

Dissociable correlates of response conflict and error awareness in error-related brain activity

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ABSTRACT

Errors in speeded decision tasks are associated with characteristic patterns of brain activity. In the scalp-recorded EEG, error processing is reflected in two components, the error-related negativity (ERN) and the error positivity (Pe). These components have been widely studied, but debate remains regarding the precise aspects of error processing they reflect. The present study investigated the relation between the ERN and the Pe using a novel version of the flanker task to allow a comparison between errors reflecting different causes—response conflict versus stimulus masking. The conflict and mask conditions were matched for overall behavioural performance but differed in underlying response dynamics, as indexed by response time distributions and measures of lateralised motor activity. ERN amplitude varied in relation to these differing response dynamics, being significantly larger in the conflict condition compared to the mask condition. Furthermore, differences in response dynamics between participants were predictive of modulations in ERN amplitude. In contrast, Pe activity varied little between conditions, but varied across trials in relation to participants' awareness of their errors. Taken together, these findings suggest a dissociation between the ERN and the Pe, with the former reflecting the dynamics of response selection and conflict, and the latter reflecting conscious recognition of an error.

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1. Introduction

The ability to detect errors, and to adapt behaviour accordingly, is a crucial function in the regulation of ongoing behaviour. An important tool in understanding error processing in humans has been provided by the discovery of neural correlates of performance monitoring. In particular, studies using event-related brain potentials (ERPs) have consistently found two components following errors: the error-related negativity (ERN) and the error positivity (Pe) (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991). The ERN is a negative deflection in the response-locked ERP immediately following an error (Falkenstein et al., 1991). Results from ERP dipole modelling (Dehaene, Posner, & Tucker, 1994), electrophysiological recording in monkeys (Gemba, Sasaki, & Brooks, 1986) and humans (Wang, Ulbert, Schomer, Marinkovic, & Halgren, 2005), and fMRI studies in humans (Carter et al., 1998; Debener et al., 2005) converge to identify anterior cingulate cortex (ACC) as the most likely source of the ERN. The neural generator of the Pe is less well characterised, but a growing body of evidence suggests that this component reflects aspects of error processing that are at least

partially dissociable from those reflected in the ERN (Overbeek, Nieuwenhuis, & Ridderinkhof, 2005).

The aim of the present study was to provide new insight into the functional significance of the ERN and Pe, using a novel variation of the flanker task (Eriksen & Eriksen, 1974) to explore the modulation of these components as a function of response dynamics, error predictability and error awareness. Our primary goal was to distinguish two broad theories of the ERN. According to one view, the ERN is associated with the process of detecting an error (Falkenstein et al., 1991; Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001; Scheffers, Coles, Bernstein, Gehring, & Donchin, 1996). In particular, recent theories emphasise the importance of error expectancy, or learnt error likelihood, as a critical determinant of ACC activity (Brown & Braver, 2005; Holroyd & Coles, 2002). In contrast, an alternative framework associates ACC activity with the detection of response conflict (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Carter et al., 1998). According to this theory, variations in ERN amplitude reflect variations in the level of conflict that develops following errors as continued task processing after an error leads to activation of the correct response (Yeung, Botvinick, & Cohen, 2004). This theory predicts that the ERN should vary primarily as a reflection of the dynamics of response conflict, rather than specifically varying with the expectedness of detected errors.

Although the error processing and conflict monitoring accounts of ACC function are conceptually distinct, in many cases these the-

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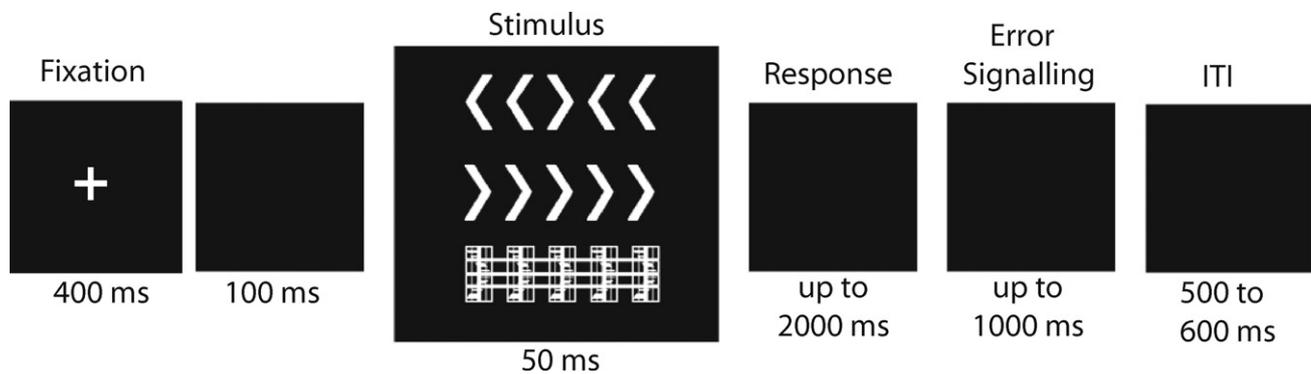


Fig. 1. Experimental procedure. Each trial began with a fixation cross followed by a blank screen. Next, a conflict (top), congruent (middle) or mask (bottom) stimulus was presented (note that only one stimulus was actually presented on any given trial). The screen remained blank during the response and error signalling response windows, and then for a varied inter-trial-interval.

ories make similar predictions. For example, error likelihood and conflict are typically confounded in the standard flanker task: On correct response trials, ACC activity is usually increased on difficult, incongruent trials (in which the central target and irrelevant flanker stimuli are associated with different responses) relative to easy, congruent trials (in which the target and flankers cue the same, correct response). The increase in ACC activity on incongruent trials could reflect the detection of conflict between the responses associated with target and flankers, but could also reflect the higher likelihood of errors on these trials. Meanwhile, on error trials, corrective response activity after the initial error might generate response conflict leading to an ERN (Rodríguez-Fornells, Kurzbuch, & Munte, 2002; Yeung et al., 2004), but might also be a correlate of processing that leads to detection of an unexpected error (Holroyd & Coles, 2002). Thus, in general, conflict and error likelihood should covary, with both increasing as a function of task difficulty. The present study therefore aimed to dissociate task difficulty and response conflict to build a greater understanding of the dynamic processes that engage these different aspects of performance monitoring.

To this end, we explored EEG activity in a modified flanker task in which errors were driven by response conflict in one condition (classic flanker task; conflict condition), and by stimulus degradation in another (mask condition; see Fig. 1 for stimuli). Previous studies have explored the effects of stimulus quality on the ERN, but have typically done so by degrading the stimulus on both congruent and incongruent trials. For example, Scheffers and Coles (2000) presented low-contrast stimuli to study the relation between ERN amplitude and subjective ratings of response accuracy, while Yeung, Ralph, and Nieuwenhuis (2007) used a similar manipulation to compare ERN amplitude on incongruent trials as a function of stimulus degradation. Here the nature and aim of the stimulus degradation manipulation was crucially different: In some blocks we replaced incongruent trials with masked congruent trials to create a condition in which errors would be driven by stimulus masking. Specifically, the level of masking was set so that the stimuli were sufficiently visible to be identified correctly on most trials, but were sufficiently masked to produce the same proportion of errors and equivalent reaction times (RTs) as incongruent stimuli in the conflict condition. Of critical interest was the contrast in error-related EEG activity between these two conditions—masked versus incongruent trials—given that they were associated with equivalent error rates.

