 items, assessing novelty seeking, harm avoidance, reward dependency, and persistence (Cloninger et al., 1994; De la Rie et al., 1998).

4.2.2. Task

We used a version of the Eriksen Flanker Task (Eriksen and Eriksen, 1974). The stimuli used for targets and flankers were the letters H and S. On each trial a five-letter string was presented. The central letter was the target, the remaining letters the flankers. During the entire task, a fixation mark was displayed above the target letter location. On congruent trials, the target letter was identical to the flankers (SSSSS of HHHHH); on incongruent trials, the target letter differed from the flankers (SSHSS or HHSHH).

The stimuli were presented on a 17″ PC monitor. The letters were white against a black background and each letter had a height and width of 0.24° visual angle. Eriksen and Eriksen (1974) showed that reaction times and error rates were highest when letters were presented close together (0.06° visual angle). To increase error-rates, we presented letters 0.05° apart. The complete five-letter string had a width of 1.43° visual angle. The fixation cross was presented 0.14° above the central target letter location.

Trials were presented in random order. 40% of the trials consisted of incongruent stimuli and 60% consisted of congruent stimuli. Flankers were presented 100 ms prior tot target onset to maximize the expected flanker compatibility effect (Kopp et al., 1996). Target and flankers disappeared simultaneously at the moment a response was made. In case no response was given; targets and flankers disappeared after 1200 ms had passed. The inter-trial interval was variable, dependent on the response, so that each trial had a total duration of 3 s. Participants received six blocks of 400 trials each. Each block of 400 trials had a total duration of 20 min. Sessions were this long because the study was also designed to investigate the effects of fatigue on error processing. However, results presented here were unrelated to time on task, so data will be presented here without reference to different blocks.

4.3. *Procedure*

Subjects were instructed to abstain from alcohol 24 h before the experiment and from caffeine containing substances 12 h before the experiment. After arrival at the laboratory at 1200 h, the subjects surrendered their watches. They had no knowledge of the length of the session other than that it would not last beyond 1800 h. Before the start of the experiment, subjects were given written task instructions and they filled out the questionnaires. Hereafter, they were trained in performing the task, for 15 min. Following the application of the electrodes, subjects were seated in a dimly lit, sound-attenuated, electrically shielded room at 1.20 m from a 17″ PC monitor. Their index fingers rested on touch-sensitive response boxes. Subjects were instructed to lift their finger from the response button as quickly as possible when a target was presented, maintaining a high level of accuracy. The experiment lasted for two hours.

4.4. *Electrophysiological recording and data reduction*

The electroencephalogram (EEG) was recorded using 4 Sn Electrodes attached to an electro cap (Electro-Cap International), from positions Fz, FCz, Cz and Pz. All electrodes were referenced to linked earlobes. The electro-oculogram (EOG) was recorded bipolarily from the outer canthi of both eyes and above and below the left eye, using Sn electrodes. Electrode impedance was kept below 5 kΩ. EEG and EOG were amplified with a 10 s time constant and a 200 Hz low pass filter, sampled at 1000 Hz, digitally low pass filtered with a cut-off frequency of 70 Hz, and online reduced to a sample frequency of 250 Hz.

All ERP analyses were performed using the Brain Vision Analyser software (Brain Products). ERPs were averaged offline. The data were further filtered with a 0.53 Hz high-pass filter and a slope of 12 dB/oct and a 40 Hz low-pass filter with a slope of 48 dB/oct. Out of range artifacts were rejected and eye movement artifacts were corrected using the Gratton et al. (1983) method. A baseline voltage averaged over the 200 ms interval preceding the event of interest was subtracted from the averages.

4.5. *Data analysis*

4.5.1. *Performance*

For the different stimulus conditions, mean reaction times (RTs) were calculated. Correct reactions occurring within a 150–1000 ms interval after stimulus presentation were considered as hits. The percentage of errors and misses were also determined. Because misses were very rare, we will focus here on hits and errors. To investigate strategic performance changes after error detection, we also analyzed RTs on trials following an error or a correct response (i.e. post-error slowing; Rabbitt, 1966). As we found no difference in post-error slowing for congruent and incongruent trials, the reported data on post-error slowing include both incompatible and compatible $n-1$ trials.

4.5.2. *ERPs*

For error trials, mean ERN/Ne and Pe amplitudes were calculated at Cz, where visual inspection showed that these components were maximal. We quantified the ERN/Ne as the most negative peak occurring in the 100 ms following the response. For statistical analyses, we used the average amplitude of the ERN/Ne in a time window starting 12 ms before the peak until 12 ms after the peak. The averaging epoch for the Pe was from 164 ms to 360 ms post-response. The same epochs were used for our analysis of the response-locked ERPs on correct trials.

