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Sensitivity to punishment and reward omission: Evidence from error-related ERP components

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ABSTRACT

In a recent experiment [Boksem, M.A.S., Tops, M., Wester, A.E., Meijman, T.F., Lorist, M.M., 2006. Error-related ERP components and individual differences in punishment and reward sensitivity. Brain Research 1101, 92–101], we showed that error-related ERP components were related to punishment and reward sensitivity. The present study was conducted to further evaluate the relationship between punishment/reward sensitivity and these ERP components. Therefore, we scored our subjects on the BIS/BAS measures of punishment and reward sensitivity. Then, subjects performed one of two versions of a Flanker task: in one, they were financially punished for committing errors; in the other, they were financially rewarded for correct performance. Analyses of ERN/Ne amplitudes indicated significant interactions between personality measures of punishment (BIS) and reward (BAS) and actual punishment and reward, while analyses of Pe amplitudes showed significant interactions between personality measures of reward sensitivity and actual reward. We suggest that ERN/Ne amplitude is related to concerns over mistakes and depends on the level of aversion experienced by individual subjects for making these mistakes. Subjects that are highly sensitive to punishment are strongly motivated or engaged in avoiding punishment, while subjects sensitive to rewards are motivated to obtain rewards and therefore show high task engagement when rewards may be earned. The error-related ERP components appear to track this level of engagement in task performance.

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1. Introduction

The ability to seek out rewards is essential for survival: to reach its goals (stay alive), any organism should try to obtain rewards (e.g. food) and at the same time should try to avoid aversive consequences (e.g. injury or death). The approach of potential rewards and the avoidance of potential punishment are fundamental to all goal directed behaviour: for something to constitute a goal, it has to be associated with a high value of predicted reward and low potential risk. From an evolutionary perspective, it is therefore not surprising that present day organisms are capable of estimating the expected reward value of various options and adjust these expectations continuously to the outcome of their choices.

In the past decades, reinforcement learning (RL) theory has been developed to describe how organisms are able to acquire these reward expectancies and how the outcomes of choices can update these expectations (Barto and Sutton, 1997). In a typical RL model, the expected outcome of every decision option starts out with a certain value. Behavioural options that have a high expected value are preferred over options with lower expected values. Whenever the expected outcome differs from the actual outcome, this is coded as a reward prediction error. This error signal is then used to update the expected reward value of the chosen behavioural option so that it better reflects the observed reward value.

The work of Schultz (Schultz et al., 1997; Schultz, 2002, 2004) suggests that these reward prediction errors are encoded in midbrain dopamine (DA) neurons. These neurons have been shown to respond with increased activity when outcomes are better than expected, while decreases in activity occur when outcomes are not as good as expected. Holroyd and Coles (2002) suggested that this negative RL error is conveyed to the anterior cingulate cortex (ACC), where it produces an error signal that can be measured as a negative event related potential (ERP) on the scalp, called the error-related negativity (ERN) or error negativity (Ne).

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Observed at fronto-central recording sites (FCz, Cz), the ERN/Ne consists of a large negative shift in the response-locked ERP occurring within 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 purely 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).

Recently, we showed that individual differences in sensitivity to punishment are reflected in the ERN/Ne (Boksem et al., 2006). In that study, we measured punishment and reward sensitivity using the BIS/BAS scale developed by Carver and White (1994). This scale is derived from the theory postulated by Gray (1987, 1989) and proposes two interacting motivational systems: the behavioural approach system (BAS) and the behavioural inhibition system (BIS). According to Gray, the BIS is sensitive to signals of punishment and inhibits behaviour that may lead to aversive or harmful outcomes. In contrast, the BAS is proposed to be sensitive to positive signals of reward. In addition, these two motivational systems are proposed to depend on separate, but interacting neural circuits: the BIS comprises cholinergic projections that inhibit dopaminergic behavioural approach systems (i.e. BAS; Gray, 1989). The BIS organizes responses to conditioned signals of punishment and its main effects are inhibition of ongoing behaviour by avoiding punishment. According to Gray, the most likely sites of interaction between the behavioural inhibition and approach systems lie in the ventral striatum and lateral septal area. Because of its involvement in RL, the ventral striatum is an ideal site at which the BIS could inhibit striatal output destined to facilitate motor behaviour aimed at the attainment of reward or non-punishment. Indeed, 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).

We found that subjects scoring high on BIS displayed larger ERN/Ne amplitudes compared to subjects scoring low on BIS (Boksem et al., 2006). As already mentioned, 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 RL theory of the ERN/Ne by Holroyd and Coles (2002), that proposes a phasic decrease in activity of mesencephalic DA neurons following the commission of an error that 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 stressed the importance of a non-dopaminergic (BIS) system in reward prediction errors that so far has received hardly any attention in theories on the ERN/Ne (for an exception see Luu and Tucker, 2001).

A possible reason for this may be that in the literature on RL and the ERN/Ne, an explicit distinction between reward omission and actual punishment has not been made. This is a pity, because it is by no means clear that in humans, these two instances of outcome over-prediction are comparable or depend on the same neural substrate: receiving no reward when a reward was expected may not be the same as receiving punishment, when no punishment was expected. The expected value of an outcome (Machina, 1987) may be conceived as ranging from positive (reward) to zero (no reward or punishment) to negative (punishment). Although both receiving nothing when the expected value was positive and receiving punishment when the expected value was zero or positive constitute a negative outcome prediction error, separate neural processes may be involved.