To the degree that ERN amplitude reflects the likelihood of detected errors, it should not differ for errors in the mask and conflict conditions, since objective error rates were matched. Importantly, our behavioural pilot testing—which we used to establish an appropriate level of masking to match difficulty with the

conflict condition—indicated that the conditions were also well matched for subjective error rates: participants signalled their awareness of errors at equivalent rates across the two tasks. Participants' responses were therefore equally predictive of accuracy both objectively and subjectively, and thus there is little reason to expect differences in ERN amplitude across conditions as a function of error expectancy or error likelihood. In contrast, although matched in overall performance, the conflict and mask conditions should differ in the dynamics of response selection and conflict, reflecting the different sources of errors in the two conditions.

Detailed computational simulations based on methods used in our prior research (Yeung & Cohen, 2006; Yeung et al., 2004) allow us to formalise the specific predictions of the conflict monitoring theory. Specifically, we contrasted a simulation of the conflict condition—modelled exactly as in our previous research (see Yeung et al., 2004 for full details of model implementation)—with a simulation of the novel mask condition. Masking was simulated as a reduction in the strength of stimulus input (reflecting the difficulty of identifying arrow direction), accompanied by a reduction in attentional focus on the central location (reflecting the fact that congruent flanker arrows need not be actively ignored). These changes resulted in an overall behavioural profile very similar to that seen in the conflict condition, with the conditions matched in terms of mean RT and error rate (Fig. 2a and b). However, the underlying response dynamics were markedly different. In particular, degradation of stimulus input reduced the level of correct response activity both on correct trials (Fig. 2c, dashed grey line) and also, critically, in the period after an error (Fig. 2c, solid grey line). As a consequence of this reduction in correct response activity on error trials, post-error conflict—the simulated ERN—was reduced in the mask condition relative to the conflict condition (Fig. 2d). Thus, although the two conditions are matched in terms of error rate, and hence the predictability of errors (cf. Brown & Braver, 2005; Holroyd & Coles, 2002), the conflict theory provides a rationale for predicting reduced ERN amplitude in the mask condition: a consequence of changes in the underlying response selection process.¹

¹ Corresponding simulation methods can also be used to formalise the predictions of error processing theories. We focused in particular on the reinforcement learning theory of the ERN (Holroyd and Coles, 2002), using the methods introduced by Holroyd, Yeung, Coles and Cohen (2005) for simulating the ERN in connectionist models of the flanker task. Holroyd and Coles (2002) propose that errors are detected, and an ERN produced, when there is activation of incorrect conjunctions of stimulus and response representations (e.g., representations of a left pointing target stimulus and a right hand response). This theory thus predicts that ERN amplitude should depend critically on whether or not a representation of the correct target stimulus is activated around the time of the incorrect response. We therefore ran additional simulations in which we analyzed the activation levels of correct stimulus represen-

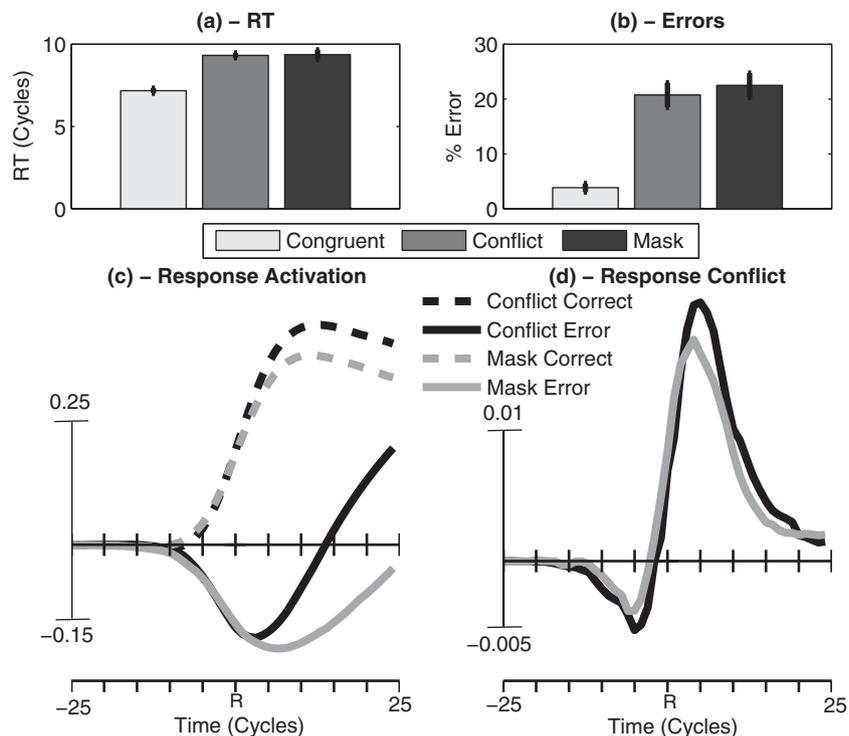


Fig. 2. Simulation results from the conflict monitoring model. (a) Mean RT and (b) error rates for the congruent, conflict, and mask stimuli. (c) Response activation profiles for conflict and mask conditions, separately for correct and error trials, calculated as the difference in activation levels between correct and incorrect response units (plotted on the y-axis). Positive values indicate greater activation of the correct than incorrect response. (d) Simulated response conflict differences between correct and error trials in the mask and conflict conditions. The x-axis indicates simulated time in panels (c) and (d), with 'R' indicating the time of the response.

The first aim of the present study was to test these predictions. To this end, we compared ERN amplitude across our empirical conflict and mask conditions, using the profile of the behavioural data and the lateralised readiness potential (LRP; Coles, 1989) as indices of the contrasting response dynamics across conditions. Rodriguez-Fornells et al. (2002) have previously demonstrated a relationship between the ERN and the post-error LRP activity: They found that quickly corrected errors were associated with a greater LRP deflection (i.e., greater activation of the correct response after the error) and an increased ERN compared with errors followed by slow corrections. In the present study, we used the LRP to investigate differences in response dynamics between conflict and mask conditions, and how these effects related to predicted modulations of the ERN.

The design of our study additionally allowed us to investigate the way in which the two conditions might differ in terms of Pe amplitude and error awareness. Recent theories of the Pe suggest that this component is associated with conscious recognition of an error (Nieuwenhuis et al., 2001; Overbeek et al., 2005). Consistent with this hypothesis, Ridderinkhof, Ramautar, and Wijnen (2009) have shown that the Pe exhibits similar prop-

erties to the P3, a component typically associated with context updating or decision making processes of motivational significance (Nieuwenhuis, Aston-Jones, & Cohen, 2005; Polich & Criado, 2006; Verleger, Jaskowski, & Wascher, 2005). For example, the amplitudes of the P3 and Pe are correlated across individuals, and show similar sensitivity to inter-trial intervals. Ridderinkhof et al. (2009) therefore suggested that the Pe is in effect a P3 to a detected error, and as such marks conscious recognition of a motivationally salient event.

In the present study, participants were asked to signal with a keypress when they thought they had made an error, to allow assessment of whether any differences in ERN amplitude could be explained simply in terms of occasional perceptual errors in the mask condition (i.e., trials on which the arrow direction was incorrectly identified). If so, one would expect consistently fewer errors to be signalled in this condition. However, as noted above, error signalling rates were comparable across conditions. This raises the interesting question of whether Pe amplitude would differ between the conflict and the mask conditions. To the extent that the ERN and Pe reflect successive stages of the same error processing sequence (Falkenstein, Hoormann, Christ, & Hohnsbein, 2000; van Veen & Carter, 2002) one might expect changes in Pe amplitude to track those of the earlier ERN, and thus to be similarly reduced in the mask condition. However, given that the ERN and Pe do not always co-vary (Overbeek et al., 2005), and the Pe has been proposed to vary specifically with error awareness (Nieuwenhuis et al., 2001), one might expect comparable Pe amplitude across conditions. The present study provided a test of these contrasting predictions.

