Journal of Motor Behavior, 2005, Vol. 37, No. 2, 157–163

Gaze-Dependent Deviation in Pointing Induced by Transcranial Magnetic Stimulation Over the Human Posterior Parietal Cortex

Paul van Donkelaar
Jaymi Adams
Department of Human Physiology
Institute of Neuroscience
University of Oregon, Eugene

ABSTRACT. Signals arising from the saccadic system influence the planning and generation of pointing movements, and the posterior parietal cortex (PPC) appears to play a vital role in that interaction. The authors demonstrate in the present study that during visual fixation, eye-position signals can dominate pointing responses when the activity in the PPC contralateral to the moving limb is disrupted with transcranial magnetic stimulation (TMS). In particular, when presented with targets in peripheral vision, participants (*N* = 5) exposed to TMS over the PPC failed to show the normal pattern of responses in which pointing movements end up farther away from the goal target. Instead, they tended to point more toward the current point of visual fixation. Those results suggest that the PPC is involved in integrating eye-position and visual information to affect reaching in the contralateral arm.

Key words: pointing movements, posterior parietal cortex, saccadic eye movements, vision

Although reaching movements tend to be preceded or accompanied by saccadic eye movements so that the object of interest can be foveated, it is not uncommon to reach for objects in peripheral vision. Under such circumstances, the visuomotor system must combine the retinal position of the object image with information concerning eye position to calculate the eccentricity of the object in a head-centered frame of reference. It can then use that information, in combination with head- and limb-position signals, to plan the details required to generate the reaching movement. Although the resulting response is relatively accurate, previous researchers have demonstrated that participants tend to overestimate the distance to the target when visually fixating (Bock, 1986; Enright, 1995; Henriques, Klier, Smith, Lowy, & Crawford, 1998). Overestimation is thought to occur because the human visuomotor system is not appropriately calibrated for reaches to objects that are not foveated at the same time (Henriques, Medendorp, Khan, & Crawford, 2002). Indeed, gaze appears to be anchored to the pointing target until the pointing response is completed (Neggers & Bekkering, 2000, 2001), implying that to plan a reach to peripheral targets, the central nervous system (CNS) must inhibit the natural tendency to select the current point of visual fixation as the reaching goal.

Our purpose in the present experiment was to examine the contribution of the posterior parietal cortex (PPC) during pointing movements to peripheral targets. We accomplished that by using transcranial magnetic stimulation (TMS) to disrupt the processing occurring within the PPC while participants generated their responses. TMS was delivered unilaterally over the left PPC while the participant maintained fixation to the left or right of straight ahead and pointed with either the left or the right hand to targets in the left or the right visual hemifield. Through those combinations of conditions, we were able to gain insight into the potential directional and hemispheric interactions between visual, eye-position, and limb motor signals in the human PPC.

Method

Participants

Five naive men (mean age = 27 ± 2.3 years) participated in the present experiment after giving informed consent. Each participant was free from neurological impairments affecting ocular or manual control and had normal or corrected-to-normal vision. The Institutional Review Board of the Office of Human Subjects Compliance at the University of Oregon had approved the experimental procedures.

Correspondence address: Paul van Donkelaar, Department of Human Physiology, Institute of Neuroscience, University of Oregon, Eugene, OR 97403-1204, USA. E-mail address: paulvd@darkwing.uoregon.edu

Task and Apparatus

The participant sat in a dimly illuminated room looking at targets projected onto a vertically oriented screen positioned about 30 cm away. Visual feedback from the hand was continuously available. The motion of the left or the right index finger was monitored by a Watsmart system (Northern Digital, Inc., Waterloo, Ontario, Canada). We used an infrared corneal reflection device (Skalar IRIS, Delft, The Netherlands) to monitor eye movements. Both systems were sampled at 200 Hz. We calibrated the Watsmart system and the eye-movement recording device by having the participant point at or fixate targets, respectively, at known eccentricities before we collected data. We used a bite bar to stabilize the participant's head.

