J Neurophysiol 108: 1954–1964, 2012.
First published July 5, 2012; doi:10.1152/jn.00157.2012.

Hand-held tools with complex kinematics are efficiently incorporated into movement planning and online control

Lee A. Baugh,[1] **Erica Hoe,**[1] **and J. Randall Flanagan**[1,2]
[1]*Centre for Neuroscience Studies, Queen's University, Kingston, Ontario, Canada; and* [2]*Department of Psychology, Queen's University, Kingston, Ontario, Canada*

Submitted 21 February 2012; accepted in final form 3 July 2012

Baugh LA, Hoe E, Flanagan JR. Hand-held tools with complex kinematics are efficiently incorporated into movement planning and online control. *J Neurophysiol* 108: 1954–1964, 2012. First published July 5, 2012; doi:10.1152/jn.00157.2012.—Certain hand-held tools alter the mapping between hand motion and motion of the tool end point that must be controlled in order to perform a task. For example, when using a pool cue, the motion of the cue tip is reversed relative to the hand. Previous studies have shown that the time required to initiate a reaching movement (Fernandez-Ruiz J, Wong W, Armstrong IT, Flanagan JR. *Behav Brain Res* 219: 8–14, 2011), or correct an ongoing reaching movement (Gritsenko V, Kalaska JF. *J Neurophysiol* 104: 3084–3104, 2010), is prolonged when the mapping between hand motion and motion of a cursor controlled by the hand is reversed. Here we show that these time costs can be significantly reduced when the reversal is instantiated by a virtual hand-held tool. Participants grasped the near end of a virtual tool, consisting of a rod connecting two circles, and moved the end point to displayed targets. In the reversal condition, the rod translated through, and rotated about, a pivot point such that there was a left-right reversal between hand and end point motion. In the nonreversal control, the tool translated with the hand. As expected, when only the two circles were presented, movement initiation and correction times were much longer in the reversal condition. However, when full vision of the tool was provided, the reaction time cost was almost eliminated. These results indicate that tools with complex kinematics can be efficiently incorporated into sensorimotor control mechanisms used in movement planning and online control.

movement planning; movement correction; sensorimotor control; tool use; visuomotor reversal

RESEARCH EXAMINING THE ABILITY of humans to modify and adjust motor performance during periods of altered visual feedback dates back over one hundred years to early prism work by Helmholtz (1867/1962). These early studies demonstrated that people can adapt to distortions introduced through the wearing of lateral displacement prisms in a number of minutes (Helmholtz 1867/1962), whereas distortions induced by inverting prisms require multiple days to weeks of exposure for people to learn to effectively interact with the world (Stratton 1897). Contemporary research has verified these findings, with many studies demonstrating a capacity for humans to adapt to altered spatial mappings between motor commands and vision (Fernandez-Ruiz et al. 2006; Flanagan and Rao 1995; Medendorp et al. 2008; Redding and Wallace 1996). Despite our ability to accurately program motor commands during periods of altered spatial mappings, there is a persistent reaction time cost, regardless of the amount of practice, associated with overriding the default mapping between the outer world and motor commands if the distortion involves a reversal between spatial mappings and motor commands (Cunningham 1989; Hommel 1993; Newport et al. 2006). Within the field of cognitive psychology, such a mismatch between the spatial location of a target stimulus and the spatial location of the required response (a stimulus-response incompatibility) has been known to increase reaction times for over 50 years (Fitts and Seeger 1953; Kornblum et al. 1990; Simon 1990). Previous research has demonstrated that much of the reaction time cost associated with situations in which the mapping between motor commands and their visual consequences has been reversed can be removed by providing participants with an understanding of a mechanical relationship between the intended movement direction and hand movement (Guiard 1983; Hommel 1993; Riggio et al. 1986; Sulzenbruck and Heuer 2012). For example, in conditions in which participants had to track a horizontally moving target with a cursor moved to the left by pushing a knob right and vice versa, performance was impaired. However, in the same study, if participants were aware that the knob was mounted on the bottom of a steering wheel they had significantly less difficulty tracking the target than when knowledge of the wheel was withheld (Merz et al. 1981). That is to say, the presence of a tool can resolve a scenario that previously resulted in a stimulus response incompatibility, reducing reaction times.

These findings demonstrating a removal of motor preparation costs fit well with research examining how novel tools are incorporated into the body schema. For a century, researchers have speculated that manipulated objects are incorporated into a constantly changing representation consisting of somatosensory and visual information that is used for acting upon our environment (Head and Holmes 1911). Recent work has established that extended tool use can change both the user's perceptual representation of peripersonal space (Berti and Frassinetti 2000; Farne et al. 2005; Witt et al. 2005) and neuronal activity of cells within premotor and parietal regions that respond to both somatosensory and visual information (Inoue et al. 2001; Maravita and Iriki 2004; Obayashi et al. 2001) as well as cells within primary somatosensory cortex (Schaefer et al. 2004). Within humans, increased neuronal activity within primary somatosensory cortex and parietal regions has been associated with short-term (e.g., 10 min) tool use. Immediately after tool use, neuronal activity quickly returns to pre-tool use levels (Inoue et al. 2001; Schaefer et al. 2004). Combining these two bodies of literature, the incorporation of tools into the body schema and the ability of tools to eliminate stimulus-

---

Address for reprint requests and other correspondence: L. A. Baugh, Sanford School of Medicine, Lee Medical Bldg., Univ. of South Dakota, Vermillion, SD 57069 (e-mail: lee.baugh@usd.edu).

response incompatibilities, one could predict that the incorporation of tools may occur at a level accessible to reflexlike behaviors.

The aim of this study was to examine whether tools with complex kinematics are incorporated into the body schema at a level used in rapid online modifications of movement trajectories. To accomplish this, we utilized a target jump paradigm in which there is a sudden displacement of the movement target shortly after the onset of movement. Previous research has shown that under normal circumstances short-latency reflexlike corrections of hand movement to accommodate the new target location are observed (Desmurget et al. 1999; Goodale et al. 1986; Gritsenko et al. 2009; Pisella et al. 2000; Prablanc and Martin 1992; Sarlegna et al. 2003). However, when reaching under a visuomotor reversal, rapid online corrections are selectively suppressed, resulting in delayed corrections, or do not take into account the required visuomotor transformation, resulting in direction errors (Gritsenko and Kalaska 2010). The work of Gritsenko and Kalaska (2010) supports the presence of two error-correction pathways, each associated with different delays in correction times (Day and Lyon 2000). The first, short-latency system appears unable to accommodate arbitrary sensorimotor mappings. In comparison, the long-latency system is able to apply arbitrary mappings between sensory input and motor output. When responding to a sudden jump in target location under an arbitrary sensorimotor mapping, the short-latency system's response must be suppressed, allowing the long-latency mechanism to correct the movement trajectory, resulting in a delayed corrective response. If the short-latency system is not suppressed, erroneous trajectory corrections will occur. Although it is not entirely clear how this suppression occurs, two plausible hypotheses are presented. First, the suppression could occur because of an explicit attempt of the participant to suppress the online corrective mechanism, as the behavioral consequences are detrimental to task performance. A second hypothesis is that a disruption in neural computations occurs as a result of the nonveridical relationship between proprioceptive and visual information and motor commands (Gritsenko and Kalaska 2010). Although the present study cannot dissociate between these theories, if, as hypothesized, complex tools are incorporated into motor plans at a low level of motor planning, one would predict a restoration of the short-latency system in response to a jump in target location under either explanation.

