



Impacts of motivational valence on the error-related negativity elicited by full and partial errors

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ABSTRACT

Affect and motivation influence the error-related negativity (ERN) elicited by full errors; however, it is unknown whether they also influence ERNs to correct responses accompanied by covert incorrect response activation (partial errors). Here we compared a neutral condition with conditions, where correct responses were rewarded or where incorrect responses were punished with gains and losses of small amounts of money, respectively. Data analysis distinguished ERNs elicited by full and partial errors. In the reward and punishment conditions, ERN amplitudes to both full and partial errors were larger than in the neutral condition, confirming participants' sensitivity to the significance of errors. We also investigated the relationships between ERN amplitudes and the behavioral inhibition and activation systems (BIS/BAS). Regardless of reward/punishment condition, participants scoring higher on BAS showed smaller ERN amplitudes in full error trials. These findings provide further evidence that the ERN is related to motivational valence and that similar relationships hold for both full and partial errors.

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1. Introduction

The commission of an incorrect response elicits an event-related brain potential (ERP) with two major components; namely, the error negativity (Ne, Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990) or error-related negativity (ERN, Gehring, Coles, Meyer, & Donchin, 1990) which is followed by the error positivity (Pe, Falkenstein et al., 1990). The neural system generating the ERN is believed to be located in the anterior cingulate cortex (ACC) (e.g., Dehaene, Posner, & Tucker, 1994). Previous studies suggested that an essential function of the neurocortical activity associated with generation of the ERN is performance monitoring, including error detection (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Holroyd & Coles, 2002) and conflict detection (e.g., Carter et al., 1998), which invokes remedial processing (e.g., Ullsperger & von Cramon, 2001) while the Pe is considered to reflect error awareness and error evaluation (e.g., Overbeek, Nieuwenhuis, & Ridderinkhof, 2005). Interestingly, the ERN is also elicited by partial errors, that is, covert activations of an incorrect response, as measured using the electromyogram (EMG)—followed by a correct

response (Masaki, Murphy, Desjardins, & Segalowitz, 2012; Masaki & Segalowitz, 2004; Roger, Bénar, Vidal, Hasbroucq, & Burle, 2010); in contrast, the Pe is not elicited by partial errors (Vidal, Hasbroucq, Grapperon, & Bonnet, 2000).

As yet, the functional significance of the ERN elicited by partial errors is not fully understood, although some studies reported that the increased amplitude of the ERN after partial-errors is associated with response interference (Masaki et al., 2012; Masaki & Segalowitz, 2004). Importantly, it has not yet been determined whether the partial-error ERN is affected by emotional and motivational aspects of the task in a similar way as has been shown for the ERN elicited by full errors. For example, Hajcak, Moser, Yeung, and Simons (2005) found that high value monetary reward contingent upon the correct response increased the ERN amplitude relative to low value reward (100 vs. 5 reward points). They also found that the ERN amplitude increased when participants were evaluated for their performance. These findings suggest that performance monitoring is influenced by the motivational significance of errors. Other studies have also confirmed motivational effects on the ERN. For example, the ERN increases with monetary loss (Potts, 2011), especially for errors associated with a larger penalty (Endrass et al., 2010). Similarly, the feedback-related negativity (FRN), elicited by external feedback indicating an undesired outcome (Miltner, Braun,

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& Coles, 1997), is affected by the affective-motivational value of the feedback signal (Stürmer, Nigbur, Schacht, & Sommer, 2011).

If the partial-error ERN resembles the full-error ERN, it should also represent affective-motivational aspects of error processing. Thus, we wanted to investigate whether the affective-motivational aspects of error processing as demonstrated for the full-error ERN generalize to partial errors. To this aim we manipulated monetary reward and punishment that have been shown to modulate the full-error ERN (Potts, 2011; Stürmer et al., 2011). In order to assess the specific effects of reward and punishment on the partial-error ERN as well as on the full-error ERN, we also included a neutral condition without reward or punishment. We expected both types of ERN to be enlarged relative to the neutral condition in the context of punishment and reward. Previous studies have shown that ERNs elicited by full errors and partial errors share similar topographies and morphologies (Masaki et al., 2012; Roger et al., 2010). Masaki et al. (2012) found that both types of ERN were larger when the stimulus-response interference was stronger, supporting their functional similarity. In addition, applying independent component analysis (ICA, Onton, Westerfield, Townsend, & Makeig, 2006), Roger et al. (2010) suggested that the ERN and partial-error ERN share common underlying neural processes. In patients with obsessive-compulsive disorders, Endrass, Klawohn, Schuster, and Kathmann (2008) found similar effects of medication both on partial-error and full-error ERNs. If both types of ERN indeed reflect the same neurocognitive processes, the partial-error ERN should also be larger when responses are rewarded or penalized in accordance with previous studies on the full-error ERN (Hajcak et al., 2005; Potts, 2011).

The most noteworthy difference between full and partial errors is probably that the former is classified as an “error” whereas the latter is formally a “correct” response because behaviorally the near error was successfully inhibited in favor of a correct response. It is intriguing to clarify whether the partial-error ERNs elicited by opposite behavioral outcomes indeed represent similar experimental variables. Thus, analyzing partial errors should be useful to understand error monitoring in initially (covertly) incorrect but behaviorally correct trials. Specifically, studying the effects of reward and punishment on partial-error ERNs should shed light on whether sub-threshold error-processing can be influenced by affective-motivational manipulations.

Because partial errors are often not consciously detected (Rochet, Spieser, Casini, Hasbroucq, & Burle, 2014), the Pe is not generally observed on partial error trials (Vidal et al., 2000). On the other hand, affective-motivational factors appear to affect the Pe. Some studies have reported that monetary valence influences the Pe. For example, Endrass et al. (2010) found that monetary punishment increased Pe amplitudes. If the Pe reflects error awareness as a function of affective-motivational manipulations (Endrass et al., 2010), it is predicted that the Pe for full errors should be larger both in the punishment and the reward conditions than in the control condition.

