Upper Limb Asymmetries in the Matching of Proprioceptive Versus Visual Targets

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Goble DJ, Brown SH. Upper limb asymmetries in the matching of proprioceptive versus visual targets. J Neurophysiol 99: 3063–3074, 2008. First published April 24, 2008; doi:10.1152/jn.90259.2008. The purpose of the current study was to determine the extent to which “sensory dominance” exists in right-handers with respect to the utilization of proprioceptive versus visual feedback. Thirteen right-handed adults performed two target-matching tasks using instrumented manipulanda. In the proprioceptive matching task, the left or right elbow of blindfolded subjects was passively extended by a torque motor system to a target position and held for 3 s before being returned to the start position. The target angle was then matched with either the ipsilateral or contralateral arm. In the second task, visual matching, circular targets were briefly projected to either side of a visual fixation point located in front of the subject. Subjects then matched the target positions with a laser pointer by moving either the ipsilateral or contralateral arm. Overall, marked arm differences in accuracy were seen based on the type of sensory feedback used for target presentation. For the proprioceptive matching task errors were smaller for the nonpreferred left arm, whereas during the visual matching task smaller errors were found for the preferred right arm. These results suggest a left arm/right hemisphere advantage for proprioceptive feedback processing and a right arm/left hemisphere advantage for visual information processing. Such asymmetries may reflect fundamental differences between the two arm/hemisphere systems during the performance of bimanual tasks where the preferred arm requires visual guidance to manipulate an object, whereas the nonpreferred stabilizes that object on the basis of proprioceptive feedback.

INTRODUCTION

Arm differences in upper limb motor behavior are evident in many activities of daily living with approximately nine of ten individuals preferring to use the right versus left arm for common tasks such as eating, drinking, and grooming (Coren and Porac 1977; Gilbert and Wysocki 1992). In this case, manual performance asymmetries have been associated with an enhanced ability of the preferred right arm, and presumably the contralateral left cerebral hemisphere, to generate motor output and/or utilize sensory feedback. Indeed, well-documented preferred arm performance advantages exist in terms of peak speed (Annett et al. 1979; Boulinguez et al. 2001; Heath and Roy 2000; Todor and Cisneros 1985; Woodworth 1899), strength (Brouwer et al. 2001; Farthing et al. 2005; Petersen et al. 1989; Provens 1967), and consistency (Elliott et al. 1999b; Peters 1976; Peters and Durdig 1979; Todor and Kyprie 1980) of voluntary movements. Based on these consistent observations, it is perhaps not surprising that the preferred and nonpreferred arms are frequently referred to as being “dominant” and “nondominant,” respectively.

Although the idea of arm dominance has persisted in the handedness literature, recent evidence in the area of motor control has provided an alternative view of upper limb asymmetries. Specifically, it has been suggested that neither arm is dominant per se but, rather, each arm is specialized for different aspects of sensorimotor performance. This is perhaps best exemplified by the dynamic dominance hypothesis of handedness, first proposed by Sainburg (2002). On the basis of multiple studies examining targeted reaching in both healthy and brain-injured individuals (Bagesteiro and Sainburg 2002, 2003; Haaland et al. 2004; Sainburg and Schaef er 2004; Sainburg and Wang 2002; Schaef er et al. 2007; Wang and Sainburg 2003, 2004a), it has been purported that the preferred arm/hemisphere of right-handed individuals is specialized for the control of movement trajectory, whereas the nonpreferred arm/hemisphere is enhanced for obtaining static arm positions or postures. One major advantage of this more bilateral approach to the study of arm asymmetries is that it highlights fundamental differences in arm function, which might be related to common bimanual activities of daily living. For example, in the task of hammering a nail, most individuals use the preferred arm to perform the trajectory-dependent movement (i.e., swinging the hammer), whereas the nonpreferred arm is used to stabilize the object (i.e., hold the nail) in a particular position based on a particular posture.

In a recent review of literature on upper limb asymmetries in sensorimotor performance, Goble and Brown (2008) also proposed a dichotomous model of arm asymmetries based on two key sources of movement-related sensory feedback: vision and proprioception. This hypothesis suggests that the preferred arm might be more reliant on visual feedback during the control of movement, whereas the nonpreferred arm is enhanced for proprioceptive feedback processing, and was also predicated on functional differences that exist between the two arms during bimanual tasks. In particular, visual attention is primarily directed to the preferred arm during bimanual activities because this arm commonly performs such tasks as object manipulation (e.g., opening the lid of a box), whereas the nonpreferred arm must therefore rely on proprioceptive feedback to perform tasks such as object stabilization (e.g., holding the box steady).