The first experiment was designed to test whether the temporal costs associated with initiating movement during a reversal between hand motion and motion of a controlled cursor can be reduced when the reversal is instantiated by a virtual tool. The tool consisted of a rod that translated through, and rotated about, a pivot point. Participants grasped the near end and were required to move the far end to targets presented to the left or right. In light of previous research using mechanical tools (Guiard 1983; Hommel 1993; Merz et al. 1981; Riggio et al. 1986; Sulzenbruck and Heuer 2012), we expected that vision of the virtual tool would reduce response preparation costs below what would be observed without vision of the tool, during conditions of visuomotor reversal. The second experiment was performed to test the novel hypothesis that vision of the tool would facilitate fast online movement corrections in response to a sudden jump in target position at movement onset; corrections were expected to be suppressed or erroneous without vision of the tool, in light of previous research demonstrating that during conditions in which a visuomotor reversal is present fast corrective mechanisms often lead to erroneous responses (Day and Lyon 2000).

MATERIALS AND METHODS

Participants

All experimental procedures were approved by the Queen's University General Research Ethics Board, and all participants provided informed consent. Participants performed the experiment with their dominant right hand, as assessed by a modified Edinburgh handedness inventory (Oldfield 1971). Sixteen undergraduates (7 men, 9 women; age 17–22 yr, mean = 19 yr) participated in *experiment 1* and performed each of the three conditions (control, visible, nonvisible) in both a reversal and a nonreversal block. Seven participants were recruited from the general university population (4 men, 3 women; age 19–36 yr, mean = 23 yr) for *experiment 2* and performed in two experimental conditions that varied the presence of vision (visible vs. nonvisible) and in a control condition in which no visuomotor transformation was required. Because of the effect sizes observed in *experiment 1*, and the omission of comparisons examining the order in which the visible tool was presented, the number of participants required for *experiment 2* was determined to be approximately half of what was required for *experiment 1*. All participants received $10 compensation for their participation.

Apparatus

Participants were seated on an adjustable chair and grasped a vertical handle attached to a lightweight (290 g) manipulandum (Phantom Haptic Interface 3.0L, Sensable Devices). The handle slid along the horizontal surface on air sleds, which allowed for near frictionless movement in a horizontal plane. Hand position was sampled at a rate of 1,000 Hz by encoders on the manipulandum. Visual stimuli (see below) were projected onto a screen by a CRT projector (Electrohome 9500 Ultra) at a refresh rate of 120 Hz. Participants viewed the screen via a mirror located midway between the screen and the horizontal plane of the handle, resulting in the visual stimuli appearing in the same plane as the handle. A participant's view of both his/her arm and hand was occluded (Fig. 1*A*). The tool was made visible by including visual information regarding the linkage of the hand cursor and tool-tip.

The virtual tool consisted of a rod (300 mm in length) connecting two circles (20 mm in diameter) (Fig. 1*B*). Participants "grasped" the tool by moving the handle of the manipulandum to the near circle, defined as the grasp point. There was a 1 to 1 relationship between hand and tool movement (that is, there was no gain applied to hand movements). Once the tool was grasped, the circle representing the grasp point moved with the handle. The far circle represented the tool-tip, and participants were required to move the tool-tip to targets.

In *experiment 1*, in which participants were required to move the tool-tip to targets presented to the left or right, the rod either translated left and right or rotated about a central pivot point. The far circle representing the tool-tip only moved left or right. Thus, when the rod rotated, the far circle slid along the rod. Participants controlled the left-right position of the tool-tip by moving the grasp point, which could also slide along the rod, sideways. Because the grasp point could slide along the rod, hand movements in the anterior-posterior direction were possible, although very little motion in this direction was observed.

In *experiment 2*, in which participants were required to move the tool-tip to targets presented on an arc distal to the start position of the tool-tip, the circles representing the grasp point and tool-tip were fixed to the rod. The rod either translated with the hand (nonreversal condition) or translated through and rotated about a pivot point, such

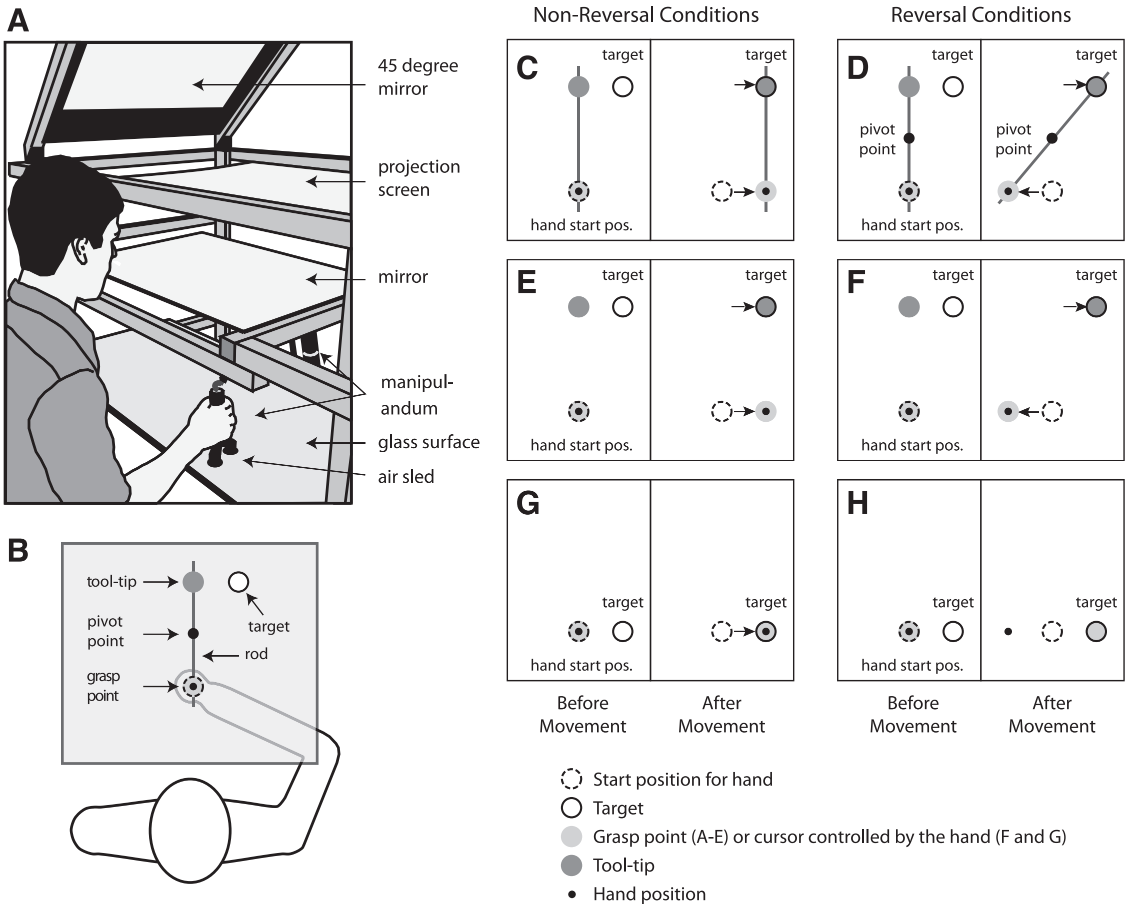

Fig. 1. Apparatus and *experiment 1* task. *A* and *B*: while seated, participants held a handle attached to a lightweight manipulandum. The handle was mounted on air sleds and easily moved over a horizontal glass surface. An image was projected onto a screen via a 45° mirror and viewed by the participant in a semisilvered mirror. This image appears at a height corresponding to the top of the handle. *C*, *E*, and *G*: nonreversal conditions in which the participant moved the hand toward the target. *D*, *F*, and *H*: reversal conditions in which the participant moved the hand away from the target. *C* and *D*: visible tool conditions in which the participant moved the tool-tip to the target either by translating the tool (*C*), in which case the hand moved toward the target, or by rotating the tool about a pivot point (*D*), in which case the hand moved away from the target. *E* and *F*: nonvisible tool conditions are the same as the visible tool conditions, except that the tool and pivot point are not presented. *G* and *H*: control condition in which the participant moved the grasp point (without the tool) to the target by moving the actual hand either toward (*G*) or away from (*H*) the target.

that there was a left-right reversal between the grasp point and tool-tip. In both cases, the tool-tip could move in both the *x* and *y* dimensions.