Another well documented behavioral after errors is the post-error slowing (PES). Typically, participants exhibit a temporary adjustment (slowing) of reaction speed following an incorrect response (Rabbitt, 1966). In this case, a different effect might be predicted. Endrass et al. (2008) did not observe PES after partial-error trials. On trials following full errors, PES was stronger in a monetary reward than in a monetary punishment condition (Stürmer et al., 2011), although it did not differ between a monetary punishment condition and a control condition (Endrass et al., 2010). According to these findings, we expected a stronger PES in the reward condition than in the punishment condition, but no effect of monetary punishment on the PES relative to the control condition.

Recent ERN studies have also shown the importance of individual differences in reactivity to errors and personality traits

(e.g., Proudfit, Inzlicht, & Mennin, 2013; Moser, Moran, Schroder, Donnellan, & Yeung, 2013). Personality traits correlate with the size of ERN, as shown primarily in clinical studies, including obsessive-compulsive disorder (e.g., Endrass & Ullsperger, 2014), schizophrenia (e.g., Weinberg, Dieterich, & Riesel, 2015), generalized anxiety disorder (e.g., Weinberg, Olvet, & Hajcak, 2010) and autism (e.g., Henderson et al., 2006). In addition, individual differences in error reactivity revealed clearer affective-motivational impacts on the ERN than comparisons of experimental conditions alone (Pailing & Segalowitz, 2004). Therefore, we also tested individual differences in responsiveness to full and partial errors when monetary reward and punishment were manipulated.

Affective-motivational processes in performance monitoring are often viewed within the conceptual framework of Gray (1970), who proposed two general motivational systems underlying human behavior and affect. The behavioral inhibition system (BIS) motivates avoidance of aversive events, whereas the behavioral approach system (BAS) is associated with positive feelings and attraction as a result of successful efforts (Carver & White, 1994).

Previous studies reported that the ERN increases as a function of BIS (Amodio, Master, Yee, & Taylor, 2008; Boksem, Tops, Kostermans, & De Cremer, 2008; Boksem, Tops, Wester, Meijman, & Lorist, 2006). Boksem et al. (2006) found that individuals scoring higher on BIS exhibited larger ERNs, suggesting that the ERN is associated with the avoidance of aversive events. Boksem et al. (2008) tested the responsiveness of the ERN to monetary reward and punishment as a function of BIS and BAS scores. In the punishment condition, the ERN was larger in high than low BIS individuals, whereas in the reward condition there was no significant correlation between BIS scores and ERN amplitudes. These results are in accordance with Gray's model assuming that BIS activates avoidance processes of threat and punishment. In addition, the ERN appears to increase with anxiety and negative affect, reflecting its sensitivity to punishment (Aarts & Pourtois, 2010; Moser et al., 2013; Olvet & Hajcak, 2009). Hajcak, McDonald, and Simons (2004) found larger ERNs for a high than for a low negative-affect group. In addition, individuals scoring high on depression anxiety stress scales (DASS; Lovibond & Lovibond, 1995) exhibited larger ERN amplitudes than individuals scoring low on DASS (Olvet & Hajcak, 2009). According to these findings, high BIS scores should be related to enhanced full-error and – possibly – partial-error ERNs in the present study.

In contrast to BIS, the relationship between BAS and the ERN is less clear. Some studies have reported smaller ERNs associated with responsiveness to reward. Although the BAS-Reward (a subscale of BAS) reflects positive responses to reward (Carver & White, 1994), Boksem et al. (2008) reported a trend of smaller ERN amplitudes for higher BAS-Reward individuals in a punishment condition. In terms of positive responses to reward, Santesso and Segalowitz (2009) found decreased ERNs for individuals with high reward sensitivity.

So far, no study has tested the relationship of BIS and BAS traits to the partial-error ERN amplitude. Given that the partial-error ERN has a functional similarity to the full-error ERN, larger ERNs should emerge in response to both partial and full errors for high-BIS individuals than for low-BIS individuals in the punishment condition. Another possibility is that we will observe smaller ERNs for individuals scoring high in BAS (Boksem et al., 2008; Santesso & Segalowitz, 2009).

Compared to the ERN, fewer findings about the relationship between Pe and BIS/BAS are available. Higher BAS individuals tend to exhibit larger Pes (Boksem et al., 2006, 2008), whereas they showed smaller Pes when errors were associated with monetary punishment (Boksem et al., 2008). To our knowledge, no study has reported a relationship between Pe and BIS. In the present study, we tested individual differences in error reactivity on Pes as well as on ERNs.

Taken together, the present study had two primary aims. First, we investigated whether the full-error and partial-error ERNs share the same functional significance with regard to affective-motivational impacts, manipulating both monetary reward and punishment. Second, we tested the relationship between performance monitoring, reflected in the two types of ERN, and individual differences in responsiveness to punishment/reward.

2. Method

2.1. Participants

Twenty-four healthy female participants (mean age = 20.4 years; SEM = 0.30) were recruited from Waseda University's Faculty of Sport Sciences. Participants had normal or corrected-to-normal vision and were paid 2400 yen (about 28 U.S. dollars) for their participation. Participants reported neither psychiatric disorders nor did they show extreme scores in relevant traits (see next paragraph). Written informed consent was obtained. The study was approved by the Waseda University Ethics Committee. We excluded one participant who showed an exceedingly large number of full errors in the control condition (i.e., 136 error trials of 216 trials in total) from further analysis.

