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Research Report

Hierarchical error processing: Different errors, different systems

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ABSTRACT

Error processing during motor control involves the evaluation of “high-level” errors (i.e., failures to meet a system goal) by a frontal system involving anterior cingulate cortex and the evaluation of “low-level” errors (i.e., discrepancies between actual and desired motor commands) by a posterior system involving posterior parietal cortex. We have recently demonstrated that high-level errors committed within the context of a continuous tracking task elicited an error-related negativity (ERN) – a component of the event-related brain potential (ERP) generated within medial–frontal cortex that is sensitive to error commission. The purpose of the present study was to demonstrate that low-level motor errors do not elicit an ERN, but may instead evoke other ERP components associated with visual processing and online motor control. Participants performed a computer aiming task in which they manipulated a joystick to move a cursor from a start to a target position. On a random subset of trials the target jumped to a new position at movement onset, requiring the participants to modify their current motor command. Further, on one half of these “target perturbation” trials the cursor did not respond to corrective movements of the joystick. Consistent with our previous findings, we found that the uncorrectable errors elicited an ERN. We also found that the target perturbations on both correctable and uncorrectable trials did not elicit an ERN, but rather evoked two other ERP components, the N100 and P300. These results suggest that medial–frontal cortex is insensitive to low-level motor errors, and are in line with a recent theory that holds that the P300 reflects stimulus–response optimization by the impact of locus coeruleus activity on posterior cortex.

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1. Introduction

Human error processing appears to be hierarchically organized such that different neural systems are tasked with different types of error evaluation (Krigolson and Holroyd, 2006; see also Doya, 2000; Doya et al., 2001). On one hand, the motor system continuously corrects for “low-level” motor errors as movements unfold. Within a hierarchical framework, low-level errors are defined as discrepancies between the actual

and appropriate motor command precipitated by neuromotor noise or by unexpected changes in the movement environment. For example, as one reaches to pick up a glass, the motor system continually adjusts the reaching trajectory so that the hand accurately finds the target. Importantly, these “low-level” errors are correctable—in the sense that such minor discrepancies can be easily overcome—and appear to be evaluated and corrected by error systems associated with posterior parts of the brain (see below). On the other hand, the

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motor system must also recognize “high-level” errors that indicate that a movement goal can not be achieved. Within the context of the above example, the motor system also determines whether or not the glass has been successfully attained so that it can plan subsequent motor commands accordingly. We have recently provided evidence that high-level errors in continuous motor tasks are processed within medial–frontal cortex (Krigolson and Holroyd, 2006). Note that within this hierarchical framework, low-level errors become high-level errors if left uncorrected. Thus, if for some reason the posterior system is not able to correct a discrepancy between the actual motor command and the appropriate motor command, then a high-level error will ensue.

Seminal research by Woodworth (1899) indicated that movements can be corrected as they unfold, a hypothesis confirmed by research demonstrating that ongoing motor plans can be rapidly adjusted during goal-directed reaching (Goodale et al., 1986). A large body of evidence suggests that the neural substrates underpinning real-time low-level error evaluation include posterior parietal cortex (PPC) and the cerebellum (Blakemore et al., 2001; Desmurget et al., 1999, 2001; Desmurget and Grafton, 2000; Gréa et al., 2002; Miall et al., 2001). Whether these online adjustments depend on a predictive forward model of control (Desmurget and Grafton, 2000; Wolpert and Ghahramani, 2000) or on a feedback-based control mechanism (Chua and Elliott, 1993; Goodale et al., 1986; Gréa et al., 2002; Heath, 2005; Khan and Lawrence, 2005; Khan et al., 2004; Khan et al., 2003; Krigolson and Heath, 2004) remains unclear. Regardless of which position is correct, it is evident that low-level error information can be used to modify ongoing motor behavior while an action is in progress.

Recent electrophysiological studies have identified a component of the event-related brain potential (ERP) associated with high-level error processing. Seminal work by two independent research groups (Gehring et al., 1993; Falkenstein et al., 1991) found that “slips” made during a speeded response task elicited a negative deflection in the ERP peaking about 100 ms after error commission (the response error-related negativity: rERN). Subsequent research by Miltner et al. (1997) demonstrated that error feedback in trial-and-error learning tasks elicited a similar negative deflection in the ERP that reaches maximum amplitude about 250 ms following feedback onset (the feedback error-related negativity: fERN). Source localisation studies of the rERN and the fERN have suggested a common source for both ERP components within anterior cingulate cortex (ACC; Holroyd et al., 2004; Miltner et al., 1997; but see Nieuwenhuis et al., 2005c). Together, the rERN and fERN are proposed to be elicited by a generic error processing system evaluating, respectively, an efference copy of the motor command and external error information. Specifically, the Reinforcement Learning theory of the error-related negativity (ERN: RL-ERN theory, Holroyd and Coles, 2002) holds that the amplitude of the ERN is determined by the impact on the ACC of a reinforcement learning signal carried by the midbrain dopamine system from the basal ganglia. Further, the theory holds that the error signal is generated by the earliest indication that events are worse than expected: A rERN is elicited when the efference copy of the motor command provides the first indication that an error has occurred, and a fERN is elicited when external information provides the first informa-

tion that an error has occurred (for a review see Holroyd et al., 2004).

The ERN also appears to be elicited by errors made during the performance of continuous motor tasks. In a recent study participants performed a continuous computer tracking task in which they attempted to keep a cursor centered between two moving barriers (Krigolson and Holroyd, 2006). In this task an error was defined as contact between the cursor and either of the barriers. We found that high-level tracking errors (cursor–barrier contact) elicited a negative deflection in the ERP, with a latency and scalp distribution consistent with the ERN. These results indicate that medial–frontal cortex is sensitive to high-level errors in continuous motor tasks. Further, we have recently replicated this finding and demonstrated that medial–frontal cortex is also sensitive to internal and external information predicting upcoming tracking errors (Krigolson and Holroyd, in press). Specifically, we found that ERNs were elicited by visual cues and by losses of joystick control when these events predicted subsequent tracking errors.