Procedure

Experiment 1. The participants completed a block of 100 trials in each of four different "tool" conditions (Fig. 1, *C–F*) in which the rod was either visible or nonvisible and the visuomotor mapping between hand movement and movement of the tool-tip was either normal or reversed. In all four conditions, there was an offset between the grasp point and tool-tip. Participants were instructed to perform the task as quickly, but as accurately, as possible and were given no information about the movement of the tool or the visual information that would be presented. At the start of each trial, the participant placed the handle of the manipulandum in the center of the grasp point, at which time the motion of the grasp point was locked to the motion of the handle. At the starting position, the hand position and tool end point were 300 mm apart, with the pivot point being located 150 mm from both the hand and tool-tip. The target location was pseudorandomly presented on the left or right side of the tool-tip at three horizontal eccentricities (35 mm, 55 mm, and 75 mm). A complete trial consisted of moving the center of the tool-tip within 10 mm of the center of the target, at which time the target changed color to signal target contact, and then returning back to the start position.

Participants also completed a block of 100 trials in each of two control conditions in which a cursor (circle 20 mm in diameter) was controlled by the handle and the handle position was vertically aligned with the cursor position (Fig. 1, *G* and *H*). At the start of each trial the participant moved the handle to the center of the cursor, at which point the motion of the cursor was locked to motion of the handle. Targets were pseudorandomly presented to the left or right of the cursor at the same three eccentricities used in the tool conditions. In the nonreversal block the participant had to move the handle toward the target to hit it with the cursor (Fig. 1, *C*, *E*, and *G*), whereas in the reversal block the participant had to move the hand in the opposite direction of the target to hit it with the cursor (Fig. 1, *D*, *F*, and *H*). Movement within the anterior-posterior direction was recorded but did not impact the displayed cursor location. This scenario best matched the tool conditions previously described, in which anterior-posterior movement did not impact the tool-tip location. The purpose of the control condition was to establish the baseline reaction times under both reversed and nonreversed conditions.

Half of the participants were randomly assigned to experience the two nonvisible tool conditions and two control conditions first, with the order randomized, followed by the two visible tool conditions, with block presentation randomized: visible nonreversal and visible reversal. The remaining 50% of participants experienced the two visible conditions and the control first and the nonvisible conditions afterwards. Before the start of each block, participants were given a practice block of 20 trials to allow familiarization with the experimental apparatus and to learn the movement required to control the cursor. The practice trials were identical to the experimental trials. The complete experiment took ~45 min to complete, and participants were given the opportunity to take breaks between blocks.

Experiment 2. Participants were instructed to perform the task as quickly, but as accurately, as possible and were given no information about the movement of the tool or the visual information that would be presented. Participants were required to move the tool-tip from its initial position to a target pseudorandomly presented at one of three positions on a circular arc of 20-cm radius located 15 cm from the pivot point (Fig. 2*A*). The target locations were straight ahead and ±30° from straight ahead. The initial position of the tool-tip was located 5 cm straight ahead from the pivot point. On 20% of trials, the target abruptly changed location 10° left or right when the tangential velocity of the handle exceeded 150 mm/s (i.e., movement onset). At the start of each trial the participant moved the handle to the center of the grasp point, at which point the motion of the grasp point was locked to motion of the handle. A complete trial consisted of moving the center of the tool-tip within 10 mm of the target and returning back to the start position.

The participants were exposed to three different conditions (see Fig. 2*A*). In the tool visible and tool nonvisible conditions the rod translated through and rotated about a pivot point, whereas in the visible nonreversal condition, the tool translated with the hand. There were 200 experimental trials in each of the conditions, and all blocks were preceded by 20 practice trials to allow the participant to discover the movement required to control the cursor and hit the target. Practice trials were identical to the experimental trials in terms of the movement of the tool and the visual information presented; however, there were no target jumps present in the practice trials. To prevent the carryover effects of vision observed in *experiment 1*, all participants began the experiment with the nonvisible condition. The complete experiment took ~45 min to complete.

Data Analysis

Tool-tip, grasp point, hand cursor, and target positions as well as trial timing information and hand velocity were collected and saved onto a Dell Pentium III computer. Hand velocity was computed as the resultant of the x and y hand positions smoothed by a low-pass Butterworth filter with a cutoff frequency of 14 Hz.

Experiment 1. Movement onset was identified when the hand velocity exceeded ±50 mm/s. Reaction times were identified as the time between target onset and movement onset. Trials in which reaction time was <150 ms were classified as early responses and not included in the data analysis. The initial direction of movement (left or right) of the tool-tip or cursor was determined from the sign of the velocity in the left-right direction at movement onset. Trials in which

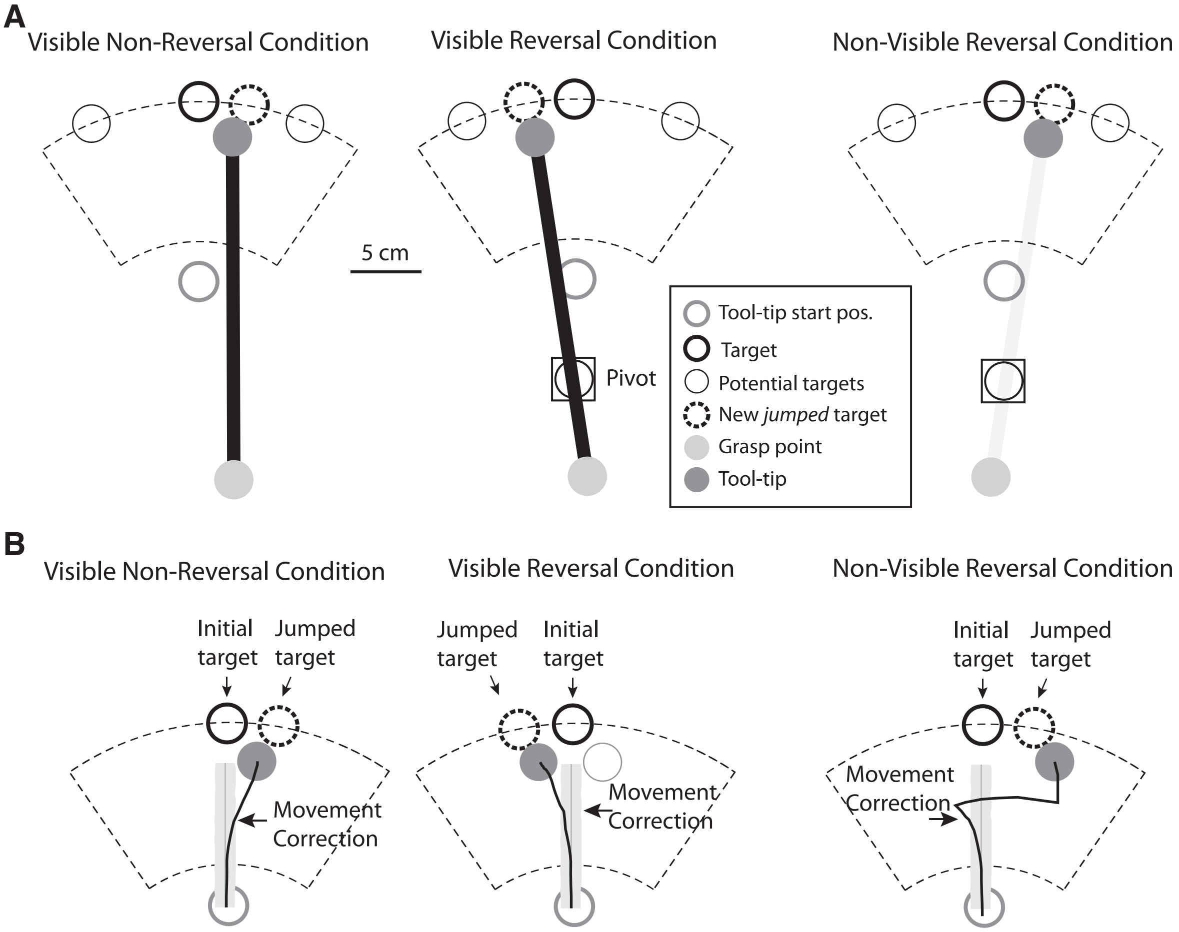

Fig. 2. *Experiment 2* task. *A*: participants moved the tool-tip to 1 of 3 targets under 3 conditions. In the visible condition, the tool moved through, and rotated around, a central pivot point. The nonvisible condition was identical, except that the bar and pivot were not visible. In the control condition, the tool translated. In 20% of the trials, the target jumped to the left or right on movement onset. *B*: the onset of a movement correction in a target jump trial was taken as the time at which the movement path deviated laterally by >2 SD from the mean of trials without a target jump. Typical movement trajectories in each of the 3 conditions and their corresponding movement corrections are provided. Note that an inaccurate movement correction is demonstrated in the movement path of the nonvisible reversal condition.