2.2. BIS/BAS scale

We used a Japanese version of the 20-items BIS/BAS scale of Carver and White (1994), translated and confirmed for reliability and validity (Takahashi et al., 2007). The BAS dimension contains the following subscales: reward responsiveness (BAS-R), drive (BAS-D), and fun seeking (BAS-F), whereas the BIS dimension does not have any subscales. The sample as a whole showed the following values on the full scales: M (BIS) = 19.61; SEM = 0.88; M (BAS) = 43.96; SEM = 1.18.

2.3. Procedure

The participants rested both forearms and palms comfortably on a Table to minimize any movements unrelated to their responses. We adopted a stimulus-response compatibility (SRC) task, classified as a spatial Stroop task (Masaki & Segalowitz, 2004). As shown in Fig. 1, a white fixation cross ($0.7^\circ \times 0.7^\circ$) on a black background was continuously presented in the center of a computer monitor, placed 1 m in front of the participant. A white arrow (visual angle: $0.7^\circ \times 0.4^\circ$) pointing either up or down was shown above or below the fixation cross with an eccentricity of 0.8° visual angle (between center of fixation and arrow). Arrow direction (pointing up or down) and location (above or below fixation) were combined orthogonally, with each combination occurring equally often across participants. Trials where arrow direction agreed with arrow location (e.g. above fixation; pointing upward) were defined as congruent; trials where this was not the case (e.g., below fixation, pointing upward) were defined as incongruent.

Each trial began with a central fixation cross shown for 300 ms; then, an arrow stimulus appeared either above or below the fixation for 150 ms. The arrow was followed by a blank screen lasting for 850 ms until the next fixation cross. Thus, the duration of each trial was 1300 ms. Participants were asked to respond quickly and accurately with a brisk finger extension according to the pointing direction of the arrow (i.e., up or down), but not to its location. If participants did not respond within 500 ms, the feedback "Too Late!" was presented for 500 ms. Omitted responses were not regarded as error, but excluded from analyses.

Responses were recorded with two microswitches mounted 150 mm apart in the mid-sagittal line. The microswitches were

operated with small cantilevers that required an upward displacement for switch closure. A plastic plate ($30 \times 20 \times 1$ mm) was attached to the end of the cantilever key, providing leverage. Participants placed their middle fingers on the end of the plastic plate. The weight of the finger at rest was enough to depress the key. The displacement of the key by lifting the finger resulted in switch closure that was defined as overt response onset. We compared three conditions: reward, punishment, and control (neutral). In the reward condition, each correct response was rewarded with a small amount of money (5 yen; about 4 cents) with a final maximum balance of 2000 yen. In this condition, errors did not result in any loss of money. In the punishment condition, participants were given a 2000 yen allotment but could lose 50 yen (about 40 cents) for each incorrect response, potentially leading to a total loss of all 2000 yen. Even after the participants had lost the total allotment (i.e., 2000 Yen), they continued performing the task believing that errors would incur financial losses. After the experiment, participants were told that their total amount could not drop below zero. Correct responses in the punishment condition did not result in monetary gains. In both the reward and punishment conditions, participants were given feedback about their current balance only at the end of each block—no feedback was given after individual trials. In the neutral control condition, participants would neither lose nor earn money and were not given any feedback.

In each condition participants performed the task for 6 blocks of 72 trials each, that is, for 108 trials in each combination of arrow direction and arrow location. Before the experiment began participants practiced the task for 72 trials without any reward/punishment. The order of the three conditions and hand-to-key assignments were counter-balanced across participants. In the reward condition, the average monetary gain was 1824 yen (SEM = 26.7) (about 15 US dollar). In the punishment condition, the average monetary loss was 3422 yen (SEM = 250.5).

2.4. EEG recording

The EEG was recorded from 128 sites with Ag/AgCl electrodes. Horizontal electrooculograms were recorded from the left and right outer canthi, and vertical electrooculograms from above and below the left eye. These were recorded with DC and 100 Hz low-passed filters, using the Biosemi Active Two system (Biosemi Inc.). Electromyograms (EMGs) were bipolarly recorded from the extensor digitorum muscles of the left and right forearms with Ag/AgCl electrodes, also using the Biosemi Active-Two system. Off-line, the EMGs were high-pass filtered with 5.31 Hz and full-wave rectified with Vision Analyzer (Brain Products) software. All physiological signals were digitized at 1024 Hz.

2.5. Data analysis

RT was measured as the interval between stimulus onset and microswitch closure. The error analysis reported here focused on incongruent trials (see procedure for definition) because in congruent trials there were only few errors. In incongruent trials we also measured the EMG-based RT (see below for details) and classified erroneous responses as full errors. Responses in incongruent trials were classified as partial errors if there were muscular activities of the incorrect response hand that did not lead to switch closure but were followed within 250 ms by corrective EMG activity, resulting in switch closure of the correct button. Hence, partial errors occurred in formally "correct" responses with initial covert erroneous EMG activity. Post-error slowing was calculated by subtracting mean RT in incongruent trials following correct responses from mean RT in incongruent trials following error responses.

To determine EMG onsets (EMG-RT), we used as threshold criterion a deflection exceeding 4.0 SDs of the rectified EMG

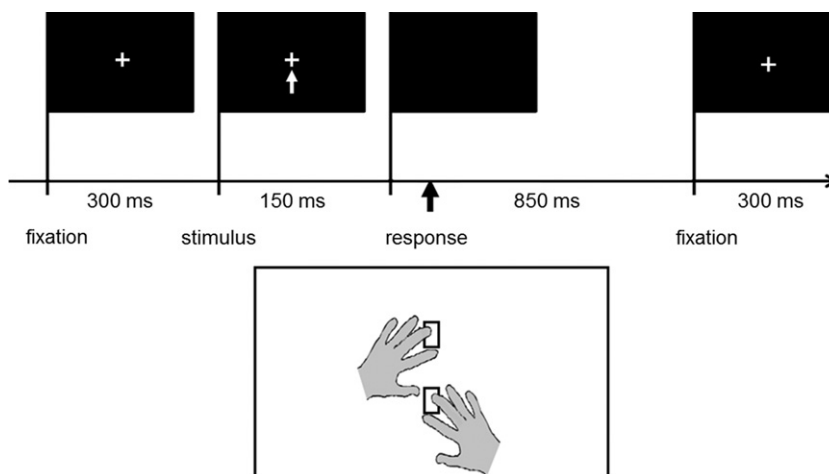


Fig. 1. Apparatus and procedure of the spatial Stroop task used in the present study. Participants were asked to respond to the pointing direction of the white arrow stimulus (i.e., up or down), but not to the arrow location.