With respect to visual feedback, Flowers (1975) was the first to compare two movement tasks that differed in sensory feedback processing demands. Although no arm asymmetries...
were found in a relatively feedback independent (i.e., ballistic) finger-tapping paradigm, the preferred arm of right-handed individuals was faster and more accurate for a sequential aiming task. Given that aiming tasks have been shown to rely heavily on visual information (Todor and Kypríe 1980), results reported by Flowers (1975) suggest an advantage for the preferred right arm in the utilization of visual feedback. In support of this conclusion, arm differences have also been demonstrated in the kinematics of visually guided aiming, especially in the case of deceleration duration, a period of time during which on-line corrections in movement trajectory based on visual feedback may occur (Carlton 1981; Elliott et al. 1999a; Ma-Wyatt and McKee 2007). In this case, deceleration duration has been found to be shorter for the preferred arm (Boulinguez et al. 2001; Elliott et al. 1995; Mieschke et al. 2001; Roy et al. 1994; Todor and Cisneros 1985), suggesting a preferred-arm specialization for the more effective processing of visual feedback. Despite this considerable evidence, however, other possibilities exist. For example, in a classic study by Annett (1979) shorter preferred-arm movement times during a peg task were found to be attributed to enhanced motor, rather than sensory, ability, allowing for fewer and faster corrective movements to be made.

In contrast to studies indicating a preferred arm advantage in the control of visually guided movement, studies of arm differences in the utilization of movement-related proprioceptive feedback have largely reported asymmetries in favor of the nonpreferred arm. Early evidence of this phenomenon came from studies involving proprioceptively guided matching of distal joint position (Colley 1984; Rio-Lu-Quinn 1991; Roy and MacKenzie 1978). More recently, Goble et al. (2005, 2006) and Goble and Brown (2007) expanded on these initial studies by comparing elbow-matching tasks of varying difficulty. Using instrumented manikulands, precise measures of elbow joint–matching error were collected, and asymmetries found, favoring greater overall accuracy of matching by the nonpreferred arm. This nonpreferred arm advantage was further shown to be enhanced when targets were of greater amplitude (Goble et al. 2006) and during more difficult tasks that required both memory and interhemispheric transfer of proprioceptively determined target information (Goble and Brown 2007).

Although intriguing, these previous studies supporting a sensory-modality–based hypothesis of handedness remain limited, given that no direct examination of upper limb asymmetries in comparable visual and proprioceptive target-matching tasks has been undertaken. Thus the purpose of the present study was to test the hypothesis that “sensory handedness” exists in healthy right-handed adults by comparing preferred and nonpreferred arm-matching accuracy during reaching tasks requiring the same motor output, but that varied with respect to the primary type of sensory information relied on during matching. Further, arm differences in matching strategy were assessed based on the kinematics associated with moving to visual versus proprioceptive targets. It was hypothesized that the accuracy of preferred arm matching would be enhanced for visually defined targets, whereas the nonpreferred arm would be more accurate for targets that were proprioceptively defined. Based on previous studies conducted by this laboratory (Goble and Brown 2007; Goble et al. 2006), it was also expected that greater asymmetries would be seen during the more difficult target-matching task (i.e., a task that involved both memory and interhemispheric transfer of target information) and when matches were made to targets of greater amplitude.

METHODS

Subjects

Approval for this study was obtained from the institutional review board at the University of Michigan. Thirteen healthy, young adults (mean age 20.1 ± 1.5 yr; six males, seven females) provided informed consent and participated in the full protocol. The total number of subjects was determined based on a power analysis using data from previous position-matching studies conducted in this laboratory (Goble and Brown 2007; Goble et al. 2006). All subjects were free of upper limb neuromuscular impairment, had normal or corrected-to-normal vision, and showed a strong right arm preference as evidenced by scores of +100 on a modified version of the Edinburgh Handedness Inventory (Oldfield 1971). In addition, the preferred arm was also associated with significantly (paired t comparisons, \( P < 0.05 \)) greater performance on several standard tests of motor ability including maximum grip strength, functional dexterity based on a peg placement test, and hand steadiness as reflected by the ability to maintain a 1-mm probe within a 2-mm hole for 10 s without touching the sides (Ranganathan et al. 2001). These performance characteristics are summarized in Table 1.

Experimental setup

Subjects in this study performed two memory-based matching tasks with similar motor output requirements, but that varied with respect to type of sensory feedback used to represent and/or achieve the target position. In the first task, proprioceptive matching (Fig. 1, top), subjects were blindfolded and seated with their forearms resting comfortably on two height-adjustable instrumented manikulands designed for measuring angular displacement of the elbow joint in the horizontal plane. Each manikuland consisted of a servomotor-driven horizontal metal support adjusted to the length of the subject’s forearm and mounted on a frictionless pivot below the elbow. Standardized starting positions for the shoulder (80° abduction, 15° flexion), elbow (75° extension), and wrist (neutral) were maintained across subjects. In addition, the effects of altering head position were minimized by means of a steel chin rest and support frame surrounding the lateral aspects of the head.