the initial direction of movement of the tool-tip or cursor was not toward the target were categorized as errors and not included in the analyses of reaction time.

Experiment 2. For all conditions, the end of movement was defined as when the center of the tool-tip was within 10 mm of the center of the target location (corresponding to the tool-tip and target overlapping in the visual display). A trial-by-trial analysis was performed on trials in which the initial target was presented at the straight-ahead position and unexpectedly jumped location left or right. The direction of the initial correction was classified as either correct (moving the tool-tip toward the target in the horizontal axis) or incorrect (moving the tool-tip away from the target in the horizontal axis) by overlaying each trial's movement trajectory on the corresponding mean trajectory from the control condition. A trajectory correction was considered to have occurred when the movement trajectory went beyond the 95% confidence interval of the mean trajectory from the control condition (see Fig. 2*B*) and remained outside of this confidence interval until the target was acquired. Trials in which a correction was not detected, or where corrections were detected earlier than 100 ms after the target jump, were treated as missing data and not included in further analyses (this resulted in the elimination of 7% of all target jump trials). Both the time of correction relative to movement onset and the direction of correction were recorded.

For both experiments, means for each participant were computed for each dependent variable. Percentage data were inspected to ensure that data transformation was not required before submission to further statistical testing. A P value of 0.05 was considered to be statistically significant.

RESULTS

Vision of a Tool Decreases Reaction Time During Visuomotor Reversal (Experiment 1)

Data from trials in which the initial direction of movement was away from the target (6.5% of trials) or those in which reaction time was <150 ms (1.7% of trials) were not included in the analysis. Main effects and interaction terms were assessed by repeated-measures analysis of variance (rANOVA). When indicated as necessary by the omnibus F-tests, corrected (Sidak) pairwise comparisons were made.

Control condition. Within the control condition there was a main effect of reversal, where the mean reaction time in the nonreversal block (mean = 306 ms, SD = 38) was significantly faster than the mean reaction time in the reversal block (mean = 409 ms, SD = 42) [$F(1,14) = 99.96$, $P < 0.001$] (Fig. 3*A*). To ensure that the reaction time benefits observed in the nonreversal block were not a result of a decrease in accuracy, an examination of directional error was performed. Relatively few direction errors were made. Across participants, the average percentage of trials in the control condition without a direction error was 91%. There was a main effect of reversal, with fewer directional errors in the nonreversal block (mean = 96% correct, SD = 2.4) than in the reversal block (mean = 87% correct, SD = 8.3) [$F(1,14) = 9.18$, $P < 0.001$] (see Fig. 3*B*). It is therefore likely that the additional reaction time observed within the reversal block enabled participants to limit the number of direction errors committed.

Experimental conditions. Main effects and interaction terms were assessed by rANOVA. When indicated as necessary by the omnibus F-tests, corrected (Sidak) pairwise comparisons were made. In assessing reaction times, a significant three-way (order × reversal × vision) interaction [$F(1,14) = 6.213$, $P < 0.0026$] was observed. Therefore, simple-effects tests were conducted on reaction times within each order.

In *order 1*, where the nonvision conditions were shown first, a significant interaction between reversal and vision was found [$F(1,7) = 7.40$, $P = 0.030$], characterized by a larger effect of vision in the reversal conditions than in the nonreversal conditions. That is, in *order 1* vision markedly decreased the reaction time cost within the reversal block but had a relatively small effect on reaction time in the nonreversal block (see Fig. 3*C*). Simple-effects tests revealed a main effect of reversal on reaction time [$F(1,7) = 46.78$, $P < 9.001$], characterized by faster reaction times within the nonreversal blocks (mean = 367 ms, SD = 46) compared with the reversal blocks (mean = 444 ms, SD = 72). Finally, a main effect of vision was also observed, with reaction times in the vision condition (mean = 383 ms, SD = 51) being faster than in the no-vision condition (mean = 428 ms, SD = 82) [$F(1,7) = 11.18$, $P = 0.012$].

In *order 2*, there was no effect of vision ($P = 0.412$) and no reversal × vision interaction was present ($P = 0.738$) (Fig. 3*D*). However, where the vision conditions were shown first, there was a main effect of reversal [$F(1,7) = 79.14$, $P < 0.001$], characterized by faster reaction times within the nonreversal blocks (mean = 318 ms, SD = 26) compared with the reversal blocks (mean = 409 ms, SD = 40). These results suggest that when participants had previously viewed the tool they could still exploit knowledge of the linkage between hand and tool-tip motion when performing the reversal task without the visible tool.

Across participants, 9% of trials contained a directional error. A main effect of reversal on direction error was observed [$F(1,14) = 9.176$, $P = 0.009$], with participants moving in the incorrect direction more often in the reversal block (12%, SD = 7) than in the nonreversal block (7%, SD = 8).

Time-based analysis of errors. To examine the issue of practice effects within the task, reaction times were binned into blocks of 10 successive trials (including 2 blocks of practice trials) and a series of Bonferroni-corrected paired-samples t-tests between each block and its predecessor were conducted (starting with the second time block) until no significant difference was found (suggesting performance had stabilized). The visible reversal, nonvisible reversal, and nonvisible nonreversal trial types demonstrated evidence of practice effects across blocks. For both the visible reversal and nonvisible nonreversal trials, performance had stabilized after 20 trials. For the nonvisible nonreversal trial type, performance stabilized within 10 trials. For all other conditions, performance had stabilized within the first 10 trials (Fig. 3*E*).

Vision of a Tool Restores Rapid Online Corrections During Visuomotor Reversal (Experiment 2)

Main effects and interaction terms were assessed by rANOVA. When indicated as necessary by the omnibus F-tests, corrected (Sidak) pairwise comparisons were made.