derived during a pre-response baseline of -700 to -550 , using a semi-automatic macro implemented in Brain Vision Analyzer. The validity of the EMG onset detection was visually inspected for each single trial; invalid EMG onsets were corrected manually. We also carefully checked incorrect EMGs in partial errors by visual inspection (Vidal et al., 2000). The extension of the middle fingers is suitable to record clear EMGs for anatomical reasons; therefore, we could detect even small EMG activities as partial errors.

All ERPs were averaged EMG-synchronized, separately for full-error and partial-error trials, using Brain Vision Analyzer. The EEG was re-calculated to average common reference and low-pass filtered at 30 Hz (roll off 12 dB). Ocular artifacts were corrected using the procedure developed by Gratton, Coles, and Donchin (1983). We excluded from averaging all trials in which response time was below 100 ms and where EEG voltages exceeded a threshold of $100 \mu\text{V}$ during the recording epoch. Mean numbers of excluded trials were 0.82 (SEM = 0.52) in the punishment condition, 0.52 (SEM = 0.16) in the reward condition, and 0.78 (SEM = 0.46) in the control condition.

The EMG-locked ERP waveforms were high-pass filtered at 0.1 Hz (roll off 12 dB). ERN amplitudes were scored at FCz as peak-to-peak amplitude by subtracting the most positive peak amplitude preceding the ERN from the negative peak amplitude of the ERN. The positive and negative peaks were determined within the time window from EMG onset and 200 ms following response onset. Using the mean voltage from -400 to -300 ms before EMG onset as baseline, we also scored mean amplitudes of the Pe in full-error trials as positive deflection at Cz within a time-window between 300 and 450 ms after response onset.

Mean RTs and error rates were subjected to two-way repeated measures analyses of variance (ANOVA) with factors Stimulus–Response congruency (congruent/incongruent) and Condition (punishment/reward/control). EMG-RTs in incongruent trials were analyzed with a two-way repeated measures ANOVA with factors Response type (full-error/partial-error/correct) and Condition (punishment/reward/control). PES was subjected to a one-way repeated measures ANOVA with factor Condition (punishment/reward/control). ERN amplitudes were assessed with a two-way repeated measures ANOVA, including the factors Condition (punishment/reward/control) and Error Type (full/partial). To analyze Pe amplitudes we used a one-way repeated measures ANOVA with factor Condition (punishment/reward/control). Degrees of freedom of F -ratios were adjusted with the Greenhouse–Geisser procedure where required, reporting epsilon values and the

original degrees of freedom. Bonferroni correction was applied to post-hoc comparisons.

3. Results

3.1. Reaction times

Fig. 2(A) shows mean reaction times in correct trials. A two-way ANOVA revealed longer RTs in incongruent than in congruent trials ($F(1, 22) = 464.94, p < .001, \eta^2_p = .96$). The main effect of condition occurred as a trend ($F(2, 44) = 2.71, p < .10, \eta^2_p = .11$). No interaction between condition and SRC was obtained ($F < 1$).

We also compared post-error slowing among conditions. A one-way ANOVA revealed a main effect of condition ($F(2, 44) = 5.89, p < .01, \eta^2_p = .21$). Post-hoc analyses showed that PES was more pronounced in the reward condition ($M = 8.1$ ms) than in the control condition ($M = -1.6$ ms) ($p < .05$) and in the punishment condition ($M = -2.8$ ms) ($p < .05$) but indistinguishable for the punishment and control conditions ($p = 1.0$).

3.2. EMG-RT

Fig. 2(B) shows EMG-RTs for errors, partial-errors, and correct responses in each condition. A two-way ANOVA revealed a main effect of condition ($F(2, 44) = 7.52, \epsilon = .80, p < .001, \eta^2_p = .26$). Post-hoc tests showed that the EMG-RTs were significantly longer in the punishment condition ($M = 239$ ms) and in the reward condition ($M = 241$ ms) than in the control condition ($M = 233$ ms) ($p < .05$ and $p < .001$, respectively). A main effect of response type on EMG-RT was also obtained ($F(2, 44) = 350.0, \epsilon = .78, p < .001, \eta^2_p = .94$). Post-hoc tests showed that RTs for full errors ($M = 211$ ms) were significantly shorter than for correct responses ($M = 285$ ms, $p < .01$). Partial-error RTs ($M = 217$ ms) were significantly shorter than for correct responses ($p < .01$). RTs for full errors tended to be shorter than for partial-errors ($p < .10$).