For the second task, visual target matching (Fig. 1, bottom), the same setup was implemented as just outlined, with the exception that subjects were not blindfolded and a back-projection system was used to present visual targets. This system consisted of a flat, translucent screen suspended directly in front of the subject on which small circular (1-cm-diameter) targets were projected from behind the screen. The screen was sufficiently large so as to limit the use of visual background information during matching (Krigolson and Heath 2004; Lemay et al. 2004). The position of the targets and fixation point were software adjusted to be along the sightline of a laser pointer fixed to the distal end of the manikuland just below eye level.

Experimental procedures

Subjects performed the two matching tasks (proprioceptive vs. visual target matching) in a sequential fashion with approximately

<table>
<thead>
<tr>
<th>Task</th>
<th>Preferred Arm</th>
<th>Nonpreferred Arm</th>
</tr>
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<tbody>
<tr>
<td>Maximum grip strength, N</td>
<td>314.6 ± 24.2</td>
<td>290.1 ± 26.3</td>
</tr>
<tr>
<td>Motor dexterity, number of pegs in 60 s</td>
<td>31.8 ± 0.9</td>
<td>29.0 ± 0.7</td>
</tr>
<tr>
<td>Hand steadiness, number of probe touches</td>
<td>8.3 ± 2.8</td>
<td>18.4 ± 5.0</td>
</tr>
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Values are means ± SE.
interhemispheric transfer of proprioceptive target information. All information, whereas the CR condition required both memory and largely consisted of the storage and retrieval of proprioceptive target [CR condition). Thus the demands associated with IR matching forearm in a mirror symmetric fashion (contralateral remembered the target (ipsilateral remembered [IR] condition), or with the opposite This was done with either the same forearm as that used to determine the elbow at a self-selected pace to the memorized target position. [Image 50x400 to 298x721]FIG. 1. Experimental setup for the proprioceptive (top) and visual (bottom) target-matching tasks.

half (n = 7) of the subject pool starting with the proprioceptive task, whereas the remaining subjects (n = 6) began with visual target matching. Prior to data collection for each task, subjects were given a full description of the experimental procedures and as many practice trials as necessary to ensure the instructions provided were understood. On average, each task lasted 0.5 h with a 10-min rest break provided between tasks. In no case were subjects given knowledge regarding the accuracy of performance.

PROPRIOCEPTIVE TARGET-MATCHING TASK. In this task, subjects performed matching of a previously determined static arm position in the absence of vision. Each trial consisted of two components: target determination and target matching. In the target-determination phase, the preferred or nonpreferred forearm was passively displaced by the torque motor system to a predetermined elbow angle (15 or 30° of elbow extension from start position) at a constant velocity of 15°/s, comparable to that used in previous studies involving the passive specification of a target joint angle by a torque motor system (e.g., Lönn et al. 2000a,b). The subject was given 3 s to memorize the target angle of the elbow based on static proprioceptive feedback. The forearm was then displaced back to the start position by the motor at a constant speed of 15°/s.

Following a 2-s delay, the target-matching phase was initiated whereby subjects responded to an auditory tone by actively extending the elbow at a self-selected pace to the memorized target position. This was done with either the same forearm as that used to determine the target (ipsilateral remembered [IR] condition), or with the opposite forearm in a mirror symmetric fashion (contralateral remembered [CR] condition). Thus the demands associated with IR matching largely consisted of the storage and retrieval of proprioceptive target information, whereas the CR condition required both memory and interhemispheric transfer of proprioceptive target information. All subjects were instructed to “focus on the end position of the reference movement and try to replicate it.” On completing the target-matching phase, subjects held their forearm steady for a minimum of 2 s prior to its being passively returned by the motor to the start position in preparation for the next trial.

VISUAL TARGET-MATCHING TASK. Similar to the proprioceptive target-matching task, the visual target-matching task also consisted of two phases. In the target-determination phase, subjects focused on a fixation point that appeared in the center of the screen directly in front of them. After 3 to 5 s, the fixation point was extinguished and a visual target appeared for 75 ms to the right or left of the fixation point. Since subjects did not have time to foveate the target, this method was used to preferentially activate the contralateral primary visual cortex (for reviews of this technique see Efron 1990; Hellige 1983).