Our primary goal in the present experiment was to identify ERP correlates evoked by the evaluation of low-level motor errors. Specifically, we hoped to demonstrate that low-level motor errors do not elicit an ERN, but instead elicit other posterior ERP components. In addition, we also hoped to provide further evidence for the hierarchical error-processing hypothesis by demonstrating that high-level errors committed in a manual aiming task also elicit an ERN. We had participants perform a computer-based manual aiming task with three experimental conditions randomly intermixed across trials. In the first experimental condition (control), participants manipulated a joystick to move a cursor horizontally from a start position to a target square. In the second experimental condition (correctable), the target square jumped to a new vertical location immediately following movement onset, forcing participants to adjust for the target perturbation with a further manipulation of the joystick. In the third experimental condition (uncorrectable), the target jumped as in the correctable condition, but the participants’ cursor failed to respond to corrective joystick movements. By creating a discrepancy between the actual motor command (joystick movement towards the original target location) and the appropriate motor command (joystick movement towards the new target location), the target perturbations in the correctable and uncorrectable conditions both resulted in low-level motor errors. Given that these errors were correctable in principle – and thus constituted low-level errors by definition – we predicted that the target perturbations would elicit posterior ERP components but not an ERN. By contrast, the failure of the joystick in the uncorrectable condition constituted a high-level error as it made the goal of

Table 1 – Behavioral data as a function of experimental condition

Condition	Reaction time (ms)	Movement time (ms)	Correctable time (ms)	Accuracy (%)
Control	519±12	1377±15	n/a	93.2
Correctable	534±14	1391±21	471±112	84.1
Uncorrectable	530±14	1441±129	470±107	0

reaching the target unattainable. In these instances we predicted that the high-level errors would elicit an ERN.

2. Results

2.1. Behavioural data

Reaction time did not differ between the three experimental conditions, $F(2,28)=2.22$, $p>0.05$ (see Table 1 for all behavioural

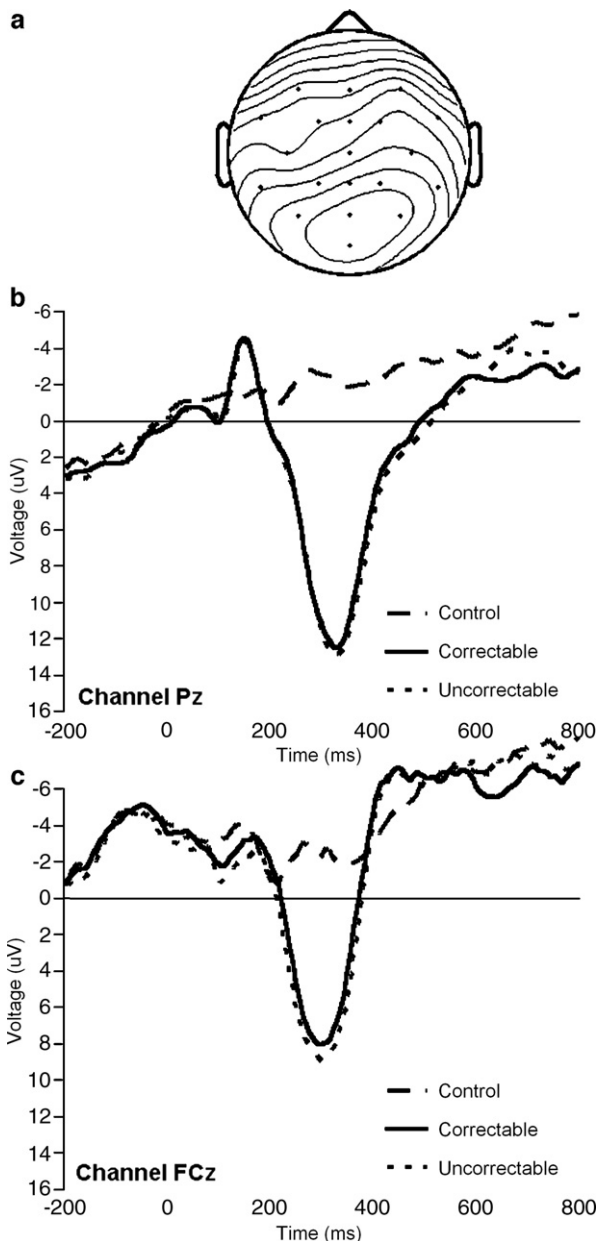


Fig. 1 – Target perturbation: Note that 0 ms corresponds to movement onset. Negatives voltages are plotted up by convention. (a) Spatial PCA factor loadings projected onto the surface of the human head for the posterior factor. (b) Averaged ERP waveforms recorded at channel Pz for the control, correctable, and uncorrectable conditions. (c) Averaged ERP waveforms recorded at channel FCz for the control, correctable, and uncorrectable conditions.