Movement correction time. The movement correction time data for trials in which the initial correction was made in the horizontally appropriate direction were separated into groups based on condition (visible reversal, nonvisible reversal, visible nonreversal) and can be seen in Fig. 3*F*. Frequency distributions of correction times of correct responses (pooled across all participants) are shown in Fig. 4, *A*–*C*. A one-way

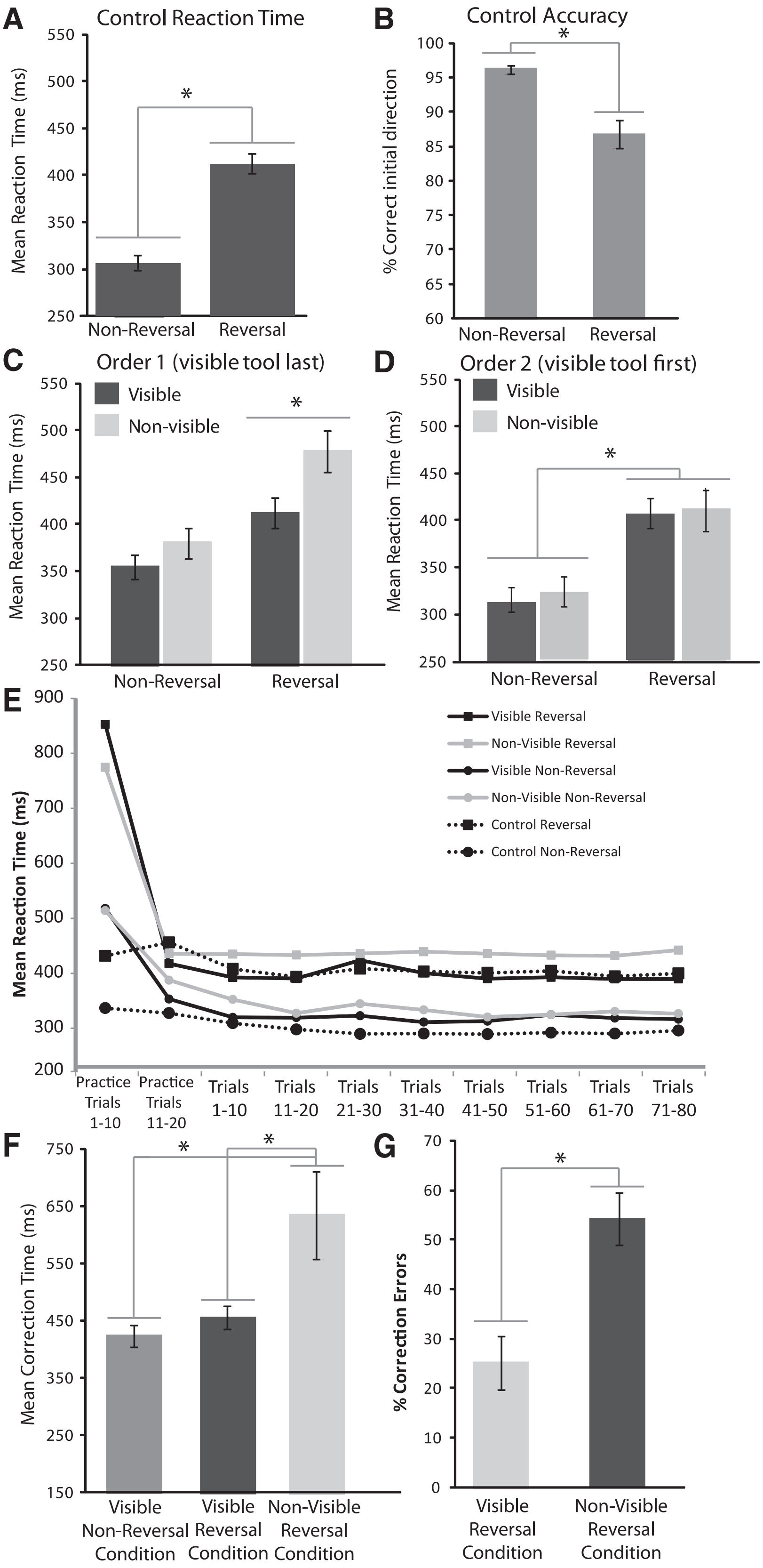

Fig. 3. Tool use and movement initiation. *A*: mean reaction time across participants in the control condition. The reversal produced a reaction time cost of ~100 ms. *B*: mean % of correct trials across participants in the control condition. Nonreversal conditions were performed significantly more accurately. *C*: mean reaction times across all participants in *order 1* for the tool visible and tool nonvisible conditions. In the reversal conditions, viewing the tool reduced reaction time to values similar to those obtained in the nonreversal conditions. *D*: mean reaction times across all subjects in *order 2* for the tool visible and tool nonvisible conditions. When the tool was displayed first, the benefit carried over to the tool nonvisible condition. *E*: learning curves for the experimental and control conditions of *experiment 1*. Performance in all groups had stabilized within 20 trials of exposure. *F*: mean correction times in the 3 conditions of *experiment 2*. Significant differences in reaction time were observed between the nonvisible and control conditions. *G*: mean % of correction errors (movements in the incorrect direction) in the visible and nonvisible reversal conditions of *experiment 2*. There were no errors in the visible nonreversal condition. Significant differences were found between the nonvisible and visible conditions. Error bars represent ±SE. *Significance at the $P < 0.05$ level.

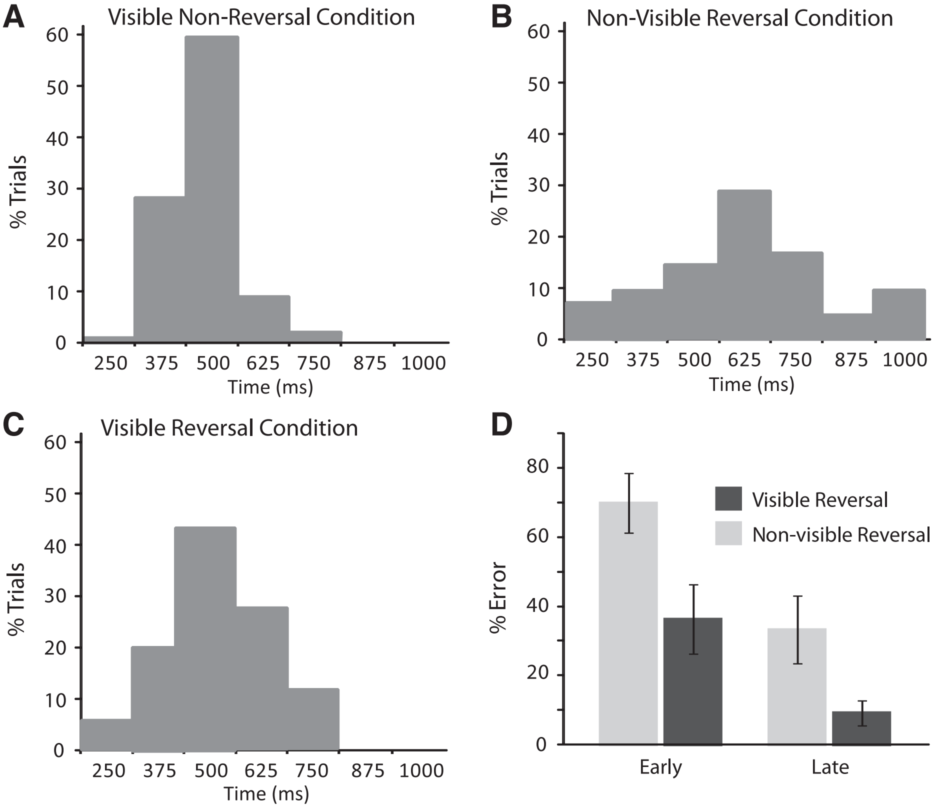

Fig. 4. Error rates as a function of the time of correction. *A–C*: frequency distributions by trial time of correct trajectory modifications for the visible nonreversal condition (*A*), nonvisible reversal condition (*B*), and visible reversal condition (*C*). Data pooled across participants. Both the mean and modal correction times occurred later in the trial in the nonvisible reversal condition than in the other 2 conditions. *D*: corrections were classified as either early (occurring before the mean correction time) or late (occurring after the mean correction time). Significant effects of both condition (tool visible vs. nonvisible) and time of correction (early vs. late) were observed on error rate. Vertical bars represent SE.

rANOVA demonstrated a significant main effect of condition [$F(2,12) = 6.34$, $P = 0.013$]. Bonferroni pairwise comparisons revealed a significant difference ($P = 0.028$) between the nonvisible reversal condition (mean = 634 ms, SD = 204) and the visible nonreversal condition (mean = 423 ms, SD = 49). However, no difference was observed between the visible reversal condition (mean = 454 ms, SD = 54) and the visible nonreversal condition ($P = 0.143$). Thus vision of the tool dramatically decreased the time required to initiate online movement corrections (in response to target jumps) during the reversal. Moreover, performance was similar to that seen without a reversal.

