Contribution of sensory and motor components to motor control asymmetries: an analytical model approach

Bernard J. Martin, Diane E. Adamo

Abstract— Proprioceptive and motor information contribute to movement representation; however, the equivalence of homologous contralateral information has received little attention. In a recent study using the matching paradigm we showed that upper limb position sense, based on feedback control, is asymmetric and this asymmetry could be associated with a difference in gain between left (L) and right (R) sensorimotor systems. The current results also show that movement sense is asymmetric in males and this asymmetry is dependent on handedness. It is assumed that a difference in gain between each sensorimotor system may be associated with asymmetric kinesthetic representations in cortical areas. Outcomes of models representing position and velocity control respectively suggest that velocity matching may be primarily controlled in a feed forward mode. Furthermore, compatibility between the models representing position control and velocity control also indicate that i) a difference between the L and R motor gains *alone* is not possible and ii) there *must be* a difference between the L and R sensory gains. Hence, the results strongly suggest a difference in movement representation between the two hand/hemisphere systems.
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I. Introduction

TO predict movement outcomes, internal models [1] must be congruent with movement representation. However, kinesthetic representations may not be identical for the left and right arm-hemisphere systems, which then imply differences between the respective internal models. Since the demonstration by Goodwin et al. [2], it is universally recognized that messages from muscle spindles contribute to kinesthesia. Hence, vibration-induced movement illusions have been extensively used to analyze the roles and properties of muscle proprioception [e.g. 3]. Yet none of the investigations using the matching paradigm evaluated the potential non-equivalence in perception and consequent movement representation between the dominant and non-dominant hand despite known systems differences [4].

Position sense asymmetry has been observed in natural [5] and altered [6] conditions. A model-based demonstration including the properties of feedback systems showed that the intrinsic asymmetry in position sense revealed by contralateral matching paradigms resulted from a difference in the gain of each respective sensorimotor system [5]. In unperturbed conditions and for right-handed individuals, the right hand overshoots the left hand reference position and the left hand undershoots the right hand reference position. Using this directional error, the model demonstrated that in right-handed individuals, the closed loop gain is higher for the left hand/right hemisphere than right hand/left hemisphere proprioceptive-based sensorimotor systems [5]. The *difference in gain concept* provides a unified interpretation of position sense asymmetries, which cannot be accounted for by an interpretation restricted to the asymmetry in transfer of information between hemispheres.

The aim of the present work was to further analyze the contribution of the sensory and motor components of each hand/hemisphere system to functional asymmetry using both empirical and analytical approaches. Concurrent matching of vibration-induced elbow flexion illusions were compared for right- and left-handed males. These movement illusions provide a kinesthetic reference based uniquely on sensory information. To test specific limb differences in movement velocity control both the right and left forearms provided the sensory reference. An analytical model was designed to support functional interpretation of the data.

II. Methods and procedures

A. Participants

Twenty young adult males (10 right-handed, laterality index [7] LI > .75; 10 left-handed, LI < -.75) participated in the experiment. All participants reported being free from any disorders. The experiments were approved by the ethic review board of the institutions to which the authors are affiliated and an inform consent was signed before each test.

B. Experimental setup and procedure

A similar apparatus was previously presented [5]. Participants were seated in a standardized symmetric posture with the forearms and hands supported by horizontal, lightweight adjustable levers free to pivot with negligible force around a vertical axis (Fig. 1). The elbow joint center of rotation was aligned with the rotation axis of each lever and the forearms were resting in pronation. Precision potentiometers coupled to the shaft of each lever measured elbow rotations.

A 100 Hz vibration, with displacement amplitude between 40-100μm, was applied perpendicularly to the distal tendon of the triceps muscle by an electrodynamic vibrator (LDS V203). The location of the application of the probe on the skin was marked to ensure that the placement was identical

B. J. Martin is with the Department of Industrial and Operations Engineering, University of Michigan (phone: 734-763-0189; fax: 734-764-3451; e-mail: martinbj@umich.edu).
D. E. Adamo is with the department of Health Care Sciences, Wayne State University

for subsequent trials. Participants were encouraged to remain relaxed in order to enhance illusory movement perception.
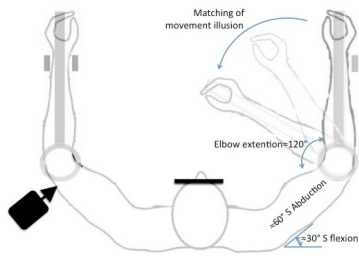

Fig. 1. Experimental setup top view. Vibration was applied to the distal tendon of either the right or left triceps (left vibration illustrated) while the forearm support was immobilized. The contralateral forearm matched the vibration-induced movement illusion concurrently.(S=shoulder).