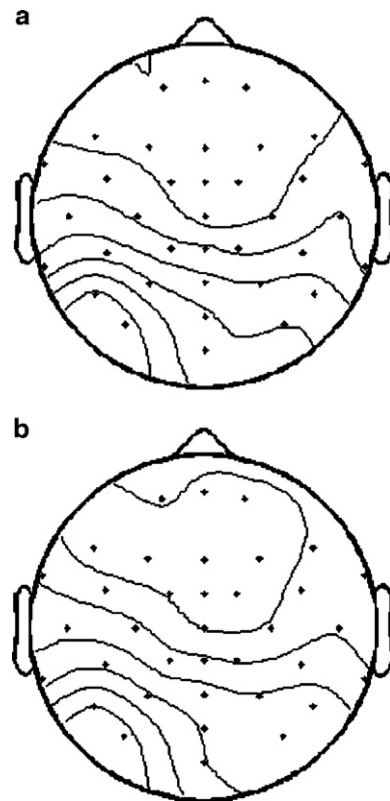


Fig. 2 – Target perturbation: (a) Scalp distribution of the N100 peak associated with the target perturbation for the correctable difference wave. (b) Scalp distribution of the N100 peak associated with the target perturbation for the uncorrectable difference wave.

results). The analysis of movement time yielded a main effect for experimental condition, $F(2,28)=7.76$, $p<0.01$, indicating that movements in the uncorrectable condition were longer than in the control ($t(14)=3.01$, $p<0.01$) and the correctable ($t(14)=2.44$, $p<0.05$) conditions. The time at which participants attempted to correct for the target perturbation did not differ between the correctable and uncorrectable conditions, $t(14)=0.25$, $p>0.05$. Participants were significantly more accurate in the control condition than in the correctable condition, $t(14)=3.60$, $p<0.01$ (note that accuracy associated with the uncorrectable condition is not meaningful as by design participants always erred on these trials). Unfortunately, an electrophysiological analysis of endpoint error could not be conducted due to an insufficient number of off-target trials in the control and correctable conditions.

2.2. Electrophysiological data: The target perturbation

A spatial PCA conducted on the three ERPs averaged to the time of the target perturbation yielded a primary spatial factor that accounted for 40.5% of the spatial variance, and that exhibited loadings that were maximal at channel Pz (see Fig. 1a). The factor scores associated with this factor were submitted to a temporal PCA, which yielded an epoch from 324 to 500 ms that accounted for 43.9% of the temporal variance. These results are consistent with the spatial distribution and latency of the P300 (Dien et al., 2003, 2004; Donchin and Coles,

1988; Spencer et al., 2001). Given these results, we examined the P300 directly by conducting peak analyses on the difference waves constructed by subtracting the control ERPs from the correctable and uncorrectable ERPs recorded at channel Pz (see above; Fig. 1b). Both the correctable ($16.5 \mu\text{V}$; $t(14)=8.18$, $p<0.001$) and uncorrectable ($16.6 \mu\text{V}$; $t(14)=8.19$, $p<0.001$) difference waves were characterized by a large positive deflection in this time range. The amplitude ($t(14)=0.72$, $p>0.05$) and latency ($t(14)=0.65$, $p=0.05$; 328 vs. 324 ms) of the peaks of the difference waves did not differ from one another. Note that the spatial PCA did not yield a front–central PCA factor consistent with the ERN. Further, peak analyses on the difference waves associated with channel FCz did not yield a statistically significant negative deflection within the time window of the ERN (100–400 ms; see Fig. 1c).

Post-hoc visual inspection of the data revealed an N100 component in the correctable and uncorrectable difference waves that peaked 140 ms following the target perturbation. The peak amplitude of the N100 was lateralised over left visual cortex, being maximal at channel PO7 (Fig. 2), where it was statistically different from zero for both the correctable ($-8.29 \mu\text{V}$; $t(14)=8.34$, $p<0.001$) and uncorrectable ($-8.19 \mu\text{V}$; $t(14)=8.30$, $p<0.001$) difference waves.¹ In sum, these results suggest that the target perturbation elicited an N100 and a P300 component, but not an ERN.

2.3. Electrophysiological data: The corrective movement

To evaluate the impact of uncorrectable errors, we conducted a STPCA on the ERP data averaged to the time of the movement correction.² This analysis yielded two spatial factors of interest: a posterior factor with maximal loadings at channels Pz (0.93) and POz (0.96) accounting for 51.2% of the spatial variance, and a frontal–central factor (Fig. 3a) with maximal loadings at channel FCz accounting for 18.0% of the spatial variance. As the posterior factor appeared to be associated with the P300 that preceded the corrective movement, we focused our analysis on the frontal–central factor. The temporal PCA on the spatial factor scores associated with the frontal–central factor yielded a temporal factor with maximal loadings from 196 to 256 ms following the attempted correction (accounting for 22.7% of the temporal variance), an epoch consistent with the latency of the fERN. Given these results, we conducted a peak analysis on the difference waves constructed by subtracting the correctable ERPs from the uncorrectable ERPs (Figs. 3b and c) for channel FCz. This analysis revealed a significant negative deflection ($t(14)=8.9$, $p<0.001$; $-5.3 \mu\text{V}$) with a latency of 248 ms and a frontal–central distribution, a result consistent with the spatial distribution and

¹ Note that Fig. 2 shows the waveforms locked to the target perturbation plotted for channel Pz. However, the statistical analysis of the N100 component was done on channel PO7 where it was maximal.

² Note that we were concerned that predictive attempts to correct for a target perturbation (i.e., a diagonal movement of the joystick) before a target perturbation occurred would bias our results. As such, if diagonal pressure was applied to the joystick before a target perturbation occurred then we removed that trial from further analysis (less than 1% of experimental trials were discarded because of this criterion).

