Evidence for Automatic On-Line Adjustments of Hand Orientation During Natural Reaching Movements to Stationary Targets

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1Département de Physiologie, 2Département de Kinésiologie, 3Research Group in Neurological Sciences, Canadian Institutes of Health Research; 4Groupe de Recherche sur le Système Nerveux Central, Fonds de la Recherche en Santé du Québec; and 5Centre de Recherche Institut Universitaire de Gériatrie de Montréal, Université de Montréal, Montreal, Quebec, Canada

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Gosselin-Kessiby N, Messier J, Kalaska JF. Evidence for automatic on-line adjustments of hand orientation during natural reaching movements to stationary targets. J Neurophysiol 99: 1653–1671, 2008. First published February 6, 2008; doi:10.1152/jn.00980.2007. Control of the spatial orientation of the hand is an important component of reaching and grasping movements. We studied the contribution of vision and proprioception to the perception and control of hand orientation in orientation-matching and letter-posting tasks. In the orientation-matching task, subjects aligned a “match” handle to a “target” handle that was fixed in different orientations. In letter-posting task 1, subjects simultaneously reached and rotated the right hand to insert a match handle into a target slot fixed in the same orientations. Similar sensory conditions produced different error patterns in the two tasks. Furthermore, without vision of the hand, final hand-orientation errors were smaller overall in letter-posting task 1 than in the orientation-matching task. In letter-posting task 2, subjects first aligned their hand to the angle of the target and then reached to it with the instruction not to change their initial hand orientation. Nevertheless, hand orientation changed during reaching in a way that reduced the initial orientation errors. This did not occur when there was no explicitly defined target toward which the subjects reached (letter-posting task 3). The reduction in hand-orientation errors during reach, even when told not to change it, suggests the engagement of an automatic error correction mechanism for hand orientation during reaching movements toward stationary targets. The correction mechanism was engaged when the task involved transitive actions directed at the target object. The on-line adjustments can occur without vision of the hand and even when target orientation is defined only by proprioceptive inputs.

INTRODUCTION

Reaching and grasping movements are an important part of human voluntary behavior. They have been the subject of extensive theoretical, behavioral, and neurophysiological study because they encapsulate many of the major issues in the control of voluntary movements, such as kinematic redundancy, sensorimotor coordinate transformations, feed-forward versus feedback control, multi-joint and -muscle coordination, control of task kinetics and muscle activity, motor adaptation, and motor skill learning.

The act of reach to grasp can be divided into three components, transport of the hand to the spatial location of the target object, orientation of the hand to align it with the spatial orientation of the object, and preshaping of the configuration of the digits and thumb in preparation to grasp the object once the hand arrives at its spatial location. The kinematics of transport, orientation, and hand preshaping/grasp are closely coordinated so that the hand is in the appropriate orientation and the digits begin to close on the target object shortly before the hand comes in contact with it (Desmurget and Prablanc 1997; Desmurget et al. 1996, 1998; Fan et al. 2006; Gentilucci et al. 1996; Jakobson and Goodale 1991; Jeannerod 1981, 1984, 1999; Jeannerod et al. 1998; Mamassian 1997; Marotta et al. 2003; Marteniuk et al. 1987; Paulignan et al. 1990; Roby-Brami et al. 2000; Torres and Zipser 2002, 2004; Wallace and Weeks 1988). While there is considerable behavioral and neurophysiological evidence that these components may be controlled by relatively separate neural circuits or “channels,” the degree to which these channels are functionally independent is still controversial (Arbib 1981; Culham et al. 2006; Desmurget et al. 1996, 1998, 1999; Fan et al. 2006; Gentilucci et al. 1991; Geyer et al. 2000; Gordon et al. 1994a,b; Jeannerod 1981, 1984, 1999; Jeannerod et al. 1998; Lacquaniti and Soechting 1982; Marotta et al. 2003; Murata et al. 2000; Paulignan et al. 1991; Rice et al. 2006; Rizzolatti and Luppino 2001; Roby-Brami et al. 2000; Soechting and Flanders 1993; Soechting and Ross 1984; Smeets et al. 2002; Stelmach et al. 1994; Torres and Zipser 2002, 2004; Zaal et al. 1998).

Compared with the large literature on hand preshaping and especially on the control of the transport phase of reaching, far fewer studies have examined the control of the orientation of the hand (Darling and Milner 1993; Desmurget and Prablanc 1997; Desmurget et al. 1996, 1998, 2000; Fan et al. 2006; Gentilucci et al. 1996; Glover and Dixon 2001a–c; Goodale et al. 1991; Mamassian 1997; Marotta et al. 2003; Roby-Brami et al. 2000, 2003; Soechting and Flanders 1993; Torres and Zipper 2002, 2004; Tunik et al. 2005; van Doorn et al. 2005). Most of these studies examined orientation in the context of combined reach-to-grasp actions and examined such issues as how hand orientation was shaped by the spatial location, spatial orientation, or optimal grasp axis of the target object, the direction of hand transport, or the initial and final postures of the arm before and after transport. There have been very few studies of the control of hand orientation per se without grasp. In one classic study, Perinini and Vighetto (1988) asked subjects to reach out and insert their hand into a slot oriented at different angles relative to vertical. Patients with optic ataxia following lesions of the parietal lobe showed marked deficits in their ability to position their hand in front of the object, the direction of hand transport, or the initial and final postures of the arm before and after transport.
the slot and to align their hand with the orientation of the slot (Perenin and Vighetto 1988). In contrast, using a similar task, Goodale et al. (1991) observed that an extensive lesion of the lateral occipital and parasagittal occipitoparietal cortex affected the ability of the patient to report the perceived orientation of a visual target but not to control the orientation of their hand while reaching to the target. Optic ataxia could reflect a breakdown of sensorimotor planning mechanisms prior to movement onset as well as of the neural mechanisms responsible for on-line adjustments to correct for errors during movement execution (Battaglia-Mayer et al. 2006; Grea et al. 2002; Torres and Zipser 2002, 2004). Finally, no studies have directly compared the control of hand orientation during reach to a target the orientation of which was defined either by vision or proprioception or compared it to the ability of subjects to perceive their hand orientation while holding their arm in a fixed posture at the target location.

The present study addressed some of those gaps in the literature on the control of hand orientation during arm movements. The paradigms used in this study were inspired by the tasks of Perenin and Vighetto (1988) and Goodale et al. (1991). We tested the ability of neurologically normal subjects to align a “match” handle that they held in their hand to the spatial orientation of a target slot at the completion of reaching movements aimed at the location of the slot (letter-posting task). We also assessed the ability of subjects to align a match handle with the spatial orientation of a target bar while holding their arm outstretched and stationary (orientation-matching task). Target orientation was defined by different combinations of visual and proprioceptive sensory input.

The performance of subjects in both the orientation-matching and letter-posting tasks was best with full visual feedback about the spatial orientation of the target and match handle and was poorest when only provided proprioceptive input about both. Performance was intermediate when subjects received only visual input about target orientation and only proprioceptive input about the orientation of their hand even though this condition required a cross-modal transfer of sensory information. Different combinations of sensory inputs produced different patterns of orientation errors in the orientation-matching and letter-posting tasks. More strikingly, subjects were better able to align their hand with the orientation of the target in the letter-posting task than in the orientation-matching task when only provided proprioceptive sensory input about hand orientation. Subsequent experiments with variants of the letter-posting task suggest that this difference in performance may at least in part reflect the engagement of an automatic on-line error correction mechanism for the control of hand orientation during the reaching movement of the letter-posting task that is not activated when the arm is held stationary in the orientation-matching task. The results also suggested that the on-line correction mechanism was preferentially engaged when the task involved transitive actions, that is, movements directed at and intended to act on a target object but not during intransitive movements that do not act directly on a target object. This work has been presented previously in preliminary form (Gosselin-Kessiby et al. 2003, 2004).

METHODS

Subjects

Eighteen right-handed subjects (9 women and 9 men, mean age: 44 yr; range: 18–64 yr) participated voluntarily in this study. Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield 1971). None of the subjects had a history of known neurological problems, and they all had normal or corrected-to-normal vision. All subjects signed a voluntary consent form. The Université de Montréal Human Research Ethics Committee approved the experimental protocol. Subjects were not informed about the specific purposes of the study.