During target matching subjects responded to an auditory tone, occurring 2 s following target presentation, by moving the forearm to direct the point of the laser attached to the manipulandum toward the memorized target position on the screen. As was the case in the proprioceptive task, this movement required 15 or 30° of elbow extension. Matching movements were made with either the forearm on the same side as the visual target (IR condition) or to a mirror image of the target using the contralateral forearm (CR condition). Once again, matching in the ipsilateral condition was thought to be less difficult than that in the contralateral condition because the former required primarily memory, whereas the latter involved both memory and interhemispheric transfer of visual target information. For both proprioceptive and visual target-matching subjects moved at a self-selected speed with an emphasis on being as accurate as possible.

Data collection and analysis

In each matching condition five trials were collected in a random block design for each combination of task (IR vs. CR), arm (preferred vs. nonpreferred), and target amplitude (15 vs. 30). Elbow joint rotations were recorded as the voltage output of precision potentiometers mounted beneath the pivot point of each manipulandum. The analog signal was then digitized at 100 Hz, filtered (fourth-order Butterworth, zero phase lag, 8 Hz), and multiplied by a displacement calibration coefficient prior to data analysis.

Three measures of matching accuracy were used in this study to characterize the accuracy of preferred and nonpreferred arm matching. Absolute error, defined as the absolute value of the difference between the target and matching positions, was used as an overall measure of endpoint matching ability. Constant errors were assessed as the signed difference between the actual and target-matching positions to determine the existence of any directional bias in matching performance. Last, the consistency of subject matching was assessed through variable error measures based on the SD of constant errors across a series of trials. For all three accuracy measures the target and matching positions were determined by differentiating displacement signals into velocity and then using a threshold-detection algorithm of ±2SDs from the baseline (zero) signal to detect movement onset and offset.

Matching movements were also analyzed for differences in several movement kinematics. Peak movement velocity (i.e., the maximal velocity achieved during the matching movement) and movement time (where both movement onset and offset were calculated as described earlier), provided indicators of the overall movement speed chosen by subjects. Time to peak velocity, measured as a percentage of total movement time, was used as a measure of temporal symmetry of velocity profiles with respect to time where 50% represented ideal symmetry. Finally, the smoothness of the matching movements was determined by the following jerk score calculation normalized for movement amplitude and duration.
\[
\text{Jerk score} = \sqrt{\left(\frac{1}{2}\right) \int \dot{j}(t) dt (\frac{d^2 \dot{j}}{dt^2})^2}
\]

where \( j \) is the third derivative of position (i.e., jerk), \( d \) is the movement duration, and \( a \) is the movement amplitude (Ketcham et al. 2002; Seidler et al. 2002).

**Statistical analyses**

For each of the visual and proprioceptive target-matching conditions, mean measures of accuracy (absolute, variable, and constant error) and movement kinematics (peak velocity, movement time, percentage time to peak velocity, and movement smoothness) were subjected to repeated-measures ANOVAs with significance set at the level of \( P < 0.05 \). Where significant main effects and/or interactions were found, data were subsequently collapsed across nonsignificant factors and tested post hoc for simple effects using Tukey’s honestly significant differences test with significance also set at \( P < 0.05 \). In the case of significant post hoc differences, effect sizes were also calculated using Cohen’s \( d \) procedure to measure the strength of relationship.

**RESULTS**

**Absolute errors**

The absolute accuracy of proprioceptive and visual target matching is shown in Fig. 2 for the preferred and nonpreferred arms in each task (ipsilateral remembered [IR] vs. contralateral remembered [CR]) and amplitude (15 vs. 30°) condition. During proprioceptive target matching, a main effect of matching arm was found such that absolute errors were smaller across all task and amplitude conditions when matching was performed by the nonpreferred versus preferred arm \( [F_{(1,12)} = 13.6; P < 0.01] \). This asymmetry, however, interacted with the type of matching task performed such that a greater nonpreferred arm-matching advantage was seen in the CR condition \( [F_{(1,12)} = 14.3; P < 0.01] \). Preferred arm errors were approximately twice as large in this condition as those seen for the nonpreferred arm. This was due largely to an increase in preferred arm error during IR versus CR matching (Tukey’s method; Cohen’s \( d = 0.7 \)). No significant differences in absolute error were seen as a function of target amplitude.

In contrast to proprioceptive matching, subjects were significantly more accurate in terms of absolute error when matching visually determined targets with the preferred arm. This main effect of matching arm \( [F_{(1,12)} = 13.3; P < 0.01] \) did not interact with task and amplitude conditions despite significant increases in absolute error for matches made by either arm during the more difficult CR task \( [F_{(1,12)} = 18.0; P < 0.001] \) and when matching the 30 versus 15° target \( [F_{(1,12)} = 24.4; P < 0.001] \). Although not statistically significant, the magnitudes of absolute errors in the visual task were, on average, greater during CR matching than those during the IR condition.