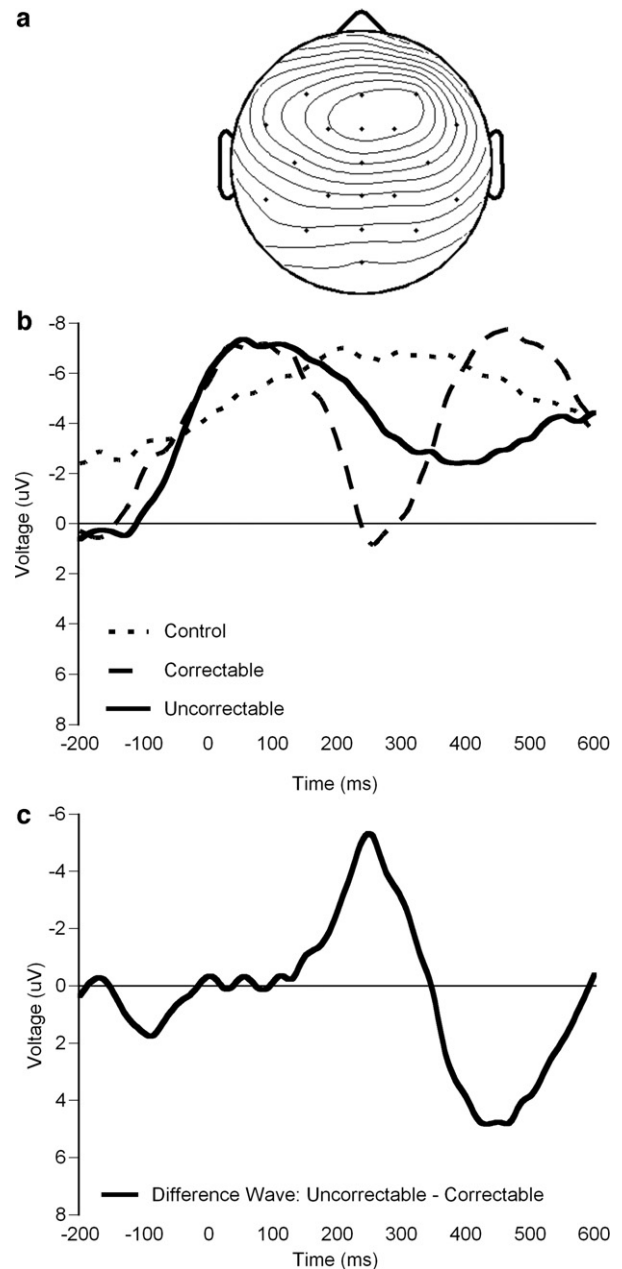


Fig. 3 – Movement correction: Note that 0 ms corresponds to movement onset. Negatives voltages are plotted up by convention. (a) Spatial PCA factor loadings projected onto the surface of the human head for the front–central factor. (b) Averaged ERP waveforms recorded at channel FCz for the control, correctable, and uncorrectable conditions. (c) Difference wave (uncorrectable – correctable) at channel FCz.

timing of the fERN (Ruchow et al., 2002; Krigolson and Holroyd, 2006; Miltner et al., 1997). Note however that the movement times were longer in the uncorrectable condition relative to the correctable condition, so this difference between the ERPs could reflect differential motor activity rather than error processing *per se*. To show that this front–central negativity was not in fact a motor potential, we created difference waves for each participant based on subsets of trials in the correctable and uncorrectable conditions that were matched

according to their movement times. In line with the previous analysis, we found a significant negative deflection ($t(14) = 3.9$, $p < 0.01$: $-9.00 \mu\text{V}$) with a latency of 260 ms and a front-central scalp distribution (see Supplementary Fig. 1). These results suggest that the uncorrectable errors in fact elicited a fERN.

3. Discussion

3.1. Low-level errors: The N100 and the P300

In this study, we sought to demonstrate that low-level motor errors do not elicit an ERN, but rather elicit other posterior ERP components associated with the processing of visual target information. Furthermore, we sought to demonstrate that high-level errors within the same trial do elicit an ERN. Participants manipulated a joystick to move a cursor from a start position on the left of a computer screen to a target position on the right. Complicating this, on some trials following movement onset, the target disappeared and jumped to a new location, requiring participants to execute a corrective motor command. Further, on one half of these target perturbation trials the joystick did not respond to the corrections. At the start of each trial, participants could not predict whether or not a target perturbation would occur, and at the time of the target perturbation, they could not differentiate the correctable from the uncorrectable trials until they attempted the movement correction. Thus, although the perturbation invalidated the current motor command, the goal of the task (moving the cursor to the target) was in principle still attainable at the time of the perturbation. For this reason, the medial-frontal system should not have evaluated the perturbation as a high-level error, and indeed we found that the perturbation did not elicit an ERN. By contrast, the perturbation constituted a low-level motor error because it resulted in a discrepancy between the actual and appropriate motor command. Thus the posterior error system should have evaluated the perturbation as a low-level error, and in fact we found that the perturbation elicited two distinct posteriorly distributed ERP components, the N100 and the P300 (Fig. 4).

The N100 was elicited shortly following the target perturbation (140 ms) and was maximal over left visual cortex. This result is consistent with previous reports that target stimuli appearing in the left or right visual field elicit a posterior N100 lateralised over the contralateral hemisphere (Kasai et al., 2003; Pazo-Alvarez et al., 2004; Spironelli et al., 2006). Because all of the target perturbations in the present study occurred in the right visual field, we believe that the left lateralised N100 component reflects the detection of the target perturbation by visual cortex. Interestingly, the timing of the N100 in the present study (140 ms) is similar to the minimum time believed to be required for feedback-reliant control processes (Desmurget and Grafton, 2000; Jeannerod, 1988; Paillard, 1996).