To look ahead briefly, the results indicated a dissociation between the ERN and the Pe, with only the former showing sensitivity to the source of error—response conflict versus stimulus masking. Therefore, to investigate further the relation between ERN and Pe, we made use of multivariate analysis techniques that allow robust estimates of the two components on individual trials (Parra et al., 2002; Parra, Spence, Gerson, & Sajda, 2005). Using this

tations at the time of error commission, separately for conflict and mask conditions. Specifically, we calculated the proportion of error trials on which correct stimulus activation exceeded a threshold at this time. The general pattern of results was unaffected by the particular threshold chosen, so for simplicity we used the same activation threshold as was used for response units in the model (0.18). The critical finding was that representations of the correct stimulus were more strongly activated on mask trial errors than on conflict trial errors, because on conflict trials the correct stimulus is laterally inhibited by incongruent flankers. In consequence, this model predicts that an ERN should be generated on a higher proportion of error trials in the mask condition (83%) than in the conflict condition (77%), and hence predicts that ERN amplitude should if anything be greater in the former condition, the opposite prediction to that derived from our simulations of the conflict monitoring theory.

approach, we investigated trial-by-trial variations in the ERN and Pe, in relation to one another and also in relation to objective and subjective measures of response accuracy. In this way, we aimed to provide a preliminary exploration of the utility of these multivariate techniques in capturing meaningful trial-to-trial variability in error-related ERP activity.

2. Methods

2.1. Participants

The study included 25 paid volunteers, 12 female and 13 male, ages 18–31 years. All participants were right-handed, had normal or corrected-to-normal vision, and had no history of epilepsy. Individuals who were taking psychoactive drugs were excluded from participating. Informed consent was obtained from each participant prior to the experimental session. Five participants were excluded from the analysis described below, two because they were unable to successfully complete one of the tasks, and three because of technical problems with the EEG recording.

2.2. Experimental procedure

Participants were seated in an electrically shielded, dimly lit room for the duration of the experimental session, 100 cm from the stimulus presentation screen. The behavioural tasks were presented using E-Prime version 1.2. Responses were collected using a computer keyboard.

Participants completed a modified flanker task comprising two different versions of the task. One was a standard flanker task in which participants indicated the direction of a central arrow, pointing to the left or right, that was flanked by four further arrows (two on each side) that could be either congruent or incongruent with the target stimulus. Henceforth we label this the “conflict” condition. In the second task, the incongruent trials were replaced by a masked stimulus. On these trials, a series of horizontal and vertical lines were presented across the arrows, which were all congruent, to make them more difficult to identify (see Fig. 1). This task was labelled the “mask” condition.

Participants completed six blocks of each condition, with 68 trials per block. Unmasked congruent stimuli were presented on 50% of the trials in all blocks; incongruent stimuli (in conflict blocks) or masked stimuli (in mask blocks) were presented on the other half of the trials. The first four trials in each block were considered as warm-up trials, and were not included in the EEG analysis. Subsequent trials were pseudo-randomly ordered such that each trial type (left vs. right target arrow; congruent vs. incongruent/masked stimuli) and each trial type transition occurred equally often. Participants completed all six blocks of one task and then all six blocks of the other task, with order counterbalanced across two groups of participants. There were no significant effects of the order in which participants completed the two tasks in either the behavioural or the ERP measures, and therefore all analyses are presented collapsed across groups.

Each trial began with a central fixation cross for 400 ms, followed by a blank screen for 100 ms. Next, the stimulus was presented in the centre of the screen for 50 ms, followed by a blank screen until 1.5–1.6 s after the participant's response. Participants responded using a standard computer keyboard, pressing the “z” key for left-pointing target arrows and the “m” key for right-pointing target arrows. Following the response a blank screen was presented for 1 s, during which time participants were instructed to make an error signalling response by pressing the spacebar if they believed that they had made an error. Finally, an inter-trial interval of 500–600 ms preceded the start of the next trial.

Participants were informed that they should respond as quickly as possible while avoiding errors. They were given feedback at the end of each block informing them of the percentage of trials in that block on which they had made an error, along with the percentage of errors they had correctly signalled. They were also told their average error rate for all the mask blocks and conflict blocks. Participants were encouraged to respond quickly, an instruction that was emphasised if their error rate dropped below 5%. This instruction emphasized only the importance of responding quickly; participants were not instructed to try to make more errors. If their error rate exceeded 20% they were instructed to respond with more care. Before the experimental trials for each of the two block types, participants completed short practice blocks of 32 trials. This practice was repeated until participants performed the tasks quickly and with error rates of roughly 10%, which typically took two blocks.

2.3. EEG recording and data pre-processing

EEG data were recorded from 34 scalp locations and an additional six sites using Neuroscan NuAmps amplifiers. External electrodes were attached to the left and right mastoids, to the outer canthi of the left and right eyes, and above and below the right eye to measure eye movement and blinks. The EEG was digitised at 1000 Hz with a 0.1–200 Hz band-pass filter, referenced to the left mastoid. The data were re-sampled offline to a 200 Hz sample rate, with a 20 Hz low-pass filter and a 0.5 Hz high-pass filter. Ocular artifact correction was conducted in Neuroscan using a regression approach (Semlitsch, Anderer, Schuster, & Presslich, 1986). Data were segmented from –1000 ms to 1500 ms relative to target onset. Bad (noisy) channels

were replaced by an interpolated weighted average from surrounding electrodes using EEGLAB in Matlab (Delorme & Makeig, 2004). Segments containing further artefacts, identified by visual inspection, were removed prior to averaging. EEG pre-processing was conducted using Neuroscan with later averaging and data handling using EEGLAB (Delorme & Makeig, 2004) and custom Matlab scripts.

2.4. ERP analysis

Our analysis of averaged ERPs focused on the ERN and Pe, which are evident as successive deflections in the response-locked ERP following errors, and on the lateralised readiness potential (LRP), an index of cortical motor activity. Response-locked ERPs were calculated by averaging relative to the response time on individual trials. Baseline activity was removed by subtracting the average voltage from –150 to –50 ms prior to the response. On the basis of the topographic distribution of the ERN and Pe, statistical analysis of these components was conducted at FCz and Pz, respectively. The LRP was calculated by averaging the difference in activity between electrode C3 and C4 for left- and right-hand responses using the equation below (cf. Coles, 1989):

$$LRP = \frac{\text{Mean (C4 - C3) left-hand} + \text{Mean (C3 - C4) right-hand}}{2} \quad (1)$$

Negative LRP values indicate activation of the correct response. LRP activity was baselined to the period from –100 to 0 ms relative to stimulus onset for both stimulus- and response-locked averages.

Where appropriate, factorial analyses were conducted using congruency (congruent, mask/conflict) and condition (mask, conflict) using the congruent trials from the two block types separately. For display purposes, we collapsed the data across congruent trials in the conflict and mask blocks, which did not differ significantly across any of the comparisons reported. The analyses reported below included both signalled and unsignalled errors. The results of analyses excluding unsignalled errors, which made up a very small proportion of the total, were essentially identical.

2.5. Single-trial analysis

As discussed in detail below, our conventional ERP analyses revealed interesting dissociations between the ERN and the Pe across the conflict and mask conditions as a function of response dynamics and error awareness. To explore these dissociations in more detail, we conducted an analysis of ERN and Pe amplitude on individual trials using the logistic-regression based linear derivation method introduced by Parra et al. (2002). This approach identifies the spatial distribution of scalp EEG activity in a given time window that maximally distinguishes two conditions—here correct versus error responses—to deliver a scalar estimate of component amplitude on each trial. The derived estimates are robust (i.e., have high signal-to-noise) because the discriminating component acts as a spatial filter that estimates component amplitude as a spatially weighted average across electrodes for each trial, in much the same way that conventional ERP analysis averages across trials to reduce noise (cf. Parra et al., 2002). We used the resulting classification values to explore the correlation between ERN and Pe amplitude across trials, and to explore variability in the ERN and Pe as a function of error awareness (signalled vs. unsignalled errors). These analyses were not possible in our raw data because of the high autocorrelation between neighbouring time windows in EEG data, and the low signal-to-noise ratio for ERPs based on small trial numbers (specifically, unsignalled errors).