A Magstim 200 stimulator (Whitland, South West Wales, U.K.) delivered single magnetic pulses through a figure-eight coil (each wing 70 mm diameter). A tight-fitting swimming cap on which marks were made aided in coil placement. Participants wore earplugs to guard against potential hearing damage. The coil was oriented with the handle pointing backward at a 45° angle from the midline and held tangential to the skull with a clamp. Before the experiment, we determined the motor threshold for eliciting electromyographic (EMG) activity (Bagnoli-2 EMG system; Delsys, Inc., Boston, MA) in the right first dorsal interroseous (FDI) muscle by stimulating over the left motor cortex. We defined the threshold as the stimulator output at which FDI activity above 50 uV could be elicited on three out of six trials (Sohn, Dang, & Hallett, 2003). We then moved the stimulating coil to the left PPC by shifting its location 7 cm posterior to the motor hot point (Terao et al., 1998; van Donkelaar, Lee, & Drew, 2000, 2002). During the experiment, stimulation was delivered to the left PPC at 110% of the threshold for eliciting FDI activity in the left motor cortex. Participants did not report any undesirable side effects resulting from the stimulation.

The events that occurred during a typical trial are displayed in Figure 1A. The participant began each trial with his left or right hand resting on a start marker located at the

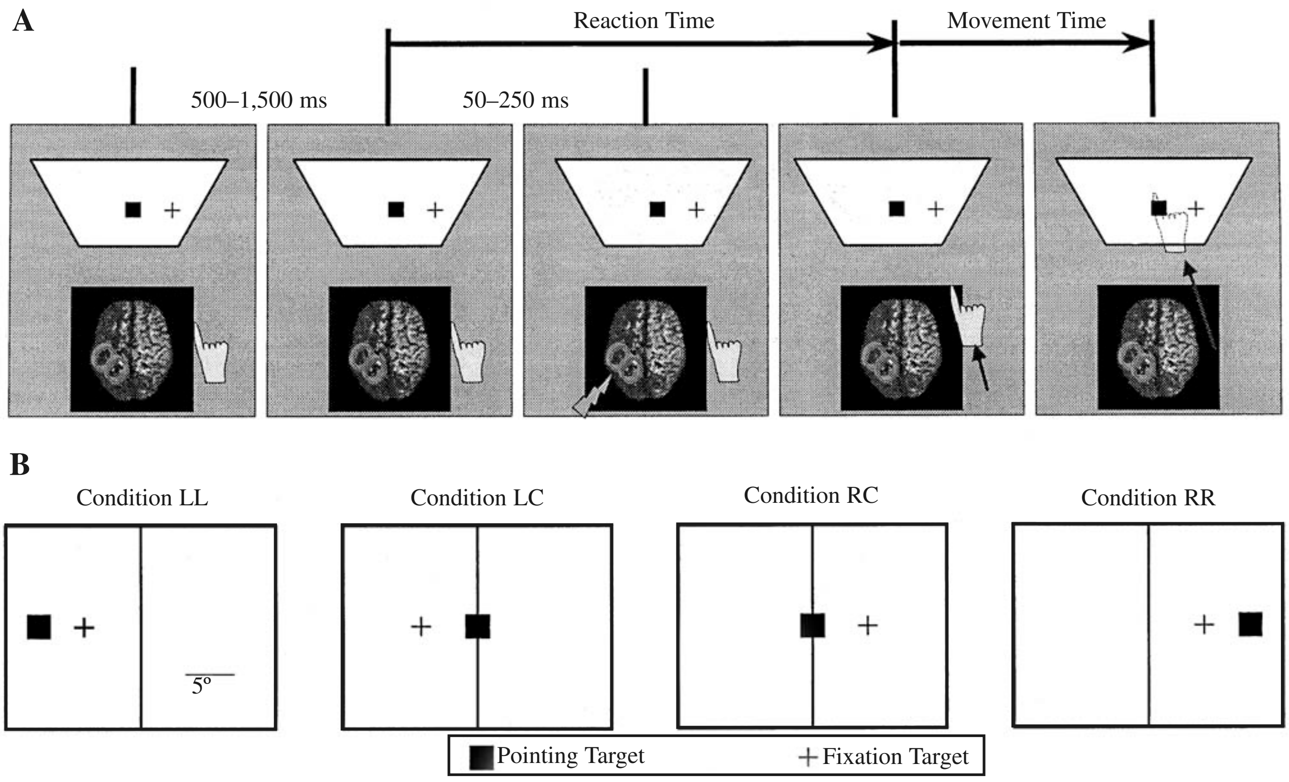

FIGURE 1. **A**. Events occurring within each trial. The fixation target initially appeared, and participants looked at it and positioned their hand (the right hand in this example) at the end of the armrest of the chair. After a variable delay, the pointing target appeared in the periphery. On transcranial magnetic stimulus (TMS) trials a single pulse of TMS was delivered 50–250 ms after that event to the left posterior parietal cortex (PPC). When the peripheral target appeared, participants were required to point to it as quickly and accurately as possible. **B**. The target configurations in the four different conditions as viewed from the participants' perspective immediately after the appearance of the peripheral (pointing) target. The vertical line represents the participants' midline and was not present in the visual display. In Condition LL, the fixation target was to the left of midline and the pointing target was to the left of the fixation target. In Condition LC, the fixation target was to the left of midline and the pointing target was at the center. In Condition RC, the fixation target was to the right of midline and the pointing target was at the center. In Condition RR, the fixation target was to the right of midline and the pointing target was to the right of the fixation target.

end of the corresponding armrest of the chair and his eyes fixating on a target (a plus sign [+] subtending ~0.5°) positioned 5° to the left or right of straight ahead. After a variable delay (500–1,500 ms), a second target (a square subtending ~0.5°) appeared 5° to the left or right of the fixation target. At that time, the participant was required to point toward the second target while maintaining his gaze on the fixation target. Instructions were given to move as quickly and accurately as possible but not to make any corrections at the end of the movement. TMS was randomly delivered over the left PPC 50, 100, 150, 200, or 250 ms after the appearance of the second target. Trials without stimulation were randomly interleaved with the TMS trials. Thus, the participant did not know if or when he would receive stimulation before each trial. The different combinations of pointing and fixation target