In addition to these response-locked ERP components, we measured the amplitudes of the stimulus-locked N2 and P3 ERP component. While mean N2 amplitude was calculated at Cz, P3 amplitude was measured at Pz, where this component had its maximum. The N2 was quantified as the average amplitude in the 400–440 ms post-stimulus time interval. The averaging epoch for the P3 was from 400 ms to 600 ms post-stimulus.

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REFERENCES

Amodio, D.M., Master, S.L., Yee, C.M., Taylor, S.E., 2005. Clarifying the neurocognitive substrates of the Behavioral Inhibition System: BIS and the No-Go N2. Psychophysiology 42 (Suppl. 1), S31.

Boksem, M.A.S., Meijman, T.F., Lorist, M.M., 2006. Mental fatigue, motivation and action monitoring. Biol. Psychol. 42 (2), 123–132.

Braver, T.S., Gray, J.R., Burgess, G.C., in press. Explaining the many varieties of working memory variation: dual mechanisms of cognitive control, In Variation in Working Memory, A.R.A. Conway, C. Jarrold, M. Kane, A. Miyake, J.N. Towse, Eds. Oxford Univ. Press, New York.

Bush, G., Luu, P., Posner, M.I., 2000. Cognitive and emotional influences in anterior cingulate cortex. Trends Cogn. Sci. 4, 215–222.

Bush, G., Vogt, B.A., Holmes, J., Dale, A.M., Greve, D., Jenike, M.A., Rosen, B.R., 2002. Dorsal anterior cingulate cortex: a role in reward-based decision making. Proc. Natl. Acad. Sci. 99 (1), 523–528.

Carver, C.S., White, T.L., 1994. Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: the BIS/BAS scales. J. Pers. Soc. Psychol. 67 (2), 319–333.

Cloninger, C.R., Pryzbeck, T.R., Svrakic, D.M., Wetzel, R.D., 1994. The Temperament and Character Inventory (TCI): A Guide to