The single-trial analysis was conducted separately for each participant by training the logistic regression classifier to discriminate error versus correct trials. Errors were pooled across mask and conflict conditions then compared with a matched number of randomly selected correct trials. Single-trial component amplitudes were calculated separately for each condition (i.e., for correct vs. error trials for the conflict and mask conditions). To increase robustness, component amplitudes were calculated as the mean across 100 permutations of the classifier analysis, with each permutation using a different randomised subset of correct trials. Classification robustness was assessed using leave-one-out cross-validation, quantified as the Az score (which corresponds to the area under the Receiver Operating Characteristic curve) (cf. Stanislaw & Todorov, 1999). Az scores were further evaluated using a bootstrap analysis in which scores were calculated for data in which truth labels were randomised. Classification was conducted for both the ERN and the Pe time windows (corresponding to those used in our standard ERP analysis). Statistical analyses of differences between signalled and unsignalled errors for each subject were conducted on the basis of means and standard deviations of the single-trial output values, using z-scores to determine the significance level of observed differences.

3. Results

We first conducted analyses of the behavioural and LRP data to establish that, as intended, the conflict and mask conditions would be matched in terms of overall performance but would differ in their underlying response dynamics. We then investigated the impact of these differing response dynamics on the ERN and Pe, as

Table 1

Behavioural performance, showing mean RTs (in ms), error rates, and error signalling performance; standard deviations are given in parentheses.

	Conflict condition		Mask condition	
	Congruent	Conflict	Congruent	Mask
Correct RT	388 (42)	495 (75)	376 (34)	490 (76)
Error RT	290 (58) ^a	380 (78)	286 (29) ^a	399 (71)
Error rate	0.02 (0.02)	0.16 (0.06)	0.02 (0.02)	0.16 (0.06)
Error signalling hits	0.82 (0.2) ^b	0.89 (0.17)	0.81 (0.21) ^b	0.82 (0.17)
Error signalling FAs	0.001 (0.002)	0.005 (0.007)	0.001 (0.002)	0.009 (0.01)
Error signalling RT	476 (187) ^a	511 (116)	431 (142) ^a	515 (126)

^a Taken from 7 participants who made at least 5 errors for congruent trials in both of the 2 tasks (mask and conflict).^b Taken from 17 participants who made at least 1 error on congruent trials in both conflict and mask blocks.

measured through conventional ERPs and our single-trial classifier analyses.

3.1. Task performance

Table 1 presents mean reaction times (RTs) and error rates for the mask and conflict blocks. Analysis of correct trial RTs revealed a significant main effect of stimulus type (congruent vs. conflict/mask), $F(1,19)=133$, $p<.001$, reflecting increased RTs in the conflict and mask trials compared to congruent trials, but there was no main effect of condition (conflict vs. mask; $F<1$) and no significant interaction between condition and congruency ($F<1$). A corresponding analysis of error rates likewise revealed a significant main effect of stimulus type, $F(1,19)=136$, $p<.001$, reflecting increased error rates on mask and conflict trials relative to congruent trials, but again no main effect of condition ($F<1$) and no condition by stimulus type interaction ($F<1$). These combined results indicate that our masking manipulation was successful in producing overall levels of performance comparable to those seen on conflict trials. This comparability also extended to performance on error trials. Error RTs on conflict/mask trials were significantly faster than correct RTs, $F(1,19)=137$, $p<.001$, but did not differ between the conflict and the mask conditions, as highlighted by the absence of a main effect of condition ($F<1$) and a non-significant condition by accuracy interaction, $F(1,19)=1.83$, $p=.19$. Error RTs for those 8 participants who made enough errors on congruent trials to calculate a reliable RT (at least 5 errors per cell), were also not significantly different between the conflict and the mask conditions ($t<1$).

In addition to exploring RTs and error rates, we compared error signalling performance between mask and conflict conditions (Table 1). For error signalling hits (correctly identified errors) there was no significant difference between mask and conflict conditions, $t(19)=1.5$, $p>.05$. We also explored error signalling hits on congruent trials in the two conditions for those seventeen participants who made at least one error in each. Again, the results did not differ ($t<1$) between conditions. Error signalling false alarms (correct responses that were signalled as errors), were significantly more frequent on mask/conflict trials than congruent trials ($F(1,19)=13$, $p<.01$), but did not differ between the two tasks (main effect of task: $F<1$; interaction between task and congruency: $F(1,19)=1.1$, $p>.05$). Finally, error signalling RTs were also well matched across the two conditions both for conflict/mask trials ($t<1$), and for congruent trials ($t<1$). These analyses show that, as with primary task performance, error processing appears to be broadly well matched between the mask and the conflict conditions.

3.2. Response dynamics: conditional accuracy and the LRP

The conflict and mask trial conditions were therefore closely matched in terms of overall performance. However, detailed analyses of the behavioural and LRP data indicate that the con-

ditions differed in terms of their underlying response dynamics. To illustrate these differences, Fig. 3a presents conditional accuracy functions across conditions, plotting accuracy after dividing the trials in each condition into twelve RT bins. For the conflict condition, accuracy was significantly below chance for the fastest trials, $t(19)=-4.5$; $p<.001$, and rose steadily for slower RT bins. Performance did not differ from chance level in the second RT bin, but was above chance (at $p<.001$) in all subsequent bins. This pattern of performance is consistent with previous findings (Gratton, Coles, & Donchin, 1992) that have been taken to reflect fast initial processing of the flanker stimuli—resulting in below-chance performance—that is followed by a gradually increasing focus on the relevant target stimulus and hence increasing accuracy (Cohen, Servan-Schreiber, & McClelland, 1992). A contrasting pattern is evident in the mask condition, for which performance was at chance in the fastest RT bin ($t<1$) and above chance thereafter ($p<.001$). A direct comparison between the two conditions revealed that conflict trials were significantly less accurate than mask trials in the first time bin, $t(19)=-4.5$; $p<.001$, with this effect reversed in the fourth fifth, sixth and seventh time bins (at $p<.05$).

These conditional accuracy data are suggestive of contrasting response selection processes across the conflict and mask conditions, a conclusion lent further weight by the results of analyses of stimulus- and response-locked LRP data. Fig. 3b plots stimulus-locked LRPs for correct trials in each condition. These data indicate that conflict trials were characterised by early activation of the incorrect response (indicated by an arrow) that was absent for mask trials and congruent trials. This early difference between conflict and mask conditions, reliable in the 220–270 ms window after stimulus onset, $t(19)=2.3$, $p<.05$, was followed by a later reversal during which there was greater activation of the correct response on conflict than on mask trials. The later difference was reliable in the time window from 350–450 ms post-stimulus centred on the peak of the LRP for conflict and mask conditions, $t(19)=2.8$; $p<.05$. These findings are consistent with our simulation results, in which activation of the correct response was reduced on mask trials (Fig. 2c) as a consequence of the degradation of stimulus information in this condition.

