



Interlimb differences in coordination of rapid wrist/forearm movements

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Abstract

We have previously proposed a model of motor lateralization that attributes specialization for predictive control of intersegmental coordination to the dominant hemisphere/limb system, and control of limb impedance to the non-dominant system. This hypothesis was developed based on visually targeted discrete reaching movement made predominantly with the shoulder and elbow joints. The purpose of this experiment was to determine whether dominant arm advantages for multi-degree of freedom coordination also occur during continuous distal movements of the wrist that do not involve visual guidance. In other words, are the advantages of the dominant arm restricted to controlling intersegmental coordination during discrete visually targeted reaching movements, or are they more generally related to coordination of multiple degrees of freedom at other joints, regardless of whether the movements are discrete or invoke visual guidance? Eight right-handed participants were instructed to perform alternating wrist ulnar/radial deviation movements at two instructed speeds, slow and fast, with the dominant or the non-dominant arm, and were instructed not to rotate the forearm (pronation/supination) or move the wrist up and down (flexion/extension). This was explained by slowly and passively moving the wrist in each plane during the instructions. Because all the muscles that cross the wrist have moment arms with respect to more than one axis of rotation, intermuscular coordination is required to prevent motion about non-instructed axes of rotation. We included two conditions, a very slow condition, as a control condition, to demonstrate understanding of the task, and an as-fast-as-possible condition to challenge predictive aspect of control, which we hypothesize are specialized to the dominant controller. Our results indicated that during as-fast-as-possible conditions the non-dominant arm incorporated significantly more non-instructed motion, which resulted in greater circumduction at the non-dominant than the dominant wrist. These findings extend the dynamic dominance hypothesis, indicating that the dominant hemisphere-arm system is specialized for predictive control of multiple degrees of freedom, even in movements of the distal arm and made in the absence of visual guidance.

Keywords Handedness · Radial/ulnar deviation · Predictive coordination · Lateralization

Introduction

Brain lateralization refers to the division of labor between the two cerebral hemispheres with respect to neurobehavioral functions. Two prominent models have been proposed that describe lateralization across a large range of neurobehavioral domains, including language, cognition, and movement. Rogers and Andrew (2008) and MacNeilage et al. (2009), proposed a model based on empirical findings of lateralized behaviors across a range of neurobehavioral domains, and across a wide range of vertebrate species. According to this model, the left hemisphere is viewed as specialized for control of well-established patterns of behavior under predictable environmental conditions, while the right hemisphere is specialized for detecting and responding

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to unexpected environmental stimuli. Dien introduced a similar model of cerebral lateralization, the Janus model, that hypothesized a behavioral planning specialization for the left hemisphere and specialization of the right hemisphere for responding to changes in environmental stimuli (Dien 2008). This model was based on lateralization in the cognitive domain, including measures such as response times to predators in fish, as well as feeding behaviors in a variety of species (Dien 2008). While these two models for hemispheric specialization were based on findings from different species and neurobehavioral domains, the models are similar in the proposed hemispheric specializations. However, neither model specifically addresses the aspects of brain lateralization that give rise to handedness.

We have proposed a model of motor lateralization, the dynamic dominance hypothesis, that provides a mechanical analog to the hemispheric specialization models of MacNeilage et al. (2009), and the Janus Model. There are two important functions in controlling movements that appear to be differentially specialized to each hemisphere: predictive control of intersegmental coordination and control of limb stability through impedance control mechanisms. When reaching with a multi-segmented arm, making accurate and smooth trajectories requires that muscle actions take account of impeding mechanical interactions between the segments of the limb. Because of neuromuscular delays, this control must exploit predictive mechanisms that rely on internal models of the body and are dependent on proprioceptive information (Sainburg 2014; Sainburg et al. 1993, 1995; Lackner and Dizio 1994; Pigeon et al. 2003). In addition, to stabilize the limb against unexpected environmental perturbations as well as to stabilize the limb at the end of movements, limb impedance must be controlled, at least in part, through feedback mechanisms that modulate reflex gains (Mutha et al. 2008; Yadav and Sainburg 2014; Woytowicz et al. 2018). These two aspects of motor control provide neuromechanical analogs to the MacNeilage and Janus models of brain lateralization described previously.