Although it may not be surprising that the target perturbations in the present study elicited an ERP component normally evoked by changes in the visual environment, our results may be considered in terms of the functional consequences of the underlying neural process. The timing of the N100 in the present study (≈ 140 ms) is too slow to simply reflect the arrival of visual information in primary visual cortex (which typically

is observed as a C1 waveform and begins 40–60 ms after stimulus onset; Clark et al., 1995). As such, it seems likely that the N100 observed in the present study may reflect neural activity associated with a more advanced stage of visual processing, such as the detection of an unexpected environmental change, the magnitude of the change, the location of the change, and so on (cf. Milner and Goodale, 1993). Importantly, these functions are necessary for the detection and correction of low-level errors by the posterior system. Although the N100 in the present study may be representative of low-level error evaluation by posterior parietal cortex, a neural region associated with the online control movement (cf. Desmurget et al., 1999), the scalp distribution of the N100 is inconsistent with this hypothesis. Alternatively, the scalp distribution of the N100 may be more consistent with the “ventral visual stream”, and recent evidence suggests that information from the ventral stream can also be utilised for the online control of movement (i.e., Krigolson and Heath, 2004; Krigolson et al., in press).

We also found that the target perturbation elicited an ERP component characterized by a timing, polarity, and scalp distribution that is consistent with the P300 (Donchin and Coles, 1988; Nieuwenhuis et al., 2005a). The P300 is a large, positive-going, parietally distributed deflection in the ERP that peaks 300 ms or later following stimulus onset (Sutton et al., 1965), and is typically elicited by surprising events. For example, in the “oddball task” participants respond to (or silently count) infrequently occurring target stimuli, which elicit a large P300 (Bekker et al., 2005; Donchin and Coles, 1988; Duncan-Johnson and Donchin, 1977; Jackson et al., 1999). Although the location(s) of the generator(s) that produce the P300 is not exactly clear, research suggests a P3 source near the temporal-parietal junction (Calhoun et al., 2006; Halgren et al., 1995; Kiss et al., 1989; Knight et al., 1989; Menon et al., 1997; Molnar, 1994; Smith et al., 1990; Verleger et al., 1994; Yamaguchi and Knight, 1991, 1992).

As with the N100, it is unsurprising that the target perturbations elicited a P300, which is normally elicited by unexpected task-relevant events. Nevertheless, our results may provide insight into the cognitive process that generates the P300. A prominent theory of the P300 holds that this ERP component indexes “context updating” (Donchin and Coles, 1988), such that it is elicited by the active updating of an internal model of the environment upon receipt of new information. It is interesting to note that an important aspect of rapid motor control involves comparing the consequences of the current motor command to the movement’s desired end-state (Desmurget and Grafton, 2000). To do so, the system must continuously predict the outcome of the current motor command while simultaneously monitoring the external environment for changes that would negate its effectiveness. This process entails the development and execution of an internal forward model of the environment that must be updated in response to unpredicted events. Given that the context-updating hypothesis proposes that the P300 is elicited by just such an occurrence (Donchin and Coles, 1988), and given the proximal location of the temporal-parietal junction to PPC, we speculate that the P300 in this task may index the revision of an internal forward model by posterior cortex and thus may reflect part of the low-level error evaluation process.

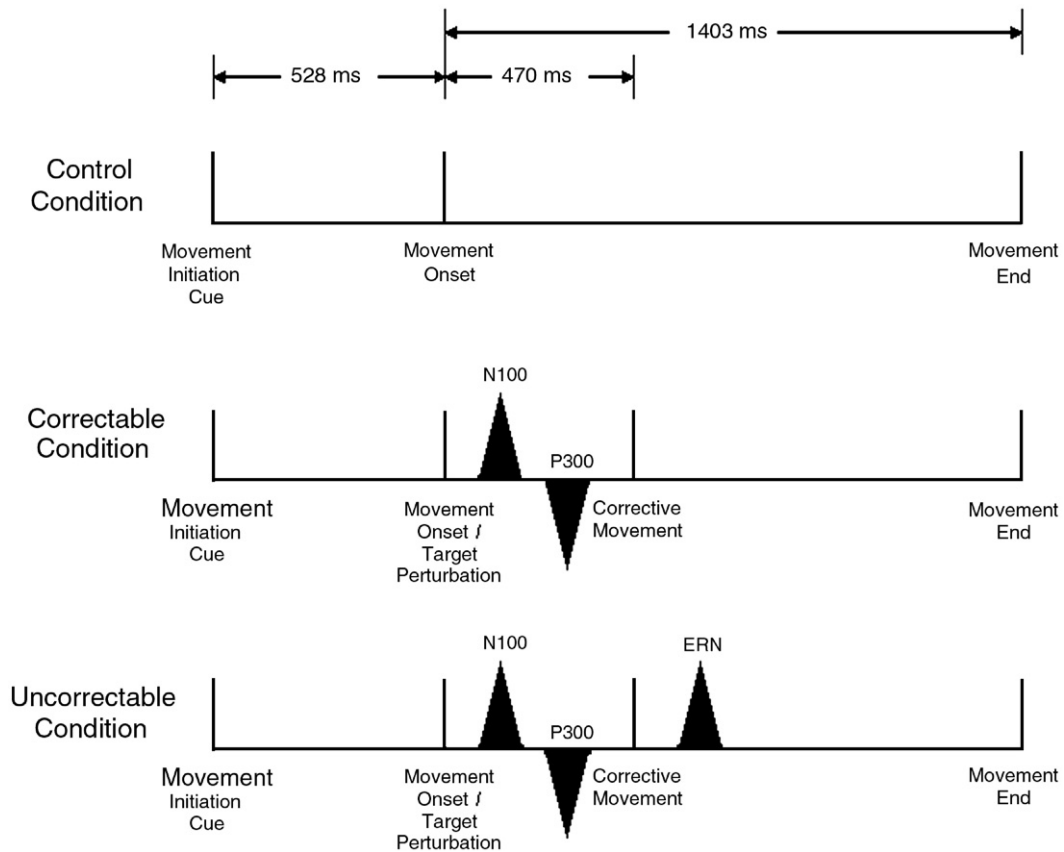


Fig. 4 – Experimental timeline: A summary of the experimental events and the evoked ERP components in the control, correctable, and uncorrectable conditions. Note that the times reported here are averages of the values reported in Table 1.

