

EVIDENCE FOR HIERARCHICAL ERROR PROCESSING IN THE HUMAN BRAIN

O. E. KRIGOLSON* AND C. B. HOLROYD

Department of Psychology, University of Victoria, PO Box 3015, Station CSC, Victoria, BC, Canada V8W 3P1

Abstract—Human goal-directed behavior depends on multiple neural systems that monitor and correct for different types of errors. For example, tracking errors in continuous motor tasks appear to be processed by a system involving posterior parietal cortex, whereas errors in speeded response and trial-and-error learning tasks appear to be processed by a system involving frontal–medial cortex. To date, it is unknown whether there is a functional relationship between the posterior and frontal error systems. We recorded the event-related brain potential from participants engaged in a tracking task to investigate the role of the frontal system in continuous motor control. Our results demonstrate that tracking errors elicit temporally distinct error-related event-related brain potentials over frontal and posterior regions of the scalp, suggesting an interaction between the subcomponents of a hierarchically organized system for error processing. Specifically, we propose that the frontal error system assesses high-level errors (i.e. goal attainment) whereas the posterior error system is responsible for evaluating low-level errors (i.e. trajectory deviations during motor control). © 2005 Published by Elsevier Ltd on behalf of IBRO.

Key words: learning, reinforcement learning, ERN, ERP, motor control, anterior cingulate cortex.

Errors differ in magnitude. A person driving a car, for example, is continually correcting small errors in the car's trajectory to accommodate the uneven surface of the road. However, a more serious error may occur when the person driving the car turns left at a street corner where they had intended to turn right. Studies in the cognitive neuroscience of motor control have indicated that such errors are processed by different neural systems (Kawato, 1999; Shadmehr and Wise, 2005; Wolpert and Ghahramani, 2000). Much of this work has focused on the role that posterior parietal cortex (PPC) plays in the online control of movement. This brain area is thought to estimate hand location in real-time and to compute motor errors (Desmurget et al., 2001) by predicting and evaluating peripheral feedback and/or an efference copy of the motor command (Desmurget and Grafton, 2000). In this manner the posterior error system can continuously modify motor output to adjust for "low-level" errors, such as updating a vehicle's trajectory to accommodate unexpected perturba-

tions. Thus impairments to this system disrupt the ability to make online motor adjustments while a movement is in progress (Desmurget et al., 1999; Grea et al., 2002). By contrast, frontal parts of the brain appear to detect and correct errors that violate "high-level" goals of the system, such as taking a wrong turn while driving. In particular, studies of the error-related negativity (ERN), a component of the event-related brain potential (ERP) sensitive to error commission, suggest that the anterior cingulate cortex (ACC) may comprise part of a generic error processing system for reinforcement learning (Brown and Braver, 2005; Holroyd and Coles, 2002; Holroyd et al., 2004, 2005). These studies have revealed that a "response ERN" is elicited when participants press the incorrect button in speeded response time tasks (Gehring et al., 1993; Holroyd and Coles, 2002; Holroyd et al., 2004, 2005), and that a "feedback ERN" is elicited when people experience an outcome that is worse than anticipated (Holroyd and Coles, 2002; Holroyd et al., 2005; Miltner et al., 1997; Nieuwenhuis et al., 2004). Both the response ERN and feedback ERN are thought to reflect error signals that indicate a violation of a "high-level" goal and that are utilized for the adaptive modification of behavior.

An important unresolved question concerns whether these different neural systems can process errors in parallel and, if so, how the systems interact. Here we demonstrate that the frontal system contributes to continuous motor control by showing that tracking errors elicit an ERN. Further, we show that these errors also elicit a subsequent negative deflection in the ERP over PPC. These results suggest a hierarchical interaction between the frontal and posterior elements of a general system for error processing.