Experimental setup

Figure 1 shows the experimental setup. Subjects sat in front of a vertical task panel on which a target was mounted. The target was either a rectangular handle (14.5 × 2.0 cm; orientation-matching task) or a slot (16.5 × 3.2 cm; letter-posting task) that could be fixed in one of six preset orientations (30, 60, 90, 120, 150, or 180°, proceeding counterclockwise from 0° at the right; Fig. 1B). The target was positioned at eye level in the middle of the visual field at a comfortable arms-length distance (i.e., at a distance reachable with near full arm extension and close to the subject’s midline). Subjects attempted to align the orientation of a rectangular match handle (14.5 × 2.0 cm) with that of the target. Eight infrared-emitting diodes (IRDs) were fixed in a circle around the perimeter of the match handle. The positions of the IRDs were recorded using an Optotrak 3020 motion capture system (Northern Digital; Waterloo, Ontario, Canada) at a sampling frequency of 100 Hz. Rotations of the match handle were made in the counterclockwise direction, starting from 0° orientation (handle horizontal and/or right wrist and forearm supine, palm up) in each trial.

The task panel and chair could not be moved during the experiment. The subjects were asked to not move their trunk and neck with respect to the chair during the entire experiment, but they were not physically restrained to avoid imposing arbitrary constraints that might alter their natural behavior (Steinman et al. 1990).

**FIG. 1.** Schematic representation of the experimental setup. A: subjects had to align the orientation of a rectangular “match” handle with the orientation of a target. In the letter-posting tasks (left), subjects held the match handle in the right hand and had to try to insert it into the target slot. In the passive orientation-matching task with full vision (right), subjects looked at the match handle to be aligned with the target but did not hold it. In all other conditions of the orientation-matching task (not shown), subjects held the match handle with their right hand. Eight infrared light-emitting diodes were fixed in a circle around the perimeter of the match handle and the spatial orientation and displacement of the handle were captured by an Optotrak 3020 motion capture system. B: the target was fixed in 1 of 6 possible orientations (30, 60, 90, 120, 150, and 180°; •, the side of the handle at which the right thumb was positioned to match the orientation of the target).
Experimental design and task structure

This study used a within-subject repeated-measure design. All 18 subjects performed all conditions of the orientation-matching task and letter-posting task 1 (see following text). Smaller subsets of the same 18 subjects also performed letter-posting tasks 2 and 3.

Each task comprised a series of trials during which the subjects attempted to align the match handle with the orientation of the target, in one of several different sensory and motor conditions. At the start of each trial, the experimenter set the target at its desired orientation. A complete data set in each sensory condition comprised five trials for each of the six target orientations (30 trials in total), in a randomized-block design.

Orientation-matching task

In the orientation-matching task, subjects aligned the orientation of the match handle to that of the target. The target was a handle identical to the match handle. Both handles were mounted on the task panel, with the match handle positioned 30 cm below the target (Fig. 1A, right). The match handle rotated freely about the axis perpendicular to the vertical plane of the task panel. Passive and active perception of spatial orientation was evaluated.

PASSIVE ORIENTATION-MATCHING TASK. After setting the spatial orientation of the target handle at the start of each trial, the experimenter gave the subject a verbal warning (“ready...go”) and then rotated the match handle smoothly (20.0 ± 5.0°/s; mean ± SD) from the back of the panel, starting at 0° in each trial, until the subjects reported verbally that it matched the orientation of the target handle. Subjects could correct the orientation by giving verbal instructions to the experimenter to rotate the match handle back and forth until they were satisfied that it was aligned with the target. Once the subject stated that the match handle was aligned with the target, the experimenter recorded the orientation of the match handle for 0.5 s (Optotrak 3020). The experimenter then recorded the orientation of the match handle back to the starting position (0°) and positioned the target at a new orientation for the next trial.

ACTIVE ORIENTATION-MATCHING TASK. Subjects held onto the match handle with their right hand. Following a verbal command from the experimenter (“ready...go”), the subjects actively rotated the handle to align it to the orientation of the target handle by rotating their right wrist and forearm at a comfortable speed, starting at 0° (hand supinated) in each trial. Subjects could correct the orientation by rotating the match handle back and forth until they reported verbally that it matched the orientation of the target. The experimenter then recorded the orientation of the match handle for 0.5 s (Optotrak 3020). Subjects held onto the match handle between trials while the experimenter rotated it back to the start position (0°), before beginning the next trial.

Letter-posting task 1: orient hand while reaching to the target

In letter-posting task 1, a target slot replaced the target handle. The match handle was a freely moving rectangular handle, instrumented with eight IREDs, that was of identical construction to the rotating match handle in the orientation-matching task. At the start of each trial, subjects held the rectangular match handle in their supinated right hand with their arm semi-flexed at the side of their body (Fig. 1A, left) while the experimenter set the target slot at the desired orientation. After a verbal command from the experimenter (“ready...go”), the subjects reached out to the target. Subjects were instructed to reach out and to simultaneously rotate the handle in a single continuous motion at a quick but comfortable speed to try to insert the match handle into the target slot without attempting to correct the handle position or orientation at the end of the reach.

Because the target slot was only slightly larger than the match handle, the subjects knew that they had to complete their planned rotation of the handle to align it with the target slot before the handle arrived at the target panel. However, it was not easy to insert the handle into the slot in one rapid continuous motion, especially in conditions in which the subjects did not see their hand (see following text). As a result, in many trials, the subjects failed to insert the match handle into the slot and contacted the task panel with the handle instead just as they were completing their hand rotation. As a result, this did not seriously perturb their performance. Whether or not they succeeded in inserting the match handle into the slot, the subjects were instructed to hold that final position until told by the experimenter to return their arm to the start location. The subjects returned their arm to the start position and rotated their hand back to the starting supine position before beginning the next trial. In all the letter-posting tasks, match handle coordinates were recorded continuously for 4 s, starting from the go command. The experimenter told the subjects to return their arm to the start position after the 4-s data-acquisition period ended.

Letter-posting task 2: orient hand and then reach to the target

Letter-posting task 2 was designed to assess whether hand orientation would remain constant or would change in some systematic way during reach to the target if the subjects perceived that their hand was already at the final desired orientation before beginning to reach. As in letter-posting task 1, subjects held the rectangular match handle in their supinated right hand with their arm in semi-flexion beside their body at the start of each trial. However, in letter-posting task 2, subjects were instructed to first rotate their wrist and forearm to align the match handle with the target slot while keeping their arm at their side. Subjects rotated the handle at a comfortable speed and could correct their hand orientation by rotating the handle back and forth until they reported verbally that they perceived that it was aligned. They were then given a verbal command by the experimenter (“ready...go”) to reach out to the target. The subjects were instructed to try to reach out to the target slot at a comfortable speed and to try not to change their initial hand orientation during the reach. At the end of each reach, the subjects held their final hand and arm position until told by the experimenter to return their arm and hand to the start position before beginning the next trial.

Letter-posting task 3: no target

Letter-posting tasks 1 and 2 had a direct target object, an oriented slot, on which the subjects attempted to act by inserting the match handle. Letter-posting task 3 was designed to assess what impact the transitive nature of those actions had on performance. This task was similar to letter-posting task 2 in that subjects were instructed to try to maintain the initial orientation of their hand while reaching out to the target panel. However, no target was presented. An opaque white circle was mounted on the target panel over the target slot, thereby concealing it. Instead of asking the subjects to align their hand to a target orientation before reaching as in letter-posting task 2, the experimenter first rotated the hand of the subjects to an orientation that was close to one of the six target orientations while the subjects’ arm was still at the start position beside their body. Initial hand orientations were set in a pseudorandom sequence across trials. After a verbal command from the experimenter (“ready...go”), the subjects reached out to contact the opaque circle with the match handle while trying to keep the initial hand orientation.

Sensory conditions

The spatial orientations of the target and/or the match handle were defined by different combinations of visual and proprioceptive sensory inputs in different sets of trials in each task.
**Task/sensory input combinations**

The study involved multiple tasks and sensory input conditions. However, not all possible combinations of tasks and conditions were tested.

The entire group of subjects \((n = 18)\) was tested in the following combinations of tasks and sensory conditions: passive orientation-matching task (3 sensory conditions), active orientation-matching task (target- and no-vision conditions), and letter-posting task 1 (3 sensory conditions), for a total of eight data sets \((240\) trials/subject). Orientation-matching and letter-posting tasks under different sensory conditions were performed in a random order, counterbalanced across subjects. In separate experimental sessions, subsets of the 18 subjects were tested in letter-posting task 2 (all 3 sensory conditions; 10 subjects) and letter-posting task 3 (full-vision and no-vision conditions; 7 of the 10 subjects who had done letter-posting task 2). Task/sensory condition combinations were again presented in random order to different subjects.