3.3. Error rates

Fig. 2(C) shows full error rates in the reward, punishment, and control conditions and for compatible and incongruent trials. Mean numbers of full errors in incongruent trials were 51.8 (SEM = 4.3) in the reward, 55.0 (SEM = 4.6) in the punishment, and 62.7 (SEM = 4.5) in the control conditions, respectively; in congruent trials there were 6.8 (SEM = 1.2) in the reward, 6.7 in the

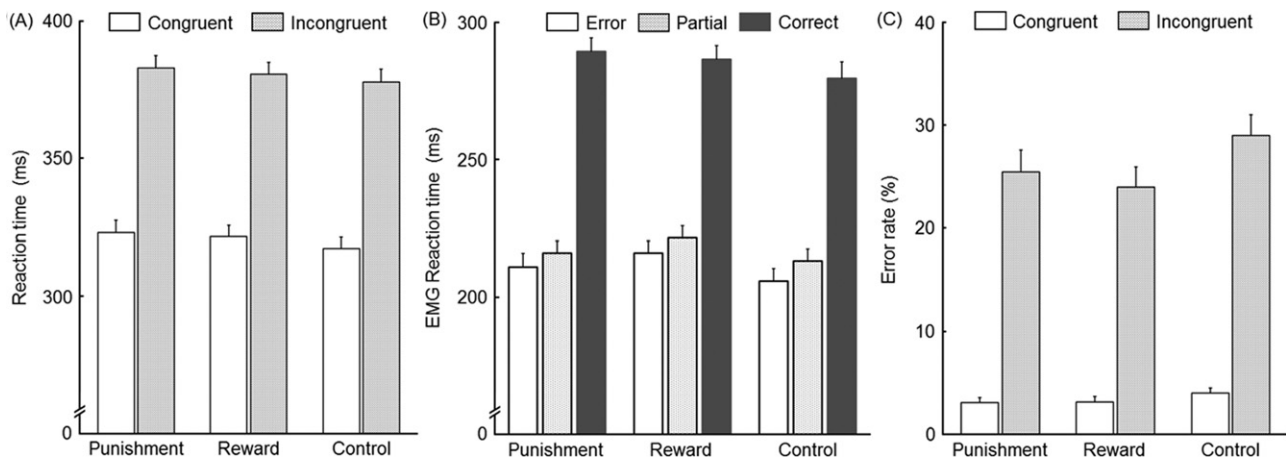


Fig. 2. (A) Mean reaction times in congruent and incongruent trials. (B) EMG reaction times (and SEMs) for both full error and partial error responses in incongruent trials. (C) Error rates in congruent and incongruent trials.

Table 1

ERN and Pe amplitudes (μV , SEM) in each condition.

	Punishment	Reward	Control
ERN (full error)	-10.4 (0.84)	-10.1 (0.73)	-9.0 (0.71)
ERN (partial error)	-9.5 (0.75)	-9.1 (0.67)	-8.2 (0.56)
Pe (full error)	4.0 (0.48)	3.5 (0.56)	2.8 (0.49)

punishment ($\text{SEM} = 1.1$), and 8.7 ($\text{SEM} = 1.1$) in the control conditions on full errors on average. A two-way ANOVA confirmed considerably more errors in incongruent than in congruent trials ($F(1, 22) = 196.92, p < .001, \eta^2_p = .90$). In addition, the main effect of condition was significant ($F(2, 44) = 6.40, \epsilon = .99, p < .01, \eta^2_p = .23$). Post-hoc tests revealed that mean error rate was higher in the control than in both the reward ($p < .05$) and punishment condition ($p < .05$). There was no interaction between condition and SRC.

Mean number of partial errors in incongruent trials in the reward, punishment, and control conditions were 43.2 ($\text{SEM} = 3.3$), 45.2 ($\text{SEM} = 3.2$), and 48.9 ($\text{SEM} = 3.2$), respectively. A one-way repeated-measures ANOVA on partial-error rates only revealed a trend for a main effect of condition ($F(2, 44) = 2.88, p = .07, \eta^2_p = .12$).

3.4. EMG-synchronized ERN

Fig. 3 depicts the grand-average ERN waveforms (at FCz), time-locked to the EMG onset. The minimum number of trials averaged for the full-error ERN was 20. Table 1 shows ERN amplitudes for both full and partial errors in each condition. A repeated-measures ANOVA on ERN amplitudes, including Condition and Error Type, revealed a main effect of Condition ($F(2, 44) = 8.48, p < .01, \eta^2_p = .28$). Post-hoc tests revealed that ERNs were larger in both the reward ($p < .05$) and punishment conditions ($p < .01$) than in the control condition; there was no difference between the reward and punishment conditions ($p = .68$). A main effect of error type was significant ($F(1, 22) = 4.30, p < .05, \eta^2_p = .16$); the ERN was larger in full than in partial error trials. The interaction between Condition and Error type did not reach significance ($F < 1$).

Additionally, we calculated the full-error ERN in the punishment condition excluding trials after the number of errors had reached 40 trials (i.e., after the allotment of 2000 yen in this condition was in financial straits). A one-way ANOVA still revealed a main effect of condition ($F(2, 44) = 7.25, p < .01, \eta^2_p = .25$). Post-hoc tests revealed larger ERN amplitudes both in the punishment ($p < .01$) and reward condition ($p = .054$) than in the control condition; there was no significant difference between reward and punishment conditions ($p = .50$).

3.5. EMG-synchronized Pe

Fig. 3 depicts the grand-average Pe waveforms (at CPz), time-locked to the EMG onset. In accordance with previous studies that did not find any Pe for partial errors (Vidal et al., 2000), it was difficult to identify the Pe in partial-error trials. Table 1 also shows mean amplitudes of Pe on full-error trials for each condition. A one-way ANOVA revealed a main effect of condition ($F(2, 44) = 3.40, p < .05, \eta^2_p = .13$). Post-hoc tests revealed larger Pe amplitudes both in the punishment than in the control condition ($p < .05$); there was no difference between reward and punishment ($p = .88$), and between reward and control conditions ($p = .48$).

3.6. BIS/BAS correlations

3.6.1. BIS

Correlations between BIS scores and full-error EMG-ERN amplitudes at FCz in each condition (punishment, reward, control) were not significant ($r_s \leq -.20$). Likewise, for partial errors, there were no significant correlations of ERN amplitudes in any condition and BIS scores ($r_s \leq .30$). Similarly, BIS scores were uncorrelated to full Pe amplitudes at Cz in any condition (for full errors; $r_s \leq .30$).