EXPERIMENTAL PROCEDURES

Fifteen undergraduate participants (six male, nine female) performed a computer tracking task by manipulating a joystick to keep a cursor centered between two moving barriers. The barriers moved in unison according to a predictable sequence of alternating left and right movements separated by brief stationary periods in the middle of the screen (*straightaway sections*). A *tracking error* was defined as a contact between the cursor and one of the barriers. Successful performance consisted of the participant maintaining the cursor in a central location between the two barriers (*on target*). In addition, on a randomly-selected subset of the straightaway sections (20%) participants encountered a *difficult corner*. At these times the barriers moved rapidly and unpredictably to the left or to the right, with an equal probability of moving in either direction. Further, on half of the difficult corners the participant maintained full control of the cursor (*unlocked difficult corners*). The speed of these barrier movements ensured that participants always made an error whenever the unlocked diffi-

*Corresponding author. Tel: +1-250-472-5393; fax: +1-250-721-6601. E-mail address: olav@uvic.ca (O. Krigolson).

Abbreviations: ACC, anterior cingulate cortex; ERN, error-related negativity; ERP, event-related brain potential; PCA, principal component analysis; PPC, posterior parietal cortex.

cult corners occurred. By contrast, on the other half of the difficult corners the computer program moved the cursor with the barriers (*locked difficult corners*) so a tracking error did not occur. For the locked corners the period of time the computer controlled the participant's cursor was matched on a trial to trial basis with the duration to barrier contact associated with the preceding unlocked difficult corner. The locked and unlocked difficult corners were identical in all other respects. Importantly, these conditions allowed a comparison of the ERPs associated with correct trials and error trials while controlling for a general effect of surprise induced by the sudden barrier movement (Holroyd, 2004). Electroencephalogram data were recorded from 38 electrodes using a 10–20 layout and were analyzed using standard techniques (see online supplementary material for more detail). For the error trials, the ERP data were averaged according to the time of the barrier contact. For the correct trials, the ERP data were averaged according to times that were matched with the barrier contact times on the error trials. Additionally, ERP data were averaged for the occasional tracking errors that occurred during the regular performance of the task, independent of the unlocked difficult corners (*regular tracking errors*).

RESULTS

Participants on average experienced 79 unlocked difficult corners, 80 locked difficult corners, and made 108 regular tracking errors throughout the course of the experiment. The ERP associated with the unlocked trials was more negative than the ERP associated with the locked trials from 26 ms before to 150 ms after the tracking error occurred. This difference was maximal at channel FCz, a finding that is consistent with previous observations of the ERN (Gehring et al., 1993; Holroyd and Coles, 2004; Holroyd et al., 2004a,b, 2005; Miltner et al., 1997) (Fig. 1a). A peak analysis of the unlocked–locked difference wave at channel FCz (Fig. 1d) demonstrated that tracking errors resulted in a significantly greater negativity than on-target performance [$t(14) = -6.51$, $P < 0.001$, $-3.61 \mu\text{V}$ difference 73 ms after the barrier contact]. Furthermore, an onset analysis (Rodriguez-Fornells et al., 2002) conducted on the difference wave indicated that this negative deflection began approximately 26 ms before the barrier contact. These findings were confirmed by the results of a spatio-temporal principal component analysis (PCA) (Dien et al., 2003) of the ERP data, which yielded 11 spatial factors that accounted for 95.6% of the total variance. The first of these spatial factors exhibited loadings with a frontal–central scalp distribution (Fig. 2a; 0.93, 0.93, 0.95 loadings over channels FC1, FCz, and FC2, respectively). A temporal PCA on the scores associated with the first spatial factor yielded a temporal factor (accounting for 34.4% of the total variance) with maximal loadings (>0.9) from 70 to 122 ms after the barrier contact. This epoch corresponded to the time of the negative peak difference recorded at channel FCz. Finally, a comparison was made between the tracking errors made during the normal tracking pattern and the locked and unlocked corners. This analysis revealed that the negativity elicited by the regular tracking errors was about the same amplitude as that of the unlocked corners [$t(14) = 0.34$, $P > 0.05$], but was significantly larger than that of the locked corners [$t(14) = 3.85$, $P < 0.001$] (see Fig. 1b).