**Pilot study of visual acuity**

In an initial pilot study, we assessed the perceptual ability of a subgroup \((n = 7)\) of the 18 subjects to align the target and match handles when they had full vision of both, accompanied by different degrees of proprioceptive input about match handle orientation. Three variants of the full-vision orientation-matching task were performed on the same day in a random order using three different sensory input combinations: condition 1: vision only (no proprioceptive information of the match handle); subjects looked at but did not hold onto the match handle while the experimenter rotated it; condition 2: vision and passive proprioceptive information of the match handle available (experimenter rotated the match handle while subjects held onto it and looked at it); and condition 3: vision and active proprioceptive information of the match handle available (subjects held and rotated the match handle themselves while looking at it).

**Data analysis**

In the orientation-matching task, match handle orientation was measured by recording the spatial coordinates of IREDs fixed on the match handle. The angle of rotation of the handle was calculated by simple trigonometry using the \((x, y, z)\) coordinates of the observable IREDs on the perimeter of the match handle. In the letter-posting tasks, the full three-dimensional (3D) spatial orientation of the match handle was also determined from the \((x, y, z)\) coordinates of the observable IREDs on the perimeter of the handle. For analysis of performance, hand orientation was defined as the projection of the 3D orientation of the handle onto the 2D vertical plane of the target panel (i.e., the orientation of the hand in the frontal plane). This did not introduce large biases in the measured hand orientations because the subjects generally succeeded in holding the match handle in a plane nearly perpendicular to that of the target panel. Reach onset in the letter-posting tasks was defined as the first time the 3D hand transport velocity exceeded 3% of peak 3D hand transport velocity and remained above that value until peak velocity was attained. Similarly, the end of the reach was defined as the first time hand transport velocity toward the panel decreased <3% of peak velocity. This often coincided with the contact of the match handle with the task panel. For the letter-posting tasks, final hand orientation was determined by calculating the mean orientation during the 50 ms immediately preceding the detected end of reach \((\text{Dyde and Milner 2002})\). This time period was used to avoid confounding the measured hand orientation with any passive mechanical rotation of the handle caused by contact with the task panel. This was a good estimate of the final orientation because the subjects timed the rotation to end as the handle approached the target panel \((\text{Fig. 2})\). Hand rotation velocities were low during that time, and the hand typically changed its orientation by <0.5° during the 50-ms sampling interval. The initial orientation corresponded to the mean handle orientation during the 50 ms immediately preceding the detected onset of the reaching movement. In the orientation-matching task, final hand orientation was the mean orientation computed over a sampling period of 0.5 s taken after the subjects had reported that the match handle was aligned with the target handle.

**Performance measures**

To compare the accuracy and precision of the spatial orientation of the match handle in the different tasks and sensory conditions, constant, absolute, and variable errors were analyzed for each target orientation. The performance of each subject in each trial was assessed by calculating the match handle orientation error, defined as the...
angular difference between the orientation of the target and the final match handle orientation, as well as for the initial hand orientation in letter-posting tasks 2 and 3. For constant error, a positive orientation error occurred when the subject made a counterclockwise rotation of the match handle past the actual orientation of the target, whereas negative errors corresponded to a counterclockwise rotation of the match handle that did not attain the target orientation. Mean constant error at each target in each data set for each subject was calculated as a function of time (s).

Statistical analysis

Constant, absolute, and variable errors for different target orientations were compared in different tasks and sensory conditions using two- or three-way ANOVAs, and post hoc pair-wise comparisons were made using Tukey HDS analyses (Statistica, Statsoft, Tulsa, OK). For all ANOVAs and Tukey HDS analyses, the threshold for statistical significance was set at 0.05. For conciseness, only main effects and interactions including either task factor (orientation-matching vs. letter-posting task 1) or time factor (letter-posting tasks 2 and 3; initial vs. final hand orientation) will usually be reported.

RESULTS

Assessment of visual acuity of spatial orientation (pilot study)

In a pilot study, subjects performed three variants of the full-vision orientation-matching task to align the match handle to the target using vision alone (condition 1), vision and passive proprioceptive input (condition 2), and vision and active proprioceptive input (condition 3; see METHODS). Orientation errors were very small and similar among the three task variants (Table 1; see METHODS). There was no significant main effect of sensory input combination on constant errors, absolute errors, or variable errors (Table 1; 2-way ANOVA; 3 visual/proprioceptive combinations × 6 target orientations).

These results showed that when subjects had full vision of both the target and match handles in the orientation-matching task, the addition of either passive proprioceptive input (condition 2) or active proprioceptive input and efference copy signals about match handle orientation (condition 3) had no significant effect on performance. As a result, only condition 1
was retained (the passive orientation-matching task, full-vision condition), and the other two conditions were not used in the main study.

**Kinematics of letter-posting task 1 (orient hand while reaching to the target)**

The overall pattern of velocity profiles of hand transport (reach) and hand rotation was similar across all tested sensory conditions. Figure 2 presents velocity profiles of hand transport and rotation for the six target orientations in a representative subject performing letter-posting task 1 in the target-vision condition without vision of the hand. The velocity profiles of hand transport and rotation were often bell-shaped and single-peaked. Peak rotation velocity increased with the desired final target orientation. Furthermore, hand rotation continued for most of the duration of the transport phase and tended to end just before the match handle arrived at or contacted the target panel for all six target orientations (Fig. 2). These observations indicated that the subjects knew that they had to align the handle to the slot before it arrived at the target panel if they were to succeed in inserting it into the slot and timed their rotation accordingly to complete it just as the match handle approached the target panel. Because the movements in Fig. 2 were made in the target-vision condition, the scaling of rotation velocity could not have been controlled only by a visual-feedback error signal of the difference between target and hand orientation. Although transport and rotation velocity profiles consistently exhibited this temporal coordination pattern, target orientation and sensory conditions had a number of effects on the kinematics of movement.

The mean duration of hand transport pooled across subjects, target orientations, and sensory conditions was 1.00 s (ranging from 0.56 to 1.65 s in different subjects and conditions). Sensory conditions had a small but significant effect on mean hand transport duration (Table 2). Target orientation had no significant influence on hand transport duration across all sensory conditions \[F(5,85) = 1.30; P > 0.05\].

Sensory conditions also influenced peak velocities. Peak transport velocities tended to decrease systematically as the amount of visual information decreased (Table 2).

Target orientation had a strong effect on hand rotational velocity and on hand transport velocity (Fig. 3). The greater the required degree of rotation of the hand during the reach, the greater the peak wrist rotation velocity \[F(5,85) = 175.66; P < 0.05\] and the greater the peak transport velocity directed toward the target panel \[F(5,85) = 47.65; P < 0.05\].

**Spatial orientation estimates: single subject**

Figure 4 presents the final orientations of individual trials in a representative subject (same as in Fig. 2) for the passive orientation-matching task and Letter-posting task 1 in the three sensory conditions tested. In both tasks, the accuracy and precision of match handle orientation paralleled the amount of visual information about the target and match orientations. In the full-vision condition, orientation errors were small and similar between the passive orientation-matching task and letter-posting task 1 (mean constant error across target orientations in the orientation-matching task: \(0.99°\); in the letter-posting task: \(-0.36°\)). The accuracy of hand orientation decreased substantially in the target-vision condition (mean constant error across target orientations in passive orientation-matching task: \(-21.78°\); in letter-posting task: \(-6.47°\)) and decreased further in the no-vision condition, i.e., when proprioceptive input was the only sensory source of information about the orientation of both the target and hand orientation (mean constant errors across target orientations: \(-23.95°\); in letter-posting task: \(-12.54°\)). The magnitude of the constant errors also tended to increase with the amount of rotation of the hand required to align the match handle to the target in the orientation-matching task. Finally, the intertrial variability increased in the target- and no-vision conditions compared with the full-vision condition. In summary, the ability of the subject to align the match handle to the target decreased as they had to rely more on proprioceptive input, and the decrease in performance was more pronounced in the passive orientation-matching task than in the letter-posting task.

**Letter-posting task 1 versus passive orientation-matching task: group performance**

The single subject in Fig. 4 displayed most of the trends of the overall subject group (Fig. 5). Accuracy and precision of hand orientation varied across tasks and sensory conditions. The performance was best in the full-vision condition and was poorest in the no-vision condition. The mean constant and absolute orientation errors were small and similar in overall magnitude across target orientations between the letter-posting and the passive orientation-matching task in the full-vision condition (Fig. 5A). This indicated that the subjects' ability to

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**TABLE 1. Visual acuity of spatial orientation—pilot study**

<table>
<thead>
<tr>
<th>Condition</th>
<th>Constant error</th>
<th>Absolute error</th>
<th>Variable error</th>
</tr>
</thead>
<tbody>
<tr>
<td>1*</td>
<td>0.27°</td>
<td>3.16°</td>
<td>1.76°</td>
</tr>
<tr>
<td>2*</td>
<td>-0.23°</td>
<td>3.72°</td>
<td>2.21°</td>
</tr>
<tr>
<td>3*</td>
<td>-0.97°</td>
<td>3.33°</td>
<td>1.77°</td>
</tr>
<tr>
<td>ANOVA</td>
<td>1.65 NS</td>
<td>2.66 NS</td>
<td>2.24 NS</td>
</tr>
</tbody>
</table>

Main effect of task conditions on errors. Two-way ANOVA (3 visual/proprioceptive combinations × 6 target orientations). *Mean error across target orientations and subjects \(n = 7\). NS: not significant, \(P > 0.05\).