Critically for our predictions regarding error-related activity, further dissociations between the conflict and the mask conditions were evident in our analysis of the response-locked LRP on error trials (Fig. 3c). As has been observed previously, error trials were characterised by a biphasic activation pattern in which initial activation of the incorrect response was followed by a swift return to baseline and even post-error activation of the correct response. Crucially, this late corrective deflection was larger following errors in the conflict condition than following mask trial errors, a difference that was reliable in the time window from –30 ms to 10 ms relative to the response, $t(19)=2.3$, $p<.05$. The increased reversal in the response-locked LRP on conflict trials was predicted by our simulations, where it reflected increased activation of the correct response following error commission. This increased corrective

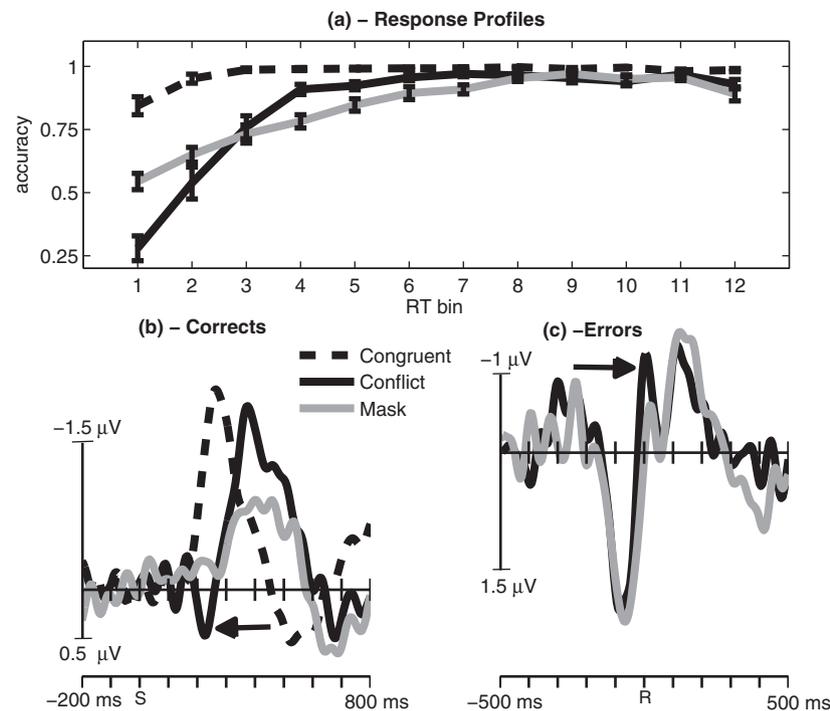


Fig. 3. Response dynamics. (a) Conditional accuracy as a function of RT, with data divided into twelve bins sorted from fastest (1) to slowest (12), separately for the congruent, mask and conflict conditions. (b) Stimulus-locked ('S') LRP for correct trials in the congruent, mask and conflict conditions. (c) Response-Locked ('R') LRP for error trials in the mask and conflict conditions.

activity is predicted to result in greater conflict with the initial error and, hence, an increased ERN. Of interest, then, are the patterns of error-related brain activity for the two conditions.

3.3. Error-related brain activity

Fig. 4a presents grand averaged response-locked ERP waveforms for the mask and conflict conditions, separately for correct and error trials. The ERN was clearly evident as a negative deflection peaking roughly 35 ms post-response, focused over frontocentral scalp locations (Fig. 4c). We therefore quantified the ERN as the average voltage at electrode FCz in a 40 ms window around its peak latency. The Pe was apparent as a longer-lasting positive deflection over posterior scalp locations (Fig. 4b and d), and was quantified as the average voltage at electrode Pz in a window from 150 to 450 ms post-response.

Analysis of the ERN time-window revealed a significant main effect of accuracy, $F(1,19) = 14.4$, $p < .001$, reflecting the presence of a robust ERN following incorrect responses. Critically, a significant condition by accuracy interaction, $F(1,19) = 5.1$, $p < .05$, indicated a difference in the amplitude of the ERN between the mask and the conflict conditions. A subsequent t -test confirmed that ERN amplitude in this time window was significantly greater for conflict trials ($-5.12 \mu\text{V}$) than mask trials ($-2.45 \mu\text{V}$), $t(19) = 2.14$; $p < .05$. This finding of an increased ERN for the conflict condition is consistent with the predictions and simulation results of the conflict monitoring theory described above, and contrast with those of error processing accounts of this component. The precise relationship between this ERN modulation and response dynamics and error processing is explored in more detail below.

Analysis of Pe amplitude revealed a significant main effect of accuracy, $F(1,19) = 71.2$, $p < .01$, highlighting the presence of a reliable Pe following errors. However, in contrast to the ERN results, for the Pe there was no main effect of condition ($F < 1$) nor any significant interaction between condition and accuracy ($F < 1$). Taken together, these results indicate that whereas errors on conflict trials

were associated with an increased ERN, no corresponding modulation was apparent for the Pe.

In a subsequent analysis, we further investigated the nature of the ERN amplitude difference between the conflict and the mask conditions. As described above, these conditions also differed in their underlying response dynamics, with the LRP results indicating greater corrective activity following errors in the conflict condition. According to the conflict monitoring theory, these two effects should be linked: Greater corrective activity should be associated with greater conflict following errors and, hence, a greater ERN. Consistent with this interpretation, individual differences in corrective LRP activity were predictive of differences in ERN amplitude, $r(19) = .526$, $p < .05$ (Fig. 5a): Participants with greater corrective activity in the conflict condition showed a greater ERN difference between the mask and the conflict conditions. In contrast, ERN amplitude was not predicted by between-condition differences in either overall error rate, $r(19) = .2$, $p > .1$ (Fig. 5b), or rate of error signalling, $r(19) = .05$, $p > .5$ (Fig. 5c). These latter results demonstrate that although the level of masking was fixed across participants rather than individually matched for difficulty with the conflict condition, idiosyncratic individual differences in error rates did not drive the observed between-condition differences in ERN amplitude. Indeed, as is evident from Fig. 5b, the relative difficulty of the mask and conflict conditions was relatively stable across participants. Taken together, therefore, these correlation results provide further support for the notion that the ERN modulation in our experiment was associated with patterns of response dynamics, not error expectancy or error awareness.

3.4. Single-trial analyses

Our final analyses used a logistic regression classifier (Parra et al., 2002) to derive measures of the ERN and Pe on individual trials. As an indication of the robustness of the measures provided by this technique, Fig. 6a presents classification (A_z) scores from each participant for the ERN and Pe components, plotted against the

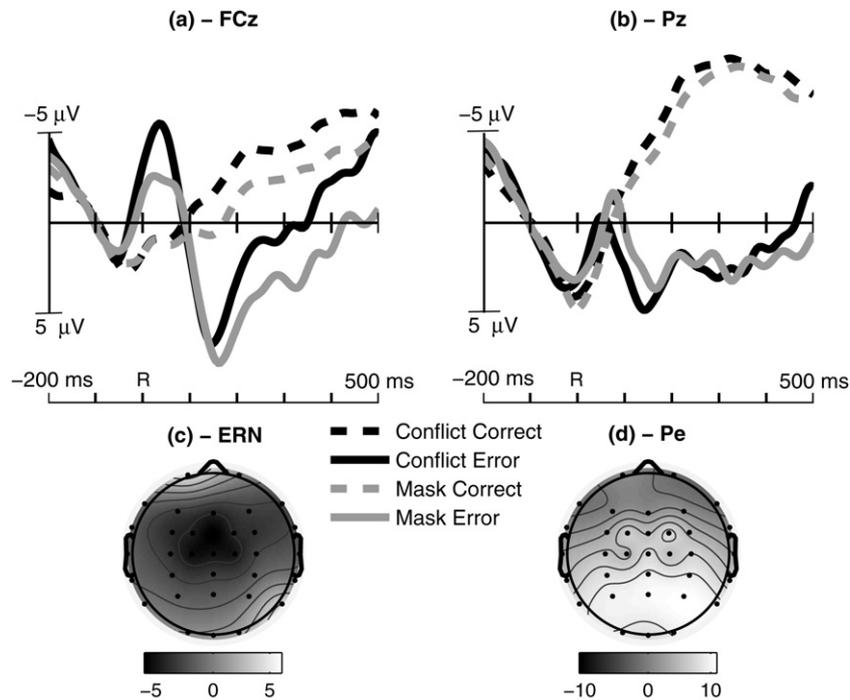


Fig. 4. Response-locked ERP data. ERP waveforms are time-locked to the response ('R') for (a) frontocentral and (b) parietal electrode sites, for correct and error trials in the mask and conflict conditions. Topographic distributions of the (c) ERN and (d) Pe components for the conflict condition were calculated as the voltage difference between error and correct trials.