The spatio-temporal PCA also revealed a second spatial factor with loadings that were maximal over posterior areas of the scalp (Fig. 2b; 0.96 and 0.89 loadings over channels POz and Oz, respectively). A temporal PCA on the scores associated with the second spatial factor yielded a temporal factor (accounting for 35.0% of the total variance) with maximal loadings (>0.9) from 146 to 166 ms after the barrier contact. To explore this finding further, we conducted a peak analysis of the locked–unlocked difference wave associated with channel POz. This analysis revealed a negativity after tracking errors that peaked 82 ms later than the frontal negativity recorded at channel FCz [$t(14) = -4.29$, $P < 0.001$, $-4.40 \mu\text{V}$ difference] (see Fig. 1c, 1d for more detail).

DISCUSSION

The ERP component observed immediately following tracking errors in the present study is consistent with previous observations of the response-ERN (Gehring et al., 1993; Holroyd and Coles, 2002; Holroyd et al., 2005) and the feedback-ERN (Holroyd and Coles, 2002; Holroyd et al., 2004; Miltner et al., 1997). Specifically, we observed during sudden barrier movements a negativity that peaked 73 ms following tracking errors but that was reduced or absent when participants remained on target. The frontal–central spatial distribution of this component is consistent with previous reports that the ERN is generated in frontal–medial cortex, probably in the ACC (Holroyd, 2004; Holroyd and Coles, 2002; Holroyd et al., 2004a,b). Nevertheless, the timing of this negativity is different from that of the response ERN and the feedback ERN, presumably because the error information associated with tracking errors becomes available to the system at a different time. Note that the onset analysis of the ERN waveform revealed that the frontal–medial system began to detect the error in advance of the actual barrier contact, rather than subsequent to the barrier contact, in which case it would have been expected to elicit a classic feedback ERN peaking about 250 ms following the error. This negativity also does not appear to depend on an efference copy of the motor command, as is the case with the response ERN (Allain et al., 2004). Rather, it appears that the frontal system can detect these errors by adopting a predictive mode of control (Desmurget and Grafton, 2000; Holroyd and Coles, 2002; Holroyd et al., 2005). Although commonly thought to be processed by posterior parts of the brain (Desmurget and Grafton, 2000; Desmurget et al., 1999, 2001; Grea et al., 2002; Kawato, 1999), these results suggest that the frontal system is sensitive to “high-level” tracking errors (i.e. barrier crossings) in a continuous motor task.

If the tracking errors in the present study are indeed evaluated by the frontal system, what then is the role of the posterior system? Previous research has demonstrated that “low-level” motor errors (i.e. trajectory modifications) are evaluated by PPC (Desmurget and Grafton, 2000; Desmurget et al., 1999, 2001; Grea et al., 2002). It has been suggested that the posterior error system residing in PPC either operates using a forward model of control