conditions are displayed in Figure 1B. The four target configurations were called Conditions LL (fixation target to left of midline, pointing target to left of fixation target), LC (fixation target to left of midline, pointing target at center), RC (fixation target to right of midline, pointing target at center), and RR (fixation target to right of midline, pointing target to right of fixation target). Eight trials were completed for each stimulation time along with 8 non-TMS trials within each condition. Thus, the participant completed a total of 192 trials in a session. Two sessions separated by at least 4 days were completed. In one session the participant used the right hand, and in the other the left hand. In both sessions only the left PPC was stimulated. The order of hand use was counterbalanced across the group.

Data Analysis

We examined eye movement to ensure that fixation was maintained. The small percentage of trials (< 3%) that contained eye motion was discarded. For that purpose, we defined *eye motion* as any displacement of the eye during the trial greater than 0.5°. Hand movement onsets, which we automatically identified by using velocity–time thresholds, could be adjusted in a graphical user interface. We defined *onsets* and *offsets*, respectively, as the point in time at which hand velocity exceeded or fell below 10% of peak velocity for at least 30 ms. Using those two variables as the starting and ending points of the reach, we calculated the following measures. *Reaction time* was defined as the period of time from the appearance of the peripheral pointing target and the onset of the hand movement. We defined *initial movement direction* as the angle formed between the start position of the finger and its position 100 ms after movement onset relative to a line from the start position of the finger to a point projected straight ahead to the vertical plane of the display screen. Initial movements to the left of straight ahead were considered negative, whereas those to the right were considered positive. We defined *peak velocity* as the maximum value achieved in pointing velocity between movement onset and offset, and *movement duration* as the time between movement onset and offset. *Movement endpoint* was defined as the distance (in cm) in the horizontal plane between the finger and the target at the end of the reach and the calibrated position of the same target. Endpoints to the left of the target were considered negative, whereas those to the right were considered positive. Although the Watsmart system reconstructed movements in all three dimensions, we used only motion in the horizontal (x, y) plane in the data analysis. Motion in the other planes was not affected in a systematic manner by the experimental manipulations to the targets or by the delivery of TMS. Each of the movement variables was compared across the relevant combinations of gaze direction, peripheral target location, pointing hand, and TMS delivery time.

Results

We used TMS to temporarily disrupt the activity in the left PPC while participants attempted to point at targets in peripheral vision. By manipulating the hand that was used, the point of visual fixation, and the visual hemifield into which the pointing response was directed relative to the hemisphere being stimulated, we were able to address how directional signals related to visual, eye-position, and limb motor information potentially interact in the human PPC. The results showed that TMS had effects on the reaching movements that were dependent upon each of those variables. However, those effects were independent of when the TMS was delivered relative to the appearance of target.

