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NEURAL CORRELATES OF STATE ESTIMATION IN VISUALLY GUIDED MOVEMENTS: AN EVENT-RELATED fMRI STUDY

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Abstract

State estimation of self-movement, based on both motor commands and sensory feedback, has been suggested as essential to human movement control to compensate for inherent feedback delays in sensorimotor loops. The present study investigated the neural basis for state estimation of human movement using event-related functional magnetic resonance imaging (fMRI). Participants traced visually presented curves with a computer mouse, and an artificial delay was introduced to visual feedback. Motor performance and brain activities during movements were measured. Experiment 1 investigated brain activations that were significantly correlated with visual feedback delay and motor error by parametrically manipulating visual feedback delay. Activation of the right posterior parietal cortex (PPC) was positively correlated with motor error, whereas activation of the right temporo-parietal junction (TPJ) was observed only in the group with a smaller increase in motor error with increased visual feedback delay. Experiment 2 involved parametric analysis of motor performance while controlling mouse movement speed during the task. Activity in the right TPJ showed a significant positive correlation with motor performance under the delayed visual feedback condition. In addition, activity of the PPC was greater when motor error was presented visually. These results suggest that the PPC plays a significant role in evaluating visuomotor prediction error, while the TPJ is involved in state estimation of self-movement during visually guided movements.

Key words: delayed visual feedback, event-related fMRI, state estimation of movements, visually guided movements, posterior parietal cortex, temporo-parietal junction

Introduction

Previous studies have indicated that human movement control is not entirely preprogrammed, with online sensory feedback information used for optimal control of self-movement (Desmurget and Grafton, 2000). In control theory, this can be realized via feedback control, in which residual error from feedback information is directly transformed into motor commands. Feedback control systems are robust, as the controller need not be precisely matched to the motor apparatus. However, the fact that feedback control is extremely sensitive to intrinsic delays represents a principal disadvantage. An inherent delay is present in human sensorimotor loops (e.g., 200-300 msec delay in visually guided movements), involving both efferent and afferent pathways. This considerable delay prevents humans from using feedback information to control self-movement, and predictive movement control is required to compensate for the delay (Miall and Wolpert, 1996; Desmurget and Grafton, 2000; Wolpert and Flanagan, 2001).

Two main approaches are available for predictive motor control: Smith (1959) predictor-based control, or model predictive observer-based control, such as the Kalman filter (Kalman and Bucy, 1961). Both models predict the consequence of movements using an internal forward model (predictor) of effectors in parallel to actual movements, and use this prediction to generate movement commands without external feedback delays. The effects of feedback-delay problems are thus mitigated. Miall et al. (1993) proposed that the Smith (1959) predictor was realized in the human movement control system. However, the Smith (1959) predictor has disadvantages, in that internal predictions cannot be optimally corrected based on sensory feedback information, since prediction error between prediction and feedback information cannot be properly evaluated. In contrast, the Kalman filter (Kalman and Bucy, 1961) can properly weight predictions and feedback information based on relative reliability: if the internal prediction is inaccurate due to noise in the effectors, the Kalman filter (Kalman and Bucy, 1961) puts more weight on the prediction error from sensory feedback compared to the prediction, and vice versa. Optimal state estimates of movements can thus be realized by properly integrating both internal predictions and prediction error from feedback information. A human behavioral study by Wolpert et al. (1995) showed that temporal propagation of measured error during a reaching task could be fully accounted for by assuming that the motor control system integrates both motor outflows and proprioceptive sensory inflows to estimate location of the hand without the vison of the hand. Such theoretical and behavioral studies indicate that the central nervous system (CNS) uses observer-based control such as the Kalman filter (Kalman and Bucy, 1961), which integrates motor commands and sensory feedback to provide optimal state estimates of self-movement.