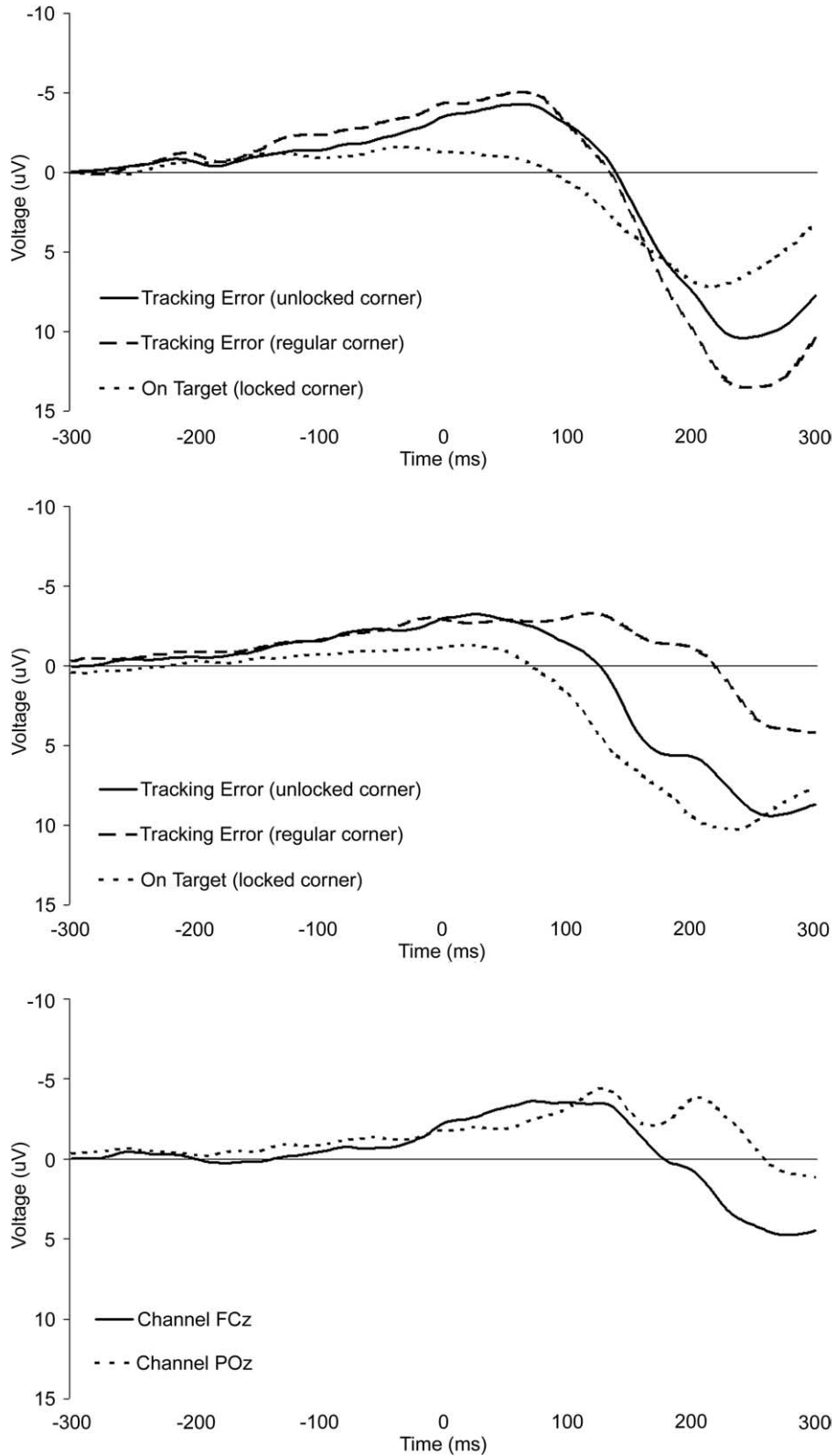


Fig. 1. (a) Averaged ERP waveforms recorded at channel FCz for unlocked tracking errors, regular tracking errors, and locked on-target events. (b) Averaged ERP waveforms recorded at channel POz for both unlocked tracking errors, regular tracking errors, and locked on-target events. (c) Averaged ERP difference waves associated with channels FCz and POz. Zero milliseconds corresponds to the time of barrier contact on error trials and to a matched point in time on correct trials (see Online Supplementary Experimental Procedures). Note that negative voltages are plotted up by convention.