Example hand paths made by the right arm of a single participant in Conditions LC and RC are displayed in Figure 2. In Condition LC (Figure 2, top), the participant visually fixated a target to the left of his midline and pointed to a second target positioned straight ahead. When the movement was made without TMS being delivered, the participant made fairly straight pointing responses that ended to the right of the target. By contrast, when TMS was delivered to the left PPC 150 ms after the appearance of the peripheral target, the hand paths were deviated toward the fixation target and ended closer to both the pointing and fixation targets. The exact opposite pattern of results was observed in Condition RC (Figure 2, bottom). Those general characteristics were quite consistent across participants and are reflected in the group measures described next. Most important, there did not appear to be any systematic effect on the dependent variables across the different TMS delivery times. Therefore, for the remainder of this report, we consider only the mean effect of TMS averaged across the different stimulation times.

Movement Endpoint

The average movement endpoints in all four conditions for each participant during trials performed with the right hand are shown in Figure 3. When no TMS was given, the movements tended to miss the pointing target in the direction opposite to the fixation target. In no case did the movement end up in a position between the fixation and pointing targets. By contrast, when TMS was delivered, the pointing

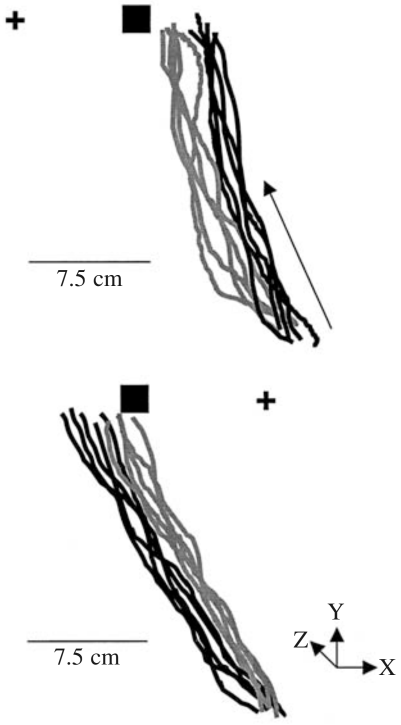

FIGURE 2. Example hand paths ($n = 5$) produced by a single participant with the right arm in conditions LC (**top**) and RC (**bottom**) with (gray) and without (black) TMS delivered over the left PPC 150 ms after the appearance of the peripheral target. The perspective is from the top, with the movements progressing in the direction of the arrow in the upper figure. The cross represents the point of visual fixation, and the black square the pointing target. X = mediolateral axis; Y = anterioposterior axis; Z = superior–inferior axis. See Figure 1 for other abbreviations.

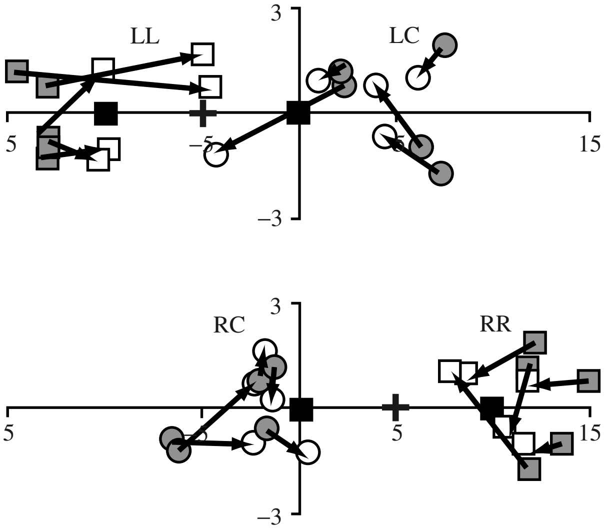

FIGURE 3. Average movement endpoints for each participant during pointing with the right hand in each condition when TMS was given (open symbols) or when TMS was not given (gray symbols). **Top**. Gaze fixated to the left of the midline (Conditions LL and LC). **Bottom**. Gaze fixated to the right of the midline (Conditions RC and RR). Without TMS, participants overshot the target (gray squares and circles), whereas with TMS, the final endpoint of the reaching movement was deviated toward the point of fixation (plus symbol) in the majority of cases. See Figure 1 for other abbreviations.