randomised control data (which establish a bootstrap significance level). The data indicate that for 19 out of the 20 participants we were able to classify reliably above chance whether the response on an individual trial was correct or incorrect on the basis of the ERP data alone: For 16 participants, above-chance classification (at $p < .01$) was possible using either the ERN or Pe time-window; for 3 other participants, above-chance classification was possible only using the Pe window classification value. Pe classification scores were numerically higher than ERN scores for all 20 participants, a difference that was reliable (at $p < .01$) for 10 participants.

Fig. 6 also presents distributions of single-trial component amplitudes (classifier output values) for correct and error trials in the two conditions (mask and conflict), averaged across participants. The figure illustrates once again that the classifier effectively distinguished correct trials (with mostly low component amplitudes) from error trials (with mostly high component amplitudes) for both the ERN and the Pe windows (Fig. 6b and c, respectively). The vertical bars in each panel indicate the grand averaged component score for errors and correct trials in the two conditions. As with our conventional ERP analysis, error-related activity more strongly distinguished the mask and conflict conditions in the ERN compared to the Pe time window: An analysis of component amplitudes

revealed a strong interaction between condition (conflict vs. mask) and response accuracy for the ERN, $F(1, 19) = 9.5$, $p < .01$, whereas the corresponding interaction was only marginally significant for the Pe time window, $F(1, 19) = 4.38$, $p = .05$. Taken together, these analyses indicate that the ERN and Pe components each provide reliable single-trial measures of response accuracy, but suggest once again that they represent at least partially dissociable aspects of error processing (cf. Overbeek et al., 2005). However, the observation that single-trial Pe classifier output values were somewhat sensitive to response conflict, although to a lesser extent than the ERN, suggests that the two components are not completely dissociable.

To explore this possibility in more detail, we correlated ERN and Pe amplitude across trials separately for each participant. These correlations were calculated separately for correct and error trials, to ensure that any correlation observed would not be driven by overall differences in error-related brain activity between correct and error trials, but rather by trial-to-trial variations for both trial types. The results of this analysis indicated that the correlation was reliably positive for error trials, $t(19) = 7.5$; $p < .001$. That is, trials with larger ERN amplitude also tended to have larger Pe amplitude. Interestingly, this relationship was also apparent on correct response trials, $t(19) = 14.9$; $p < .001$. Nevertheless, the correlation

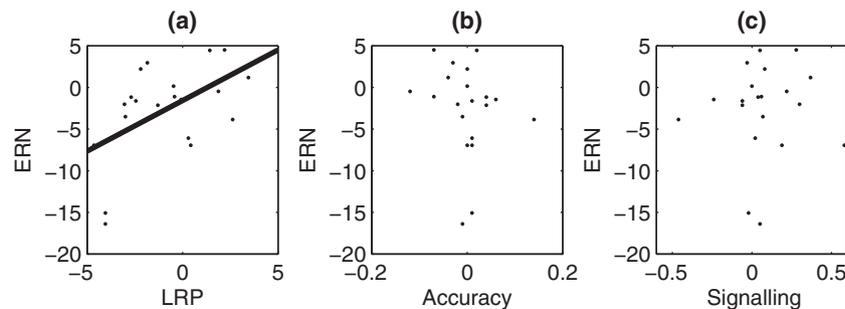


Fig. 5. Correlation between the ERN amplitude difference between mask and conflict conditions and the corresponding between-condition difference in (a) error-correcting activity evident in the LRP, (b) objective error rate, and (c) error signalling rate.

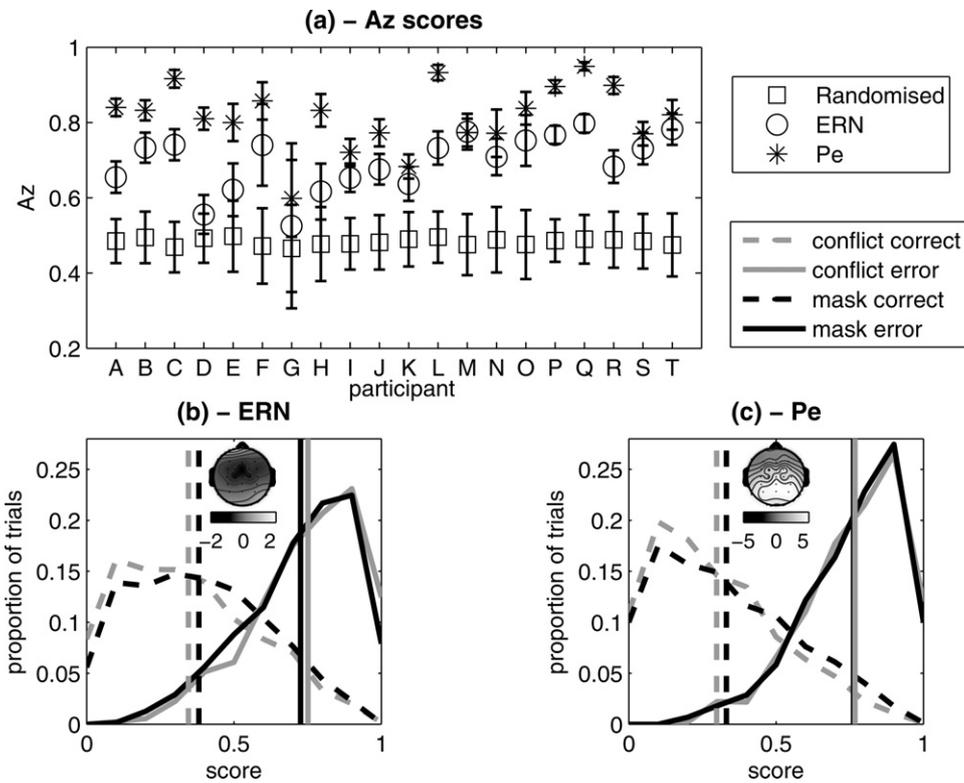


Fig. 6. Logistic regression classifier results. (a) Cross-validated Az classifier scores for the ERN and Pe component time intervals, compared against classification on randomised data (to establish bootstrap significance level) for each participant (labelled A to T). Error bars indicate standard deviations obtained from 100 permutations of the logistic regression classifier. (b and c) Distribution of single trial classifier output values for the ERN and Pe respectively. These histograms are formed for each participant by calculating the proportion of trials in each bin of width of 0.1 for the four conditions, before averaging together the individual participants. The vertical lines represent the mean of single trial classifier output for each condition. Topographic plots show the scalp projections obtained from the logistic regression classifier for each time window.

coefficients were relatively modest (correct trials: mean $r = .228$; range $-.03$ to $.44$; error trials: mean $r = .244$; range $.09$ – $.32$), suggesting that, although there may be common information in the ERN and Pe, there is also a large degree of independent variance in the two components.