Correction direction errors. The percentages of direction errors in the visible reversal and nonvisible reversal conditions are shown in Fig. 3*G*. The data from the visible nonreversal condition are not shown because participants made zero errors in the direction of initial movement trajectory correction. A one-way rANOVA (visible reversal vs. nonvisible reversal) revealed a significant effect of condition [$F(1,6) = 55.46$, $P < 0.001$], with a greater proportion of initial corrections in the incorrect direction in the nonvisible trials compared with the visible trials where vision of the tool was presented (54%, SD = 14 vs. 25%, SD = 14).

To further quantify the effects of tool visibility on the accuracy of corrections, and to confirm that early correction errors in the nonvisible trials were likely to be erroneous, the direction error was further split into two groups (early vs. late) based on the time of correction within a trial using a mean split (Fig. 4*D*). A 2 (visible vs. nonvisible) × 2 (early vs. late) rANOVA revealed significant effects of both condition [$F(1,6) = 16.41$, $P = 0.008$] and time [$F(1,6) = 15.63$, $P = 0.007$]. Therefore, participants in the nonvisible condition were more likely to make movements in the incorrect direction, regardless of the time of correction. Additionally, the corrective action was more likely to be toward the new target location if the correction occurred later in the trial for both groups of participants.

Movement duration and duration of corrective movements. Further analyses were conducted on the movement duration and the duration of the corrective movement. A significant effect of condition was observed for both movement duration [$F(2,12) = 58.75$, $P < 0.001$] and the duration of the corrective response [$F(2,12) = 21.79$, $P < 0.001$]. Bonferroni-corrected pairwise comparisons revealed that movement duration in the nonvisible reversal condition (mean = 1,417 ms, SD = 358 ms) was significantly longer than that in either the visible reversal condition (mean = 712 ms, SD = 169 ms) or the visible nonreversal condition (mean = 598, SD = 155 ms) ($P < 0.001$ in both cases). However, no difference was observed between the visible reversal condition and the visible nonreversal condition ($P = 0.06$). Pairwise comparisons between durations of the corrective response revealed the same pattern of results. The duration of the corrective movement in the nonvisible reversal condition (mean = 782 ms, SD = 350) was significantly longer than that in either the visible reversal condition (mean = 257 ms, SD = 130 ms) ($P = 0.006$) or the visible nonreversal condition (mean = 175 ms, SD = 120 ms) ($P = 0.010$). However, no significant difference ($P = 0.526$) was observed between the visible reversal condition and the visible nonreversal condition.

Time-based analysis of errors. To examine the issue of practice effects within the task, for each condition a series of Bonferroni-corrected paired-samples *t*-tests between each trial in which a target jump occurred and the preceding target jump trial were conducted on movement correction times (starting with the second jump trial) until no significant difference was found between these two trials (suggesting performance had stabilized). No significant differences were found across jump trials in any of the conditions.

DISCUSSION

The present study demonstrates that the presence of a virtual tool can reduce the temporal costs associated with response preparation during a visuomotor reversal (*experiment 1*) and can restore movement correction times in response to a sudden displacement in target location performed under a visuomotor reversal scenario to equivalent times as when no visuomotor reversal was present. To our knowledge, these results provide the first evidence that tools with complex kinematics are incorporated into the body schema at a level that enables them to be incorporated in rapid, online modifications of movement trajectories. This finding fits well with contemporary research demonstrating functional changes in the body schema associated with active tool use. Previous research has shown that extended tool use can change both the user's perceptual representation of peripersonal space (Berti and Frassinetti 2000; Farne et al. 2005; Witt et al. 2005) and neuronal activity of cells within premotor and parietal regions that respond to both sensory and visual information (Inoue et al. 2001; Maravita and Iriki 2004; Obayashi et al. 2001). Additionally, recent research has shown that extensive tool use can alter somatosensory representations of intrinsic properties of arm configuration (Cardinali et al. 2009).

The present study focused on two specific measurements of motor performance during a visuomotor reversal: the reaction time required for initiating movements (*experiment 1*) and the time required to initiate online corrections in response to a target suddenly jumping location (*experiment 2*). We found that the presentation of a virtual tool that visually represented the transformation that was required was sufficient to reduce the reaction times and to restore corrective mechanisms used to respond to a jump in target location. Analyses on the movement duration and the duration of the corrective response were consistent with these findings, with both movement duration and the duration of the corrective response suggesting more efficient movement planning and control in the visible tool condition compared with the nonvisible tool condition. Overall, the reaction time data of the control condition are in line with previous studies. Specifically, a reaction time of up to 300 ms to a visual stimulus requiring a movement-related response and a reversal effect of ~100 ms have been reported for a number of similar tasks (Dean et al. 2011; Fernandez-Ruiz et al. 2011; Gritsenko and Kalaska 2010; Sommer et al. 2001). Although there has been evidence that physical tool use can restore stimulus response compatibility and thus reduce reaction times during reversal scenarios (Guiard 1983; Hommel 1993; Riggio et al. 1986), this is the first behavioral study to demonstrate that tool use is incorporated in fast corrective mechanisms that are considered to represent low-level, automatic responses (Gritsenko and Kalaska 2010; Pelisson et al. 1986; Pisella et al. 2000).

The presence of a main effect of reversal on reaction time in both the control condition and the tool conditions of *experiment 1* confirmed that there is a reaction time cost associated with performing visuomotor reversals under these conditions. Previous research has demonstrated similar movement initiation costs with a variety of methodologies including antipointing (Fischer and Weber 1997; Guitton et al. 1985; Neely and Heath 2009), cursor-target remapping (Fernandez-Ruiz et al. 2007; Newport et al. 2006), and reversing prisms (Cunningham 1989). It is therefore not surprising that in all conditions a main effect of reversal was demonstrated. The present results demonstrate that a toollike visual representation of the reversal can decrease this cost in initiating movements, as reflected in the significant interaction between vision and reversal on the reaction times in participants who experienced the nonvisible conditions before the visible conditions (i.e., *order 1*). When these participants were presented with a visible tool, the temporal costs associated with response preparation toward the targets under the visuomotor reversal were significantly reduced. Interestingly, the benefit of visual information related to the tool is present in a relatively short period of time, within just a few trials for most conditions. This incorporation of the tool appears to occur much faster than the exposure previously reported to induce changes at the neuronal level in the monkey within the parietal lobes (Hihara et al. 2006; Iriki et al. 1996), but in a timeline consistent with human neuroimaging work (Schaefer et al. 2004), suggesting that perhaps previous experience we have using the simplistic tools employed in the present experiment allows for their rapid incorporation into movement planning (see also Ingram et al. 2010). Within humans, neuronal plasticity within primary somatosensory cortex (Schaefer et al. 2004) and posterior parietal cortex (PPC) (Inoue et al. 2001) related to tool use was observed during brief exposure to a simplistic tool. Future studies examining more complicated and/or novel tools for which participants would have no previous experience may shed additional light on this question.

It is important to note that there was an increase in the percentage of errors in both the visible and nonvisible conditions of *experiment 2* compared with the control condition in which no reversal was required. Although successful incorporation of the virtual tool into movement planning occurred within the first 20 practice trials, the error data suggest that this incorporation is not present for all participants and/or is not successful during all trials. Future research would be well served by specifically examining individual differences in the ability to utilize this information across participants.