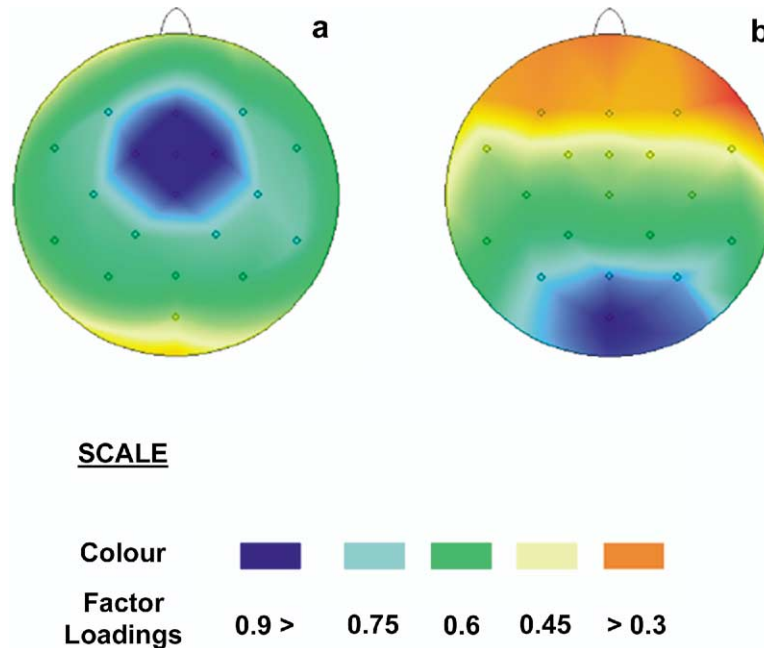


Fig. 2. Spatial PCA factor loadings projected onto the surface of the human head for the first (a, frontal-central, accounting for 42.7% of the total variance) and second (b, posterior, accounting for 32.0% of the total variance) factors. The top of each map points toward the nose.

(Desmurget and Grafton, 2000; Wolpert and Ghahramani, 2000) or in an online manner using visual feedback (Elliott et al., 2001; Goodale et al., 1986, 2004). Interestingly, the results of the present study revealed a negative deflection in the ERP that was distributed over occipital–parietal regions of the scalp and that peaked about 82 ms after the ERN. To our knowledge these data comprise the first ERP evidence of a posterior error system.

One may ask why posterior activity was not revealed in the ERP during the period before the tracking error occurred. In the present study the errors elicited by the unlocked difficult corners occurred very rapidly (on average about 218 ms following the onset of the corner) and unpredictably. Although the posterior system may have attempted to prevent a tracking error from occurring, the speed and the unpredictability of the unlocked difficult corners may have been beyond its capacity to correct. This inference is in line with models that suggest the posterior motor control system depends on visual feedback during a movement (i.e. Goodale et al., 2004) and is supported by the results of goal-directed reaching experiments that have demonstrated that participants are not able to adjust movement trajectories during very rapid movements (Carlton, 1981; Desmurget et al., 1999). Furthermore, the unpredictable nature of the unlocked difficult corners may have negated the ability of a predictive error system to utilize a forward model of control. Instead, in the present study the frontal–medial system appears to have determined that these tracking errors violated a high-level goal of the system, namely, to avoid crossing the barriers. It seems likely that an optimal movement control strategy would most likely involve both frontal and posterior systems operating in both feedback and feedforward manners (Desmurget and Grafton, 2000; Holroyd and Coles, 2002; Seidler et al.,

2004). As such, one possible explanation for timing of the frontal–central and posterior ERP components in the present study may be that the high-level error information, once evaluated by the frontal system, was then communicated to the posterior system for the adaptive modification of behavior.

CONCLUSION

In summary, we have observed for the first time that tracking errors in a continuous movement task elicit both an ERN and a subsequent ERP component that is distributed over posterior regions of the scalp. These results indicate that the frontal–medial system is sensitive to errors in a computational domain normally associated with posterior parts of the brain, and suggest an interaction between the frontal and posterior elements of a hierarchically organized system for error processing.

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APPENDIX

Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi: [10.1016/j.neuroscience.2005.10.064](https://doi.org/10.1016/j.neuroscience.2005.10.064).

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