The Dynamic Dominance hypothesis was originally based on studies of motor asymmetries in typical adults (Sainburg and Schaefer 2004; Mutha et al. 2013; Yadav and Sainburg 2014; Sainburg et al. 2016), and was later supported through verified predictions of hemisphere dependent motor deficits in stroke survivors, with specific left and right hemisphere lesions (Sainburg and Duff 2006; Schaefer Haaland and Sainburg 2009; Mani et al. 2013). These studies quantified differences in intersegmental coordination between the two arms, and suggested that control of the inertial torques that are propagated along the segments of a moving limb is specialized to the left-hemisphere in right-handers. This accounts for a dominant arm advantage in specifying movement trajectories, and making smooth and energetically efficient movements, regardless of variations in intersegmental

torques (Sainburg 2002, 2014). In contrast, we hypothesized that specialization for control of limb impedance is localized to the right hemisphere. This accounts for robust responses to unanticipated and unpredictable dynamic conditions, such as perturbations (Bagesteiro and Sainburg 2002) or unpredictable force fields (Yadav and Sainburg 2014), as well as the ability to stabilize objects during bilateral tasks (Woytowicz et al. 2018). In fact, Yadav and Sainburg (2014) verified the plausibility of this hypothesis using control-theory based forward dynamic simulations of reaching movements. However, this hypothesis was developed based on the findings in studies of discrete visually guided reaching movements made predominantly at the shoulder and elbow joints. Thus, the generality of this hypothesis to non-discrete movements at other joints that do not invoke visual guidance or targeting remains unknown. We now ask whether the dominant arm specialization of this hypothesis can be extended to more distal joints in the arm and to continuous movements that do not involve visual guidance or targeting. We do not assess the non-dominant aspect of coordination here, as continuous movements do not have a constant position phase.

We now examine interlimb differences in control of wrist movements in a single, instructed degree of freedom, wrist radial-ulnar deviation. All of the muscles that cross the wrist have moment arms with respect to more than one degree of freedom, and each muscle that crosses the wrist has both redundant actions with regard to other muscles, and coupled actions with regard to multiple axes of rotation. In our task, the elbow is stabilized by resting the forearm on a surface, while the three degrees of freedom at the wrist and forearm (pronation/supination, ulnar/radial deviation, and flexion/extension) are not restricted. The forearm/wrist muscles with moment arms in these degrees of freedom that are not primary elbow flexors or extensors include: pronator teres, supinator, extensor carpi radialis longus, extensor carpi radialis brevis, extensor carpi ulnaris, extensor digitorum communis, extensor digiti minimi, flexor carpi radialis, flexor carpi ulnaris, flexor digitorum superficialis, abductor pollicis longus, and palmaris longus. Because all of these muscles have moment arms in two or more degrees of freedom, coupling between motion in these degrees of freedom is a natural consequence of activating any of these muscles (Ettema et al. 1998; Nichols et al. 2015; Gonzalez et al. 1997; Ramsay et al. 2008). Therefore, the ability to limit motion to one degree of freedom requires multi-degree of freedom coordination.

This study tests the hypothesis that handedness reflects, in part, dominant hemisphere/arm specialization for predictive coordination of multiple degrees of freedom, during continuous wrist movements, that do not involve visual monitoring or visual targeting. Eight healthy young adults (18–30 y/o) performed a rapid alternating wrist ulnar/radial deviation task. Movements were instructed at ‘slow’ and ‘as

fast as possible' speeds. The slow trials provided a control-condition to assure that the task could be performed, while the fast trials were intended to challenge the requirements for predictive coordination of the wrist and forearm muscles.

Methods

Participants

Participants were eight healthy, right-handed individuals (two male/six female) aged 21–25 years old. The handedness of each of the subjects was determined using the Handedness Quotient of the Edinburg Handedness Inventory, and the average laterality score was 100, i.e., all participants were strongly right handed. Informed consent was given prior to subject participation which was approved by The Pennsylvania State University's Institutional Review Board. Each subject received payment as compensation for his or her participation.

Experimental setup

Participants were seated in a chair with a forearm supporting apparatus attached to the side with either arm bent at a 90° angle at the elbow and their hand in a neutral, vertical position with their thumb facing up and palm facing medially towards the body midline. The forearm was supported in the neutral position but was unconstrained in all three degrees of freedom. Each participant's wrist and forearm movements were tracked using 6 DOF magnetic sensors (Ascension Trackstar) placed on the hand and upper arm at 116 Hz.