**TABLE 2. Letter-posting task 1—kinematics**

<table>
<thead>
<tr>
<th></th>
<th>Full-Vision*</th>
<th>Target-Vision*</th>
<th>No-Vision*</th>
<th>ANOVA [F(2, 34)]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean hand transport duration, s</td>
<td>0.99</td>
<td>0.92</td>
<td>1.08</td>
<td>8.85**</td>
</tr>
<tr>
<td>Mean hand transport peak velocity, mm/s</td>
<td>581.6</td>
<td>570.4</td>
<td>550.8</td>
<td>0.59 NS</td>
</tr>
<tr>
<td>Mean hand rotation peak velocity, °/s</td>
<td>333.8</td>
<td>316.9</td>
<td>275.16</td>
<td>7.03**</td>
</tr>
</tbody>
</table>

Main effect of sensory conditions on kinematics. Two-way ANOVA (3 sensory conditions × 6 target orientations). *Mean error across target orientations and subjects \(n = 18\). **Significant, \(P < 0.05\); NS: not significant, \(P > 0.05\).
align their hand orientation to a target at the end of a single continuous reach-and-orient movement with full vision of the hand and target was very similar to their perceptual ability to align the two handles visually when given as much time as they wished to adjust and correct the match handle orientation. In contrast, the magnitude of constant and absolute orientation errors tended to increase with the orientation angle of the target in the passive orientation-matching task in the target- and no-vision conditions when the subjects could no longer see their hand and the match handle (Fig. 5, B and C). This trend was much less prominent (constant error) or absent (absolute error) in the letter-posting task in those same sensory conditions. The magnitude of variable errors also increased as the subjects were progressively deprived of visual input and had to rely more on proprioceptive inputs about target and match handle orientation in both the letter-posting and orientation-matching tasks but was fairly similar across target orientations.

Those general trends were supported by statistical analyses. First, separate three-way ANOVAs (2 tasks × 3 sensory conditions × 6 target orientations) were performed on the constant, absolute and variable errors made by subjects in the passive orientation-matching task and letter-posting task 1. For constant errors, there were significant main effects of task \( F(1,17) = 140.00; P < 0.05 \), sensory condition \( F(2,34) = 34.75; P < 0.05 \), and target orientation \( F(5,85) = 24.12; P < 0.05 \). There was also a significant interaction among these three factors \( F(10,170) = 2.66; P < 0.05 \), whereby mean constant errors were significantly larger for the passive orientation-matching task than the letter-posting task only in the target- and no-vision conditions and got progressively larger for target orientations requiring greater wrist

![Graph showing peak velocities for hand transport and hand orientation.](http://jn.physiology.org/)

**FIG. 3.** Peak velocities for hand transport and hand orientation. Mean of peak velocities of hand transport toward the panel (●) and hand orientation (○) across all subjects \( n = 18 \) and all sensory conditions tested for movements aimed at the 6 target orientations (30, 60, 90, 120, 150, and 180°) in letter-posting task 1. Axes represent the hand transport velocity (mm/s) and the hand orientation velocity (°/s) as a function of time (s). Error bars represent SE.

![Graph showing final orientations of the match handle relative to the target.](http://jn.physiology.org/)

**FIG. 4.** Final orientations of the match handle relative to the target in letter-posting task 1 and the passive orientation-matching task in a representative subject. Final orientations of the match handle of 1 representative subject across 30 movements aimed to the 6 target orientations (30, 60, 90, 120, 150, and 180°), for all sensory conditions in Letter-posting task 1 and the passive Orientation-matching task. Each of the marked circles represents the trials for 1 target orientation. The arrows next to the circles represent the target orientation. The lines inside each circle represent the 5 individual trials for each orientation.
rotations. Accordingly, post hoc tests showed significantly smaller constant errors in letter-posting task 1 than in the passive orientation-matching task for target orientations larger than the vertical (120, 150, and 180°) in the target-vision condition ($P < 0.05$) and for all target orientations except vertical (i.e., for 30, 60, 120, 150, and 180°) in the no-vision condition ($P < 0.05$).

Similar results were observed for absolute errors. There were significant main effects of task [$F(1,17) = 16.40; P < 0.05$], sensory condition [$F(2,34) = 73.16; P < 0.05$], and target orientation [$F(5,85) = 9.09; P < 0.05$] as well as a significant interaction among these three factors [$F(10,170) = 5.53; P < 0.05$]. There were significantly smaller absolute errors in letter-posting task 1 than in the passive orientation-matching task for target orientations greater than vertical (120, 150, and 180°; $P < 0.05$) in the target-vision condition and for target orientations corresponding to the vertical and larger (90, 120, 150, and 180°; $P < 0.05$) in the no-vision condition.

In contrast to constant and absolute errors, there was no main effect of task on variable errors [$F(1,17) = 0.21; P > 0.05$]. However, there was a main effect of sensory condition [$F(2,34) = 72.23; P < 0.05$] and target orientation [$F(5,85) = 7.39; P < 0.05$]. There was also a significant three-way interaction among task, sensory condition, and target orientation [$F(10,170) = 2.55; P < 0.05$], but no specific post hoc comparisons were significant.

**Letter-posting task 1 versus orientation-matching task**

**OBLLIQUE EFFECTS IN PERCEPTION AND ACTION.** The subjects showed evidence of an oblique effect in their visual perception of cardinal versus oblique orientations of the target in the full-vision passive orientation-matching task. Constant, absolute, and variable errors were all systematically smaller for the 90 and 180° orientations than for the oblique orientations (Figs. 4 and 5A; 1-way ANOVA, main effect of orientation $P < 0.05$ for each error type). Furthermore, post hoc tests showed that absolute and variable errors were similar at 90 and 180° ($P > 0.05$) but were statistically smaller than all other target orien-
tations \( (P < 0.05) \) with the sole exception of the absolute errors at 120 versus 180° \( (P > 0.05) \). The mean bias (constant errors) was also smaller for the cardinal orientations than the oblique orientations, but the constant errors were small and the differences in constant errors were statistically significant for only some post hoc comparisons (90 vs. 150°; 180 vs. 30, 60, and 150°; \( P < 0.05 \)). These findings showed that there was a robust oblique effect in the full-vision passive orientation-matching task expressed by a greater dispersion (absolute errors) and intertrial variability (variable errors) for the oblique orientations than for the cardinal orientations, but the effect was somewhat less robust for constant errors. In contrast, there was almost no evidence of an oblique effect in the full-vision letter-posting task 1 in which constant, absolute, and variable errors were more similar across all target orientations. In particular, absolute and variable errors were statistically identical at all orientations (Fig. 5A; 1-way ANOVA, main effect of orientation \( P > 0.05 \); all post hoc tests, \( P > 0.05 \)). There was also some evidence of an oblique effect in the target- and no-vision conditions of the orientation-matching task, but that effect was dominated by the rotation-dependent error trend (Fig. 5, B and C).

In the target- and no-vision conditions of letter-posting task 1, in contrast, the subjects showed evidence of a different type of “sensorimotor” oblique effect. They tended to overshoot the target angle at 30° and especially at 120° and to undershoot the target at 60 and 150° (Fig. 5, B and C). This was stronger in the no-vision condition than the target-vision condition. This trend indicates that the final hand orientations tended to deviate away from the actual intermediate diagonal target angles toward the central diagonals of 45 and 135° as less visual information was available in letter-posting task 1. This trend was not evident in the corresponding sensory conditions of the orientation-matching task.

**ACTIVE ROTATION OR ACTIVE REACH?** The greatest difference in performance between the passive orientation-matching task and the letter-posting task occurred in the target- and no-vision conditions (Fig. 5). In these two sensory conditions, the subjects held onto the match handle, but there were two main differences between the tasks. In letter-posting task 1, the subjects reached out to the target and also actively rotated their hand’s orientation to align the match handle to the target. In contrast, the subjects held their arm outstretched and stationary in the passive orientation-matching task, and the experimenter passively rotated the subjects’ hand. The better accuracy of the subjects in the target- and no-vision conditions of the letter-posting task 1 than in the passive orientation-matching task, especially for larger target orientations, may have been due mainly to the active reaching or active hand rotation components in the former task. To assess the contribution of those two factors, we performed the following comparisons.