The human ventral striatum indeed shows a strong outcome-related response when a reward occurs unexpectedly or an activity decrease when an expected reward is omitted (Pagnoni et al., 2002; McClure et al., 2003; O'Doherty et al., 2003, 2004; Ramnani et al., 2004), resembling a prediction error signal similar to the dopaminergic midbrain signal in the primate (Schultz and Dickinson, 2000). However, under conditions of punishment, prediction errors are primarily associated with increased activations of amygdala and/or lateral orbitofrontal cortex (Breiter et al., 2001; Kahn et al., 2002; Glascher et al., 2005; Seymour et al., 2005). This is in accordance with a growing number of studies that show increased activation in lateral orbitofrontal cortex, insula and also ACC when subjects evaluate their choices negatively because they lost money or were punished (O'Doherty et al., 2003; Ullsperger and von Cramon, 2003; Liu et al., 2007; Kuhnen and Knutson, 2005; Gottfried and Dolan, 2004; Yacubian et al., 2006).

A second error-related ERP component, the error positivity (Pe), 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). Although the functional significance of the Pe is far from clear, this component 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). In our previous study, we showed that Pe amplitude was positively correlated with BAS-scores (Boksem et al., 2006). We suggested that Pe amplitude may reflect proactive engagement after error commission, to prevent future errors and maximize future rewards (i.e. approach motivation/reward seeking, as measured by the BAS).

The present study was conducted to evaluate the respective contributions of a reward seeking system (BAS) and a punishment avoidance system (BIS) to error-related ERP components, under conditions of either punishment or reward omission. Therefore, we had our subjects fill out the BIS/BAS Scales (Carver and White, 1994), which are based on Gray (1987, 1989) biopsychological theory of personality. The BAS scale has three subscales: fun seeking (BAS-F), reward responsiveness (BAS-R) and drive (BAS-D). The BIS scale has no such subscales. Subjects performed a version of the Eriksen flanker task (Eriksen and Eriksen, 1974) under conditions in which they either lost money when they provided an erroneous response (punishment condition) or were rewarded for providing the correct response (and so were confronted with reward omission when they provided the incorrect response; reward omission condition). ERPs were recorded during task performance.

2. Experimental procedure

2.1. Subjects

Twenty-nine healthy participants (12 males), between 18 and 29 ($M = 21.8$, S.D. = 3.0) years of age, were recruited from the university population. They were paid for their participation and had normal or corrected-to-normal vision. Written informed consent was obtained prior to the study.

2.2. Measures

2.2.1. BIS/BAS-scale

Gray (1987, 1989) proposed that two general motivational systems underlie behaviour and affect: a behavioural inhibition system (BIS) and a behavioural activation system (BAS). We used the Dutch version (Franken et al., 2005) of the 24-item BIS/BAS-scale created by Carver and White (1994) to assess dispositional BIS and BAS sensitivities. The BAS dimension contains the following subscales: BAS reward responsiveness (BAS-R), BAS drive (BAS-D), and BAS fun seeking (BAS-F). The BIS has no subscales.

2.2.2. 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). Subjects were instructed to respond to the central target letter 'S' by pressing the button under their right index finger and to press the button under their left index finger when the central target letter was an 'H'. Responses occurring between 100 and 1000 ms after stimulus onset were registered as hits.

The stimuli were presented on a 17 in. PC monitor. The letters were white against a black background and each letter had a height and width of .24° visual angle. Eriksen and Eriksen (1974) showed that reaction times and error-rates are highest when letters were presented close together (.06° visual angle). To increase error-rates, we presented letters .05° apart. The complete five-letter string had a width of 1.43° visual angle. The fixation cross was presented .14° above the central target letter location.

Trials were presented in random order. Forty percent of the trials consisted of incongruent stimuli and 60% consisted of congruent stimuli. Flankers were presented 100 ms prior to target onset to maximize the expected flanker compatibility effect (Kopp et al., 1996). Target and flankers disappeared simultaneously at 500 ms after target onset. Following a 900 ms fixation interval, feedback was presented for 500 ms. The inter trial interval was 1000 ms, so that each trial had a total duration of 3 s. Participants completed 500 trials (25 min) in one of the two different conditions described below.

2.2.3. Reward

In this condition (n = 15), participants were told that for each correct answer they would be credited with a small amount of money, and that they could earn up to €10. It was stressed that errors would not result in loss of money. Feedback on the accuracy of the given response was provided .14° above fixation and could be 'Error' or 'Correct + €€' (in green). In addition, feedback could be 'Too Slow' when the subject was slower than his RT in the practice session plus one standard deviation. This was done to prevent subjects from slowing down to achieve greater accuracy.

2.2.4. Punishment

In the punishment condition (n = 14), participants were given €10 and were told that for each incorrect response, they would lose a small amount of money, and that they could lose up to €10. It was stressed that correct responses would not result in winning money. Feedback could be 'Error − €€' (in red) or 'Correct'. In addition, feedback could be 'Too slow' when the subject was slower than his RT in the practice condition plus one standard deviation.

