

Proprioceptive target matching asymmetries in left-handed individuals

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Abstract In right-handers, the ability to reproduce proprioceptive targets has been shown to be asymmetric, favoring the non-preferred left arm. The present study sought to determine whether a similar arm/hemisphere asymmetry exists for left-handers. Ten strong left-handed adults used the left or right arm to perform proprioceptive target matching tasks that varied in processing demands (i.e., need for memory, interhemispheric transfer) and target amplitude (20, 40°). Similar to right-handers, left-handed individuals had smaller total errors when matching with the non-preferred arm. This asymmetry was greatest in conditions with increased processing demands and larger amplitude targets. These results provide the first evidence to date of right arm/left hemisphere dominance for proprioceptive target matching in left-handers that is the “mirror image” of right-handers.

Keywords Handedness · Sensory feedback · Proprioception · Task complexity · Kinesthesia · Upper limb · Laterality

Introduction

It has been estimated that approximately 90% of the population prefers using the right arm when performing funda-

mental movement tasks, such as writing on a piece of paper or eating with a spoon (Gilbert and Wysocki 1992; Perelle and Ehrman 2005). This behavioral asymmetry, more commonly known as “right-handedness”, has remained relatively stable over time (Coren and Porac 1977) and is thought to reflect specialization of the contralateral left hemisphere for skilled motor activities (Liepmann 1920; Goodale 1988).

The high proportion of right-handed individuals in the population has led to a bias in the study of sensorimotor abilities, with most experiments focusing only on right-handed subjects performing tasks with their preferred right arm. This approach is advantageous, of course, in that it reduces experimental design complexity inherent to comparisons of the left versus right arm, as well as eliminates difficulties associated with recruiting left-handed subjects. However, this approach is limited in its ability to determine important sensorimotor differences that may exist between the preferred and non-preferred arms, and/or between left and right-handed individuals (for review see Elliott and Roy 1996).

Proprioception can be defined as one’s ability to determine body positions and movements in the absence of vision and is derived from muscle, skin and joint receptors (for review see Gandevia et al. 2002). Despite evidence that electrical stimulation of afferent proprioceptive pathways elicits a similar response for the left and right arms (Aimonetti et al. 1999), it has typically been shown that right-handed subjects perform proprioceptive target matching tasks with greater accuracy when using the non-preferred left thumb (Roy and MacKenzie 1978; Nishizawa 1991) or elbow (Kurian et al. 1989; Goble et al. 2006; Goble and Brown 2007, 2008c). These findings suggest a left arm/right hemisphere specialization for the utilization of proprioceptive feedback, which might relate to general use of the

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non-preferred arm for proprioception-based object stabilization tasks. This is particularly relevant in the context of bimanual activities, where vision is often diverted to the preferred arm for object manipulation (for review see Goble and Brown 2008b).

Several additional lines of support exist for a non-preferred arm/right hemisphere asymmetry in the processing of proprioceptive information. Studies of individuals with unilateral brain lesions/excisions, for example, showed that right versus left hemisphere deficits were associated with larger impairments in proprioceptive matching tasks (Leonard and Milner 1991a, b; Goble et al. 2009). In addition, neural activation underlying proprioceptive illusions of joint position/movement appears to exhibit a right hemisphere dominance in healthy, right-handed individuals (Naito et al. 2005, 2007), while the neural signals associated with processing information regarding performance of proprioceptively guided movement are also thought to be right hemisphere lateralized (Grunewald et al. 1987).

The purpose of the present study, therefore, was to explore the extent to which left-handed individuals might show asymmetry for proprioceptive target matching, as has been shown previously for right-handers. Left-handedness is not necessarily expressed as the mirror image of right-handedness, and, therefore, the degree of lateralization relies on the particular sensorimotor process being tested. Studies of sensorimotor abilities in left-handers have revealed patterns of asymmetry that are either (1) identical to those of right-handers (e.g., reaction time in Boulinguez et al. 2001, sensorimotor adaptation in Chase and Seidler 2008); (2) less lateralized or non-existent (e.g., arm selection for picking up objects in Gonzalez et al. 2006, 2007, reaction to a visual stimulus in Velay and Benoit-Dubrocard 1999, finger tapping speed/variability in Schmidt et al. 2000); or (3) the reverse of that displayed by right-handers (e.g., visually guided targeted reaching accuracy in Wang and Sainburg 2006).