To assess the effect of active hand rotation, we compared performance of the subjects in the active and passive orientation-matching tasks in the target- and no-vision conditions. There was no significant main effect of task for any error measure [constant error, \( F(1,17) = 4.04, P > 0.05 \); absolute error, \( F(1,17) = 4.07, P > 0.05 \); and variable error, \( F(1,17) = 0.777, P > 0.05 \); 3-way ANOVA; 2 tasks \( \times \) 2 sensory conditions \( \times \) 6 target orientations]. There were, however, a significant task by target orientation interaction for constant errors \( [F(5,85) = 5.40; P < 0.05] \) and absolute errors \( [F(5,85) = 3.53; P < 0.05] \). Post hoc tests showed that subjects made significantly smaller constant errors in the active than the passive orientation-matching task for the 90 and 120° target orientation \( (P < 0.05) \) and significantly smaller absolute errors in the active than the passive orientation-matching task for the 120° target orientation only \( (P < 0.05) \). Therefore while there were a few significant differences, these findings suggested that active hand rotation had a relatively minor overall effect on performance in the orientation-matching task.

Next we assessed the effect of reaching on hand orientation. We compared performance in the target- and no-vision conditions of letter-posting task 1 and the active orientation-matching task. Subjects always made active hand rotations in both tasks but reached only in the letter-posting task. Separate three-way ANOVAs (2 tasks \( \times \) 2 sensory conditions \( \times \) 6 target orientations) were performed on the constant, absolute, and variable errors.

For constant errors, there was a significant main effect of task \( [F(1,17) = 59.8; P < 0.05] \). There was also a significant task by sensory condition interaction \( [F(1,17) = 10.99; P < 0.05] \). Post hoc tests of that interaction revealed that for both sensory conditions, the constant errors in letter-posting task 1 were significantly smaller than in the active orientation-matching task \( (P < 0.05) \), that subjects made larger errors in the no-vision condition than in the target-vision condition in both tasks, and that this increase was more pronounced in the active orientation-matching task than in the letter-posting task \( (P > 0.05) \). Finally, there was a significant task by target orientation interaction \( [F(5,85) = 6.78; P < 0.05] \). Post hoc tests revealed that constant errors in hand orientation were significantly smaller in letter-posting task 1 than in the active orientation-matching task for the 30, 120, 150, and 180° target orientations \( (P < 0.05) \).

For absolute errors, there was a significant main effect of task \( [F(1,17) = 21.8; P < 0.05] \) as well as a significant three-way interaction among task, sensory condition, and target orientation \( [F(5,85) = 2.48; P < 0.05] \). Subjects made significantly smaller absolute errors in letter-posting task 1 than in the active orientation-matching task for the 150 and 180° target orientations \( (P < 0.05) \) in both the target- and no-vision conditions.

For variable errors, there was no main effect of task \( [F(1,17) = 0.15; P > 0.05] \). There was a significant three-way interaction \( [\text{task} \times \text{sensory condition} \times \text{target orientation}; \quad F(5,85) = 2.66; P < 0.05] \), but no significant differences were found at any specific target orientation in post hoc tests.

In summary, the ANOVA results confirmed that the performance of the subjects in the active orientation-matching task was much more similar to that in the passive orientation-matching task than in letter-posting task 1 in the target- and no-vision conditions. This suggested that the act of reaching accounted for most of the improvement in performance of the subjects in letter-posting task 1 compared with the two conditions of the orientation-matching task.

**Letter-posting task 2: initial versus final hand orientation**

To further investigate the effect of reaching on hand orientation, we tested the performance of 10 of the 18
subjects who had done letter-posting task 1 in letter-posting task 2, in which they attempted to align the match handle to the target before reaching and then to maintain the initial orientation of the match handle as they reached to the target. Subjects generally tended to under-rotate their initial hand orientation, and the degree of under-rotation increased from full vision to no-vision conditions (constant errors, Fig. 6). Most importantly, the constant orientation errors tended to be smaller at the end of the reaching movement than prior to movement onset even though the subjects had been instructed not to change the orientation of the hand during the reach (Fig. 6).

This trend was supported by statistical analyses. Separate three-way ANOVAs (2 times 3 sensory conditions x 6 target orientations) were performed on the constant, absolute and variable initial and final errors made by subjects. For constant errors, there was a main effect of time [initial vs. final hand orientation; F(1,9) = 23.5; P < 0.05] as well as a significant three-way interaction among time, sensory condition, and target orientation [F(10,90) = 5.41; P < 0.05]. Constant errors in hand orientation were significantly smaller (P < 0.05) at the endpoint than before the onset of reaching movements for several target orientations in the full-vision (60, 90, 150, and 180°), target-vision (30, 60, 150, and 180°), and no-vision conditions (30, 60, 120, and 150°).

For absolute errors, there was a significant main effect of time [initial vs. final, F(1,9) = 20.9; P < 0.05] with smaller overall absolute errors at the end of reaching than prior to movement onset. There was also a time by target orientation interaction [F(5,45) = 3.96; P < 0.05] with significantly smaller absolute errors of final than initial hand orientation at the 60 and 150° target orientations (P < 0.05) across all three sensory conditions.

For variable errors, there was a significant main effect of time [F(1,9) = 16.5; P < 0.05], indicating a small but very consistent reduction of trial-to-trial variable error at the reaching endpoint compared with movement onset, averaged across all three sensory conditions (mean initial variable error: 3.35°, mean final variable error: 3.01°).

**FIG. 6.** Initial and final error in hand orientation in letter-posting task 2. Mean error in hand orientation in letter-posting task 2 across subjects (n = 10). Mean of constant, absolute and variable errors are shown in different columns. Sensory conditions are presented in different rows (A: full vision; B: target vision; C: no vision). The axes represent the errors in orientation as a function of target orientation (in degrees). Error bars represent SE. ■, final hand orientation; □, initial hand orientation.
Letter-posting task 3: influence of a defined target for action on hand orientation

To evaluate whether the reduction of hand orientation errors from before to after the reach movement in letter-posting task 2 depended on the presence of an explicit target orientation, we tested the performance of 7 of the 10 subjects who had done letter-posting task 2 in letter-posting task 3. This was similar to letter-posting task 2 except that there was no explicitly defined target for action. Instead the experimenter put the right hand of the subjects at an angle that corresponded to one of the six target orientations prior to the reaching movement in each trial (see METHODS).

Subjects showed an overall reduction in absolute hand orientation errors after reaching in letter-posting task 2 (Fig. 7; grand mean error: \(-2.17^\circ\) pooled across both sensory conditions; all negative values at each target orientation with the exception of target orientation 120° in the no-vision condition). In striking contrast, subjects exhibited a general increase in absolute errors in letter-posting task 3 (Fig. 7; grand mean error: \(4.14^\circ\) pooled across both sensory conditions; all positive values at all target orientations).

Three-way ANOVA (2 tasks × 2 sensory conditions × 6 target orientations) revealed a significant main effect of task \([F(1,6) = 17.1; P < 0.05]\) as well as a significant interaction between task and target orientation \([F(5,30) = 4.22; P < 0.05]\). Post hoc tests revealed that when the target was present (letter-posting task 2), errors were significantly reduced compared with letter-posting task 3 for target orientations 30, 60, and 150° \((P < 0.05);\) data pooled across both sensory conditions).

These results indicated that the final hand orientations in letter-posting task 2 tended to converge onto the desired target orientation at the end of the reaching movement, compared with initial orientations prior to reach (cf. Fig. 6). In contrast, in letter-posting task 3, final hand orientations tended to be more broadly dispersed compared with their initial orientations prior to reach when the subjects simply reached out to contact the target panel with the match handle rather than attempting to insert it into the target slot.

**Discussion**

**Principal findings**

There were several main findings in this study. First, constant, absolute, and variable errors were small in the full-vision condition of both the orientation-matching task and letter-posting task 1. In contrast, the ability of subjects to align their right hand to the target was significantly better at the end of a single continuous reaching movement in the target- and no-vision conditions of letter-posting task 1 than in the corresponding conditions of the orientation-matching task, in particular for target orientations that required greater rotations of the hand. Second, two perceptual error patterns, an oblique effect in the perception of object orientation in the full-vision condition and a progressive increase in hand orientation errors with greater required rotations of the right (match) hand in the target-vision and no-vision conditions, were seen in the orientation-matching task. However, these did not result in corresponding error patterns in letter-posting task 1. Third, under those same target- and no-vision conditions, a different error pattern emerged in letter-posting task 1 whereby final hand orientations migrated away from the desired diagonal target orientations toward the central diagonals (45, 135°) as less visual input was available. Fourth, letter-posting tasks 2 and 3 suggested that the transitive actions of letter-posting task 1 engaged an automatic on-line correction mechanism for hand orientation during the reaching movements to stationary targets. The correction mechanism could function when the only available sensory input about hand orientation and even of target orientation came from proprioception (target- and no-vision conditions of letter-posting tasks 1 and 2). Fifth, the overall magnitude and specific patterns of orientation errors of both orientation-matching and letter-posting tasks were strongly influenced by the combinations of sensory inputs by which the orientation of the target and match handles were sensed or controlled. Finally, the peak velocity of both hand rotation and hand transport toward the target increased with the magnitude of required hand rotation, indicating a functional coupling between these two components of reach-to-grasp movements. These findings will be discussed in the following sections.