3.6.2. BAS

We calculated correlations between BAS scores and full-error ERN amplitudes at FCz in each condition (Fig. 4). There were significant weak and moderate positive correlations between BAS scores and ERN amplitudes in all conditions (punishment: $r = .44, p < .05$, reward: $r = .53, p < .01$, control: $r = .57, p < .01$), indicating that individuals with higher BAS scores showed smaller ERN amplitudes. In contrast, for partial errors there were no significant correlations of ERN amplitudes in any condition with BAS scores (punishment: $r = .18, p = .40$, reward: $r = .36, p < .10$, control: $r = .22, p = .31$).

When correlations were calculated between BAS-subscale scores and ERN amplitudes, we found positive correlations between the BAS-Reward scores and ERN amplitudes in the reward condition ($r = .49, p < .05$), and in the control ($r = .56, p < .01$). There was no significant correlation between the BAS-Reward scores and ERN amplitudes in the punishment condition ($r = .40, p = .06$). A positive correlation between the BAS-Fun seeking scores and ERN amplitudes was also obtained in the control condition ($r = .50, p < .05$). There were no significant correlations between BAS-Fun seeking and ERN amplitudes in the reward ($r = .41, p = .052$) or punishment condition ($r = .29, p = .17$). In contrast, the BAS-Drive scores did not correlate with ERN amplitudes ($r_s < .30$).

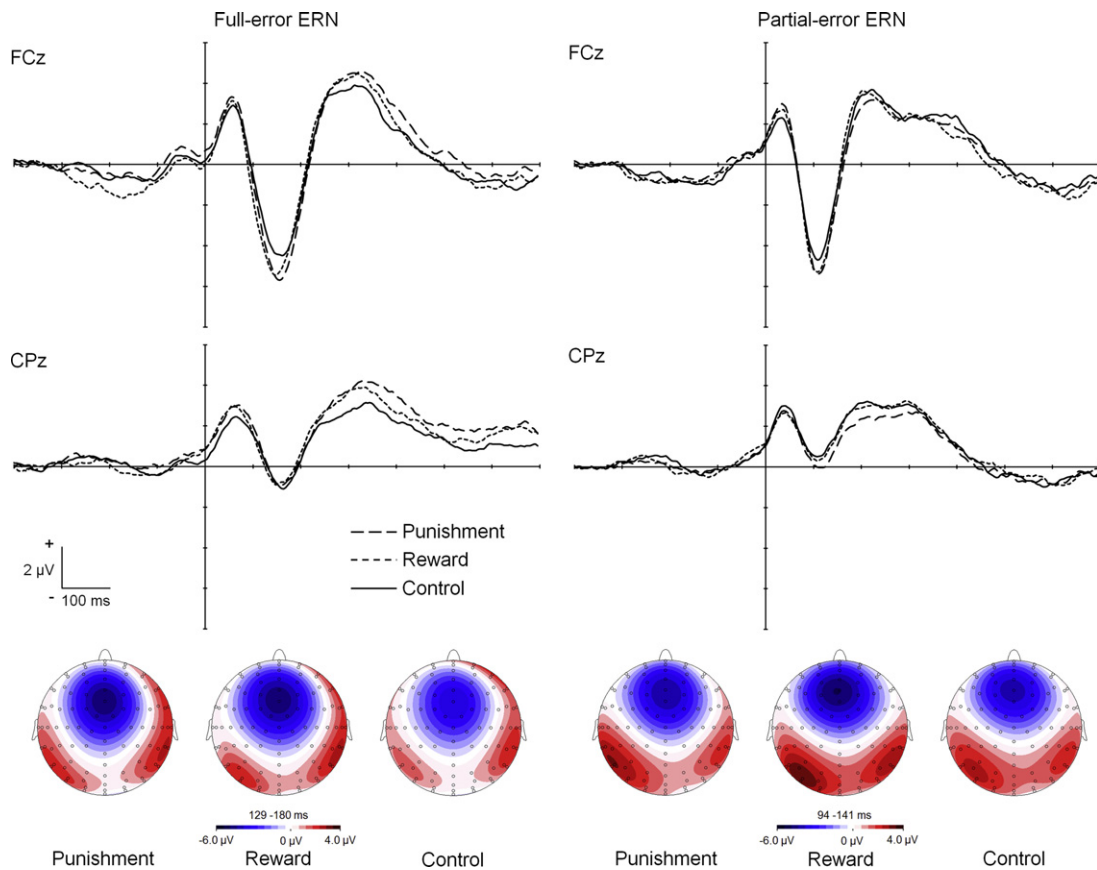


Fig. 3. EMG-locked grand average waveforms ($N=23$) at FCz and Cz for full-error trials (left panel) and partial error trials (right panel). Topographies represent activities across a time window of 50 ms, only for illustrative purposes.