In reality, no money was ever lost; all subjects received €5 extra payment.

2.3. Procedure

Before the start of the experiment, subjects were given written task instructions and they filled out the questionnaire. Then they were trained in performing the task, for 15 min (300 trials). 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 in. PC monitor. Their index fingers rested on response buttons. Subjects were instructed to press the response button as quickly as possible when a target was presented, maintaining a high level of accuracy. Upon completion, subjects were debriefed and paid.

2.4. Electrophysiological recording and data reduction

Electroencephalographic recordings (EEG) were made on 49 locations using active Ag–AgCl electrodes (Biosemi ActiveTwo, Amsterdam, Netherlands) mounted in an elastic cap. Horizontal EOGs were recorded from two electrodes placed at the outer canthi of both eyes. Vertical EOGs were recorded from electrodes on the infraorbital and supraorbital regions of the right eye placed in line with the pupil. The EEG and EOG signals were sampled at a rate of 256 Hz, and offline rereferenced to an averaged mastoid reference.

All ERP analyses were performed using the Brain Vision Analyser software (Brain Products). ERPs were averaged offline. The data were resampled at 100 Hz and further filtered with a .53 Hz high-pass filter and a slope of 48 dB/oct and a 40 Hz low-pass filter also with a slope of 48 dB/oct. Artefacts were rejected and eye movement artefacts were corrected, using the Gratton et al. (1983) method. A baseline voltage averaged over the 100 ms interval preceding events of interest was subtracted from the averages.

2.5. Data analysis

2.5.1. BIS/BAS-scale

The scores on the four dimensions of the BIS/BAS-scale were standardized, such that people who scored 0 on these measures had an average score on that measure.

2.5.2. Performance

For the different stimulus conditions, mean reaction times (RTs) were calculated for both correct and incorrect responses. The percentage of hits, errors and misses were also determined. Correct reactions occurring within a 100–1000 ms interval after stimulus presentation were considered as hits. 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; Rabbit, 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. Because of technical problems, post-error performance was not recorded for two subjects, so data on post-error performance will be reported for 27 subjects.

2.5.3. ERPs

For error trials, mean ERN/Ne and Pe amplitude were calculated at Cz, where in our previous study (Boksem et al., 2006) the interactions between BIS, BAS and these components were observed. We quantified the ERN/Ne as the most negative peak occurring in the 100 ms following the erroneous response. For statistical analyses, we used the average amplitude of these peaks in a time window starting 20 ms before the peak until 20 ms after the peak. Because the Pe is such a broadly distributed (in time) component, the Pe was quantified as the average amplitude between 150 and 350 ms after response. The same epochs were used for our analysis of the response-locked ERPs on correct trials.

Although feedback was presented following every trial, thus potentially allowing for looking at feedback-related ERPs, this feedback was not that informative because the task is so simple that subjects are well aware of making an error before feedback is presented. Feedback was only used to induce reward and punishment contexts. Therefore, feedback-related ERPs will not be presented.

2.5.4. Statistical analyses

To test for effects of BIS/BAS measures on the dependent variables of interest in the two conditions, we performed linear regression analyses with BIS/BAS scores, condition and the interaction BIS/BAS × condition as predictors. When significant interactions were found, we performed simple slope analyses to test whether this difference between conditions was present for subjects high (1S.D. above the mean) or low (1S.D. below the mean) on BIS/BAS.

3. Results

3.1. BIS/BAS-scale

BIS-scores were found to be negatively correlated with BAS-scores, $r = -.38$, $p < .05$. Of the BAS subscales, only BAS-F displayed this negative correlation with BIS, $r = -45$, $p < .05$ (Table 1).

Although subjects were randomly assigned to the two experimental conditions, a t-test showed that subjects in the punishment condition scored higher on BAS-F (M = 13.3, S.D. = 2.5) compared to the reward condition (M = 11.3, S.D. = 1.8), $t(27) = -2.53$, $p < .05$. No such difference between conditions was observed for the other measures.

3.2. Task performance

Independent samples t-tests revealed no difference in reaction times or accuracy (number of errors committed) between the two experimental conditions (reward omission and punishment), $t(27) = -.35/1.10$, n.s.

To further investigate task-related performance, reaction times and number of errors were calculated for the two trial types (congruent and incongruent) separately. For reaction times, repeated-measures GLM with experimental condition as a between-subject factor indicated a significant main effect for trial type, $F(1,27) = 146.06$, $p < .001$: subjects responded slower on incongruent trials (432 ms) compared to congruent trials (370 ms). This effect was not different for the two experimental conditions, $F(1,27) = .06$, n.s. The same analyses also revealed a main effect of trial type for accuracy, $F(1,27) = 76.98$, $p < .001$: the number of errors made on incongruent trials (9.8%) was substantially larger than the number of errors committed on congruent trials (1.4%). Again, we found no interaction with experimental condition, $F(1,27) = 2.25$, n.s.