Previous research investigating the online control of goal-directed movement has shown that, when presented with a double-step paradigm in which the target jumps to a new location at reach movement onset, participants are able to make fast corrections to their initial trajectory to accommodate the shift in target location (Day and Brown 2001; Day and Lyon 2000; Gritsenko and Kalaska 2010; Paulignan et al. 1991; Pisella et al. 2000; Prablanc and Martin 1992). It is thought that these rapid corrections are generated in part by the PPC, through the combination of multisensory information resulting in a current arm state estimate that can then be used to generate a rapid online correction at a level before conscious perception of target location is achieved (Desmurget et al. 2004; Kalaska et al. 1983; Mulliken et al. 2008). Indeed, participants are normally unaware of small target jumps that occur immediately before, during, or shortly after gaze shifts to the initial target, in part as a result of the saccadic suppression of the image displacement phenomenon (Bridgeman et al. 1975). Additionally, these reach errors that result from such jumps are within the range of errors that can be expected because of normal movement variability (Goodale et al. 1986; Pelisson et al. 1986), making such error corrections commonplace for the visuomotor system.

It is important to note that the movement correction times reported in the present study are significantly higher than most previously cited studies that utilized a double-step paradigm. For example, Day and Lyon (2000) reported corrective response latencies occurring as early as 120 ms, whereas we find responses to a jump in target location occurring at 420 ms in the visible tool nonreversal condition. These baseline response latencies are likely a function of the experimental setup, the specific experimental task, and the analysis employed to detect when a movement correction has been made. However, within an experiment, these factors should remain constant across conditions. Therefore, we interpret the fact that the movement corrections for both the visible nonreversal and visible reversal condition occurred at the same time to mean that a partial restoration of the corrective response was achieved. However, an alternate hypothesis is that all movement corrections reported (even those that did not require a reversal) were on a timescale consistent with voluntary cognitive responses. The present study is unable to experimentally distinguish these two competing hypotheses.

Day and Lyon (2000) examined whether participants had cognitive control of these corrective movements. In their study, there was an observable shift of target location 25 ms after movement onset. Participants were instructed either to follow the target to its new location or to move in the opposite direction. When participants were explicitly instructed to point away from the target, 24% of trials contained movement corrections within the 125–160 ms "automatic" latency range. Movement directions of trials within this latency range could not be reversed, with participants continuing to point to the target's new location. Similar results were obtained in a study in which a change in target color instructed participants whether they should incorporate the new target location into their movement or interrupt their movement upon noticing that the target had changed color. In this experiment, participants often made automated corrections to a target jump, despite instructions to do otherwise. However, when a color change in target was used as an instruction as to which act participants were to perform, such fast corrections were not observed (Pisella et al. 2000).

Recently, Gritsenko and Kalaska (2010) examined double-step task performance in a visuomotor reversal scenario. These authors trained participants to generate target-directed reaching movements under a left-right visuomotor reversal and found that, even when the visuomotor reversal was highly practiced, movement trajectory corrections occurred 100–200 ms later than in normal, nonreversed, reaching. Furthermore, those trajectory modifications occurring on a timescale consistent with early automatic corrections were significantly more likely to be incorrectly performed, resulting in hand movements in the same direction as the target jump and cursor movements in the opposite direction (Gritsenko and Kalaska 2007, 2010). These results indicate that learning a visuomotor reversal may result in a volitional suppression of the fast online correction system that is typically responsible for correcting small displacements in target location, but does not result in its adaptation. In normal circumstances such a limitation makes sense, as we are unlikely to encounter situations in which sensory inputs and outgoing motor commands would have a reversed relationship. In contrast to previous research, when shown a visible tool that instantiated a visuomotor reversal participants in *experiment 2* were able to modify their movement trajectories at time intervals on par with conditions in which no visuomotor reversal was present. This suggests that the reversal limitation in the online correction mechanism is not fundamentally grounded in the direction of the required arm movement itself but is instead related to the direction of required movement of the controlled end point, which may be opposite the direction of the hand when using a tool with complex kinematics.

Pisella and colleagues (Pisella et al. 2000) report on a patient who failed to demonstrate fast, online correction in response to a sudden jump in target location after bilateral PPC damage, suggesting that the dorsal stream of visual information is a likely substrate for online corrections in movement trajectory. This finding is supported by recent transcranial magnetic stimulation (TMS) studies demonstrating that when a TMS pulse was applied over the left PPC during target presentation, a disruption of normal movement path corrections occurred (Desmurget et al. 1999). Additionally, the location of the PPC between areas where elementary stimulus analysis and motor output generation occur (MacKay 1992; Sakata and Taira 1994) makes it a prime candidate for such computations. The PPC has also been implicated in the integration of tools into the body schema. Specifically, the visual receptive fields of bimodal neurons within the intraparietal sulcus (IPS) have been shown to elongate from the hand along the body of a utilized tool to the tip when a monkey was trained to use a rake to retrieve food (Iriki et al. 1996). Similar results have been found with PET and human participants, with tool-dependent activation observed within the IPS (Inoue et al. 2000). Therefore, it appears that tool use and rapid responses to sudden jumps in target locations are utilizing similar brain regions, and this may facilitate the interaction of these mechanisms. An interesting follow-up to partially address this possible interaction would be the examination of parietal lobe-damaged patients' abilities to incorporate tools into the body schema, as opposed to the general examinations of ideomotor apraxia that commonly arises after left hemisphere parieto-frontal damage.

Apart from a better understanding as to how tools are incorporated into movement plans, the presented results may also have direct implications for the type of information virtual reality and teleoperative devices should provide to the people using them. Although these systems typically provide visual (and sometimes haptic) feedback of effector end points to the operator, the present findings suggest that visual representations of the linkages between the user's hand movements and the resultant movements of the effector's end points would provide a better integration of the teleoperative device. This could have substantial implications where speed and accuracy are a necessary requirement of the system.

GRANTS

This work was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC), and the Canadian Institutes of Health Research (CIHR). L. A. Baugh was supported by an NSERC CREATE training grant.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: L.A.B., E.H., and J.R.F. conception and design of research; L.A.B. and E.H. performed experiments; L.A.B. and E.H. analyzed data; L.A.B., E.H., and J.R.F. interpreted results of experiments; L.A.B. and J.R.F. prepared figures; L.A.B. drafted manuscript; L.A.B. and J.R.F. edited and revised manuscript; L.A.B., E.H., and J.R.F. approved final version of manuscript.

REFERENCES

Berti A, Frassinetti F. When far becomes near: remapping of space by tool use. *J Cogn Neurosci* 12: 415–420, 2000.

Bridgeman B, Hendry D, Stark L. Failure to detect displacement of the visual world during saccadic eye movements. *Vision Res* 15: 719–722, 1975.

Cardinali L, Frassinetti F, Brozzoli C, Urquizar C, Roy AC, Farne A. Tool-use induces morphological updating of the body schema. *Curr Biol* 19: R478–R479, 2009.

Cunningham HA. Aiming error under transformed spatial mappings suggests a structure for visual-motor maps. *J Exp Psychol Hum Percept Perform* 15: 493–506, 1989.

Day BL, Brown P. Evidence for subcortical involvement in the visual control of human reaching. *Brain* 124: 1832–1840, 2001.

Day BL, Lyon IN. Voluntary modification of automatic arm movements evoked by motion of a visual target. *Exp Brain Res* 130: 159–168, 2000.

Dean HL, Marti D, Tsui E, Rinzel J, Pesaran B. Reaction time correlations during eye-hand coordination: behavior and modeling. *J Neurosci* 31: 2399–2412, 2011.

Desmurget M, Epstein CM, Turner RS, Prablanc C, Alexander GE, Grafton ST. Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nat Neurosci* 2: 563–567, 1999.

Desmurget M, Gaveau V, Vindras P, Turner RS, Broussolle E, Thobois S. On-line motor control in patients with Parkinson's disease. *Brain* 127: 1755–1773, 2004.

Farne A, Iriki A, Ladavas E. Shaping multisensory action-space with tools: evidence from patients with cross-modal extinction. *Neuropsychologia* 43: 238–248, 2005.

Fernandez-Ruiz J, Diaz R, Moreno-Briseno P, Campos-Romo A. Ojeda R. Rapid topographical plasticity of the visuomotor spatial transformation. *J Neurosci* 26: 1986–1990, 2006.