Prior to the experiment, two practice trials were performed to determine individual sensitivity to the vibration in eliciting a perception/illusion of movement. Participants were required to close their eyes before and during the application of vibration to the reference arm and then, when the illusion was perceived, reproduce the ongoing illusory movement with the opposite (matching) arm with instruction to match the velocity. In the event that vibration did not elicit an illusion of movement during the practice trials, the individual was excluded from further testing; hence two individuals were excluded. Vibration was applied for 10 s. The reference arm was stabilized in a fixed position (Fig.1) by clamping the lever arm to the chair. The matching arm was positioned in an identical starting position and the elbow was free to rotate in the flexion direction. A 15 s rest break was provided between trials. During the rest breaks participants were encouraged to open their eyes and "shake out" their hands or produce isometric contractions in order to eliminate any residual post vibration effects and reset muscle proprioception [8]. Two practice trials were followed by a series of five test trials. The two experimental conditions (2 reference arms) were randomized between participants.

C. Data processing and analysis

The analog signal from the matching side was digitized at 1000Hz and low pass filtered (Fourth order, zero phase Butterworth filter, 6 Hz cutoff frequency) using customized software (LabVIEW™). Additional custom designed software was used for offline data processing. Position profiles were presented on a display for visual inspection and processing of each trial. Two vertical cursors shifted along the time axis captured the sections of the recordings corresponding to the reproduction of the perception of movement elicited by vibration. The slope (Δ position/Δ time) of each section was recorded to determine the velocity of the matching movement. Hence, eventual periods corresponding to an absence of movement, most likely due to a temporary fading of illusion, were eliminated from the velocity computation. The average of the velocity over all "movement" segments of each trial was used as the trial perceived velocity. Left and right hand movement trajectories differed only in slope.

A two-way repeated measure ANOVA was conducted to test for the main effects of hand preference (right, left), matching arm (right, left) and interaction effects for (Δ position/Δ time) of each section was recorded to determine the velocity of the matching movement. Hence, eventual periods corresponding to an absence of movement, most likely due to a temporary fading of illusion, were eliminated from the velocity computation. The average of the velocity over all "movement" segments of each trial was used as the trial perceived velocity. Left and right hand movement trajectories differed only in slope.

A two-way repeated measure ANOVA was conducted to test for the main effects of hand preference (right, left), matching arm (right, left) and interaction effects for movement velocity. To determine which factors influenced interaction effects, Tukey HSD post-hoc tests were conducted. Significance was set at $\alpha \leq .05$.

III. RESULTS

The ANOVA indicated a significant difference between right and left handed groups and a significant asymmetry in velocity matching within each group. For right-handed participants right arm vibration resulted in left arm matching (RVLM) velocity (mean $\pm$ SE) of 2.9 $\pm$ 0.3 °/s, while matching velocity was 1.5 $\pm$ 0.1 °/s in the reverse condition (LVRM). For left-handed participants, right arm vibration induced left arm matching (RVLM) velocity (mean $\pm$ SE) of 1.88 $\pm$ 0.7 °/s, while matching velocity was 2.98 $\pm$ 0.7 °/s in the reverse condition (RVLM), as illustrated in Fig.2. Hence, the asymmetry is reversed in left-handed individuals.
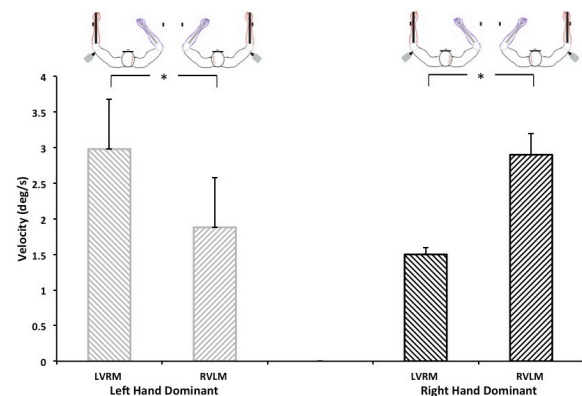

Fig. 2. Mean (+ SE) matching velocity for left (▨) and right (▨) handed groups in the L vibration R match (LVRM) and R vibration L match (RVLM) conditions. Asymmetry is significant for each group. * P < .05

IV. DISCUSSION AND MODEL

The results showed that an asymmetric perception and/or reproduction of movement is inverted between right- and left-handed males. These findings bring new perspectives in movement representation, the assessment of perceptual differences based on vibration-induced movement illusions and use of matching paradigms. The present discussion focuses on a modeling approach to determine the mode of control for matching movements and to understand the relative contribution of the sensory and motor

components to hand/hemisphere specific movement asymmetry.