To investigate whether there were differences in performance for subjects scoring high or low on the BIS/BAS measures, linear

Table 1
Correlations between BIS/BAS scores

	BAS	BAS-D	BAS-F	BAS-R
BIS	−.38*	−.23	−.45*	−.21
BAS		.86**	.85**	.68**
BAS-D			.61**	.47**
BAS-F				.38*

Note: For all correlations: $n = 29$.
* $p < .05$.
** $p < .01$.

regression analyses were performed on the performance data. Results showed a significant interaction between accuracy in the two conditions and scores on BAS-R, $R^2 = .37$, $\beta = -.80$, $t = 3.59$, $p < .005$ (Fig. 1). Simple slope analyses revealed that the difference in accuracy between conditions was significant for subjects scoring low on BAS-R (1S.D. below the mean, $\beta = .79$, $t = 3.48$, $p < .005$), while this difference failed to reach significance for subjects scoring high on BAS-R (1S.D. above the mean, $\beta = -.37$, $t = -1.63$, n.s.). Moreover, in the reward condition, accuracy was positively correlated with BAS-R, $r = .54$, $p < .05$, while in the punishment condition, accuracy was negatively correlated with BAS-R, $r = -.68$, $p < .01$. The interactions between accuracy in the two conditions and scores on BIS and BAS-F were non-significant, while these interactions with BAS and BAS-D were marginally significant, $R^2 = .17$, $\beta = -.65$, $t = -1.89$, $p = .07$; $R^2 = .15$, $\beta = -.53$, $t = -1.79$, $p = .09$, respectively.

No difference in post-error performance was observed between the two experimental conditions, $t(25) = -.98$, n.s. However, linear regression performed on post-error performance data showed a significant interaction between experimental condition and BIS-scores, $\beta = .87$, $t = 2.71$, $p < .05$ (Fig. 2). Simple slope analysis revealed that subjects scoring high on BIS (1S.D. above the mean), slowed down significantly more after committing an error in the punishment condition than in the reward condition, $\beta = .78$, $t = 2.95$, $p < .01$. This effect failed to reach significance for subjects scoring low on BIS, $\beta = -.32$, $t = -1.14$, n.s. In the punishment condition ($n = 12$), error slowing was positively correlated to BIS-scores, $r = .65$, $p < .05$, while in the reward condition ($n = 15$), BIS-scores tended to be negatively related to error slowing, but this failed to reach significance, $r = -.39$, n.s.

3.3. ERPs

A large negative deflection following an erroneous response (ERN/Ne) was observed that was significantly larger, $F(1,28) = 146.61$, $p < .001$, than the deflection following a correct response (CRN). One-way ANOVAs showed no difference in ERN/Ne, CRN or Pe amplitude between the two experimental conditions. We found no significant effects on response-locked ERPs on correct trials (CRN), so data on this component will not be considered further.

The mean number of error trials that went into the analyses was 25.2 (S.D. = 17.3) in the reward condition and 20.4 (S.D. = 10.9) in the punishment condition. The number of trials in the two conditions were not significantly different, $t(27) = .88$, n.s.

3.3.1. ERN/Ne

Linear regression showed an interaction between BIS-scores and experimental condition on ERN/Ne amplitudes, $R^2 = .31$, $\beta = .87$, $t = 2.68$, $p < .05$ (Fig. 3). Subjects scoring high on BIS displayed a larger ERN/Ne amplitude in the punishment condition than in the reward condition (although marginally significant, $\beta = .47$, $t = 1.92$, $p = .06$). Conversely, subjects scoring low on BIS displayed a larger ERN/Ne in the reward condition, compared to the punishment condition, $\beta = -.58$, $t = -2.11$, $p < .05$. In the punishment condition, BIS-scores were positively related to ERN/Ne amplitude, $r = .63$, $p < .05$, while no significant correlation between BIS-scores and ERN/Ne amplitude was observed in the reward omission condition.

Similar analyses revealed no interaction between BAS, BAS-D and BAS-F and experimental condition on ERN/Ne amplitude. BAS-R, however, was shown to interact with experimental condition, $R^2 = .22$, $\beta = -.60$, $t = -2.40$, $p < .05$ (Fig. 4). Subjects scoring high on BAS-R displayed a larger ERN/Ne in the reward omission condition than in the punishment condition, $\beta = -.52$, $t = -2.07$, $p < .05$, while ERN/Ne for subjects low on BAS-R did not differ significantly between conditions, $\beta = .34$, $t = 1.35$, n.s. In the punishment condition, high BAS-R scores tended to be associated with small ERN/Ne amplitudes, $r = -.51$, $p = .06$, while no such correlation was observed in the reward omission condition.

To make sure that ERN/Ne amplitude was not confounded by pre-response, stimulus-locked activity, we scored the positivity occurring prior to erroneous responses (possibly a direct correlate of the stimulus-locked P3) relative to a pre-stimulus baseline of 200 ms. We then tested whether this positivity in any way affected our results by including this pre-response positivity in our regression model and by calculating partial correlations. These analyses did not change the observed pattern of results in any way and will therefore not be considered further.