Previous studies have suggested that the posterior parietal cortex (PPC) is involved in online control of movement based on internal state estimates (Desmurget and Grafton, 2000; Blakemore and Sirigu, 2003). The PPC along the intraparietal sulcus (IPS) is involved in visuomotor transformation (Rizzolatti et al., 1997; Culham and Kanwisher, 2001), and sensory signals from numerous modalities, in addition to efferent copy signals from motor-related areas, are integrated in the PPC (Andersen et al., 1997). Neuropsychological studies have described cases in which PPC lesions disrupt online control of visually guided movement (Pisella et al., 2000; Grea et al., 2002). Based on a visually guided pointing task, Desmurget et al. (1999, 2001) proposed that the PPC computes dynamic motor error for use by motor centers to correct ongoing trajectories by building internal representations of instantaneous hand location. Wolpert et al. (1998a) suggested that an internal representation of body state created from sensory and motor signals is maintained and updated in the PPC. Furthermore, the PPC is involved in self-monitoring of actions, evaluating the temporal congruency of peripheral (visual) and central (efference copy) signals associated with self-generated movements (Sirigu et al., 1999; MacDonald and Paus, 2003).

These previous studies suggest that the PPC is involved in online state estimation of self-movement. However, a unifying theoretical explanation describing these neural components based on predictive control theory has yet to be reported. The framework of observer-based control such as the Kalman filter (Kalman and Bucy, 1961) includes 2 principal processes: internal generation of state estimation; and evaluation of prediction error. In the first process, an internal state estimation of the motor system is generated, using the previous state estimate and efference copy of motor commands as inputs. In the second process, this state estimation is compared with actual feedback information from effectors, and prediction error is evaluated and integrated into state estimation (Miall and Wolpert, 1996; Desmurget and Grafton; 2000, Wolpert and Flanagan, 2001; Wolpert and Ghahramani, 2000).

The present study directly investigated the neural basis for these 2 components in state estimation of human movement using event-related functional magnetic resonance imaging (fMRI). Participants performed visually guided movements with an artificial delay introduced into the actual visual feedback during movement. Under the delayed visual feedback condition, movement control based purely on feedback information is impaired, so prediction of self-movement could be used to maintain relatively accurate performance in the presence of feedback delays. This internal state estimation is then compared with actual feedback information, and prediction error is used to optimize the estimated state. This study investigated the neural basis of state estimation and prediction error of self-movement by analyzing correlations between motor performance and brain activity under delayed visual feedback conditions.

Behavioral data from subjects were measured during the task and used as explanatory variables in event-related fMRI analyses. This parametric fMRI analysis based on motor performance from each subject could reveal relationships between motor performance and brain activity. In Experiment 1, brain activations displaying positive correlations with delayed feedback and motor error were investigated by parametrically manipulating visual feedback delay (0 msec, 200 msec and 500 msec). In Experiment 2, based on the brain areas observed in Experiment 1, parametric analysis of motor error was performed while controlling mouse movement speed during the task. Furthermore, relationships between brain activation and visual feedback information were investigated by adding a condition in which no visual feedback information about motor error was available.

Materials and Methods

Participants

In Experiment 1, 19 neurologically normal subjects (10 women, 9 men; mean age: 24.9 years; range: 20-31 years) participated. Of these, 2 subjects (1 woman, 1 man) were excluded from analysis due to excessive head movement during scans thus 17 subjects were analyzed. In Experiment 2, 15 neurologically normal subjects (5 women, 10 men; mean age: 24.7 years; range: 20-31 years) participated. Nine subjects participated in both experiments. All subjects were right-handed according to the improved version of the Edinburgh Inventory scale (Oldfield, 1971) and had normal or corrected-to-normal visual acuity. All subjects were familiar with manipulating a computer mouse. Informed written consent was obtained from each subject, and the protocol was approved by the ethics committee of Advanced Telecommunication Research Institute.

Task

A curve-tracing task was used as a visually guided movement. The curve-tracing movement requires continuous visual feedback for both the target and self-movement, so this task is appropriate when investigating the online effects of delayed visual feedback on motor performance. Experimental stimuli were run using a personal computer outside the MRI scanner, and presented on a liquid crystal display projected onto a custom-