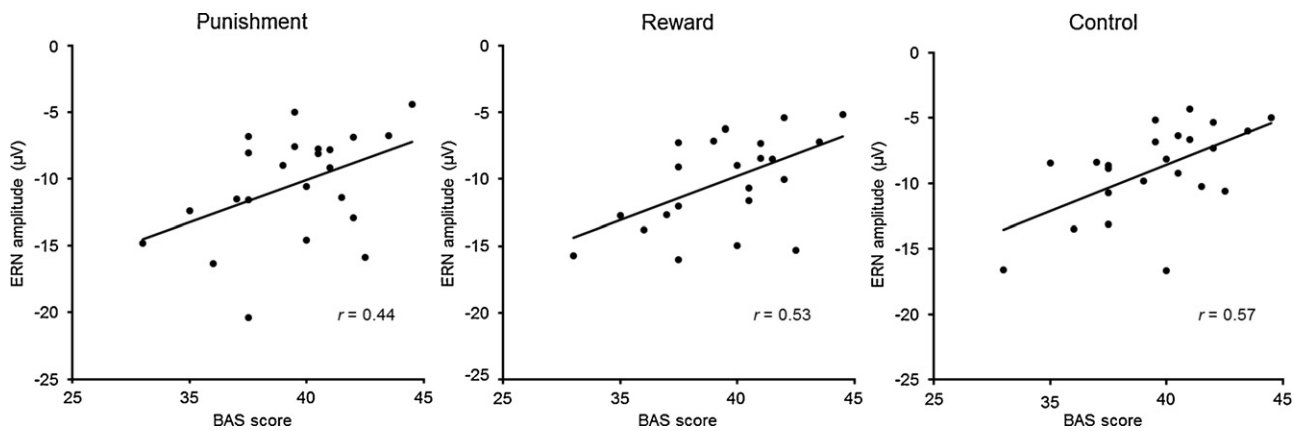


Fig. 4. Scatter plots and correlations between scores for the behavioral activation system (BAS) scale and ERN amplitudes in each condition.

Concerning Pe, no correlations between BAS score and Pe amplitude were found regardless of condition (for full errors; $r_s \leq .20$). Also, Pe amplitude for full errors did not correlate with BAS-subscale scores regardless of condition ($r_s < .35$).

4. Discussion

We compared a monetary reward-only and a punishment-only condition with a neutral control condition to investigate whether the partial-error ERN shows similar affective-motivational modulations as the full-error ERN. Full error rates were significantly lower in both the reward and punishment conditions than in the control condition, suggesting that inhibition of incorrect responses was

stronger in association with monetary reward/punishment. This result also suggests that the significance of errors was higher in both reward and punishment conditions than in the control condition. In contrast, such an effect was not obvious for partial errors. Contrary to error rates, overall RTs did not differ among conditions. On the other hand, post-error slowing was found only in the reward condition, suggesting a stronger remedial function in association with monetary reward. The ERNs were larger in both reward and punishment conditions than in the control condition regardless of error type, although the full-error ERN tended to be larger than the partial-error ERN. The Pe was larger in the punishment condition than in the control condition.

The current findings are consistent with previous reports (Hajcak et al., 2005; Potts, 2011), establishing the sensitivity of the full-error ERN to motivational values. Hajcak et al. (2005) found that the ERN was larger in their high-reward than in their low-reward condition. Although their monetary manipulations did not influence behavioral measures, the ERN amplitude indeed reflected the value of errors induced by monetary reward for correct trials. However, Endrass et al. (2010) reported an increased ERN in a punishment condition where monetary loss was given contingent upon incorrect responses. According to these findings, it is reasonable to conclude that the higher significance of errors was responsible for the increased ERNs in both partial and full error conditions of the present study.

To our knowledge, this is the first demonstration of an effect of punishment and reward on the partial-error ERN. Partial error trials are classified as behaviorally correct responses after successful inhibition of covert incorrect muscular activity. However, when partial errors, which appear to have similar neural manifestations as full errors, are classified as correct trials – as common – they may blur the distinction between the processing of fully correct and fully incorrect trials. Therefore, the separation of partial errors from full errors and fully correct responses may also foster research on the two latter.

Previous studies reported that partial errors elicit an ERN, although its peak latency was shorter than for the full-error ERN (e.g., Masaki & Segalowitz, 2004). Based on results from ICA, Roger et al. (2010) concluded that partial-error and full-error ERNs are based on a common neural system. In terms of affective-motivational modulations, our results revealed a further functional similarity between partial-error and full-error ERNs. Both types of ERNs increased in amplitude in both punishment and reward conditions compared to a neutral control condition.

Given that the partial-error EMG occurs in correct responses, both types of ERN may reflect the affective significance of errors, regardless of whether error awareness actually occurs. Previous studies suggested that the Pe reflects error awareness and error evaluation (e.g., Overbeek et al., 2005). In accordance with this notion, we found larger amplitudes of Pe for full errors, presumably representing enhanced error awareness with affective-motivational manipulations (Endrass et al., 2010). In addition, previous studies suggested that Pe is not elicited by partial errors because partial errors are less often consciously detected (Rochet et al., 2014). Thus, even though participants may not be aware of partial errors, increased partial-error ERNs in reward and punishment conditions might be ascribed to a motivationally triggered error monitoring system.

Although there was no difference in ERN amplitudes between the reward and punishment conditions, significantly longer RTs on post-error trials (i.e., stronger remedial action) were found in the reward condition as compared to the other conditions. These findings are in accordance with a report by Stürmer et al. (2011) who manipulated monetary punishment and reward in a Simon task. They found larger post-error slowing in a reward condition and suggested that monetary reward might promote remedial action. Therefore, monetary reward might enhance behavioral adjustments after error trials as compared to monetary punishment, indicating that participants were more cautious to avoid further errors in the reward condition than in the punishment condition. These results might also indicate that the ERN amplitudes are less discriminative between reward and punishment processes than performance measures. However, there are also alternative positions that consider the ERN to better represent affective-motivational processes than behavioral data (e.g., Hajcak et al., 2005).

In the punishment condition, monetary penalty was contingent only upon incorrect responses and there was no opportunity

for financial gain. Even in this situation, the significance of errors should be enhanced, because the participants should try to protect their initial allotment of money. The ERN elicited by full errors was larger in the punishment condition than in the control condition when we calculated the full-error ERN only for trials before participants had lost their allotments. Because errors caused monetary loss, committing errors should have been much worse for the participants in the punishment than in the reward condition where errors were monetarily inconsequential. However, ERN amplitudes did not differ between the punishment and reward conditions. This suggests that ERN amplitude might reflect motivational significance of errors themselves rather than its consequences.