**Variable errors**

Matching consistency, as determined by variable error, is shown in Fig. 3. Similar to the absolute error findings, a main effect of arm was seen in the proprioceptive task for variable error with significantly smaller errors across all conditions for matches made by the nonpreferred compared with the preferred arm \( [F_{(1,12)} = 48.7; P < 0.001] \). This arm asymmetry did not, however, interact with the type of matching task because similar arm differences were seen in both the IR and the CR conditions. Further, arm differences did not interact with the magnitude of the target position, although there was a main effect of amplitude, indicating greater errors during the 30 versus 15° target-matching condition \( [F_{(1,12)} = 5.3; P < 0.05] \).

In the visual target-matching task, the pattern of variable errors was different from that observed during proprioceptively guided matching. Overall, preferred arm variable errors were significantly smaller than those seen for the nonpreferred arm \( [F_{(1,12)} = 5.5; P < 0.05] \). This main effect was mediated, however, by a significant interaction with target amplitude \( [F_{(1,12)} = 8.7; P < 0.05] \) where a preferred arm advantage was
Constant errors

Constant errors in the direction of target matching are provided in Fig. 4 where positive errors represent target overshoooting and negative errors indicate undershoooting. In the proprioceptive task, where subjects’ responses were largely biased toward overshoooting, arm asymmetries were seen only in the CR condition [task × arm interaction: $F_{(1,12)} = 9.5$; $P < 0.05$]. In this case, preferred arm matches showed significantly greater overshoooting compared with the nonpreferred arm (Tukey’s method; Cohen’s $d = 0.7$) and compared with either arm in the IR condition (Tukey’s method; Cohen’s $d = 0.8$).

In contrast to the overshoooting that was observed during proprioceptive target matching, the visual task was associated with greater undershoooting. During IR matching, the degree of target undershoooting was, on average, 1° for both the preferred and nonpreferred arms. Although the preferred arm maintained this level of undershoooting for the CR task, nonpreferred arm errors interacted with target amplitude [$F_{(1,12)} = 13.7$; $P < 0.01$]. In this case, 15° target matching showed essentially no direction bias, whereas 30° target matching was characterized by undershoooting of about 3°.

Movement kinematics

Ensemble-averaged velocity profiles from a representative subject are shown in Fig. 5 as a general indicator of how subjects moved during the different experimental conditions. On the whole, subject movement kinematics appeared similar for matches made to proprioceptive and visual targets. As seen in Fig. 6A, for both modalities, there was a main effect of
amplitude on peak velocity for both the proprioceptive \[F(1,12) = 37.6, P < 0.001\] and visual \[F(1,12) = 26.5; P < 0.001\] target tasks, such that higher maximum speeds were observed in the 30 versus 15° condition. This scaling effect did not interact with either the matching arm or type of matching condition (i.e., IR vs. CR). However, a significant main effect of peak speed was found where slower speeds occurred in the CR compared with IR matching of both proprioceptive \[F(1,12) = 4.9; P < 0.05\] and visual \[F(1,12) = 5.1; P < 0.05\] targets. Similar to these findings for peak velocity, main effects of target amplitude and matching task were also seen for movement time (Fig. 6B). Subjects made longer-duration movements (i.e., had greater movement times) when targets were larger in amplitude \[\text{proprioceptive task: } F(1,12) = 61.9, P < 0.001; \text{visual task: } F(1,12) = 37.7, P < 0.001\] and when matching was performed in a CR versus IR fashion \[\text{proprioceptive task: } F(1,12) = 29.5, P < 0.001; \text{visual task: } F(1,12) = 7.2, P < 0.05\].

Matching movements in the present study were temporally asymmetric with time to peak velocity occurring approximately one third into the movement regardless of arm, task, or target amplitude condition for both proprioceptive and visual targets (Fig. 6C). Based on the mean normalized jerk scores from the group data (Fig. 7A), it was found that the overall smoothness of matching did not differ between arms in either the visual or proprioceptive target-matching task. There was, however, a main effect of matching task such that IR matching was smoother than CR matching regardless of whether the target was proprioceptive \[F(1,12) = 9.0; P < 0.05\] or visual \[F(1,12) = 7.0; P < 0.05\]. In general, velocity profiles were smooth and stereotyped during the acceleratory phase, whereas movement deceleration was more irregular in nature with a number of secondary velocity peaks (Fig. 7B).