**Entire arm contributes to the spatial orientation of the hand**

This study examined the ability of human subjects to perceive and control the spatial orientation of their hand in the frontal plane. The subjects were given no instructions as to how to rotate their hand in the tasks. Direct observation revealed that most of the rotation occurred at the wrist and
forearm but that torsional rotations about the long axis of the humerus also occurred. It is well established that proximal arm joints contribute to the final spatial orientation of the wrist and hand in unconstrained arm movements (Desmurget et al. 1996, 1998; Fan et al. 2006; Marotta et al. 2003; Soechting and Flanders 1993; Tillery et al. 1995; Torres and Zipser 2002, 2004). However, the relative contribution of different joints to hand orientation was not the objective of this study, and we did not measure proximal joint angles. The findings of this study should be interpreted as reflecting the subjects’ estimate of the orientation of the hand relative to that of the target and not their estimate of wrist pronation/supination angle per se.

**Accuracy of hand orientation at the end of a reaching movement: evidence for on-line correction for orientation errors**

This study provides further evidence that hand orientation is adjusted by an on-line correction mechanism during reaching movements (Fan et al. 2006; Glover 2004; Glover and Dixon 2001a–c; Tunik et al. 2005) even though in this study, the target orientation was stationary and did not change during reach (cf., Fan et al. 2006; Tunik et al. 2005) nor was it subject to an optical illusion (cf., Glover 2004; Glover and Dixon 2001a–c).

Final orientation errors increased from the full-vision to the target- and no-vision conditions of letter-posting task 1 consistent with a role for visual feedback about the hand and the target for the on-line adjustments of movement (Connolly and Goodale 1999; Ma-Wyatt and McKee 2007; Messier and Kalaska 1999; Sarlegna et al. 2003, 2004; Saunders and Knill 2003–2005; Sheth and Shimojo 2002).

On-line adjustment is also supported by the reduction in hand-orientation errors from the beginning to the end of the reaching movements in letter-posting task 2. This finding is all the more striking because control of hand orientation during the act of reaching could be prone to execution errors due to inaccuracies in outgoing motor commands and to passive mechanical perturbations of the hand away from its desired orientation. This was demonstrated in letter-posting task 3 in which there was an increased divergence of hand orientations from the beginning to the end of reaching movements without an explicit target, unlike the convergence of final hand orientations on the desired target orientation in letter-posting task 2. This finding further indicates that the improvement in hand orientation after reaching in letter-posting task 2 likely depended on an active on-line correction process that compensated for the errors in the initial hand orientation estimates prior to reaching as well as for errors resulting from motor planning and passive mechanical perturbations during reach execution.

The correction mechanism appears to be automatic. In all letter-posting tasks, the subjects were asked to make no voluntary movement corrections. Nevertheless in letter-posting task 2, hand-orientation errors decreased after the reach even though the subjects had presumably perceived that their hand was already at the desired orientation before beginning to reach and were told to keep their hand in that initial orientation during the reach. Finally, letter-posting task 3 revealed that the reduction in orientation errors was dependent on the presence of a physical target for action with a defined orientation.

Many studies have reported automatic on-line adjustments for hand spatial location and grip aperture (Bard et al. 1999; Connolly and Goodale 1999; Day and Lyon 2000; Desmurget and Grafion 2000; Desmurget et al. 1999, 2001; Goodale et al. 1986; Grea et al. 2002; Pélisson et al. 1986; Prablanc and Martin 1992; Prablanc et al. 2003; Schenk et al. 2005; Saunders and Knill 2003–2005; Supuk et al. 2005; Turrell et al. 1998; Van Sonderen et al. 1989), but few have investigated such mechanisms for hand orientation (Fan et al. 2006; Glover and Dixon 2001a–c; Tunik et al. 2005). Most of those studies involved corrections for abrupt unexpected changes in target location, size, or orientation. In contrast, our findings suggest that an on-line correction mechanism for hand orientation is also engaged during reaching movements to a stationary target (Glover 2004; Glover and Dixon 2001a–c). These findings are consistent with a recent study of continuous on-line control during movement execution (Rice et al. 2006) and with other reports of on-line correction for the variability and errors in the initial kinematics of reaching movements to stationary targets (Blouin et al. 1993, 1996; Desmurget et al. 2005; Gordon et al. 1994a,b; Ma-Wyatt and McKee 2007; Messier and Kalaska 1999; Sheth and Shimojo 2002).

A key finding of the present study is that movement per se is not sufficient to engage the on-line correction mechanism. The nature and goal of the movement also is a critical factor (Bridgeman et al. 2000; van Doorn et al. 2005). The reaching movements of letter-posting tasks 1 and 2 were transitive actions in the sense of being directed at a target object, a slot with a defined orientation, on which the subjects intended to act with the goal of inserting a handle. The sensory conditions in which they were performed did not alter their underlying transitive nature. In contrast, the reaching movements of letter-posting task 3 were intransitive because there was no target object on which the subjects attempted to act. Likewise, the initial hand orientations prior to reach in letter-posting task 2 were intransitive in that they were guided by the orientation of the target but were performed before the subjects attempted to act on the target. This resulted in initial orientation errors that were subsequently reduced when the subjects reached out to the target to attempt to insert the match handle into the target slot. These findings suggest that the on-line correction mechanism is preferentially activated when the object the physical properties of which guide action is also the direct object of that action. Alternatively, it is rendered relatively ineffective in the absence of a direct target object for the action.

**Perception versus action dichotomy**

Many studies have reported that error patterns observed during perceptual tasks do not always determine the performance errors of the same subjects in corresponding sensorimotor tasks (Goodale and Milner 1992; Milner and Goodale 1995). This implies that the processing of sensory information for perception and action can occur in parallel, rather than having a strictly serial order, and that sensory processing in the two systems is prone to different types of errors (Goodale and Milner 1992; Milner and Goodale 1995; van Doorn et al. 2005). Most of the evidence for a perception/action dichotomy has come from studies that have exploited various optical illusions (e.g., Bridgeman et al. 1981, 2000; Dyde and Milner 2002; Glover and Dixon 2001a–c; Goodale 2001; Goodale
et al. 2005; Haffenden and Goodale 1998) or from studies of the sensorimotor capacities of patients with lesions of the dorsal or ventral visual streams (e.g., Goodale et al. 1991, 2005; Milner and Goodale 1995). The present study provided two potential examples of this distinction between perception and action in neurologically intact subjects in tasks that did not evoke optical illusions.

First, one finding of this study was that in the full-visibility condition, the overall ability of subjects to align their hand with the orientation of a target at the end of a continuous reaching movement (letter-posting task 1) was similar to that observed in the passive orientation-matching task, when the subjects simply had to align the match handle to the target by vision and had ample opportunity to instruct the experimenter how to position the match handle’s orientation. Nevertheless, in the latter task, subjects showed a visual perceptual oblique effect in which the accuracy and precision of their ability to match the cardinal orientations (90°, 180°) was significantly better than for oblique angles (Appelle 1971; Cuijpers et al. 2000; Hermens and Gielen 2003; Hermens et al. 2006; Kappers 1999, 2002–2004; Kappers and Koenderink 1999; van Doorn et al. 2005). This effect was especially robust for absolute and variable errors. An oblique effect, however, was largely absent in the letter-posting task 1, and in particular, absolute and variable errors were small and constant across all target orientations (van Doorn et al. 2005). This would appear consistent with a dichotomy between perception and action, although it is also possible that the small errors at each target orientation may represent a performance limit in the precision and accuracy of active reaching movements that masks an equally small oblique effect in full-visibility letter-posting task 1.