Our final single-trial analysis investigated the relationship between the ERN, Pe and error awareness. Participants were asked to signal with a keypress when they thought they had made an error, and generally did so very accurately. Indeed, twelve participants signalled almost every error they made, leaving too few unsignalled errors (mean = 2.4 trials, range = 0–5) to permit a reasonable comparison of signalled and unsignalled errors even for our robust classifier analysis. We therefore only analyzed data for the eight participants with at least 6 unsignalled errors, as previous research suggests that this is a reasonable number of trials to use to explore these components (Olvet & Hajcak, 2009). These participants correctly signalled 75.7% of their errors (S.D. = 15), indicating that their error signalling performance was nevertheless highly reliable overall. Results for these participants are shown in Fig. 7. Fig. 7a plots classifier output values in the ERN time window on single-trials for these participants, contrasting signalled errors (grey circles) with unsignalled errors (black asterisks). Although ERN amplitude was somewhat smaller for unsignalled than signalled errors, this difference was not reliable, $t(7) = 2.0$; $p > .05$. In contrast, the difference between signalled and unsignalled errors was greater, and statistically reliable, in an analysis of the Pe time window, $t(7) = 3.0$; $p < .05$ (Fig. 7b). Follow-up analyses indicated that signalled errors were associated with significantly higher Pe amplitude than unsignalled errors for 6 out of the 8 participants (at $p < .01$). These results indicate that error-related brain activity, in particular in the Pe time window, was predictive of error signalling responses. Given the small number of unsignalled errors

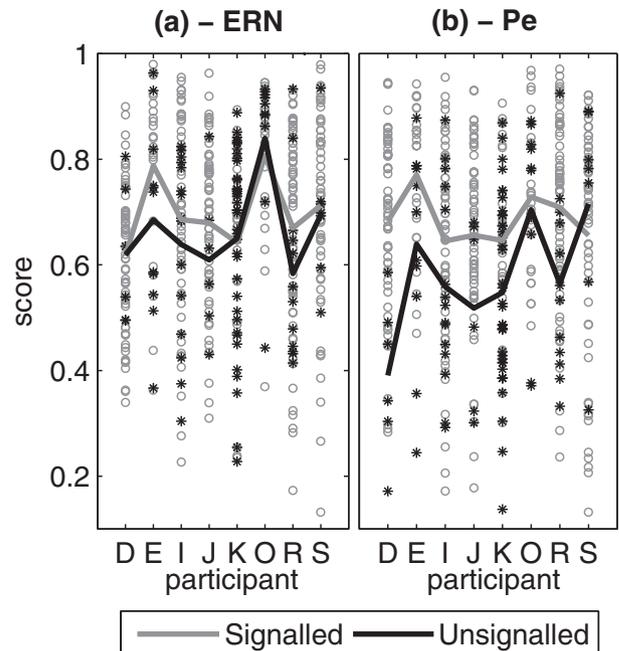


Fig. 7. Single-trial classifier output values for signalled and unsignalled errors. Classifier output values for signalled (grey circles) and unsignalled (black asterisks) errors are shown for those participants (labelled by letter) with at least 6 unsignalled errors separately for (a) the ERN and (b) the Pe. The horizontal lines represent the mean of the distribution of classifier output values for signalled (grey) and unsignalled (black) errors.

in most participants, it is not surprising that this difference did not affect overall ERP amplitude, as noted above. Nonetheless, this result demonstrates that Pe activity in the current task was associated with error awareness, extending previous reports which have observed a corresponding relationship in oculomotor tasks with very high proportions of undetected errors (e.g., Nieuwenhuis et al., 2001).

4. General discussion

The present study explored the influence of error expectancy, error signalling and response dynamics on error-related brain activity. Participants performed a modified version of the Eriksen flanker task, in which errors were primarily driven by incongruent stimulus information in one condition (conflict trials) and by stimulus degradation in a second (mask trials). Our behavioural data confirmed that these two conditions were similar in terms of error rate, the proportion of errors signalled, and mean RTs. However, the tasks differed in terms of their detailed response dynamics. In particular, in contrast to the mask condition, the conflict condition showed below-chance accuracy for the fastest responses, accompanied by LRP evidence of transient activation of the incorrect response (cf. Gratton et al., 1992). Critically, the response-locked LRP indicated that errors on conflict trials were followed by a greater level of corrective activity, and hence greater response conflict, than were errors in the mask condition. Thus, whereas the two conditions were well-matched in terms of objective and subjective expectancy of errors, they differed in terms of the underlying dynamics of response selection and response conflict. In this way, we aimed to produce a dissociation between overall task difficulty and response conflict, two factors that are typically confounded. Of critical interest was the impact of this dissociation on error-related EEG activity.

4.1. ERN, conflict, and error expectancy

The dissociation between error expectancy and conflict dynamics was primarily intended to distinguish two broad accounts of ACC function as it is reflected in the ERN, the conflict monitoring and error processing theories. According to the conflict monitoring theory (Botvinick et al., 2001; Yeung et al., 2004), the ERN can be explained in terms of conflict that develops following errors when continued processing of the stimulus leads to activation of the correct response, creating conflict with the incorrect response just produced. Critically, as predicted by our computational simulations, the LRP data indicated that post-error corrective activity was greater in the conflict condition than in the mask condition. Thus, the conflict monitoring theory would predict greater ERN amplitude in the former condition, an effect that was apparent in the empirical data.

Moreover, if differences in ERN amplitude between the two conditions were driven by differences in response conflict, we should also observe a correlation between the magnitude of the correcting response and the size of the ERN. This prediction was also borne out in the data, with individual differences in LRP amplitude predictive of differences in ERN amplitude between the conflict and the mask conditions. Rodriguez-Fornells et al. (2002) have previously explored the association between LRP and ERN activity, observing differences associated with the speed with which participants made an error-correcting response. Our findings demonstrate that in two different conditions—matched in terms of overall performance but with differing response dynamics—LRP and ERN amplitude appear to covary, and do so in the manner predicted by the conflict monitoring theory.

Our findings are harder to reconcile with theories that associate the ERN with the detection of unexpected errors (Brown & Braver, 2005; Holroyd & Coles, 2002). Simulations based on Holroyd and Coles' (2002) reinforcement learning theory, which proposes that errors are detected as incorrect conjunctions of stimulus and response representations, led to a prediction of greater ERN amplitude in the mask condition, contrary to our empirical results. Along similar lines, Brown and Braver (2005) have proposed that ACC activity reflects the learnt likelihood of making an error. However, given that our conflict and mask conditions were well-matched in terms of objective error rate and levels of error awareness (as reflected in the proportion of errors signalled), such that the stimuli and responses in the two conditions were equally predictive of errors, this theory provides little reason to expect the observed difference in ERN amplitude between conditions. Moreover, we found no evidence of a relationship between ERN amplitude and individual differences in error rate or error signalling accuracy.

However, it might be argued that an alternative explanation of the present findings could be consistent with these error processing theories. Specifically, perhaps participants deliberately made errors or fast guesses in the mask condition to ensure that error rates were matched across the two conditions (despite our instructions solely emphasising response speed). One would expect ERN amplitude to be reduced for these deliberate guesses (Stemmer, Witzke, & Schonle, 2001), such that adopting this strategy would lead to a reduced ERN for the mask condition. Similarly, corrective activity in the LRP should be reduced for errors that were deliberate guesses rather than genuine (but flawed) attempts to respond quickly and accurately. In this case, although our findings might still provide useful evidence about the neural correlates of errors with different causes, they would not fully discriminate between the conflict and the error processing theories as intended.