Recent work by Wang and Sainburg (2006) is particularly relevant to the present study, given that they also assessed target reaching accuracy (albeit in the presence, rather than absence, of vision). These researchers showed that, following adaptation to rotated target feedback with the opposite limb, non-preferred right arm accuracy in left-handers was greater than that of the preferred left arm, when exposed to the same rotation. This mirror image result to that seen for right-handed individuals (see Sainburg 2005 for review) led to the hypothesis in the present study that left-handers would also show a mirror image asymmetry to that typically expressed by right-handers for proprioceptive target matching tasks. Specifically, it was expected that the non-preferred right arm of left-handed individuals would make larger matching errors and that these errors would be enhanced with manipulations of task

difficulty (i.e., increased target amplitude and task demands). Beyond this main prediction, an alternative hypothesis was that lateralization of proprioceptive matching would not be seen for left-handers. This hypothesis is in line with the results of earlier studies on proprioception-related asymmetries in small samples of left-handers, which failed to reveal consistent arm/hemisphere differences for either the stimulation of afferent neural pathways (Aimonetti et al. 1999) or the magnitude of brain potentials (Grunewald et al. 1987). Overall, the results of the present study contribute to the basic understanding of lateralized control for proprioceptive target matching tasks, demonstrating the degree to which left and right-handed individuals might share a common behavioral/neurophysiological substrate for the utilization of proprioceptive feedback.

Methods

Participants

Ten healthy adults (mean \pm SD age = 23.2 \pm 4.6 years; six females) with no history of neuromuscular impairment were recruited from the University of Michigan student population. Participants provided written, informed consent prior to testing and demonstrated left arm preference, as evidenced by a laterality quotient (mean \pm SD laterality quotient = -75 ± 10.5 ; range = -65 to -90) calculated from a ten-item version of the Edinburgh Handedness Inventory (Oldfield 1971). Subjects also demonstrated a left arm dexterity advantage (mean \pm SD pegs left arm = 31.4 \pm 2.9; mean \pm SD pegs right arm = 29.1 \pm 2.2) measured on a 60 s peg placement task (Purdue pegboard, Lafayette Instrument Co). The local institutional review board approved all experimental procedures ensuring compliance with the standards laid down in the 1964 Declaration of Helsinki.

Experimental setup

The setup for this study has previously been described (for more details see Goble and Brown 2007, 2008c). Briefly, blindfolded participants were seated upright with forearms affixed to separate instrumented manipulanda designed for measuring angular elbow position in the horizontal plane. Each manipulandum consisted of a length-adjustable aluminum support lever mounted on frictionless pivot below the elbow that could be rotated at 10°/s by a torque motor system. Standardized start positions for the shoulder (80° abduction, 15° flexion), elbow (70° flexion) and wrist (neutral) were maintained across subjects. The head was supported by a steel frame with chin rest.

Experimental tasks/procedure

Prior to data collection, subjects were given multiple practice trials to become familiar with three types of matching tasks to be performed in the experiment. These tasks varied in processing demands (i.e., the need for memory and/or interhemispheric transfer) and consisted of two phases: target establishment and target matching. In the *ipsilateral remembered* (IR) task, target elbow angles were established with the preferred or non-preferred elbow through passive elbow extension (20 or 40°) from the start angle. The target angle was then held for 3 s before the elbow was passively returned to the start angle. Following a verbal “match” command, the target matching phase began whereby subjects actively reproduced the target elbow angle based on proprioceptive memory with the same (i.e., ipsilateral) arm.

In contrast to the IR task, *contralateral concurrent* (CC) matching did not have a memory requirement. In this case, a passively determined target elbow extension angle of 20° or 40° (target establishment phase) was held throughout the task to provide a concurrent, “online” reference for active target matching (in a mirror symmetric fashion) with the opposite (i.e., contralateral) elbow. Although this manipulation eliminated the need for proprioceptive memory, greater demands were placed on interhemispheric transfer of proprioceptive information to plan and execute matching with the opposite elbow.

In the third type of task, *contralateral remembered* (CR) matching, key aspects of the IR and CC tasks were combined to maximize the proprioceptive processing demands placed on the subject. Specifically, the subject’s preferred or non-preferred elbow was passively extended to the target angle of 20° or 40° (target establishment phase), held for 3 s and then returned to the start angle. Next, during the target matching phase, subjects actively replicated in a mirror symmetric fashion the target elbow angle with the opposite (i.e. contralateral) elbow. This task, therefore, required both memory and interhemispheric transfer of proprioceptive information regarding target position to achieve the desired matching elbow angle. For each task type, the same instruction was given: “memorize the angle of your elbow without focusing on how the elbow was brought to that position”. Subjects were not provided information regarding matching accuracy to avoid potential learning effects.