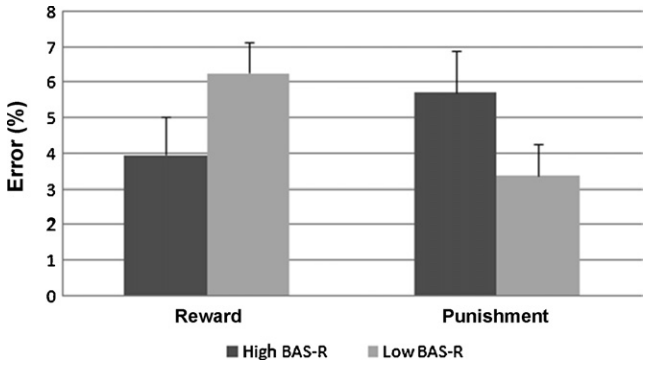

Fig. 1. Percentage of errors in the two experimental conditions, for subjects scoring high and low on BAS-R (groups formed by a median split procedure, only for illustrative purposes). In the reward omission condition, subjects that scored high on BAS-R committed less errors than subjects scoring low on this measure. Conversely, subjects scoring high on BAS-R in the punishment condition committed more errors that subjects that scored low on BAS-R. Bars represent standard errors.

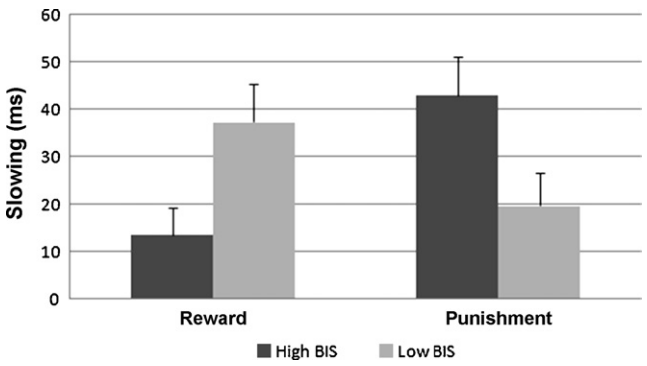

Fig. 2. Post-error slowing in the two experimental conditions, for subjects scoring high and low on BIS (groups formed by a median split procedure, only for illustrative purposes). Subjects that scored high on BIS slowed down more in the punishment condition, compared to the reward omission condition. Moreover, high scores on the BIS were related to increased slowing in the punishment condition. Bars represent standard errors.

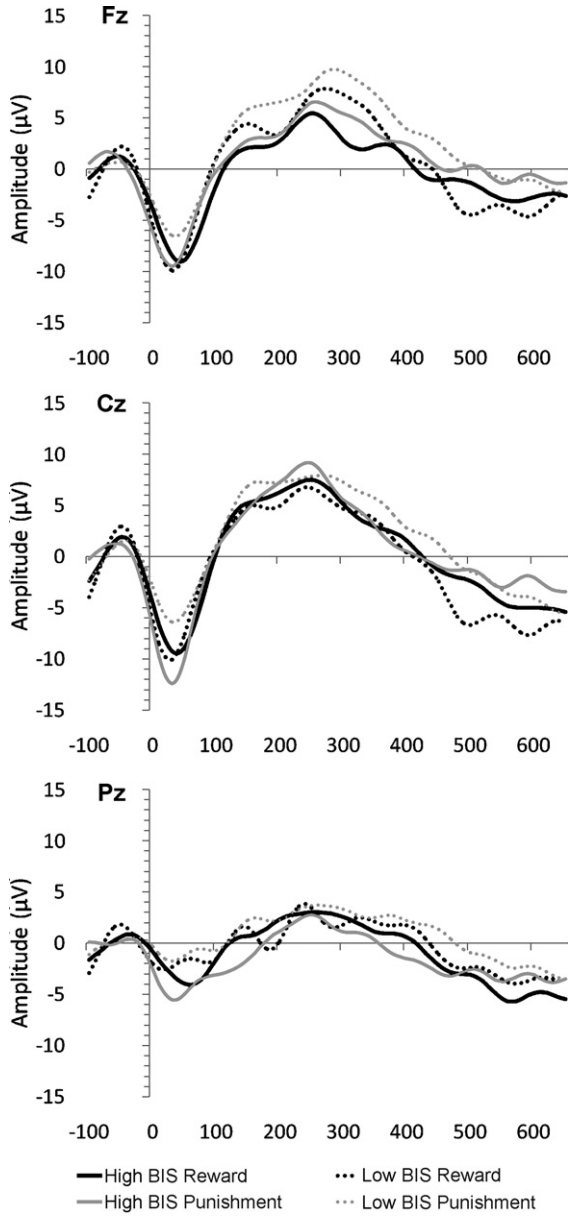

Fig. 3. Grand-averaged, response-locked ERPs at Cz for subjects high and low on BIS (groups formed by a median split procedure, only for illustrative purposes) in the two experimental conditions. High scores on the BIS were related to larger ERN/Ne amplitudes in the punishment condition. Moreover, ERN/Ne amplitudes were larger in the punishment condition, compared to the reward omission condition for subjects scoring high on BIS.