Fernandez-Ruiz J, Goltz HC, DeSouza JF, Vilis T, Crawford JD. Human parietal "reach region" primarily encodes intrinsic visual direction, not extrinsic movement direction, in a visual motor dissociation task. *Cereb Cortex* 17: 2283–2292, 2007.

Fernandez-Ruiz J, Wong W, Armstrong IT, Flanagan JR. Relation between reaction time and reach errors during visuomotor adaptation. *Behav Brain Res* 219: 8–14, 2011.

Fischer B, Weber H. Effects of stimulus condition on the performance of antisaccades in man. *Exp Brain Res* 116: 191–200, 1997.

Fitts PM, Seeger CM. S-R compatibility: spatial characteristics of stimulus and response codes. *J Exp Psychol* 46: 199–210, 1953.

Flanagan JR, Rao AK. Trajectory adaptation to a nonlinear visuomotor transformation: evidence for motion planning in visually perceived space. *J Neurophysiol* 74: 2174–2178, 1995.

Goodale MA, Pelisson D, Prablanc C. Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature* 320: 748–750, 1986.

Gritsenko V, Yakovenko S, Kalaska JF. Integration of predictive feedforward and sensory feedback signals for online control of visually guided movement. *J Neurophysiol* 102: 914–930, 2009.

Gritsenko V, Kalaska JF. Rapid online correction is selectively suppressed during movement with a visuomotor transformation. *J Neurophysiol* 104: 3084–3104, 2010.

Gritsenko V, Kalaska JF. Learning a new visuomotor transformation does not change early online correction in humans (Abstract). In: *Soc Neurosci Abstr* 33, 2007.

Guiard Y. The lateral coding of rotations: a study of the simon effect with wheel-rotation responses. *J Mot Behav* 15: 331–342, 1983.

Guitton D, Buchtel HA, Douglas RM. Frontal lobe lesions in man cause difficulties in suppressing reflexive glances and in generating goal-directed saccades. *Exp Brain Res* 58: 455–472, 1985.

Head H, Holmes HG. Sensory disturbances from cerebral lesions. *Brain* 34: 102–254, 1911.

von Helmholtz H. *Treatise on Physiological Optics*. New York: Dover, 1867/1962.

Hihara S, Notoya T, Tanaka M, Ichinose S, Ojima H, Obayashi S, Fujii N, Iriki A. Extension of corticocortical afferents into the anterior bank of the intraparietal sulcus by tool-use training in adult monkeys. *Neuropsychologia* 44: 2636–2646, 2006.

Hommel B. Inverting the Simon effect by intention—determinants of direction and extent of effects of irrelevant spatial information. *Psychol Res* 55: 270–279, 1993.

Ingram JN, Howard IS, Flanagan JR, Wolpert DM. Multiple grasp-specific representations of tool dynamics mediate skilful manipulation. *Curr Biol* 20: 618–623, 2010.

Inoue K, Kawashima R, Satoh K, Kinomura S, Goto R, Sugiura M, Ito M, Fukuda H. A PET study of visuomotor learning under optical rotation. *Neuroimage* 11: 505–516, 2000.

Inoue K, Kawashima R, Sugiura M, Ogawa A, Schormann T, Zilles K, Fukuda H. Activation in the ipsilateral posterior parietal cortex during tool use: a PET study. *Neuroimage* 14: 1469–1475, 2001.

Iriki A, Tanaka M, Iwamura Y. Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport* 7: 2325–2330, 1996.

Kalaska JF, Caminiti R, Georgopoulos AP. Cortical mechanisms related to the direction of two-dimensional arm movements: relations in parietal area 5 and comparison with motor cortex. *Exp Brain Res* 51: 247–260, 1983.

Kornblum S, Hasbroucq T, Osman A. Dimensional overlap: cognitive basis for stimulus-response compatibility—a model and taxonomy. *Psychol Rev* 97: 253–270, 1990.

MacKay WA. Properties of reach-related neuronal activity in cortical area 7a. *J Neurophysiol* 67: 1331–1345, 1992.

Maravita A, Iriki A. Tools for the body (schema). *Trends Cogn Sci* 8: 79–86, 2004.

Medendorp WP, Beurze SM, Van Pelt S, Van Der Werf J. Behavioral and cortical mechanisms for spatial coding and action planning. *Cortex* 44: 587–597, 2008.

Merz F, Kalveram KT, Huber K. Der Einfluss kognitiver Faktoren auf Steueleistungen. In: *Erkennen, Wollen, Handeln*, edited by Tent L. Gottingen, Germany: Hogrefe, 1981, p. 327–335.

Mulliken GH, Musallam S, Andersen RA. Forward estimation of movement state in posterior parietal cortex. *Proc Natl Acad Sci USA* 105: 8170–8177, 2008.

Neely KA, Heath M. Visuomotor mental rotation: reaction time is not a function of the angle of rotation. *Neurosci Lett* 463: 194–198, 2009.

Newport R, Brown L, Husain M, Mort D, Jackson SR. The role of the posterior parietal lobe in prism adaptation: failure to adapt to optical prisms in a patient with bilateral damage to posterior parietal cortex. *Cortex* 42: 720–729, 2006.

Obayashi S, Suhara T, Kawabe K, Okauchi T, Maeda J, Akine Y, Onoe H, Inki A. Functional brain mapping of monkey tool use. *Neuroimage* 14: 853–861, 2001.

Oldfield RC. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9: 97–113, 1971.

Paulignan Y, MacKenzie C, Marteniuk R, Jeannerod M. Selective perturbation of visual input during prehension movements. *Exp Brain Res* 83: 502–512, 1991.

Pelisson D, Prablanc C, Goodale MA, Jeannerod M. Visual control of reaching movements without vision of the limb. II. Evidence of fast unconscious processes correcting the trajectory of the hand to the final position of a double-step stimulus. *Exp Brain Res* 62: 303–311, 1986.

Pisella L, Grea H, Tilikete C, Vighetto A, Desmurget M, Rode G, Boisson D, Rossetti Y. An "automatic pilot" for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia. *Nat Neurosci* 3: 729–736, 2000.

Prablanc C, Martin O. Automatic control during hand reaching at undetected two-dimensional target displacements. *J Neurophysiol* 67: 455–469, 1992.

Redding GM, Wallace B. Adaptive spatial alignment and strategic perceptual-motor control. *J Exp Psychol Hum Percept Perform* 22: 379–394, 1996.

Riggio L, Gawryszeqski L, Umilta C. What is crossed in crossed-hand effects? *Acta Psychol (Amst)* 62: 1986.

Sakata H, Taira M. Parietal control of hand action. *Curr Opin Neurobiol* 4: 847–856, 1994.

Sarlegna F, Blouin J, Bresciani JP, Bourdin C, Vercher JL, Gauthier GM. Target and hand position information in the online control of goal-directed arm movements. *Exp Brain Res* 151: 524–535, 2003.

Schaefer M, Rothemund Y, Heinze H, Rotte M. Short-term plasticity of the primary somatosensory cortex during tool use. *Neuroreport* 15: 1293–1297, 2004.

Simon JR. The effects of an irrelevant directional cue on human information processing. In: *Stimulus-Response Compatibility: An Integrated Perspective*, edited by Proctor RW, Reeve TG. Amsterdam: North-Holland, 1990, p. 31–86.

Sommer M, Classen J, Cohen LG, Hallett M. Time course of determination of movement direction in the reaction time task in humans. *J Neurophysiol* 86: 1195–1201, 2001.

Stratton GM. Some preliminary experiments on vision without inversion of the retinal image. *Psychol Rev* 3: 611–617, 1897.

Sulzenbruck S, Heuer H. Enhanced mechanical transparency during practice impedes open-loop control of a complex tool. *Exp Brain Res* 218: 283–294, 2012.

Witt JK, Proffitt DR, Epstein W. Tool use affects perceived distance, but only when you intend to use it. *J Exp Psychol Hum Percept Perform* 31: 880–888, 2005.