Data acquisition and analysis

Subjects performed six blocks (one for each combination of matching task and matching arm) with the two target amplitudes randomized within each block. Conditions were further counterbalanced via a different, random presentation of the blocks for each subject. Data were collected as the voltage output from precision potentiometers located below the

pivot points of the manipulanda at a resolution of 0.1 deg. The analog voltage signal was digitally sampled at 100 Hz, filtered (fourth order Butterworth, zero phase lag, 8 Hz) and converted to angular displacement via a standard multiplication factor. Three measures of target error were calculated to characterize matching accuracy. Constant error and variable error were used as measures of central tendency and variability, respectively (Schutz and Roy 1973). In addition, total error was calculated according to the method of Henry (1974), as a composite measure of proprioceptive acuity. For each dependent measure, a mean value was calculated for each subject within the various matching task conditions. Mean values were then subjected to a 3 (task) \times 2 (amplitude) \times 2 (arm) analysis of variance with repeated measures. Effects were decomposed where appropriate by collapsing across non-significant factors and using the method of Tukey corrected for multiple comparisons. Statistical significance was set at the $p < 0.05$ level. In the case of significant post hoc differences, effect sizes were also calculated using Cohen’s d procedure to provide a measure of relationship strength.

Results

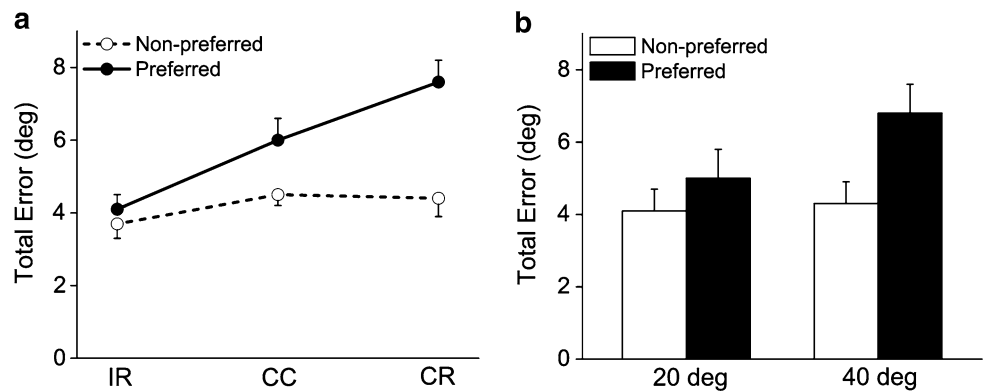
Total (composite) matching errors

Total errors showed that left-handed individuals were significantly less accurate (i.e., made greater errors) when matching with the preferred versus non-preferred arm (arm main effect: $F_{1,9} = 23.3$; $P < 0.001$). This arm asymmetry was influenced by the processing demands associated with the task (Fig. 1a; arm \times task interaction: $F_{1,9} = 14.1$; $P < 0.01$) and target amplitude (Fig. 1b; arm \times amplitude interaction: $F_{1,9} = 7.6$; $P < 0.05$). Specifically, while non-preferred right arm total errors were similar ($\sim 4^\circ$) for all task and amplitude conditions, preferred left arm errors were negatively influenced by increased task demands and increased target amplitude. This resulted in significantly greater non-preferred arm advantages during matching in the most complex, CR task condition (Tukey’s method; Cohen’s $d = 1.3$) and for larger, 40° targets (Tukey’s method; Cohen’s $d = 1.1$).

Central tendency and variability of matching

With respect to the direction and variability of matching performance, no arm differences were seen for measures of constant or variable error, respectively. Constant errors were, however, significantly worse when matching 20° (mean = 2.1° overshooting) versus 40° (mean = 0.1° overshooting) targets (amplitude main effect: $F_{1,9} = 15.1$; $P < 0.01$). In contrast, variable errors were larger in the 40°

Fig. 1 Mean (\pm standard error) total error of proprioceptive target matching as influenced by (a) processing demands and (b) target amplitude



(mean = 3.6°) versus 20° (mean = 2.6°) target condition (amplitude main effect: $F_{1,9} = 11.0$; $P < 0.01$). Variable errors were also significantly increased when matching was performed in the CR (mean = 3.4°) and CC (mean = 3.4°) compared to the IR (mean = 2.7°) task (main effect of task: $F_{1,9} = 10.4$; $P = 0.01$; Tukey's method; Cohen's d for IR vs CC = 0.5; Cohen's d for IR vs CR = 0.5).