A discussion about physiological, structural and neural mechanism supporting asymmetry in motor control is beyond the scope of the present work; these are reported in a submitted manuscript. In brief, it is presumed that hemisphere dimorphisms relative to cortical representations of the dominant and non-dominant upper limb contribute to functional differences including movement perception and/or their reproduction.

In the context of this matching task, a model representing the respective components involved in the control of movement may be proposed to determine the most likely mode of control of velocity. This model also helps provide a initial estimate of the relative role of each component to the overall gain of each system. For the sake of simplicity the model will represent the case of right-handed individuals.

1) Position sense versus movement sense: Our position control model demonstrated that position sense asymmetry in right-handed individuals results from a closed loop sensorimotor gain higher for the left than right sensorimotor system [5]. If velocity control was also based on a closed loop control mode then the matching velocity (V) would be larger for the LVRM than RVLM conditions, however this is not the case. The present study shows the opposite result ($V_{RVLM} > V_{LVRM}$), which implies that velocity matching is controlled in an open loop mode whose gain is greater for *right sensory input – left motor output* than *left sensory input - right motor output* systems. The existence of separate control mechanisms for position and velocity has been demonstrated by vibration-induced perturbation of movement control [9]. Further support for an open loop control mode is derived from position and velocity profiles which show monotonous change in position with sporadic movement interruptions, but rarely large multiple corrections indicative of a feedback control mode. These types of movement patterns concur with forward predictive models showing smoother movements than negative feedback control models, particularly for movements performed in the absence of visual feedback [10]. Therefore, higher movement velocities for the left than right arm do not contradict asymmetries of position sense. Movement sense asymmetry rather emphasizes the importance of the mode of control (feedback vs feed forward) and supports a sensorimotor closed loop gain higher for the left than the right limb and an open loop gain higher for the right than left limb, as indicated by our results and supported below.

2) Differences in systems and component gains: As shown in Fig. 3, a simplified model of the respective open loop systems can be used to support the interpretation of the current results and propose a hypothesis regarding the sensory and/or motor origin of the difference in gain between the right and left limb systems. In the Laplace domain, the transfer function of each element is characterized by a gain in the input-output relationship of a system , as follow:

$$Y = I \bullet Kf \bullet (Gc \bullet Gm) \quad (1)$$

where, *Y* represents the output or active movement velocity, *I* the input corresponding to the illusory movement velocity based on proprioceptive activity, *Gc* the gain of the controller or motor command, *Gm* the gain of the muscle and *Kf* the gain of the proprioceptive sensory system. In the LVRM case, the matching movement output can be represented by:

$$Yr = Il \bullet Kfl \bullet (Gcr \bullet Gmr) \quad (2)$$

where, *r* and *l* denote the right and left sides.

Considering the following:

i) The present results show that *Yl > Yr*, hence

$$Ir \bullet Kfr \bullet Gcl \bullet Gml > Il \bullet Kfl \bullet Gcr \bullet Gmr \quad (3)$$

ii) Closed loop position control excludes a difference between the respective motor components *only*. Indeed, if only the right and left motor gains (*Gc • Gm*) were different, then proprioceptive feedback would contribute to reducing the error significantly, and equality in perceptions would correspond to equality in final positions but not in matching asymmetry [5].

If we assume that the motor components are not significantly different (*Gcl • Gml ≈ Gcr • Gmr*)

then (3) implies that $\qquad Ir \bullet Kfr > Il \bullet Kfl \quad (4)$

which would show that in such context the gain of the sensory component would be greater for the right than the left hand system. This result is also in agreement with the closed loop gain (see 5).