Although the ERN was susceptible to monetary punishment in the present study, a previous study also reported similar results concerning effects of punishment. A loud unpleasant noise (100 dB) contingent upon an error increased the ERN amplitude (Riesel, Weinberg, Endrass, Kathmann, & Hajcak, 2012). It is possible that other types of aversive punishment have the same effect as monetary punishment. It is likely that motivational processes controlled by the basal ganglia strongly affected the ACC in the punishment studies, resulting in larger ERNs (Potts, 2011). The punishment contingent upon an error might be a critical factor to increase ERN amplitude.

Contrary to our hypothesis, we did not find any significant correlation between BIS scores and ERN amplitudes. In fact, Boksem et al. (2006) and Amodio et al. (2008) reported a relationship between BIS but not BAS scores and ERN amplitudes. Boksem et al. (2008) replicated the correlation only in the monetary-punishment condition, ascribing the larger ERN associated with the BIS trait to a stronger tendency of negative emotion exhibited by high-BIS individuals compared to low-BIS individuals. In our opinion, the discrepancy between these studies and the present one might be due to different experimental procedures; neither Boksem et al. (2006) nor Amodio et al. (2008) manipulated monetary reward and punishment, and Boksem et al. (2008) adopted a between-subjects design, comparing punishment and reward groups.

On the other hand, we found that higher BAS individuals showed overall smaller ERN amplitudes regardless of condition. These findings extend previous research, reconfirming the relationship between sensitivity to reward and ERN amplitude. Boksem et al. (2008) found that ERNs in the punishment condition tend to be smaller for individuals high rather than low in the BAS-Reward subscale. In line with this assumption, Santesso and Segalowitz (2009) found that a higher sensitivity to reward measured with a questionnaire (sensitivity to punishment and sensitivity to reward questionnaire: SPSRQ, Torrubia, Avila, Moltó, & Caseras, 2001) resulted in smaller ERNs. In general, these results suggest that increased sensitivity to reward is associated with smaller ACC activity.

However, the above-mentioned relationship (i.e., smaller ERNs associated with higher BAS scores) was ambiguous when we calculated correlations of ERN with BAS-subcales. For the BAS-Reward trait that is associated with positive responsiveness to reward and punishment expectation, we obtained significant correlations only in the reward and control conditions, but not in the punishment condition. For the BAS-Fun seeking trait that is associated with impulsiveness to novelty stimulus and reward, a significant correlation was obtained only in the control condition. These findings suggest that the trait responsiveness of ERN to affective-motivational situations could be obvious in a neutral situation, whereas affective-motivational manipulations might obscure the ERN responsiveness. There might be two reasons for the attenuation of the correlation between BAS subscales and ERN amplitudes. Affective-motivational manipulations would induce a trait and state interaction that resulted in unequal increases in ERN amplitude across participants both in the reward and the punishment

condition. Alternatively, because of a ceiling effect, some individuals might not show full scale increases of ERN amplitudes with monetary manipulations. Either case would diminish the correlations of ERN with BAS-subcales.

Gray et al. (2005) investigated the relationship between the BIS/BAS and activities of the dorsal ACC in a working memory task using fMRI. They found that high-BAS individuals show reduced activation of the dorsal ACC. This finding suggests that high-BAS individuals exhibit higher neural processing efficiency; hence, they may need less mental effort to perform the task than low-BAS individuals. It is possible that higher neural processing efficiency manifests as deactivation of the dorsal ACC. Thus, Gray et al., emphasized the relationship between the BAS trait and ACC functions. Indeed, the small ERNs in control condition for high-BAS individuals in our study are consistent with the findings of Gray et al. (2005). Interestingly, we found weakened correlations between BAS subscale scores and ERN amplitudes in the reward and the punishment conditions, supporting the sensitivity of the ERN to the interaction between the trait aspect of BAS and the state aspect manipulated by reward and punishment. The motivational manipulation might decrease the neural processing efficiency.

For partial errors the overall relationship with motivational aspects showed a high similarity to that of full errors; namely, a statistical trend for a weak positive relation for BAS in the reward condition but none for BIS. This correlation pattern for partial errors appears to be a diluted version of the pattern for full errors. Given that ERN is smaller in partial errors than in full errors in the present study, awareness of errors might be a necessary condition to obtain a significant correlation between BAS and ERN. Similarly, in a study that tested sleepiness, the ERN also tended to be smaller than during an alert condition (Murphy et al., 2006). Although this study concerned only full errors, the findings suggest that the ERN amplitude could be modulated by awareness of errors. Further studies are needed to confirm the relationship between BAS scores and partial-error ERNs. In accordance with previous studies (Boksem et al., 2006, 2008), we did not find any relationship between BIS and Pe amplitudes. However, our results did not support previous findings that Pe amplitude is associated with BAS (Boksem et al., 2006, 2008).

A limitation of our study might be the assumptions on the subjective effects of monetary reward and punishment. It is possible that our monetary manipulations provided participants with subjectively higher probabilities of winning more than losing even in the punishment condition (0 yen vs. loss 50 yen). A study that would reward participants only on – for example – 20–30% of total trials in all conditions is needed to control for frequency effects in reward and punishment. Another possibility might be that subjective values of outcome possibly did not differ between the reward and punishment conditions. Both reward and punishment are operationalized as winning more money the fewer errors are committed, although there was a difference in monetary value between punishment and reward conditions. However, post-error slowing was present specifically in the reward condition, even though ERN did not differ between reward and punishment conditions. Further studies need to be conducted whether there are differences in influence between punishment and reward as a function of the magnitude of these factors or – more generally – of the subjective value of the different conditions.

In sum, we found that partial-error ERNs are modulated by the affective-motivational significance of errors. If the errors are important for participants, ERN amplitudes are larger even on partial-error trials. This suggests that similar mechanisms underlie both the full-error ERN and the partial-error ERN. We also found that higher BAS individuals showed smaller ERNs on the full error trials, and tended to show smaller ERN on partial-error trials in the reward condition. Together, the present findings provide further

evidence that the ERN is related to motivational valence and that similar relationships hold for both full and partial errors.

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