responses ended up closer to the fixation target. The fact that most of the arrows connecting each participant's data point inward toward the point of fixation allows one to appreciate that finding. To measure that influence, we calculated the difference between the movement endpoints on trials without TMS and the average of the movement endpoints for all of the stimulation times for each of the participants. The group means for the change in movement endpoint induced by TMS are plotted for each hand in Figure 4. As is clear from the figure, the change in movement endpoint resulting from the delivery of TMS was dependent upon the limb used and the visual hemifield in which the peripheral target was presented. However, eye position with respect to the midline did not have an influence. We confirmed that finding with a two-way repeated measures analysis of variance (ANOVA) for the right-handed pointing movements (Figure 4, top), which revealed a significant difference in the change in movement endpoint across the left and right hemifields, $F(1, 4) = 8.196$, $p = .036$, but not across the left and right eye positions, $F(1, 4) = 3.24$, $p = .126$. In addition, the interaction between those two variables did not reach significance, $F(1, 4) = 0.394$, $p = .56$. The limb dependence was revealed by the fact that when the left hand was used to respond, the influence of TMS on the movement endpoints was no longer present (Figure 4, bottom). A two-way repeated measures ANOVA applied to the data from the left hand revealed no significant effects: hemifield effect, $F(1, 4) = 0.055$, $p = .826$; eye-position effect, $F(1, 4) = 0.218$, $p = .665$; interaction, $F(1, 4) = 0.025$, $p = .881$.

Initial Movement Direction

The affect of TMS on the initial movement direction was dependent on the limb that was being used, the visual hemifield in which the pointing target appeared, and the position of the eye with respect to the midline. The eye position- and visual-hemifield dependence for right-handed movements (top) and the absence of an effect for left-handed movements (bottom) are shown in Figure 5. As in Figure 4, plotted in each part of Figure 5 is the average change induced in initial movement direction within each condition for all the TMS delivery times combined relative to the mean initial movement direction when no TMS was delivered. For example, when the right hand was used to reach for a target positioned straight ahead while the eyes fixated a second target to the right of center (Condition RC, Figure 5, top), TMS caused the initial movement direction to be deviated

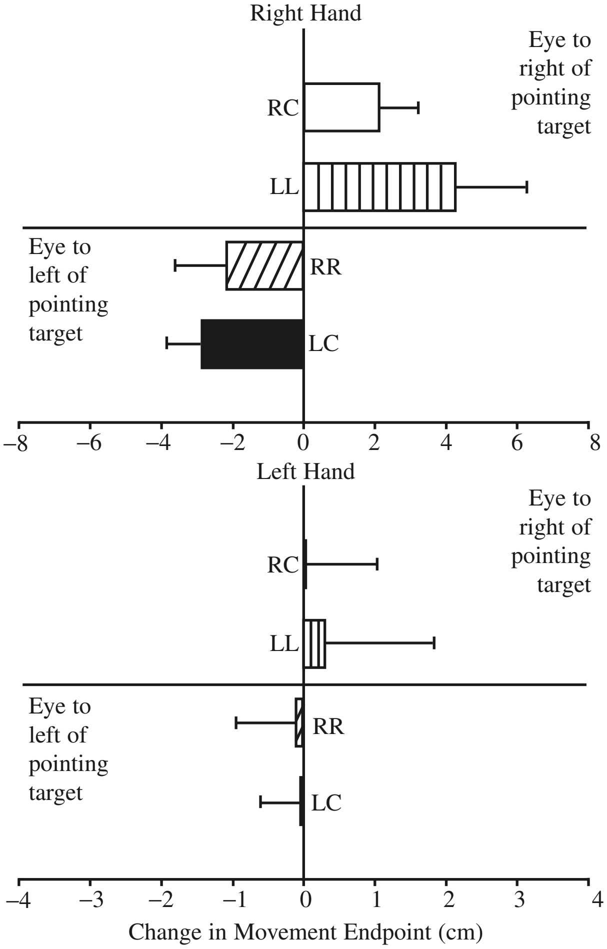

FIGURE 4. Group means for the change induced in movement endpoint by TMS during pointing movements with the right hand (**top**) or left hand (**bottom**). The conditions are grouped according to the eye position relative to the pointing target. When the right hand was used, TMS caused a deviation in the movement endpoint toward the point of fixation. That was not the case when the left hand was used. Error bars = 1 intersubject standard error. See Figure 1 for other abbreviations.