its Development and Use. Centre for Psychobiology of Personality, St. Louis Missouri.
De Bruijn, E.R.A., Hulstijn, W., Verkes, R.J., Ruigt, G.S.F., Sabbe, B.G.C., 2004. Drug-induced stimulation and suppression of action monitoring in healthy volunteers. Psychopharmacology 177, 151–160.
De la Rie, S.M., Duijsens, I.J., Cloninger, C.R., 1998. Temperament, character, and personality disorders. J. Pers. Disord. 12 (4), 362–372.
Dehaene, S., Posner, M.I., Tucker, D.M., 1994. Localization of a neural system for error detection and compensation. Psychol. Sci. 5, 303–305.
Depue, R.A., Collins, P.F., 1999. Neurobiology of the structure of personality: dopamine, facilitation of incentive motivation, and extraversion. Behav. Brain Sci. 22, 491–569.
Dickerson, S.S., Kemeny, M.E., 2004. Acute stressors and cortisol responses: a theoretical integration and synthesis of laboratory research. Psychol. Bull. 130, 355–391.
Dikman, Z.V., Allen, J.J.B., 2000. Error monitoring during reward and avoidance learning in high- and low-socialized individuals. Psychophysiology 37, 43–54.
Eriksen, B.A., Eriksen, C.W., 1974. Effects of noise letters upon the identification of target letters in visual search. Percept. Psychophys. 16, 142–149.
Falkenstein, M., Hohnsbein, J., Hoormann, J., Blanke, L., 1990. Effects of errors in choice reaction tasks on the ERP under focused and divided attention. In: Brunia, C.H.M., Gaillard, A.W. K., Kok, A. (Eds.), Psychophysiological Brain Research. Tilburg Univ. Press, Tilburg, pp. 192–195.
Falkenstein, M., Hoormann, J., Christ, S., 2000. ERP components on reaction errors and their functional significance: a tutorial. Biol. Psychol. 51 (2–3), 87–107.
Falkenstein, M., Hielscher, H., Dziobek, I., Schwarzenau, P., Hoormann, J., Sundermann, B., Hohnsbein, J., 2001. Action monitoring, error detection and the basal ganglia: an ERP study. NeuroReport 12, 157–161.
Falkenstein, M., Willemssen, R., Hohnsbein, J., Hielscher, H., 2005. Error processing in Parkinson's disease. J. Psychophysiol. 19 (4), 305–310.
Franken, I.H.A., Muris, P., Rassin, E., 2005. Psychometric properties of the Dutch BIS/BAS scales. J. Psychopathol. Behav. Assess. 27 (1), 25–30.
Gehring, W.J., Willoughby, A.R., 2002. The medial frontal cortex and the rapid processing of monetary gains and losses. Science 295, 2279–2282.
Gehring, W.J., Coles, M.G.H., Meyer, D.E., Donchin, E., 1990. The error-related negativity: an event-related brain potential accompanying errors. Psychophysiology 27, S34.
Gehring, W.J., Himle, J., Nisenson, L.G., 2000. Action-monitoring dysfunction in obsessive–compulsive disorder. Psychol. Sci. 11 (1), 1–6.
Gratton, G., Coles, M.G., Donchin, E., 1983. A new method for off-line removal of ocular artifact. Electroencephalogr. Clin. Neurophysiol. 55, 468–484.
Gray, J.A., 1987. The neuropsychology of emotion and personality. In: Stahl, S.M., Iverson, S.D., Goodman, E.C. (Eds.), Cognitive Neurochemistry. Oxford Univ. Press, Oxford, pp. 171–190.
Gray, J.A., 1989. Fundamental systems of emotion in the mammalian brain. In: Palermo, D.S. (Ed.), Coping with Uncertainty: Behavioral and Developmental Perspectives. Lawrence Erlbaum, Hillsdale, NJ, pp. 173–195.
Gray, J.R., Braver, T.S., 2002. Personality predicts working-memory-related activation in the caudal anterior cingulate cortex. Cogn. Affect Behav. Neurosci. 2 (1), 64–75.
Hajcak, G., Simons, R.F., 2002. Error-related brain activity in obsessive–compulsive undergraduates. Psychiatry Res. 110 (1), 63–72.
Hajcak, G., McDonald, N., Simons, R.F., 2003a. Anxiety and error-related brain activity. Biol. Psychol. 64, 77–90.
Hajcak, G., McDonald, N., Simons, R.F., 2003b. To err is autonomic: error-related brain potentials, ANS activity, and post-error compensatory behavior. Psychophysiology 40 (6), 895–903.
Hajcak, G., McDonald, N., Simons, R.F., 2004. Error-related psychophysiology and negative affect. Brain Cogn. 56, 189–197.
Hajcak, G., Moser, J.S., Yeung, N., Simons, R.F., 2005. On the ERN and the significance of errors. Psychophysiology 42 (2), 151–160.
Hendriks, A.A.J., Hofstee, W.K.B., De Raad, B., 1999. Handleiding bij de five-factor personality inventory (FFPI); manual to the five-factor personality inventory (FFPI). Swets Test Publishers, Lisse.
Hermann, M.J., Römmler, J., Ehlis, A.C., Heidrich, A., Fallgatter, A.J., 2004. Source localization (LORETA) of the error-related-negativity (ERN/Ne) and positivity (Pe). Cogn. Brain Res. 20, 294–299.
Hoebel, B.G., Rada, P.V., Mark, G.P., Pothos, E.N., 1999. Neural systems for reinforcement and inhibition of behavior: relevance to eating, addiction, and depression. In: Kahneman, D., Diener, E., Schwarz, N. (Eds.), Well-being: The Foundations of Hedonic Psychology. Russell Sage Foundations, New York.
Holroyd, C.B., Coles, M.G.H., 2002. The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity. Psychol. Rev. 109 (4), 679–709.
Holroyd, C.B., Yeung, N., 2003. Alcohol and error processing. Trends Neurosci. 26, 402–404.
Holroyd, C.B., Praamstra, P., Plat, E., Coles, M.G., 2002. Spared error-related potentials in mild to moderate Parkinson's disease. Neuropsychologia 40, 2116–2124.
Holroyd, C.B., Larsen, J.T., Cohen, J.D., 2004. Context dependence of the event-related brain potential associated with reward and punishment. Psychophysiology 41, 245–253.
Knutson, B., Westdorp, A., Kaiser, E., Hommer, D., 2000. FMRI visualization of brain activity during a monetary incentive delay task. NeuroImage 12, 20–27.
Kopp, B., Rist, F., Mattler, U., 1996. N200 in the flanker task as a neurobehavioral tool for investigating executive control. Psychophysiology 33, 282–294.
Leuthold, H., Sommer, W., 1999. ERP correlates of error processing in spatial S-R compatibility tasks. Clin. Neurophysiol. 110, 342–357.
Luu, P., Tucker, D.M., 2001. Regulating action: alternating activation of midline frontal and motor cortical networks. Clin. Neurophysiol. 112, 1295–1306.
Luu, P., Collins, P., Tucker, D.M., 2000. Mood, personality, and self-monitoring: negative affect and emotionality in relation to frontal lobe mechanisms of error monitoring. J. Exp. Psychol. Gen. 129, 43–60.
Mark, G.P., Weinberg, J.B., Rada, P.V., Hoebel, B.G., 1995. Extracellular acetylcholine is increased in the nucleus accumbens following the presentation of an aversively conditioned taste stimulus. Brain Res. 688, 184–188.
Mathalon, D.H., Whitfield, S.L., Ford, J.M., 2003. Anatomy of an error: ERP and fMRI. Biol. Psychol. 64, 119–141.
Mathewson, K.J., Dywan, J., Segalowitz, S.J., 2005. Brain bases of error-related ERPs as influenced by age and task. Biol. Psychol. 70, 88–104.
Nieuwenhuis, S., Ridderinkhof, K.R., Blom, J., Band, G.P.H., Kok, A., 2001. Error-related brain potentials are differentially related to awareness of response errors: evidence from an antisaccade task. Psychophysiology 38, 752–760.
Overbeek, T.J.M., Nieuwenhuis, S., Ridderinkhof, K.R., 2005. Multiple processes in error-monitoring: on the functional significance of the Pe vis-à-vis the ERN/Ne. J. Psychophysiol. 19 (4), 319–329.
Pailing, P.E., Segalowitz, S.J., 2004. The error-related negativity as a