Experimental task

Participants were instructed to make smooth alternating movements of the hand, moving only in radial/ulnar deviation. They were instructed to move either "slow enough to isolate the movement to a single plane" for a 10 s interval, or "as fast as possible" for 10 s. The desired movement was modeled by the experimenter, and was also demonstrated through passive movement, both under the slow condition. Order of condition and hand were randomized between participants. Each participant performed the sequence of trials twice. The first sequence was a familiarity trial to orient individuals to the task and the second was the test sequence. Both sequences were recorded but only the test sequence was analyzed. All subjects performed two 'slow' trials and two 'fast' trials with each hand. All trials were 10 s long and only the second trial was analyzed for each condition. The sequence of trials, i.e., condition and hand, was randomized between participants.

Kinematic analysis

Two 6-DOF magnetic trackers (Trackstar) were placed on the hand and upper arm segments. The index finger, 2nd MCP joint, medial and lateral wrist points, medial and lateral epicondyles of the humerus, and the lateral acromion process were digitized at 116 Hz. Custom software (Kinereach®) was used to estimate joint centers, and calculate 10-DOF at the shoulder, elbow, forearm, and wrist. All joints distal to the wrist (MCP and IP) were splinted in extension throughout the trials. Because the forearm was supported, shoulder and elbow movements were restricted. Once recorded, trials were segmented into individual cycles, reflecting one full down and up motion of the hand, for further analyses.

For each cycle, we quantified angular displacement at each of the three available degrees of freedom: pronation/supination, flexion/extension and ulnar/radial deviation. We normalized displacement in the non-instructed degrees of freedom (pronation/supination; flexion/extension) to displacement in the instructed degree of freedom (ulnar/radial deviation) to provide a measure of the amount of motion (degrees) in each non-instructed degree of freedom per degree of motion in the instructed degree of freedom. This accounted for differences in instructed displacement between subjects and conditions. We quantified frequency of each cycle of hand movement as $\text{Frequency} = \frac{1}{\text{cycle duration}}$. Cumulative hand-path distance was calculated using the following formula:

$$\text{Distance} = \sum_{n=0}^{n=\text{points in cycle}} \sqrt{(x_{n+1} - x_n)^2 + (y_{n+1} - y_n)^2 + (z_{n+1} - z_n)^2},$$

where x , y and z refer to the spatial coordinates of the finger digitization at each point of the movement. This measure yields the cumulative distance traveled during each cycle. Peak velocity was calculated using the first time derivative of hand displacement. The maximum value was taken as peak velocity. Finally, we quantified wrist circumduction as the area circumscribed by the hand-path in the frontal plane divided by the cumulative distance during the cycle. To calculate cumulative hand-path area, each cycle of movement was first segmented into separate segments, if the hand path intersected itself (see Fig. 1). For each segment, we summed each consecutive triangular area defined between the initial hand path location (n_0) and each two consecutive locations (n_i, n_{i+1}) to determine the area of the closed path. The area of each segment (if more than one) was summed, and then divided by cumulative hand path distance to provide a measure of hand-path shape (circumduction) that was normalized to movement amplitude. The formula for circumduction is as follows: $\text{Circumduction} = \frac{\sum_{n=0}^{n=i+1} \text{Area of each segment } n}{\text{Cumulative Distance}}$.

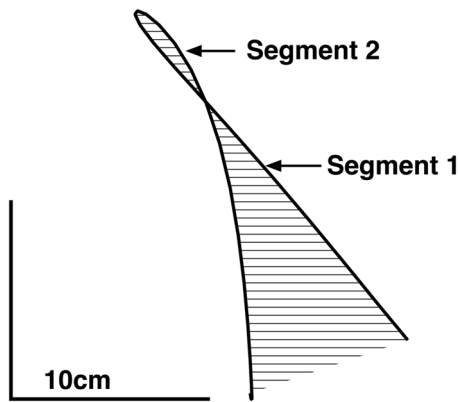


Fig. 1 Representative hand path which shows a path separated by the intersection point into two segments. The area of each segment (shaded) is calculated via triangular integration. The resulting areas of the two segments are summed to provide the total area circumscribed by the hand path