It is therefore critical that several features of our data argue strongly against this alternative interpretation of the ERN difference between conditions. First, if errors in the mask condition disproportionately reflected deliberate guesses, one would expect Pe amplitude to be reduced in this condition as well, since the Pe is strongly associated with awareness and evaluation of the motivational significance of errors (Ridderinkhof et al., 2009). However, Pe amplitude was equally large for mask and conflict trials. Second, if errors in the mask condition reflected a specific strategic choice that was distinct from the cause of conflict trial errors, one would expect this difference to be reflected in the behavioural and neural profile of these errors. However, error RTs were no faster and no more variable in the mask condition, contrary to the hypothesis that they contained an unusual number of fast guesses or deliberate errors. Correspondingly, the distribution of ERN amplitudes revealed by the single-trial analysis gave no indication (e.g., in terms of bimodality) that mask condition errors comprised a unique mix of "real" errors and deliberate guesses that should produce no ERN. Rather, trial-to-trial variation in ERN amplitude was similar across the two conditions, but overall amplitude was consistently lower in the mask condition. It is also notable that our model simulations captured these empirical findings without requiring a reduced response threshold in the mask condition to increase the number of errors. Finally, to the degree that fast guesses are defined as responses produced before the stimulus is fully processed, such responses are highly unlikely to be restricted to the mask condition: All current theories of the ERN assume that fast guesses are an important contributing factor to errors even in the standard conflict condition of the flanker task (e.g., Holroyd, Yeung, Coles, & Cohen, 2005; Scheffers & Coles, 2000; Yeung et al., 2004).

These considerations suggest that ERN differences across conditions did not reflect qualitatively different underlying processes, but rather reflected quantitative differences in response dynamics. Our interpretation is that these differing response dynamics led

directly to changes in ERN amplitude, reflecting conflict detection in ACC, but our data do not entirely rule out the possibility that the relationship is less direct than this. In particular, the observation of below-chance performance on the fastest trials in the conflict condition indicates that some errors in this condition reflect “informed” responding—specifically, responding that is informed by the irrelevant flankers—a factor that is not evident for errors in the mask condition. It is possible that error processing might differ in as yet unspecified ways for these informed errors compared with other error types. However, until this account can be shown to account fully for the detailed pattern of behavioural and ERP results we have observed—such as the relative absence of Pe differences across conditions—we would continue to favour the hypothesis that ERN differences across conditions are a direct reflection of their differing response dynamics.

In this way, the present findings suggest that the ERN reflects monitoring of the ongoing dynamics of response selection and response conflict, rather than an explicit process of detecting or predicting errors. In this regard, our findings converge with other recent evidence suggesting that ACC activity in speeded decision tasks primarily reflects the current level of cognitive demand, as reflected in the degree of response conflict, rather than the retrospective coding of past performance in specific contexts (Yeung & Nieuwenhuis, 2009). This conclusion might initially appear inconsistent with other theories that emphasise the role of ACC in value-based decision making (Rushworth, Walton, Kennerley, & Bannerman, 2004). However, these theories are in broad agreement that ACC is involved in the optimization of behaviour and action selection (Botvinick, 2007), and it seems plausible that both past experience and current demands must be taken into account to ensure effective behavioural control. As such, these apparently contrasting conclusions might be reconciled within a wider view of ACC function in terms of the integration of long-term influences (such as learned reward contingencies) and short-term constraints (such as experienced difficulty or effort) in decision making and cognitive control.

4.2. Relationship between the ERN and the Pe

Although the initial focus in the present study (and in the foregoing discussion) has been on the ERN as a measure of ACC function, the present findings also bear on the relationship between this component and the Pe. In contrast to the ERN, Pe amplitude was relatively insensitive to the difference in response dynamics across the conflict and mask conditions. Instead, our single-trial analysis revealed that the Pe was significantly increased for signalled as compared to unsignalled errors. It is important to note the caveat that this analysis was conducted using only a subset of participants who, in fact, were the worst at error signalling—although they still detected the vast majority of their errors. Nevertheless, the observed effect is consistent with previous work suggesting that the Pe may be a correlate of conscious detection of an error (Nieuwenhuis et al., 2001; Ridderinkhof et al., 2009). However, whereas many previous studies of error signalling and error awareness have used saccadic eye movement tasks (e.g. Klein et al., 2007; Nieuwenhuis et al., 2001) or difficult tasks in which participants are unaware of a large number of errors (Scheffers & Coles, 2000; Steinhauser & Yeung, 2010), the present study was able to demonstrate this relationship between Pe amplitude and error awareness using a more typical speeded manual decision task.

As such, the present findings add to the growing body of evidence that the ERN and Pe reflect at least partially dissociable processes (Overbeek et al., 2005). The relative insensitivity of the Pe to between-condition differences is particularly striking in this regard, given that ERN amplitude was reduced by 48% in the mask condition relative to the conflict condition. This finding seems on

the surface to challenge the notion that the two components reflect sequential stages of error processing (Falkenstein et al., 2000; van Veen & Carter, 2002): If so, one would expect modulations of the ERN to result in corresponding downstream modulations of the Pe. However, detailed aspects of the present data paint a more nuanced picture of the ERN/Pe relationship. In particular, our single-trial analysis revealed that the amplitudes of the two components were consistently correlated across trials, that ERN amplitude showed some relationship with error awareness (albeit a weak and inconsistent one), and that Pe amplitude varied subtly across the conflict and mask conditions. These observations suggest that it may be premature to reject the hypothesis that the ERN and Pe are functionally linked, rather than simply being coincident indices of two independent processes. For example, it could be that the Pe reflects a transformation of the information contained in the ERN, in which information specific to error processing is extracted from a more general signal relating to the response selection process (and perhaps also combined with other, more general information, for example regarding the motivational significance of ongoing events; Ridderinkhof et al., 2009).

Interestingly, the correlation between ERN and Pe amplitude was apparent on trials with correct responses as well as on error trials, suggesting that monitoring processes reflected in the two components are not specific to errors, but instead provide a continuously varying output that is present to some degree on all trials. This conclusion would be consistent with theories proposing that the ERN reflects the operation of a general performance monitoring system, rather than being specifically related to error detection (e.g., Vidal, Hasbroucq, Grapperon, & Bonnet, 2000; Yeung et al., 2004). The conclusion might also provide useful constraints on developing theories of the Pe component (Ridderinkhof et al., 2009), where it perhaps indicates that the Pe reflects a stage of error processing prior to a binary, categorical decision about response accuracy (cf. Steinhauser & Yeung, 2010). Taken together, therefore, the present findings provide new insight into the monitoring processes reflected in the ERN and Pe, and the relationship between these components.

5. Conclusions

The present study employed a novel variant of the Eriksen flanker task to explore the modulation of error-related brain activity associated with response conflict, while controlling for error-likelihood and error awareness. Our ERP analyses demonstrated that variations in the dynamics of response selection and conflict are associated with modulations of ERN amplitude, consistent with the predictions of the conflict monitoring theory, but contrary to theories that associate the ERN with learned error expectancy in specific task contexts. In contrast to the ERN, the Pe was relatively insensitive to these between-condition differences in response dynamics. Our single-trial analyses demonstrated that Pe amplitude instead varied as a function of participants' awareness of having made an error, but was also partially predictable on the basis of the earlier ERN. These findings support the hypothesis that the ERN and Pe index related but partially dissociable performance monitoring functions, and provide important constraints on what these functions might be. In addition, an important methodological goal of the present study was to provide a preliminary exploration of recently developed multivariate analysis techniques for estimating ERP component amplitudes on individual trials (Parra et al., 2002, 2005). Our analyses indicate that these techniques can indeed provide robust single-trial measures of the ERN and Pe. Crucially, these measures appear to capture meaningful variance that can provide useful insight into the functional significance of these components. Exploitation of this fine-grained information may prove

very valuable in future research that attempts to probe further the relationship between the ERN and the Pe in order to better understand the cognitive and neural basis of performance monitoring.

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