state and trait measure: motivation, personality, and ERPs in response to errors. Psychophysiology 41 (1), 84–95.
Rabbitt, P.M.A., 1966. Errors and error correction in choice reaction tasks. J. Exp. Psychol. 71, 264–272.
Ridderinkhof, K.R., DeVlugt, Y., Bramlage, A., Spaan, M., Elton, M., Snel, J., 2002. Alcohol consumption impairs detection of performance errors in mediofrontal cortex. Science 298, 2209–2211.
Ridderinkhof, K.R., Ullsperger, M., Crone, E.A., Nieuwenhuis, S., 2004. The role of the medial frontal cortex in cognitive control. Science 306, 443–447.
Savitz, J.B., Ramesar, R.S., 2004. Genetic variants implicated in personality: a review of the more promising candidates. Am. J. Med. Genet. Pt. B 131B, 20–32.
Schultz, W., 2002. Getting formal with dopamine and reward. Neuron 36, 241–263.
Tieges, Z., Ridderinkhof, K.R., Snel, J., 2004. Caffeine strengthens action monitoring: evidence from the error-related negativity. Cogn. Brain Res. 21 (1), 87–93.
Tops, M., Boksem, M.A.S., Wester, A.E., Lorist, M.M., Meijman, T.F. Task engagement and the relationships between the error-related negativity, agreeableness, behavioral shame proneness and cortisol. Psychoneuroendocrinology, in press.
Tucker, D.M., Hartry-Speiser, A., McDougal, L., Luu, P., deGrandpre, D., 1999. Mood and spatial memory: emotion and right hemisphere contribution to spatial cognition. Biol. Psychol. 50, 103–125.
Tucker, D.M., Luu, P., Frishkoff, G., Quiring, J., Poulsen, C., 2003. Frontolimbic response to negative feedback in clinical depression. J. Abnorm. Psychol. 112 (4), 667–678.
Ullsperger, M., Von Cramon, D.Y., 2003. Error monitoring using external feedback: specific roles of the habenular complex, the reward system, and the cingulate motor area revealed by functional resonance imaging. J. Neurosci. 23 (4), 4308–4314.
Vidal, F., Hasbroucq, T., Grapperon, J., 2000. Is the error negativity specific to errors? Biol. Psychol. (2–3), 109–128.
Walton, M.E., Bannerman, D.M., Alterescu, K., Rushworth, M.F.S., 2003. Functional specialization within medial frontal cortex of the anterior cingulate for evaluating effort-related decisions. J. Neurosci. 23 (16), 6475–6479.
Watson, D., Wiese, D., Vaidya, J., Tellegen, A., 1999. The two general activation systems of affect: structural findings, evolutionary considerations, and psychobiological evidence. J. Pers. Soc. Psychol. 76 (5), 820–838.
Wijers, A.A., Boksem, M.A.S., 2005. Selective attention and error processing in an illusory conjunction task: an event-related brain potential study. J. Psychophysiol. 19 (3), 216–231.