The results of the present study are also compatible with a more recent theory that holds that the P300 is evoked by the impact of phasic activity of the locus coeruleus (LC)–norepinephrine (NE) system on posterior cortex (Nieuwenhuis et al., 2005a,b). Phasic activity of the LC–NE system is associated with the presentation of task relevant stimuli (Aston-Jones and Bloom, 1981; Aston-Jones et al., 1994; Foote et al., 1980; Nieuwenhuis et al., 2005a,b) and appears to be time-locked to the behavioural response initiated by the stimulus (Bouret and Sara, 2004; Clayton et al., 2004; Rajkowski et al., 2004). In this context, the LC–NE system appears to increase the gain of target neurons in cortex, the thalamus, and the cerebellum to optimize the decision-making process (Servan-Schreiber et al., 1990).

In the present experiment the target perturbation created a low-level motor error which forced participants to rapidly change their current motor command. Given that phasic activity of the LC–NE system appears to facilitate rapid decision making, it seems reasonable to assume that the target perturbation would activate this system. The LC–NE system projects to parietal cortex (amongst other brain regions; Aston-Jones et al., 1984; Berridge and Waterhouse, 2003) and thus may have a direct impact on PPC, a neural region associated with the online control of movement (Desmurget et al., 1999, 2001; Gréa et al., 2002). If the LC–NE theory of P300 generation is correct (Nieuwenhuis et al., 2005a,b), then this process would also elicit a P300. Consistent with this inference, it appears

that the P300 in this task may reflect a rapid adjustment by the posterior system to low-level motor errors.

Of equal importance is the result that the target perturbations did not elicit an ERN. Within a hierarchical framework, errors are only evaluated as “high-level” by the medial–frontal system if they indicate that the movement goal is no longer attainable. Within the context of the present study, at the time of the target perturbations participants did not know whether or not they would lose vertical control of the cursor. As such, the target perturbations in the present study construed low-level motor errors as they resulted in discrepancies between the actual and the desired motor commands. However, the target perturbations did not indicate that the goal of the task was unattainable, and thus an ERN was not elicited as the medial–frontal system was not activated by these errors.

3.2. High-level errors and the error-related negativity

The second goal of this study was to demonstrate that high-level errors committed during the performance of a discrete manual aiming task elicited an ERN. In the uncorrectable condition of the present experiment corrective joystick movements were prevented. As such, the low-level errors brought about by the target perturbations in this condition became high-level errors when joystick control was reduced. Interestingly, we found that the blocking of corrective joystick movements elicited a deflection in the ERP that exhibited a latency

and scalp distribution consistent with the fERN (Holroyd et al., 2004; Miltner et al., 1997), which is thought to be produced in medial-frontal cortex (Holroyd and Coles, 2002; but see Nieuwenhuis et al., 2005c).

It may be asked why such errors would elicit a fERN as opposed to a rERN (e.g., Gehring et al., 1993). Recall that the RL-ERN theory holds that the ERN is elicited by the first indication that ongoing events are worse than expected. According to the theory, the rERN is elicited by an efference copy of the motor command, and as such occurs relatively quickly following the error response (~100 ms), whereas the fERN is elicited by an external feedback stimulus and thus occurs following feedback presentation (~250 ms). Importantly, participants in this task attempted to correct the low-level errors on both correctable and uncorrectable trials, so in both conditions the efference copy would have indicated that the system was producing the appropriate response. Instead, participants relied on visual feedback from the cursor to determine whether or not their error correction was successful. When the joystick failed, this external visual feedback indicated that the system goal would be violated and elicited a fERN. These results are consistent with a previous finding that high-level errors made during the performance of a continuous tracking task also elicited an ERN (Krigolson and Holroyd, 2006, *in press*).

An alternative explanation for the frontal-central negativity elicited by the blocked joystick movement is that it is a motor potential. There is some evidence to suggest that enhanced motor potentials are associated with increased force production or movement duration (i.e., Slobounov and Ray, 1998). In the present experiment it is possible that motor-related differences between correctable and uncorrectable trials gave rise to the frontal-central negativity observed in the difference wave. However, the frontal-central negativity was not lateralised over left motor cortex, suggesting that it was not directly elicited by the motor correction. Furthermore, the ERPs associated with the correctable and uncorrectable conditions began to differ from one another approximately 120 ms following the attempted movement correction (Fig. 3). Considering the long delay before participants responded to the target perturbation (~470 ms), 120 ms would seem to be too little time for the system to both detect the error and initiate the correction (Fig. 4). On the other hand, the scalp distribution and latency of the negativity is exactly consistent with the fERN. For these reasons we believe that the front-central negativity in the present experiment is in fact a fERN.

3.3. A theory of hierarchical error processing

The results of the present study, together with our previous work examining the ERN in the context of a continuous tracking task (Krigolson and Holroyd, 2006, *in press*), suggest that the error processing system is organized hierarchically: high-level errors are evaluated by a neural system involving medial-frontal cortex, and low-level errors are evaluated by a neural system involving posterior and occipital cortex. The present study complements the previous work by demonstrating that low-level errors elicit an N100 and a P300, but not an ERN. Although it seems likely that the N100 and P300 do not directly reflect the sensorimotor transformations implemen-

ted by PPC for the online control of movement, they may instead reflect processes that support PPC function (such as context-updating, or LC-NE optimization of response execution). Conversely, our results indicate that only high-level errors elicit an ERN, suggesting that the medial-frontal system is concerned with only whether or not the motor command will be ultimately successful.