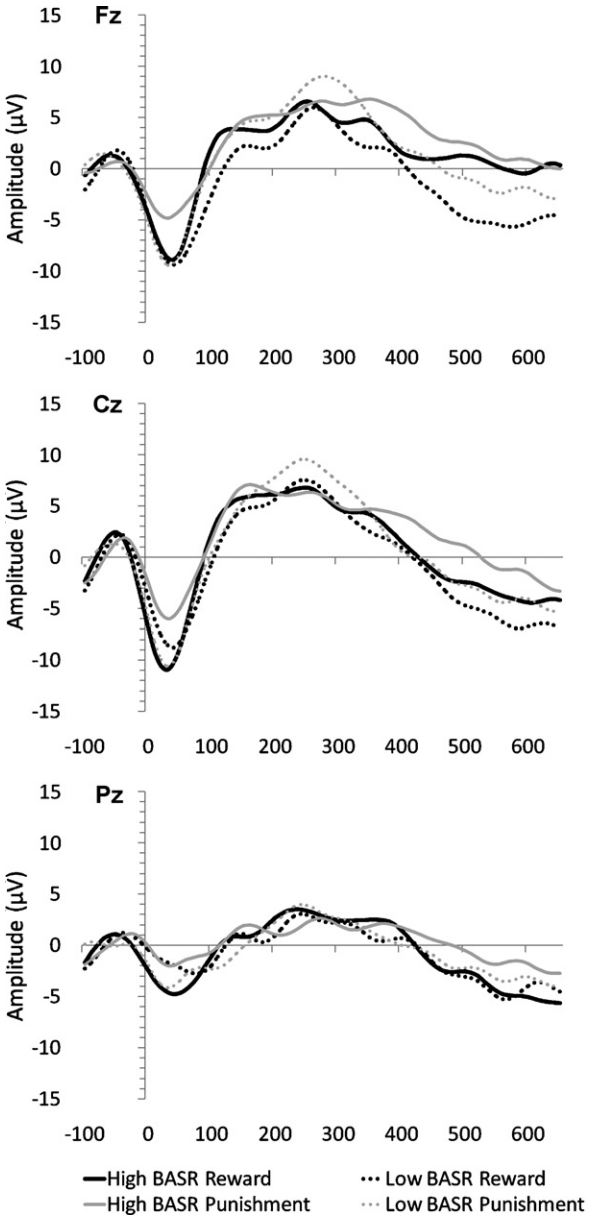

Fig. 4. Grand-averaged, response-locked ERPs at Cz for subjects high and low on BAS-R (groups formed by a median split procedure, only for illustrative purposes) in the two experimental conditions. High scores on the BAS-R subscale were related to larger ERN/Ne amplitudes in the reward omission condition, compared to the punishment condition.

3.3.2. Pe

Error positivity amplitudes were also submitted to a linear regression for analysis. Results indicate a significant interaction between BAS-D scores and experimental condition, $R^2 = .38$, $\beta = -.94$, $t = -3.69$, $p < .001$ (Fig. 5). Simple slope analyses revealed that subjects high on BAS-D tended to display a larger Pe in the reward omission condition compared to the punishment condition, $\beta = -.45$, $t = -1.93$, $p = .07$, while subjects low on BAS-D showed a larger Pe in the punishment condition, $\beta = .77$, $t = 3.42$, $p < .005$. Moreover, BAS-D scores were positively related to Pe amplitude in the reward condition, $r = .54$, $p < .05$, while BAS-D scores were negatively related to Pe amplitude in the punishment condition, $r = -.67$, $p < .01$.

4. Discussion

In this study, we further investigated the effect of personality differences in punishment and reward sensitivity (i.e. BIS and BAS) on error-related ERP components. Subjects were either punished for incorrect responses (punishment condition) or failed to receive a reward when responding incorrectly (reward omission condition). The results show that subjects high on punishment sensitivity (BIS) displayed a larger ERN/Ne in the punishment condition compared to the reward omission condition, while subjects high on reward sensitivity (BAS-R) showed a larger ERN/Ne in the reward omission condition compared to the punishment condition.

The ERN/Ne has been proposed to reflect a reward over-prediction error, consistent with predictions from RL theory