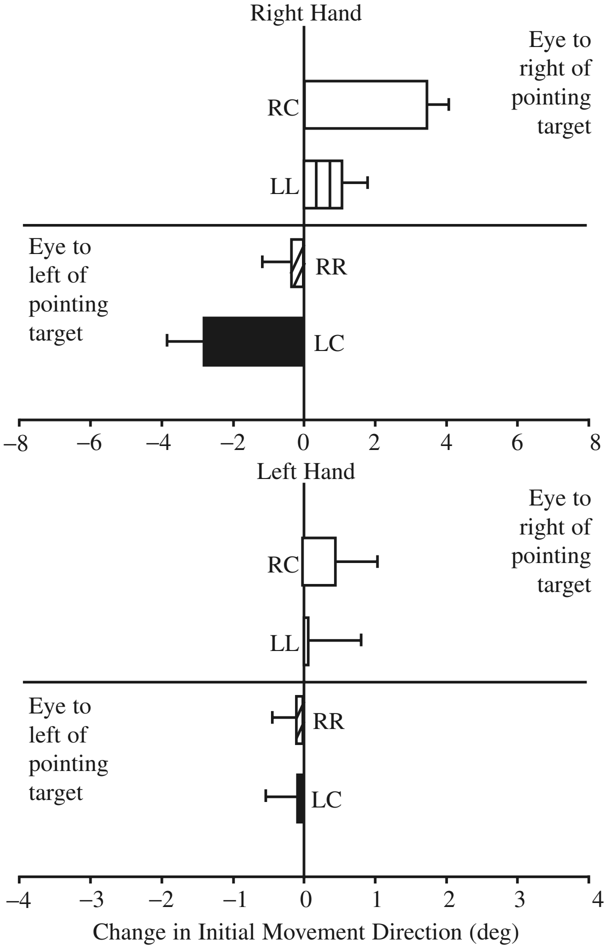

FIGURE 5. Comparison between group means for the change in initial movement direction for each condition when TMS and when it was not given during pointing movements with the right hand (**top**) or left hand (**bottom**). The conditions are grouped according to the eye position relative to the pointing target. When the right hand but not the left hand was used, TMS caused a deviation in the initial movement direction toward the point of fixation. Error bars = 1 intersubject standard error. See Figure 1 for other abbreviations.

rightward toward the fixated target. The opposite was true when the eyes were fixating on a target to the left of center (Condition LC)—pointing movements aimed to a target positioned straight ahead were initially deviated to the left. That trend in the data was less apparent when the hand pointed to a target more eccentric than the visual fixation target (Conditions LL and RR). Moreover, the magnitude of the deviation in initial movement direction was larger when the eyes fixated to the right (Conditions RC and RR) than when they fixated to the left (Conditions LC and LL). Those effects were captured in a two-way repeated measures ANOVA, which revealed a significant difference in the change in initial movement direction across the left and right hemifields, $F(1, 4) = 19.38$, $p = .012$, and the left and right eyes, $F(1, 4) = 6.91$, $p = .041$, but a nonsignificant interaction, $F(1, 4) = .984$, $p = .26$. In contrast to the effects of left PPC stimulation on right hand movements, no significant deviation of the initial movement direction toward the point of fixation occurred when the left hand was used (Figure 5, bottom). A two-way repeated measures ANOVA applied to the data from the left hand revealed no significant effects: hemifield effect, $F(1, 4) = 0.241$, $p = .649$; eye-position effect, $F(1, 4) = 0.401$, $p = .561$; interaction, $F(1, 4) = 0.079$, $p = .792$.

Reaction Time, Peak Velocity, and Movement Duration

The remaining movement variables did not display any systematic changes associated with the different combinations of eye position, limb used, or TMS delivery times.

There was, however, a general speeding up of reaction time during TMS trials as compared with that in non-TMS control trials. In particular, averaged across the different TMS delay times, reaction time was significantly faster when TMS was delivered than when it was not for both the left (TMS trials, 399 ms; non-TMS trials, 436 ms; *t* test, $p < .05$) and right (TMS trials, 405 ms; non-TMS trials, 431 ms; *t* test, $p < .05$) hands. That type of general TMS effect has been observed previously (Sawaki, Okita, Fujiwara, & Mizuno, 1999) and most likely represents the influence of intersensory facilitation (Hughes, Reuter-Lorenz, Nozawa, & Fendrich, 1994) associated with the auditory and somatosensory stimulation occurring during the TMS pulse.