**DISCUSSION**

Upper limb asymmetries in motor behavior have traditionally been viewed from the standpoint of preferred arm dominance for both the generation of motor output and the utilization of sensory feedback. More recently, however, theories such as the dynamic dominance hypotheses of handedness have suggested that the preferred and nonpreferred arm/hemispheres are each specialized for different aspects of sensorimotor performance. In line with this more current thinking, the aim of the present study was to elucidate whether the preferred and nonpreferred arms could be differentiated on the basis of the type of sensory feedback (vision vs. proprioception) primarily relied on during targeted reaching. It was found that the nonpreferred left arm was enhanced for matching proprioceptively determined targets, whereas the preferred right arm was more adept at obtaining visual targets. These results provide the best evidence to date of a sensory-modality–based hypothesis of handedness, whereby the nonpreferred and preferred arms differ on the bases of their relative affiliation for proprioceptive versus visual information during targeted movements.

Mounting evidence from studies of joint position matching concurs with the idea that the nonpreferred left arm is more
accurate when making targeted movements in the absence of vision (i.e., based on proprioceptive feedback). Perhaps the earliest example of this was provided by Roy and MacKenzie (1978) who found a nonpreferred left arm advantage for the matching of previously experienced thumb, but not arm, positions. Subsequent to this finding, a nonpreferred thumb advantage was also shown in studies by Colley (1984) and Riolo-Quinn (1991), although Nishisawa (1991) was unable to show differences between preferred and nonpreferred thumb matching. Further, no arm differences were found for matching proprioceptively determined endpoints in two-dimensional (Carson et al. 1990) and three-dimensional (Chapman et al. 2001) space. A recent study from this laboratory explained these equivocal results on the basis of increased proprioceptive processing demands (Goble and Brown 2007). In this study, a large nonpreferred arm advantage was seen during the more difficult CR task requiring both memory and interhemispheric transfer of proprioceptively determined target positions. This result was in contrast to the smaller asymmetries found in matching tasks that involved only memory (IR) or interhemispheric transfer (contralateral concurrent) of proprioceptive information.

Given the preferential role of the contralateral hemisphere in the control of arm movements, such a nonpreferred left arm advantage for proprioceptive target matching may reflect right hemisphere specialization for processing of proprioceptive feedback. Relevant support for this hypothesis comes from two separate lines of research. First, studies of brain-injured individuals have shown that patients with right versus left frontal and/or medial temporal damage have greater difficulty reproducing the movement extent of passively determined kinesthetic targets (Leonard and Milner 1991a,b; Rains and Milner 1994). Specifically, large right hemisphere excisions affected subjects’ ability to monitor proprioceptive feedback during the presentation of proprioceptive targets and/or plan/execute the proprioceptively guided matching movement.

Further support for hemispheric differences in the processing of proprioceptive feedback comes from studies of healthy adults using functional brain-imaging techniques. In a study of goal-directed reaching, Butler and colleagues (2004) compared activation of the left versus right hemisphere during both visual and proprioceptively guided reaching to remembered targets. When comparing the two modalities it was found that during the proprioceptive task subjects showed preferential activation of a subset of areas in the temporoparietal cortex of the right hemisphere. Although similar results were not obtained in a more recent study by Darling et al. (2007), Naito et al. (2005, 2007) also found increased activation in several higher-order somatosensory processing areas of the right hemisphere during the perception of movement illusions at the wrist. Interestingly, in the Butler et al. (2004) and Naito et al. (2005, 2007) studies, the preferred right arm was often used as a primary source of proprioceptive information. This may indicate that the right hemisphere is dominant for proprioceptive processing during...
movements of both the preferred and nonpreferred arms of right-handers, with preferential access of the nonpreferred left arm to the right hemisphere, leading to the proprioceptive advantages described in the present, and previous, matching studies.

In the case of vision, preferred-arm accuracy advantages for visually guided tasks have been described since the time of Woodworth (1899). It is only during the past three decades, however, that attempts to describe the specific role of vision in determining handedness have been undertaken. Based, in part, on the work of Flowers (1975), preferred-arm advantages for accurately obtaining visual targets of progressively smaller size have most often been attributed to arm differences in the ability to utilize visual feedback for making small corrective movements during the latter stage of reaching (Carson et al. 1993; Elliott et al. 1995; Mieschke et al. 2001; Roy et al. 1994; Todor and Cisneros 1985; Todor and Doane 1978; Todor and Kyprie 1980). Indeed, this asymmetry in visual feedback processing has also been inferred from the kinematics of visually guided reaching movements where the amount of time spent post peak velocity—a period of time thought to rely heavily on the use of visual feedback to monitor and correct movement (Carlton 1981; Elliott et al. 1999a)—has been shown to be shorter for preferred arm movements (Boulinguez et al. 2001; Elliott et al. 1995; Mieschke et al. 2001; Roy et al. 1994; Todor and Cisneros 1985). Although these results are intriguing, it should be noted that it is difficult to compare these previous results to those of the present study. This is particularly true given that reaching movements in the present study were made at a self-selected speed with a high emphasis on target accuracy, whereas previous studies required subjects to move as fast and as accurately as possible.