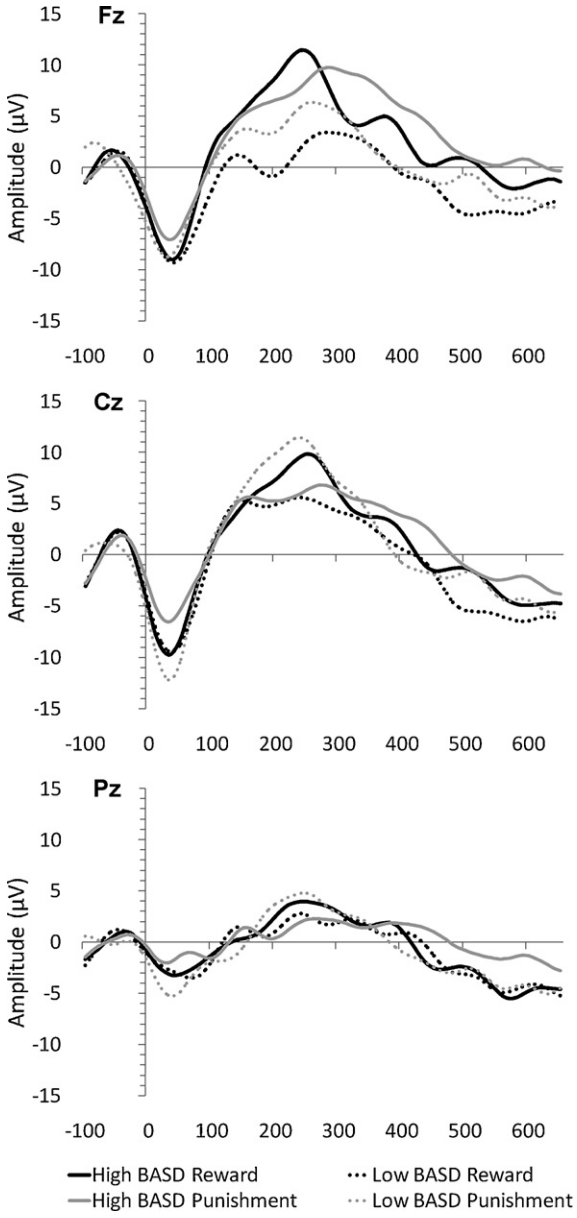

Fig. 5. Grand-averaged, response-locked ERPs at Cz for subjects high and low on BAS-D (groups formed by a median split procedure, only for illustrative purposes) in the two experimental conditions. High scores on the BAS-D subscale were related to larger Pe amplitudes in the reward omission condition, compared to the punishment condition, while subjects low on BAS-D showed a larger Pe in the punishment condition.

(Holroyd and Coles, 2002). Our findings show that punishment and reward omission result in quantitative differences in this error signal for subjects that are sensitive to either reward or punishment. In other words, it would seem that there are greater differences between predicted and received rewards in the punishment condition for subjects that are highly sensitive to punishment, compared to subjects that are sensitive to rewards. In contrast, this difference between predicted and actually received rewards would seem to be larger in the reward omission condition for subjects sensitive to rewards.

When we focus on the reward omission condition, the interpretation that subjects with high BAS-R scores would expect more rewards for themselves than subjects low on BAS-R would seem plausible. The BAS is proposed to be related to the approach of reward and the experience of positive emotions such as hope, elation and happiness (Gray, 1990; Carver and White, 1994). Therefore, subjects scoring high on BAS-R may have high expectations of the potential rewards for their actions. Omission of this reward, because of an unexpected incorrect response, may result in greater error responses for high BAS-R subjects, compared to subjects without such high expectations.

The results we obtained from the punishment condition are more difficult to reconcile with the RL model of the ERN/Ne. The larger ERN/Ne for subjects scoring high on punishment sensitivity would suggest that these subjects experienced a larger reward over-prediction error upon receiving punishment compared to subjects low on punishment sensitivity. The BIS, however, is related to the avoidance of potentially negative or harmful outcomes and the experience of anxiety and negative affect. Therefore, subjects scoring high on BIS are more likely to expect punishment in a situation when punishment may occur, compared to subjects low on BIS. Receiving punishment when already expecting punishment (BIS) should lead to a smaller reward prediction error than receiving punishment when expecting no punishment (BAS). This is not what we observe in our data.

These results are consistent, however, with a growing number of studies demonstrating a relationship between negative affectivity/punishment sensitivity 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; Boksem et al., 2006; Tops et al., 2006). To integrate these findings in a RL account, we have argued that, while a prediction error may be part of what generates the ERN/Ne, its amplitude is strongly dependent on the subjective value of the prediction error to the individual subject (Boksem et al., 2006; Tops et al., 2006; see also Hajcak et al., 2005; Bush et al., 2000; Pailing and Segalowitz, 2004). That is, subjects high on negative affect/punishment sensitivity experience this error as more aversive than subjects low on these personality measures when they are punished for committing errors. Similarly, subjects high on positive affect/reward sensitivity experience this prediction error as more aversive when they were in a position to acquire rewards but failed to do so. This latter observation is in accordance with a number of studies that have related measures of positive affect to increased ERN/Ne amplitudes (Tucker et al., 1999; Luu et al., 2000; Santesso et al., 2005; Tops et al., 2006).

It seems that ERN/Ne amplitude depends the most on how concerned subjects are over making mistakes. Indeed, both measures of negative affectivity (i.e. anxiety, neuroticism) and positive affectivity (i.e. agreeableness; DeNeve and Cooper, 1998) relate to concerns over social evaluation (e.g. Tops et al., 2006). In modern day life, the most prevalent and salient error signals are probably of a social nature, and negative social evaluation is probably one of the most potent ones, leading to strong physiological responses (Dickerson and Kemeny, 2004). While both subjects high on negative affect and subject high on positive affect are concerned over mistakes, these concerns may have different underlying causes. While subjects high on negative affect fear being negatively evaluated by others, subjects high on positive affect may be overly concerned with doing well.

The behavioural data provide some support for this. Subjects high on BIS slowed down more after having committed an error in the punishment condition than in the reward condition (Fig. 2). As most errors in this sort of tasks are so called 'slips' caused by responding prematurely, slowing down after such a slip reduces the probability of committing another error. Because punishment was experienced as more aversive than reward omission by these subjects, this behavioural adaptation to error commission was observed only in the punishment condition. In contrast, in the reward omission condition, subjects high on BAS-R showed lower error-rates than subjects low on BAS-R. In the punishment

condition, high BAS-R subjects committed even more errors than subjects low on BAS-R. Again, this is compatible with the view that these subjects were more concerned with performing well, especially when they were in the position to obtain rewards for good performance.