Furthermore, the closed loop model also showed that the closed loop gain is greater for the left than the right hand system *Hl > Hr* [5], in which

$$Hl = (Gcl \bullet Gml)/(1 + Kfl \bullet Gcl \bullet Gml) \qquad \text{and}$$
$$Hr = (Gcr \bullet Gmr)/(1 + Kfr \bullet Gcr \bullet Gmr)$$

then $(1/(Gcr \bullet Gmr)) + Kfr > (1/(Gcl \bullet Gml)) + Kfl \quad (5)$

this equation indicates that if *Kfl* was equal to *Kfr* then

$$Gcr \bullet Gmr < Gcl \bullet Gml \quad (6)$$

which is not possible *individually*. Therefore, the respective sensory gains cannot be equivalent.

Further, it is not excluded that the gain representing the interhemispheric transfer (see Fig. 3) may be greater from right reference to left matching limb than in the opposite direction [11]. However, a significant difference would reduce the left hand undershoot and exacerbates the right hand overshoot in contralateral position matching, which is not the case since these position matching errors are of similar magnitude [5].

In sum, the required compatibility of the sensory and motor components included in the *"position"* and *"velocity"*
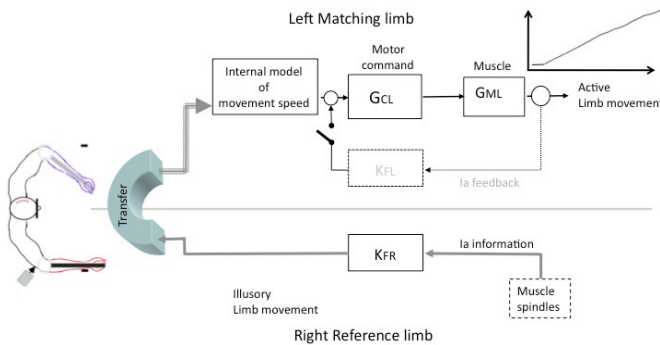
Fig. 3. Open loop velocity control model (Laplace domain representation). The model illustrates "left arm matching of the movement illusion elicited in the right arm - RVLM" (see inset drawing). K_F, G_C and G_M correspond to the gains of the respective transfer functions representing the Ia sensory information, motor command and muscle components. R and L denote right and left limb. K_F represents the gain of the proprioceptive path while $G_C \cdot G_M$ represents the gain of the motor path.

models shows that i) a difference between the L and R motor gains *alone* is not possible and ii) a difference between the L and R sensory gains exists. Although it is reasonable to assume that for a given individual vibration-induced activations of muscle spindles were similar at the source (Roll and Ribot-Ciscar, personal communication), they lead to different reproductions of movement velocities. It is inferred that, whether large or small, the difference in matching speed reflects primarily a difference in the gain of the sensory component of each upper limb system (L vs R). Nevertheless, the present results do not exclude a possible *concurrent* difference in gain between the L and R motor components but tend to emphasize the primary role of perception in the differentiation of motor outcomes when each system attempts to reproduce the perception elicited in the other. A difference between L and R motor components is likely since muscle strength commonly differ between the dominant and non-dominant arm; however the influence of this difference is rather small in the present context since the amount of force required to produce the active match is $\leq 1\%$ MVC (slow movement velocity to displace a virtually frictionless lever – force measure derived from calibrated biceps EMG in typical participant). Alternatively, left hand feedback and right hand feedforward velocity control, as suggested by the specialization of each arm/hemisphere system [12], could be envisaged since $Ir \cdot Kfr > Il \cdot Kfl$. and $Gcr \cdot Gmr \approx Gcl \cdot Gml$ in the present context. However, movement trajectories do not exhibit significant differences permitting to confirm this alternative in the present context.

V. CONCLUSION AND FUTURE DIRECTION

Overall, our results suggest that the sensory component plays a significant role in kinesthetic asymmetry. Structural and processing dimorphisms may modify the extent to which the respective sensorimotor gains differ that, in turn, likely contribute to inter-individual differences and differences between left and right-handed individuals. Although the asymmetry is significant in left-handed males, the average difference is less pronounced and variability was larger for that group. This may not be surprising since in a predominantly right-handed world, left-handed individuals may frequently use their non-dominant hand and thus adapt proprioceptive assistance to movement control as a function of hand use [13]. Furthermore, movement sense and position sense asymmetry point to asymmetry in kinesthetic representations. This phenomenon suggests that matching experiments and their interpretations deserve specific attention as past studies using both limbs have pooled left and right hand matching data. Finally, as the difference in gain of the respective motor component cannot be excluded, a quantification of their contribution beyond a simple difference in muscle strength must be addressed in future experiments. Finally, this modeling approach may be used to identify the component(s) of sensorimotor systems affected by neurological disorders and assess the efficacy of rehabilitation procedures.

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