The second and more striking example arose in the target- and no-vision conditions of the orientation-matching task and letter-posting Task 1. In those conditions, the subjects had no vision of their hand (target-vision condition) or of either the hand or target (no-vision condition), and their only other sensory source of orientation information was proprioception. The subjects showed increasingly large errors in their estimation of hand orientation in the passive and active orientation-matching task as a function of the degree of required rotation of the hand even though they simply had to adjust their hand orientation while holding their arm outstretched and stationary and had ample opportunity to correct hand orientation. However, the perceptual trend of progressive over-estimation of the orientation of the hand did not translate into corresponding performance errors in letter-posting task 1 and subjects showed smaller constant and absolute errors overall (Fig. 5). These findings suggest that the perception/action dichotomy may be particularly striking in the proprioceptive domain when proprioception is the only sensory source of information about motor performance or about target properties (Dijkerman and de Haan 2007; Fiehler et al. 2007). The overwhelming majority of prior studies of the perception/action dichotomy have focused on visual processing within the dorsal and ventral visual streams (Goodale 2001; Goodale and Milner 1992; Goodale and Westwood 2004; Goodale et al. 2005 Milner and Goodale 1995; Rice et al. 2007; Shmuelof and Zohary 2005; Valyear et al. 2006).

As already noted, the present study also indicated that one critical factor determining performance of the letter-posting task was whether or not the task involved transitive or intransitive actions. Indeed virtually every prior study that has revealed a psychophysical dissociation between perception and action performance used transitive action tasks in which the sensory object guiding action was also the target of that action. In contrast, the nominally perceptual tasks often required the subjects to perform some form of intransitive gesture with their hand or arm to report to the experimenter their estimate of object size, orientation, or other properties. Similarly, the active hand rotations of the target- and no-vision orientation-matching task in this study were intransitive actions that were guided by the same sensory input about target orientation as in letter-posting task 1 but were not directed at the target or intended to act on it. Instead, their goal was to rotate a second object (the match handle) at a separate spatial location to align it to the orientation of the target. One could argue that this is a transitive movement by definition since the subjects rotated a handle. However, the critical distinction is that the subjects performed those movements not to act on the object guiding their behavior but rather to report their estimate of their introspectively perceived hand orientation relative to that object. It is noteworthy that the passive orientation-matching task required the subjects simply to report verbally to the experimenter when they perceived that their hand orientation was aligned to that of the target as the experimenter rotated their hand. Nevertheless, the error patterns in the passive and active orientation-matching task were similar and clearly different from that in letter-posting task 1, indicating that the former errors were primarily influenced by perceptual processes, whereas the latter were subject to other factors.

It is interesting to note that the difference in the sensitivity to oblique effects in the full-visibility orientation-matching and letter-posting task 1 of this study are very similar to that seen in a visual-matching versus target-catching paradigm using oriented bars when the subjects physically captured the target bars, a transitive action (van Doorn et al. 2005), but not in a study in which the catch was simulated, an intransitive act (Hermens and Gielen 2003). Furthermore, the present study provided evidence that the transitive actions of letter-posting task 1 appeared to engage an automatic on-line correction mechanism. This suggests that another possible reason for the difference in performance in the orientation-matching and letter-posting tasks is not that the former is necessarily more “perceptual” in nature than the latter, but that it requires intransitive actions that do not engage an on-line adjustment mechanism as effectively as does the Letter-posting task.

Taken together, these findings could be interpreted as supporting an alternative model of sensorimotor performance, the so-called planning/control model (Glover 2004) in which the initial planning of action uses sensory representations that are susceptible to illusions and other perceptual errors. The perception-dependent planning errors are subsequently reduced by on-line correction mechanisms during movement execution (Glover 2004; Glover and Dixon 2001a–c). However, the present study was not designed specifically to compare the perception/action versus planning/control models. Furthermore, it is clear that action is not completely refractory to performance errors resulting from perceptual illusions (Glover 2004; Glover and Dixon 2001a–c; Dyde and Milner 2002; Hermens and Gielen 2003; Milner and Goodale 1995; van Doorn et al. 2005), nor do we believe that the perception/action and planning/control models are mutually exclusive.
On-line corrections mediated by proprioceptive input

This study emphasizes the potential contribution of proprioception to on-line adjustments for hand orientation. A few studies have evaluated reaching or grasping in situations that were similar or identical to our target-vision condition (Bridge- man et al. 2000; Connolly and Goodale 1999; Dyde and Milner 2002; Fukui and Inui 2006; Ghez et al. 1995; Glover and Dixon 2001a–c; Gordon et al. 1994a; Haffenden and Goodale 1998; Hu et al. 1999; Prablanc et al. 1986; Schenk and Mai 1999; Schettino et al. 2003). In our target-vision condition, vision of the target was prevented during the reach (no knowledge of the results), and vision of the hand was always prevented. Therefore the only source of real-time sensory input to guide movement execution, including any on-line correction process, was from proprioception.

The contribution of proprioception for the planning and on-line control of movement has been suggested by studies in deafferented patients (Blouin et al. 1993, 1996; Ghez and Sainburg 1995; Ghez et al. 1995b; Messier et al. 2003; Nougier et al. 1996; Vercher et al. 2003) and by tendon vibration studies (Redon et al. 1991; Sittig et al. 1987; Steryvers et al. 2001; Vercher et al. 2003; Verschueren et al. 1999). Other studies using perturbations of target or hand position also suggest a role for proprioception for on-line correction of movement (Bagheire et al. 2006; Sarlegna et al. 2003, 2004). However, in all studies using reaching movements the target was defined by visual input. Indeed, Glover and Dixon (2001a–c) used a visually induced illusion to produce errors in the initial estimation of target orientation that were corrected on-line during reach execution. This study is the first to our knowledge to provide evidence for an on-line correction mechanism for hand orientation when the only sensory input available about both the desired target orientation and current hand orientation (no-vision condition) came from proprioception.

Proprioception was not the sole source of information to guide hand orientation during letter-posting task 1 in the target- and no-vision conditions. In the target-vision condition, a visual representation of target orientation stored in short-term memory could have contributed after the target was masked during the reach. Furthermore because the task involved active reach and rotation of the arm, an effference copy of the motor command could also have contributed to the difference in performance compared with the orientation-matching task. However, the active orientation-matching task also involved outgoing motor commands to produce the active hand rotations, but the subjects showed similar error patterns to that in the passive orientation-matching task rather than to the letter-posting task (Fig. 5, B and C). Similarly, letter-posting tasks 2 and 3 both required active reach movements of the arm but their error patterns differed (Fig. 7). This indicates that an effference copy of an outgoing motor command is not in itself sufficient to account for the difference between orientation-matching and letter-posting tasks.

Optimal combination of vision and proprioception during perception and control of hand orientation

This study is consistent with many previous studies that showed better perception or control of arm and hand position when vision is available than when only proprioceptive information is available (Adamovich et al. 1998; Berkinblit et al. 1995; Ma-Wyatt and McKee 2007; Smeets et al. 2006; Tillery et al. 1991; Zelaznik et al. 1983) and with previous studies that suggested a dominant role of vision in the perception of hand location in space when both vision and proprioception are available (Flanagan and Riao 1995; Hagura et al. 2007; Smeets et al. 2006; Wolpert et al. 1994). The assumption is that visual input is less noisy and more reliable than proprioceptive input and that the CNS optimally combines both sources of sensory information by weighting the visual input more heavily to guide movement or estimate hand spatial location when both vision and proprioception are available (Carrozzo et al. 1999; Ernst and Banks 2002; Knill and Pouget 2004; Kording and Wolpert 2006; Rossetti et al. 1995; Smeets et al. 2006; Sober and Sabes 2003, 2005; van Beers et al. 1996, 1998, 1999, 2002). This study provides two new possible examples of the optimal combination of visual and proprioceptive inputs.

In theory, the full-vision orientation-matching and letter-posting tasks could be performed exclusively in extrinsic or allocentric visual spatial coordinates while the no-vision tasks could be performed entirely in intrinsic or egocentric proprioceptive coordinates. In contrast, the target-vision condition in which the target orientation was defined by visual input but match handle orientation was sensed by proprioception would appear to require an inter-modal sensory coordinate transformation, which could introduce an extra source of estimation errors. Nevertheless performance was always intermediate in the target-vision condition, showing larger constant, absolute, and variable errors than the full-vision condition but smaller errors than in the no-vision condition. The increased errors compared with the full-vision condition could reflect the lack of visual feedback-driven on-line adjustments of hand orientation during reach in the target-vision condition. However, the smaller errors in this intermodal condition compared with the intramodal no-vision condition could reflect the benefit of the visual input about target orientation prior to the onset of reach.