It is appealing to attribute the preferred right-arm advantages for accurately obtaining visual targets in this study to specialization of the contralateral left-hemisphere for visual feedback processing. Evidence in support of this notion, however, is limited. One interesting observation that lends support to the notion of a left-hemisphere advantage for the processing of visual information is the large proportion of individuals who demonstrate right-eye dominance. In this case, it has been shown that 65% of the population prefers the right eye for monocular tasks (Porac and Coren 1976, 1978) and that visual information from the nasal (i.e., crossed) fibers of this eye, leading to the left hemisphere, exhibit processing dominance over the temporal (i.e., uncrossed) fibers traversing to the right hemisphere (Crovetz 1964; Hubel and Wiesel 1959, 1962). In addition, studies of visual acuity have also shown a left-hemisphere advantage in terms of temporal resolution (for review see Okubo and Nicholls 2005). In a study by Nicholls (1994), for example, the threshold for detecting fusion of two light flashes that were presented in quick succession was examined in a group of healthy, right-handed adults. Based on this paradigm, it was found that subjects were most accurate for stimuli presented in the right visual field (i.e., left hemisphere). Last, anatomical differences between the left and right visual cortices also exist where the left occipital lobe extends further anterior and is wider than the right (Galaburda et al. 1978; Geschwind and Galaburda 1985). This structural arrangement may lead to greater volume of neural substrate available to the left visual cortex.

In accordance with previous proprioceptive matching studies conducted by this laboratory (Goble and Brown 2007; Goble et al. 2006), asymmetries in absolute and constant matching errors favoring the nonpreferred arm were particularly pronounced in the contralateral remembered proprioceptive task. Given that this task is dependent on the interhemispheric transfer of memorized proprioceptive feedback prior to making an accurate matching movement (Fabri et al. 2001; Sperry et al. 1969), one may logically conclude that subjects more readily transferred this information from the left to the right hemi-

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**FIG. 7.** A: mean group differences in movement smoothness are shown for matches made to proprioceptive and visual targets in each task condition across target amplitudes. Error bars represent between-subject variability in the form of SE. B: representative velocity profiles from the 40° target condition are provided demonstrating the smoothness of matching in the IR and CR conditions for targets based on proprioception or vision.
sphere. This directional bias with respect to the interhemispheric transfer of memorized positional information has previously been reported in studies assessing the transfer of learning following opposite-arm training in a visuomotor rotation task. It has been shown specifically that previous experience with the unseen preferred arm (i.e., left hemisphere) under rotated feedback conditions enhances the final position accuracy of the unseen nonpreferred arm (i.e., right hemisphere), but not vice versa (Sainburg and Wang 2002; Wang and Sainburg 2003, 2004b).

Although absolute errors in this study provided the clearest indication of a subject’s overall ability to accurately match target positions, it should be noted that this measure of performance is a complex combination of variable and constant errors (Schutz and Roy 1973). In this case, variable errors represent the consistency of matching performance and have been associated with noise in the sensorimotor system, whereas constant errors are more reflective of the central representation of target position (McIntyre et al. 2000). Compared with absolute errors, variable errors in this study showed a similar pattern of arm differences for the different sensory feedback types, with enhanced nonpreferred arm performance in the proprioceptive task and greater preferred arm accuracy during, at least, the 15° visual target-matching condition. Surprisingly, there was a lack of arm asymmetries in the visual-matching task for the 30° target, which was not initially expected based on a previous proprioceptive target-matching study conducted by this laboratory (Goble et al. 2006). This result, however, may reflect the influence of task workspace on arm asymmetries during visually guided reaching tasks. Wang and Sainburg (2006), for example, recently demonstrated that arm asymmetries when reaching to a visual target were found only if the task was performed in a shared arm space around the body midline and not when the arms performed in their own hemispaces. In this case, it might have been expected that asymmetries in the visual task of the present study would be seen only for the 15° target amplitude because it was performed closer to the body midline than was the 30° target amplitude.

The constant errors observed in this study were biased in the direction of overshooting for proprioceptive targets and undershooting for visual targets. This result is comparable to that reported by Adamovich and colleagues (1998) who demonstrated a similar tendency for subjects to reach beyond proprioceptively determined targets, while falling short of targets that were obtained under visual guidance. Although the neurophysiological basis for this pattern of errors remains unclear, it has been suggested that these results likely reflected a modality-specific difference in the representation of space (Adamovich et al. 1998). In this case, the perception of kinesthetic space was thought to be subject to a relative “stretching” along the lateral direction, whereas there may have been a comparable “contraction” in visual space.