Discussion

The present study provides the first known evidence of a non-preferred right elbow accuracy advantage in left-handed individuals for proprioceptive target matching. In agreement with previous matching studies of right-handers, this asymmetry was significantly greater during more difficult conditions, including those requiring greater processing demands (Goble et al. 2005; Goble and Brown 2007, 2008a, c, 2009) and/or larger target amplitudes (Goble et al. 2006; Goble and Brown 2008c). These results suggest that this aspect of sensorimotor performance is the “mirror image” of right-handers, with right arm/left hemisphere specialization likely for the utilization of upper limb proprioceptive feedback.

While two previous proprioception-related studies involving small samples of left-handed individuals found no evidence of lateralization (Aimonetti et al. 1999; Grunewald et al. 1987), a corollary might be made between the present results and recent work involving the accuracy of reaching to visual targets by Wang and Sainburg (2006). These researchers assessed inter-limb transfer for left-handers on a visuomotor rotation task conducted in a virtual reality environment. Subjects were trained to make reaching movements with the preferred or non-preferred arm in the presence of distorted (rotated 30°) visual feedback. Following adaptation, subjects attempted the same task with the opposite arm. Left-handed individuals in this study showed a mirror image pattern of results as that previously found for right-handers, in agreement with previous work by this research group (see Sainburg 2005 for review of the

dynamic dominance hypothesis of handedness). In this case, transfer of position-related information occurred only in the direction of the non-preferred right arm. Although it is not certain to what extent this non-preferred arm accuracy advantage represents a common neurophysiological phenomenon as that seen in the present study, it can be proposed that this performance asymmetry is related to functional differences between the preferred and non-preferred arms during bimanual tasks. Indeed, it is typically the role of the non-preferred arm to stabilize an object in a particular position using proprioception (e.g., holding a piece of paper), while that object is dynamically interacted with using visual guidance of the preferred arm (e.g., writing on the paper). Over time, conditioning of the arms in this manner could result in use-dependent neuroplastic changes of the contralateral hemisphere to each hand (i.e., through learning-based mechanisms) and, thus, serve as the basis for the observed proprioceptive asymmetries seen in the present study.

To what degree subjects coded the elbow displacement rather than target elbow angle information in this experiment is not known. However, there are several reasons to believe that target elbow angle was more important than the spatiotemporal characteristics of the elbow displacement. First, subjects were instructed to focus on the final elbow angle and replicate it without paying attention to how the elbow was moved to the target. Second, it has previously been shown that, in situations where subjects are required to use a matching strategy based on limb displacement versus target position, increased errors (Marteniuk 1973; Marteniuk et al. 1972) and directional biases (Imanaka and Abernethy 1992a, b) are found. This demonstrates that a displacement matching strategy is likely to be a less effective and, therefore, not chosen by subjects. Lastly, the kinematic characteristics of the passive limb displacements made by the servomotor system were in no way similar to those demonstrated by subjects when they actively moved to the target position. Servomotor-driven movements were relatively slow and followed a constant velocity trajectory, whereas subjects

made faster movements with more typical, bell-shaped velocity profiles.

Another point of note in this study was that asymmetries were captured only by the composite error measure (total error), and not by measures of bias/central tendency (constant error) or variability (variability). Given the relationship between these measures of target accuracy (Henry 1974; Schutz and Roy 1973), it is, however, reasonable to assume that total errors must have been influenced to some degree by both a target bias and increased variability. With respect to bias (undershooting versus overshooting), a recent study by Adamo and Martin (2009) provided evidence that when greater constant errors are seen for matches made with the opposite (i.e., CC and CR conditions) versus same (i.e., IR condition) wrist, underlying differences in proprioceptive gain for the preferred versus non-preferred arms is possible. In addition, Haggard et al. (2000) found arm differences using both constant and variable error when right-handed subjects matched the felt location of either the preferred or non-preferred fingertip with the opposite fingertip in different locations across the workspace. These results suggested not only that separate representations exist for each arm effector, but also that there is increased accuracy for matches made in the far left space.

Recent brain imaging studies have revealed distinct differences in neural activation between left and right-handed subjects during upper limb movements (Dassonville et al. 1997; Kim et al. 1993; Lutz et al. 2005). Dassonville et al. (1997), for example, found a negative correlation between ipsilateral brain activity and strength of handedness in left and right-handedness groups. Since participants in the present study could be categorized as having strong left-handedness (as indicated by the Edinburgh Handedness Inventory and the pegboard task), they might also be expected to show more lateralized patterns of brain activity. To this point, right-handed individuals are known to have right hemisphere specialization for the perception of vibration-induced proprioceptive illusions (Naito et al. 2005, 2007). Given the results of the present study, a similar assessment of hemispheric dominance for proprioceptive feedback processing in left-handed individuals now seems warranted.

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