Second, in the full-vision letter-posting task 1, hand-orientation errors were small and nearly uniform across all target orientations. In contrast, as the subjects were increasingly deprived of visual input and became progressively more dependent on proprioceptive input to guide their performance in the target- and no-vision conditions of letter-posting task 1, they showed evidence of a different type of “sensorimotor” oblique effect. Their estimates of hand orientation for the diagonal target orientations regressed increasingly toward the central diagonals of 45° and 135°. Although speculative at this point, this trend suggests that as subjects had to rely increasingly on potentially noisier information about hand and target orientation from proprioception or effference copies, the control of hand orientation during reaching tended to be biased away from the desired target diagonal angles (30, 60, 120, 150°) toward the more central diagonals (45, 135°), which may be more familiar or easier to estimate. A similar central tendency under conditions of increasing uncertainty has been seen for estimates of elbow angle during active and passive movements (Grilzenko et al. 2007). It is noteworthy that the trend was not evident in the active and passive orientation-matching task in the same sensory conditions, which showed different error patterns. This is a potential reverse example of the perception/action dichotomy, whereby motor perfor-
performance is prone to errors not evident in perceptual psychophysics.

However, when visual input was available in the full-vision condition of letter-posting task 1, the “sensorimotor oblique effect” was not evident, and orientation errors were much more similar to those in the purely visual perceptual orientation-matching task (Fig. 5A). Furthermore, when the subjects gained access to proprioceptive inputs and efference copy signals about hand orientation by holding onto and actively rotating the match handle (conditions 2 and 3 of the orientation-matching task in the pilot study), there was also no evidence of the sensorimotor oblique effect and no significant change in performance compared with the purely visual perceptual condition. These observations all indicate that when complete visual information was available for planning and on-line correction, potentially less reliable information (proprioception, efference copy) had a significantly reduced influence on performance of both the orientation-matching and letter-posting tasks (Ernst and Banks 2002; Sober and Sabes 2003, 2005; van Beers et al. 1996, 1998, 1999, 2002).

**Proprioceptive/kinesthetic perception of hand orientation**

When the subjects attempted to align their unseen right hand to the target in the orientation-matching task, they tended to fall short of the degree of required rotation. This error increased as the required degree of rotation increased. This trend was evident whether the hand was rotated passively by the experimenter or actively by the subjects and was stronger in the no-vision condition than in the target-vision condition. These findings suggest that without vision, the subjects perceptually overestimated the degree of rotation of their right hand in the present task conditions.

The under-rotation of the hand in the target-vision and the no-vision orientation-matching task could have arisen from biomechanical constraints if the degree of rotation required to reach target orientations approaching 180° required the subjects to pronate their wrist and forearm into increasing extreme or uncomfortable positions. However, that does not appear to be the case. High accuracy was observed for all target orientations, including 180°, in conditions 2 and 3 of the pilot full-vision orientation-matching task in which the subjects held onto the match handle as well as in the full-vision letter-posting task 1. Moreover subjects with normal mobility can readily rotate their hand well past 180° (i.e., beyond a posture of horizontal pronation with the palm facing downward) while holding the match handle with their arm outstretched in front of them. Therefore the results in the orientation-matching task likely reflect perceptual overestimates of hand orientation or of the change in hand orientation from the initial supine (palm-up) orientation rather than biomechanical constraints.

The subjects were instructed to align the match handle to the spatial orientation of the target. Besides their estimate of spatial orientation of their hand, per se, the subjects may have also used an estimate of the degree to which their hand was parallel to the target as a second cue. There have been a number of studies on the sense of spatial parallelism using haptic or visual input (Appelle 1971; Cuijpers et al. 2000; Hermens and Gielen 2003; Hermens et al. 2006; Kaas and Mier 2006; Kappers 1999, 2002; Kappers and Koenderink 1999; Kappers and Viergever 2006; van Doorn et al. 2005; Volcic et al. 2007; Zuidhoek et al. 2003, 2004). These studies also found evidence of similar visual and haptic oblique effects and showed that errors in estimates of spatial parallelism are strongly dependent on such factors as the spatial location and spatial separation between the two objects or the two hands, and by the spatial orientation of the target object, in the horizontal, vertical fronto-parallel, and vertical mid-saggittal planes.

The consensus of many of these studies is that errors in haptic estimates of spatial orientation and parallelism depend on a weighted combination of representations of the spatial orientation of the objects in different spatial locations in allocentric coordinate systems (Kappers 2002–2004; Kap- pers and Viergever 2006; Volcic et al. 2007). However, in most of those studies, the subjects attempted to estimate and report the relative spatial orientation of two objects that they explored with their hands or to rotate a match bar by various means until it was perceived as aligned to a target bar rather than to align their hand physically with a target object as was the case in this study. Furthermore the target and match handles in this study were fixed in adjacent spatial locations in the vertical axis at the subjects’ midline, and changes in orientation errors were related to differences in sensory and motor conditions and to the required degree of rotation of the hand in that fixed location not to different weighted interactions between spatial orientation estimates at different locations in allocentric coordinates. However, this factor may have contributed to the errors in initial alignment of the hand with the target before reach in letter-posting task 2.

The under-rotation of the hand observed in the target-vision and the no-vision orientation-matching task was consistent with observations from studies of haptic perception of spatial hand orientation that showed an overestimation (undershoot) of the right-hand match orientation compared with the left-hand reference orientation when subjects attempted to align two bars presented in the horizontal plane (Kaas and Mier 2006; Kappers and Viergever 2006). A similar trend of under-rotation was observed in this study performed in the vertical plane for bars presented one below the other. This suggests that proprioceptive perceptual under-rotation observed in this study is not related to any physical characteristic of the experimental setup per se.

As was the case for many of the haptic studies of parallelism, our no-vision condition required an inter-manual transfer of orientation signals from the left to the right arm that was not required in the other sensory conditions. This may have contributed to the increased errors in the no-vision condition. Haptic estimates of parallelism are comparable or better when subjects perform the tasks unimanually than bimanually (Appelle and Countryman 1986; Gentaz and Hatwell 1995; Kappers 2002, 2003; Kappers and Koenderink 1999). Performance may have been better if we had asked the subjects to explore the target orientation with the right hand first and then to attempt to match it with the same hand. However, this would have introduced two new confounds. There would be a delay between the initial haptic exploration and the subsequent attempt to match. More importantly, the paradigm would no longer be a true matching task as in the full- and target-vision conditions. Instead it would require the subjects to replicate a proprioceptive or sensorimotor state recently experienced by
the same hand and arm. As a result, we did not use this strategy in the no-vision condition.

**Significant interaction among target angle, hand rotation velocity, and hand transport velocity**

In a task similar to the full-vision condition of our letter-posting task 1, Fan et al. (2006) asked subjects to reach to and grasp objects in six different orientations (30–150°) at two different spatial locations. Consistent with their results, our data showed that the hand began to rotate at the onset of hand transport, that peak rotation velocity increased with the degree of hand rotation required from the original supine orientation, and that total movement duration did not vary significantly with final target orientation. These results indicate that hand orientation is specified early in the planning of reach-to-grasp actions (Fan et al. 2006). Because this was also observed in the target-vision and no-vision conditions, our study extends this into the proprioceptive domain.

However, we found that the peak of hand transport velocity increased significantly with greater target orientations. This interaction among target orientation, wrist rotation velocity, and hand transport velocity had the paradoxical effect that when the hand had to rotate a full 180°, it approached the target panel at a peak transport velocity that was nearly 30% faster than when it only had to rotate only 30° (mean peak transport velocity 647.2 vs. 499.2 mm/s, respectively). Despite this interaction, total movement duration did not vary significantly with target orientation. This can be explained by a subtle change in the hand transport velocity profiles with target orientation. For targets requiring large hand rotations, velocity curves tended to become more sharply peaked (Fig. 2) so that the hand spent less time traveling near the peak velocity.

This coupling between the kinematics of hand orientation and hand transport is consistent with a number of other findings of temporal coordination and interactions among the transport, orientation, and grasp components of reach-to-grasp movements (Connolly and Goodale 1999; Desmurget et al. 1996, 1998; Gentilucci et al. 1991; Marotta et al. 2003; Marteniuk et al. 1987; Paulignan et al. 1990, 1991; Soehting and Flanders 1993; Torres and Zipser 2002, 2004). Our finding is also consistent with earlier demonstrations that larger target objects resulted in faster transport velocities (Bootsma et al. 1994; Gentilucci et al. 1991; Jakobson and Goodale 1991; Marteniuk et al. 1990; Zaal and Bootsma 1993). Together, those earlier studies and the present findings all indicate that while transport, orientation, and grasp may be separate behavioral components of reach-to-grasp movements (Fan et al. 2006), there is considerable functional coupling of the neural circuits implementing each component of the action during normal unconstrained motor behavior. This may reflect a shared mechanism required to coordinate each component of reach-to-grasp actions (Jeannerod 1999).

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