How do the posterior and frontal error systems work together? Within a motor learning context, high-level error information can be utilised to improve the accuracy of subsequent motor commands. For instance, it has been proposed that once a motor command is put into execution, the posterior system monitors and corrects low-level errors in real-time via a forward model of control (i.e., Desmurget and Grafton, 2000; Wolpert and Ghahramani, 2000), feedback-based control (Chua and Elliott, 1993; Goodale et al., 1986; Gréa et al., 2002; Heath, 2005; Khan and Lawrence, 2005; Khan et al., 2003, 2004; Krigolson and Heath, 2004), or both. Conversely, a growing body of evidence suggests that the medial-frontal system (including the basal ganglia) plays an important role in error evaluation (i.e., Holroyd and Coles, 2002). While this frontal system may receive error information during a movement, it does not appear to act on this information unless a high-level goal is not achieved. When this occurs, the frontal system elicits the ERN. Converging evidence from monkey studies have demonstrated that the midbrain dopamine system carries a temporal difference prediction error from the basal ganglia to frontal cortex (Schultz et al., 1997; Schultz and Dickinson, 2000), including the ACC, where the impact of this signal may generate the ERN (Holroyd and Coles, 2002). Interestingly, it has recently been demonstrated that a temporal difference prediction error system can be used to train forward models (Branning et al., 2005). Thus, one potential function of the high-level error signal generated in medial-frontal cortex could be to train the forward models implemented by the posterior error system.

Although the neural generators that support the type of feed-forward control outlined above remain unclear, they likely involve the supplementary motor area (Hikosaka et al., 2002; Matsumura et al., 2004), the cerebellum (Floyer-Lea and Matthews, 2004; Wolpert et al., 1998), and/or the basal ganglia (Doyon and Benali, 2005; Hikosaka et al., 2002). The results of the present study, along with our previous research (Krigolson and Holroyd, 2006, *in press*), provide evidence that these feed-forward error signals are also sent to ACC in order to modify subsequent motor output (cf. Holroyd and Coles, 2002).

3.4. Conclusion

We have proposed that errors come in two kinds: high-level errors that occur when a task goal has been violated and low-level errors that reflect a currently invalid but correctable course of action. Our results indicate that low-level errors associated with a target perturbation elicit two posteriorly distributed ERP components, an N100 and a P300, but do not elicit an ERN. We suggest that the ERP components evoked by the target perturbation reflect processes that support the online control of movement. Specifically, we propose that the N100 reflects detection by the visual system of changes in the

target location. We also suggest that the P300 reflects the updating of an internal model of the visual environment, which in turn facilitates an updating of the PPC's current forward model of control. Furthermore, we speculate that the P300 may also reflect the impact of phasic LC-NE activity on PPC to optimize the corrective movement. The scalp distribution and proposed neural generators of the N100 and P300 are consistent with these suggestions. In addition, our results also indicate that high-level errors elicit the ERN. Given that the ERN appears to be generated in ACC, these data support the hypothesis that the medial-frontal system, which includes the basal ganglia and the ACC, plays a role in the detection and evaluation of high-level errors in continuous motor tasks. Taken together with our previous findings, these results support our hypothesis that that human error processing is hierarchically organised.

4. Experimental procedures

4.1. Participants

Fifteen right-handed college aged participants (9 males, 6 females) with no known neurological impairments and with normal or corrected-to-normal vision took part in the experiment. All of the participants were volunteers who received extra-credit in a first or second year psychology course for their participation. The participants provided informed consent approved by the Office of the Vice-President, Research, University of Victoria, and the study was conducted in accordance with the ethical standards prescribed in the 1964 Declaration of Helsinki.

4.2. Apparatus and procedure

Participants were seated comfortably in front of a computer monitor in an electromagnetically shielded, soundproof booth and used a standard USB joystick to perform a computerized aiming task (written in MATLAB [Version 7.1, Mathworks, Natick, USA] using the Psychophysics Toolbox extension (Brainard, 1997); the computer code can be downloaded from the website of the Brain and Cognition Laboratory at the University of Victoria, Victoria, Canada). To perform the task, participants used a joystick to move a cursor (a 0.5 cm×0.5 cm red square) 24 cm from a start position square (a 1.5 cm×1.5 cm white square) on the left-hand side of a computer display to target position (a 1.5 cm×1.5 cm white square) on the right-hand side of a computer display. Pressure applied to the joystick in the desired direction moved the cursor in the corresponding direction. The cursor moved at a constant velocity, irrespective of the amount of pressure applied. Participants could direct the cursor only in the up/down and rightward directions; leftward movements (away from the target) were not possible. Note that this control structure allowed for diagonal forward movements (i.e., to the right and up, to the right and down). Once a movement started, the cursor's trajectory could be modified along the vertical axis but not along horizontal axis; the forward movement could only be stopped, not reversed. To stop the cursor, participants returned the joystick to its resting position.

The experiment consisted of 300 trials that were divided between three randomly intermixed aiming conditions (100

trials in each condition). Each trial began with a 2-s visual preview period during which the participant could see the start position, the target position, and the cursor. At the end of the preview period the cursor changed colour from white to green, indicating to the participants that the movement could begin. If the participant applied pressure to the joystick before the cursor changed colour, then the trial was immediately cancelled, an error message was presented, and another trial (selected at random) began.