Discussion

In the present experiment, we demonstrated that reaching movements to targets in the visual periphery require normal processing in the PPC. In particular, when PPC activity is disrupted with TMS, reaching movements are deviated toward the point of visual fixation, implying that eye-position signals play a greater role under those conditions. That finding is consistent with the hypothesis that the PPC normally participates in the transformation of reach-related signals from an eye- to a limb-centered frame of reference (Batista, Buneo, Snyder, & Andersen, 1999; Buneo, Jarvis, Batista, & Andersen, 2002). Moreover, the effects of TMS were more substantial on the affected measures that occurred early in the response than on those that occurred later. In particular, the effect of TMS on initial movement direction was modulated by both the visual hemifield in which the pointing target appeared and the position of the eye with respect to the midline. By contrast, the effect of TMS on final movement endpoint was modulated only by the visual hemifield in which the peripheral target was presented. The absence of a consistent eye-position effect later in movement most likely reflects the fact that participants were able to modify their responses online as a result of visual feedback and cognitive corrections. In that sense, the modulation of initial movement direction more purely reflects the effects of the stimulation.

Pointing to a target in peripheral vision usually leads to an overestimation of the eccentricity of the target (Bock, 1986; Enright, 1995; Henriques et al., 1998). The reason for the overestimation is thought to be individuals' relative lack of experience in pointing to targets at which their gaze is not also directed, which leads to an inappropriately calibrated frame of reference in that situation. More generally, it implies that information related to eye position plays a significant role in generating accurate pointing responses. Indeed, there is compelling evidence that the CNS normally plans reaches so that the reacher can avoid having to point into the periphery. In particular, Neggers and Bekkering (2000, 2001) have shown that saccades to a suddenly presented peripheral target are delayed if the current point of fixation is the goal of an ongoing reaching movement. In other words, gaze is anchored to the target of the reach.

Clearly, when the task demands it and a pointing movement is made to a target in the periphery during visual fixation, the default association between gaze position and reach plans must be inhibited. The fact that TMS over the PPC increases the influence of eye-position signals on pointing responses under such circumstances suggests that the PPC makes a significant contribution to the inhibitory process. That result is similar to the clinical syndrome known as *magnetic misreaching* (Carey, Coleman, & Della Sala, 1997; Carey, Della Sala, & Ietswaart, 2002). The patient described in that case study had bilateral parietal lobe degeneration that resulted in an inability to reach to any location other than the one at which she was looking. One interpretation of that finding is that the PPC normally overrides the default association between pointing responses and the direction of gaze, allowing reaches to be made into the peripheral visual fields. In this particular patient's case, PPC damage led the hand to become a slave to the eye.

Three main effects were observed in the present study. The clearest effect was the substantial difference in the influence of TMS over the left PPC between right-handed and left-handed movements. That effect is consistent with the substantial projections from the left PPC to the left motor areas of the brain (Wise, Boussaoud, Johnson, & Caminiti, 1997). Furthermore, it implies that the changes induced by the TMS were not a simple visual phenomenon.

The next most obvious effect was related to the visual hemifield in which the target appeared. In particular, TMS led to changes in the initial movement direction and the final movement endpoint that were in opposite directions to each other when pointing targets appeared in the right and left visual hemifields. That contrasts with the visual field effect typically observed following unilateral PPC damage, in which reaches into the visual hemifield contralateral to the damaged hemisphere are most inaccurate (Perenin & Vighetto, 1988). However, the current visual-hemifield results are consistent with previous brain imaging results (Kertzman, Schwartz, Zeffiro, & Hallett, 1997) as well as the TMS effects observed by Desmurget et al. (1999). In particular, the latter authors found that TMS over the left PPC markedly reduced the appearance of limb trajectory adjustments in response to the sudden change in target location regardless of whether the target shifted into the right or left visual hemifield. On the other hand, it appears to be contradictory that trajectory adjustments were present in our study (as implied by the different pattern of results for initial movement direction than for movement endpoint) during TMS trials but were blocked by TMS in the study by Desmurget and colleagues. The differences may have resulted from the fact that in the latter study, TMS was delivered closer in time to the period when trajectory adjustments were required (i.e., at movement onset, as opposed to ~100–300 ms before movement).

Finally, a subtle effect was observed for eye position in that initial movement direction was influenced more by the TMS when the eyes were directed to the right of the midline than when they were directed to the left. That result is consistent with brain imaging data showing increased left PPC activation during right-handed movements when the eyes are directed rightward (DeSouza et al., 2000).

ACKNOWLEDGMENTS

This work was partially supported by Grants BCS-9982019 and BCS-0121916 from the National Science Foundation to the first author. J. A. was supported by the University of Oregon Summer Program for Undergraduate Research.