High valuation of performing well/not making mistakes results in high task engagement. Interestingly, a large meta-analysis of PET studies (Paus et al., 1998) showed that the common denominator of ACC (the proposed source of the ERN/Ne) activation across many task conditions is the level of task engagement, i.e. the amount of effort, which has to be engaged in a task (see also Winterer et al., 2002). Accordingly, engagement (Luu et al., 2000; Tops et al., 2006) and 'investment of attentional resources' (Pailing and Segalowitz, 2004) have been proposed to be reflected in ERN/Ne amplitude.

In our previous study, we showed that Pe amplitude was positively correlated with BAS-scores (Boksem et al., 2006). We suggested that Pe amplitude reflected proactive engagement after error commission, to prevent future errors and maximize future rewards (i.e. approach motivation/reward seeking, as measured by the BAS). It is interesting to note that in the present study, this correlation only emerged in the reward omission condition, and only for BAS-D. In the punishment condition BAS-D was even shown to be negatively related to Pe amplitudes.

BAS-D appears to be associated with extraversion and positive emotionality. When we take a closer look at the specific items of this sub-scale, BAS-D particularly measures persistence in pursuing desired goals. BAS-D scores correlate moderately with positive affectivity (Carver and White, 1994), assertiveness (Jackson and Smillie, 2004; Knyazev et al., 2004) and impulsivity (Jackson and Smillie, 2004). It has been suggested (Knyazev and Slobodskoj-Plusnin, 2007) that BAS-D probably captures some aspects of personality that relates to positive emotionality and sensitivity to positive reinforcement (see, e.g. Depue and Collins, 1999). In a recent study by Knyazev and Slobodskoj-Plusnin (2007), BAS-D discriminated between subjects high and low on sensitivity to rewards. Our finding that subjects high on BAS-D displayed the largest Pe amplitudes in the condition where they were able to obtain rewards for accurate performance, tentatively supports our suggestion that Pe amplitude may reflect engagement in order to prevent errors and maximize rewards.

Previously, we showed that ERN/Ne amplitude was positively correlated with BIS-scores (Boksem et al., 2006). It is interesting to note that in the present study, this correlation only emerged in the punishment condition. This would suggest that under conditions without explicit reward or punishment for doing well or committing errors, subjects may perceive making mistakes as punishing. This could be explained by concerns subjects may have over negative evaluation: they are well aware that the experimenter monitors their performance and in general they do not want to let the experimenter down by screwing up the experiment (Hawthorne Effect).

The observed interactions between punishment sensitivity and ERN/Ne amplitude under conditions of punishment and the positive correlation between BIS and ERN/Ne amplitude in neutral (no explicit punishment or reward) task settings are consistent with the notion that the neural substrate of the BIS proposed by Gray (1987, 1989) may be involved in generating the ERN/Ne. Gray suggests that the first response to prediction error and punishment is mediated by a cholinergic BIS system. In turn, this system inhibits dopaminergic approach-related activity in the ventral striatum, consistent with the model of the ERN/Ne proposed 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.

Results obtained by Ullsperger and von Cramon (2003) provide some additional support for this. These authors observed activation of the anterior insula and habenula complex in response to negative feedback after committing an error. Receiving projections from the basal forebrain, the habenular nuclei project to the ventral tegmental area, inhibiting DA neurons (Christoph and Leonzio, 1986). In addition, the insula has also been shown to be involved in the processing of costs and punishments (Small et al., 2001; Paulus et al., 2003; Sarinopoulos et al., 2006; Nitschke et al., 2006).

Recently, Matsumoto and Hikosaka (2007) showed that the primate lateral habenula is an important source of negative reward-related signals in DA neurons. These authors recorded the activity of habenula neurons and DA neurons while rhesus monkeys were performing a task with differential reward outcomes, based on their performance. Many habenula neurons were excited by non-reward-predicting stimuli and were inhibited by reward-predicting stimuli.

As expected, DA neurons showed the opposite pattern of activation and were excited by rewards and inhibited by non-reward-predicting stimuli. Importantly, in unrewarded trials, the excitation of habenula neurons preceded the inhibition of DA neurons, suggesting an inhibition of these DA neurons by habenula activity. The authors suggest, comparable with Gray (1987, 1989) theory, that the lateral habenula is involved in negative reward processing, while DA neurons are involved in positive reward processing.

In summary, we found that ERN/Ne amplitude is related to sensitivity to punishment when subjects are punished for making mistakes and to sensitivity to reward when subjects are rewarded for correct performance. We suggest that ERN/Ne amplitude is related to concerns over mistakes and depends on the level of aversion experienced by individual subjects for making these mistakes. Subjects that are highly sensitive to punishment are strongly motivated or engaged in avoiding punishment, while subjects sensitive to rewards are motivated to obtain rewards and therefore show high task engagement when rewards may be earned. The error-related ERP components appear to track this level of engagement in task performance. In addition, our results tentatively suggest a neural substrate for the ERN/Ne that has so far received little attention in the literature.

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