In the first aiming condition (control), participants were required to move the cursor horizontally from the start position to the target position. In the second (correctable) and third (uncorrectable) aiming conditions, the target simultaneously disappeared and re-appeared at a new location immediately following movement onset (within one refresh cycle), either up or down 8 cm from its initial position (equal probability for each direction). As such, trials in these conditions required participants to correct their initial movement by shifting pressure on the joystick from a horizontal to a diagonal direction. However, in the uncorrectable condition, the cursor was unresponsive to diagonal displacements of the joystick. Thus, it was possible to correct for the target perturbations in the correctable condition but not in the uncorrectable condition. Note that participants could not determine at the start of each trial which condition would occur, as the target perturbations always followed movement onset. Furthermore, following a perturbation, participants could differentiate the uncorrectable from the correctable conditions only by attempting a corrective movement.² Participants were instructed to be as accurate as possible and to stop the cursor so that it made contact with the target.

Participants performed five blocks of 60 trials with 20 trials from each of the three conditions randomly intermixed within each block. Between blocks participants relaxed during self-paced rest periods. The base aiming task (the control condition) was explained to participants before the experiment. Participants were also told that on some trials (the correctable and uncorrectable conditions), the target would jump to a new location, and that on some of these trials the joystick would not work and as such they would be unable to reach the movement target. Participants then completed five practice trials in each of the aiming conditions before the experiment began.

4.3. Behavioural analysis

The aiming program recorded reaction time (the time from when the cursor changed colour to movement onset in ms), movement time (the time from movement onset to movement offset in ms), and the time of the corrective movement in the correctable and uncorrectable conditions (in ms).³ Accuracy was recorded as a binary value (whether the cursor ended the trial on-target or off-target). Participants also completed a short questionnaire upon completion of the experiment. Behavioural data were analysed using a univariate ANOVA

³ For comparison purposes we also examined the ERP data for the control condition. As there was no corrective movement in this condition, we averaged the ERP data for the control condition on a trial-by-trial basis according to the time of the corrective movement on each preceding correctable or uncorrectable trial.

with post-hoc comparisons done by simple effects analysis. An α level of 0.05 was assumed for all statistical tests.

4.4. Data acquisition

The electroencephalogram (EEG) was recorded from 41 electrode locations using BrainVision Recorder software (Version 1.3, Brainproducts, GmbH, Munich, Germany). The electrodes were mounted in a fitted cap with a standard 10–20 layout and were referenced to the average. The vertical and horizontal electrooculograms were recorded from electrodes placed above and below the right eye and on the outer canthi of the left and right eyes, respectively. Electrode impedances were kept below 10 k Ω . The EEG data were sampled at 250 Hz, amplified (Quick Amp, Brainproducts, GmbH, Munich, Germany) and filtered through a passband of 0.017 Hz–67.5 Hz (90 dB octave roll off).

4.5. Data analysis

The EEG data were filtered through a (0.1 Hz–20 Hz passband) phase shift free Butterworth filter and re-referenced to linked mastoids. Ocular artefacts were removed using the algorithm described by Gratton et al. (1983). Trials in which the change in voltage at any channel exceeded 35 μ V per sampling point were also discarded. In total, less than 1% of the data were discarded. All waveform segments (regardless of marker position) were baseline corrected to a 200-ms epoch from 500 to 300 ms before the movement initiation cue.

To evaluate the effect of the target perturbation on the ERP, 1000-ms epochs of data (from 200 ms before movement onset to 800 ms after movement onset) were extracted from the continuous EEG for each trial, channel, and participant for each of the three experimental conditions. ERPs were then created by averaging the EEG data by condition for each electrode, channel, and participant. These data were submitted to a spatiotemporal principal component analysis (STPCA: see below) to identify electrophysiological activity that co-varied across electrodes and time. Subsequent to this analysis two separate difference waves were created by subtracting the control waveform from the correctable and uncorrectable waveforms for each channel and participant. A peak detection analysis was conducted on each of the difference waves for channels of interest identified by the STPCA. The ERN was identified as the maximum negative deflection in the difference wave from 100 to 400 ms and the P300 (see below) was identified as the maximum positive deflection in the difference wave from 200 to 500 ms.

To analyse the corrective movements associated with target perturbations, a 1000-ms window of data was extracted and averaged with respect to the time of the first diagonal (corrective) movement of the joystick in the correctable and uncorrectable conditions (400 ms before the corrective movement, 600 ms after). These data were submitted to a STPCA. Following the STPCA difference waves were created by subtracting the correctable ERPs from the uncorrectable ERPs for each channel and participant. A peak analysis was conducted on this difference waveform using the criteria outlined above.

The amplitudes of the difference waves were tested against zero with a one sample t-test. Amplitudes and latencies of the

difference waves were compared directly with paired samples t-tests. For all statistical tests, an α level of 0.05 was assumed.

4.6. Spatiotemporal principal component analysis

As noted above, the ERP data were submitted to STPCA (analysed using the MATLAB PCA toolbox; Dien, 2002 and Dien et al., 2003; see also Krigolson and Holroyd, 2006). First, spatial factor loadings were obtained by submitting to a PCA the observations (for the target perturbation analysis: 750 ERP samples, 250 time points \times 3 conditional waveforms; for the movement correctable analysis: 600 ERP samples, 200 time points \times 3 conditional waveforms) for each participant and electrode (Varimax rotation, no Kaiser correction). Next, the spatial factor scores for each spatial factor were submitted separately to a temporal PCA. For display purposes, the spatial factor loadings were plotted using custom MATLAB scripts built on the open source EEGLAB toolbox (Delorme and Makeig, 1994; <http://sccn.ucsd.edu/eeglab>).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.brainres.2007.04.024](https://doi.org/10.1016/j.brainres.2007.04.024).

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