One limitation of the present study was that, during the visual target-matching task, proprioceptive feedback was available for use during the matching phase of each trial. In this case, it could be argued that any asymmetry in matching performance might be due to a preferred arm advantage for the utilization of vision and/or proprioceptive feedback, rather than only vision itself. Even though the specific contribution of each source of feedback was not determined in the present study, previous research using visuo-proprioceptive mismatch paradigms would suggest that our subjects were heavily reliant on visual feedback during both the target-presentation and target-matching phases of the visual task. In particular, these studies have shown that the planning of movement direction (Bagesteiro et al. 2006; Lateiner and Sainburg 2003; Sober and Sabor 2003) and movement extent (Sarlegna and Sainburg 2007) are highly dependent on visual information, with weighting estimates as high as 90% for visual feedback compared with only 10% for proprioceptive feedback (Sober and Sabor 2005). It should be acknowledged, however, that in the present study a mismatch situation was not utilized (i.e., visual and proprioceptive feedback were not perturbed) and thus it remains possible that a significant contribution was made by the proprioceptive system during the visual target-matching task.

With respect to movement kinematics, peak velocity was found to scale with movement amplitude in both the ipsilateral remembered and contralateral remembered tasks, as has been shown to be an invariant characteristic of goal-directed reaching movements (e.g., Brown and Cooke 1981, 1984, 1990; Gottlieb 1998; Gottlieb et al. 1990; Pfann et al. 1998). In contrast to these studies, however, the matching movements made in the present study were rather slow (average movement time <2 s) and thus were more typical of those that have been reported for targeted movements made in the absence of speed constraints and where a heavy emphasis has been placed on accuracy (Fisk and Goodale 1985; Goble and Brown 2007; Goble et al. 2005, 2006; Milner 1992; Milner and Ijaz 1990). In particular, velocity profiles often consisted of a primary movement component, characterized by a gradual rise to peak velocity, and a prolonged, irregular deceleration phase with multiple subpeaks (Novak et al. 2002; Soechting 1984). Greater irregularities in the velocity profile were seen during contralateral remembered matching in both the visual and proprioceptive target-matching tasks. This finding likely reflects the need for subjects to make an increased number of feedback-based corrections in the on-line movement trajectory to achieve a more uncertain target end position (Fishbach et al. 2007; Milner and Ijaz 1990; Rohrer et al. 2002). Importantly, no arm differences were found related to movement kinematics, further strengthening the argument that arm asymmetries in movement accuracy were likely related to feedback processing.

To what extent subjects in the present study may have utilized amplitude- versus position-matching strategies is not certain, although it seems fair to assume that the final arm position was the primary basis for planning matching movements. The basis for this assumption lies in both the instruction given to subjects (i.e., focus on the final arm position and try to replicate it) and on research examining errors in proprioceptively guided matching of movement extent versus target location. In this case, it has been shown that when subjects are required to utilize a movement amplitude strategy only, increased errors (Marteniuk 1973; Marteniuk et al. 1972) and directional biases (Imanaka and Abernethy 1992a,b) are seen with respect to the target position. The tasks used in this study were also memory-based and thus it might be argued that subjects, in theory, might not have utilized sensory feedback for on-line control (i.e., participants may have constructed a movement plan in advance of response cuing) at all. Despite this, however, it seems highly likely that both on-line and off-line control mechanisms were used for the matching movements made in this experiment, as has recently been shown to
be possible by Heath and Westwood (2003) and Heath (2005). With respect to off-line control, for example, planning of the matching movement would require an internal representation (memory) of the target position, which itself was based on the subject’s sensory experience of the target. Similarly, in the case of on-line control, subjects likely used sensory feedback during the movement to determine a current estimate of the arm’s position (proprioceptive task) or the laser’s endpoint (visual task) to determine when it had achieved the desired location.

Overall, the results of the present study provide strong evidence supporting a sensory-modality–specific hypothesis of asymmetries in motor behavior. It has been shown that the nonpreferred left arm of right-handed individuals was more accurate when matching targets that are proprioceptive in nature, whereas the preferred arm is more accurate for visual-target matching. To what extent these results reflect different roles for the preferred and nonpreferred arms during the performance of many activities of daily living remains somewhat unclear. However, given the use-dependent neural plasticity that is now known to exist within the sensorimotor system (for review see Monfils et al. 2005), it seems plausible that neural networks within the left and right hemispheres may have evolved to more adequately process proprioceptive versus visual feedback, respectively. In this case, left-hemisphere specialization for visual-feedback processing would allow for greater interactions between the preferred arm and objects in the external environment (e.g., reaching out for a glass of water). In contrast, specialization of the right hemisphere for proprioceptive feedback would be important for maintaining objects in a particular location outside of visual attention (e.g., holding a piece of bread) prior to their being manipulated by the preferred arm (e.g., buttering it with a knife).

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