REFERENCES

Batista, A. P., Buneo, C. A., Snyder, L. H., & Andersen, R. A. (1999). Reach plans in eye-centered coordinates. *Science, 285,* 257–260.

Bock, O. (1986). Contribution of retinal versus extraretinal signals towards visual localization in goal-directed movements. *Experimental Brain Research, 64,* 476–482.

Buneo, C. A., Jarvis, M. R., Batista, A. P., & Andersen, R. A. (2002). Direct visuomotor transformations for reaching. *Nature, 416,* 632–636.

Carey, D. P., Coleman, R. J., & Della Sala, S. (1997). Magnetic misreaching. *Cortex, 33,* 639–652.

Carey, D. P., Della Sala, S., & Ietswaart, M. (2002). Neuropsychological perspectives on eye-hand coordination in visually-guided reaching. *Progress in Brain Research, 140,* 311–327.

Desmurget, M., Epstein, C. M., Turner, R. S., Prablanc, C., Alexander, G. E., & Grafton, S. T. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nature Neuroscience, 2,* 563–567.

DeSouza, J. F., Dukelow, S. P., Gati, J. S., Menon, R. S., Andersen, R. A., & Vilis, T. (2000). Eye position signal modulates a human parietal pointing region during memory-guided movements. *Journal of Neuroscience, 20,* 5835–5840.

Enright, J. T. (1995). The non-visual impact of eye orientation on eye-hand coordination. *Vision Research, 35,* 1611–1618.

Henriques, D. Y., Klier, E. M., Smith, M. A., Lowy, D., & Crawford, J. D. (1998). Gaze-centered remapping of remembered visual space in an open-loop pointing task. *Journal of Neuroscience, 18,* 1583–1594.

Henriques, D. Y., Medendorp, W. P., Khan, A. Z., & Crawford, J. D. (2002). Visuomotor transformations for eye-hand coordination. *Progress in Brain Research, 140,* 329–340.

Hughes, H. C., Reuter-Lorenz, P. A., Nozawa, G., & Fendrich, R. (1994). Visual-auditory interactions in sensorimotor processing: Saccades versus manual responses. *Journal of Experimental Psychology: Human Perception and Performance, 20,* 131–153.

Kertzman, C., Schwarz, U., Zeffiro, T. A., & Hallett, M. (1997). The role of posterior parietal cortex in visually guided reaching movements in humans. *Experimental Brain Research, 114,* 170–183.

Neggers, S. F., & Bekkering, H. (2000). Ocular gaze is anchored to the target of an ongoing pointing movement. *Journal of Neurophysiology, 83,* 639–651.

Neggers, S. F., & Bekkering, H. (2001). Gaze anchoring to a pointing target is present during the entire pointing movement and is driven by a non-visual signal. *Journal of Neurophysiology, 86,* 961–970.

Perenin, M. T., & Vighetto, A. (1988). Optic ataxia: A specific disruption in visuomotor mechanisms. I. Different aspects of the deficit in reaching for objects. *Brain, 111,* 643–674.

Sawaki, L., Okita, T., Fujiwara, M., & Mizuno, K. (1999). Specific and non-specific effects of transcranial magnetic stimulation on simple and go/no-go reaction time. *Experimental Brain Research, 127,* 402–408.

Sohn, Y. H., Dang, N., & Hallett, M. (2003). Suppression of corticospinal excitability during negative motor imagery. *Journal of Neurophysiology, 90,* 2303–2309.

Terao, Y., Fukuda, H., Ugawa, Y., Hikosaka, O., Hanajima, R., Furubayashi, T., et al. (1998). Visualization of the information flow through human oculomotor cortical regions by transcranial magnetic stimulation. *Journal of Neurophysiology, 80,* 936–946.

van Donkelaar, P., Lee, J.-H., & Drew, A. S. (2000). Transcranial magnetic stimulation disrupts eye-hand interactions in the posterior parietal cortex. *Journal of Neurophysiology, 84,* 1677–1680.

van Donkelaar, P., Lee, J.-H., & Drew, A. S. (2002). Cortical frames of reference for eye-hand coordination. *Progress in Brain Research, 140,* 301–310.

Wise, S. P., Boussaoud, D., Johnson, P. B., & Caminiti, R. (1997). Premotor and parietal cortex: Corticocortical connectivity and combinatorial computations. *Annual Review of Neuroscience, 20,* 25–42.

Submitted September 4, 2003
Revised February 11, 2004