Statistical analysis

We employed a within-subjects repeated-measures ANOVA with two factors, hand (left, right), and condition (fast, slow). This 2×2 ANOVA tested for main effects of condition, main effects of hand, and whether an interaction occurred between these variables. The Greenhouse–Geisser correction is used to assess the change in a continuous outcome with three or more observations across time or within-subjects. In cases in which the assumption of sphericity was violated for this within-subjects analysis, the Greenhouse–Geisser correction was implemented. Post-hoc analysis (Tukey HSD) was used to compare the means of every treatment to the means of every other treatment; that is, it applies simultaneously to the set of all pairwise comparisons. Our use of the Tukey HSD controls for the family-wise error rate (Barnette and McLean

2005). For each participant, mean values for each dependent variable was calculated under each level of each factor, and then subjected to ANOVA using a repeated measures model.

Results

Figure 2 shows frontal plane profiles for example slow and fast movements made by a sample participant with each hand (2a) and the velocity profiles associated with those movements (2b).

These frontal plane projections show that for the slow condition, the motion of both right and left hands overlapped the upward and downward motions, within the frontal plane. However, for the fast condition, the frontal plane hand-paths did not overlap and were more ovoid. This implies circumduction of the wrist among more than one degree of freedom. The 3-D tangential velocity profiles were similar between the left and right hands; Fig. 5 shows the peak velocity measure in detail. The multi-peaked profiles for the slow movements are characteristic of very slow hand motions (Summa et al. 2016).

Figure 3 shows that the mean frequency of each cycle of hand movement was similar between hands, but significantly different between conditions. When instructed to move as fast as possible, participants made movements under the fast conditions with a mean frequency of 4.0 Hz (± 0.31 Hz), and under the slow condition, they moved with a frequency of 0.65 Hz (± 0.07 Hz). Our ANOVA showed a main effect of condition ($F(1,7) = 103.35$, $p < 0.0001$), but no main effect of hand nor interactions between factors. Qualitatively, both hands and participants were remarkably consistent in the number of cycles performed at each speed, despite the fairly open-ended instructions to move ‘slow’ and ‘as fast as possible’.

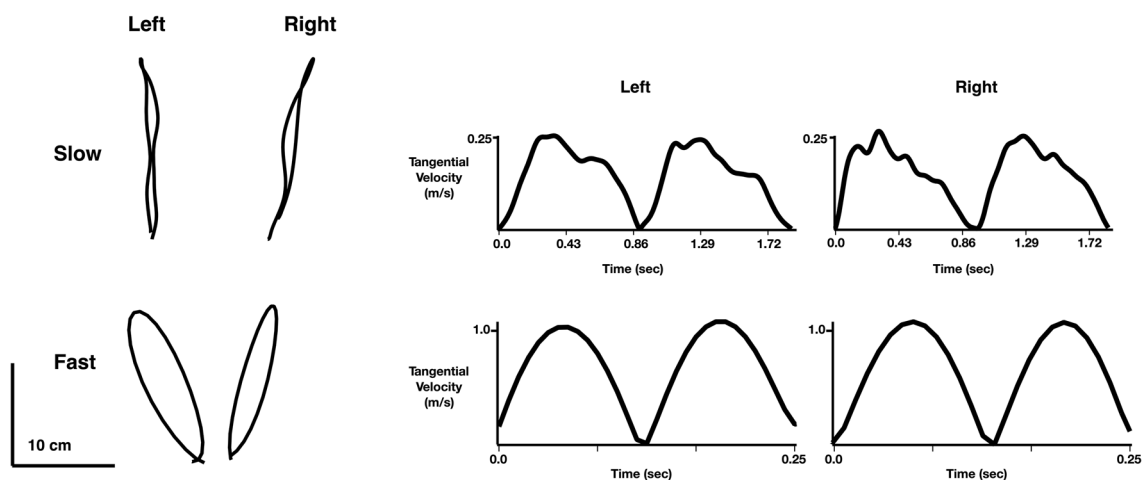


Fig. 2 a Sample hand paths (finger trace in frontal plane) b Tangential velocity of the finger (m/s)

Fig. 3 Frequency vs. condition. Participant’s mean frequency of movement throughout a full cycle compared in fast and slow conditions with error bars representing SE. Asterisk signifies a significant difference between fast and slow conditions

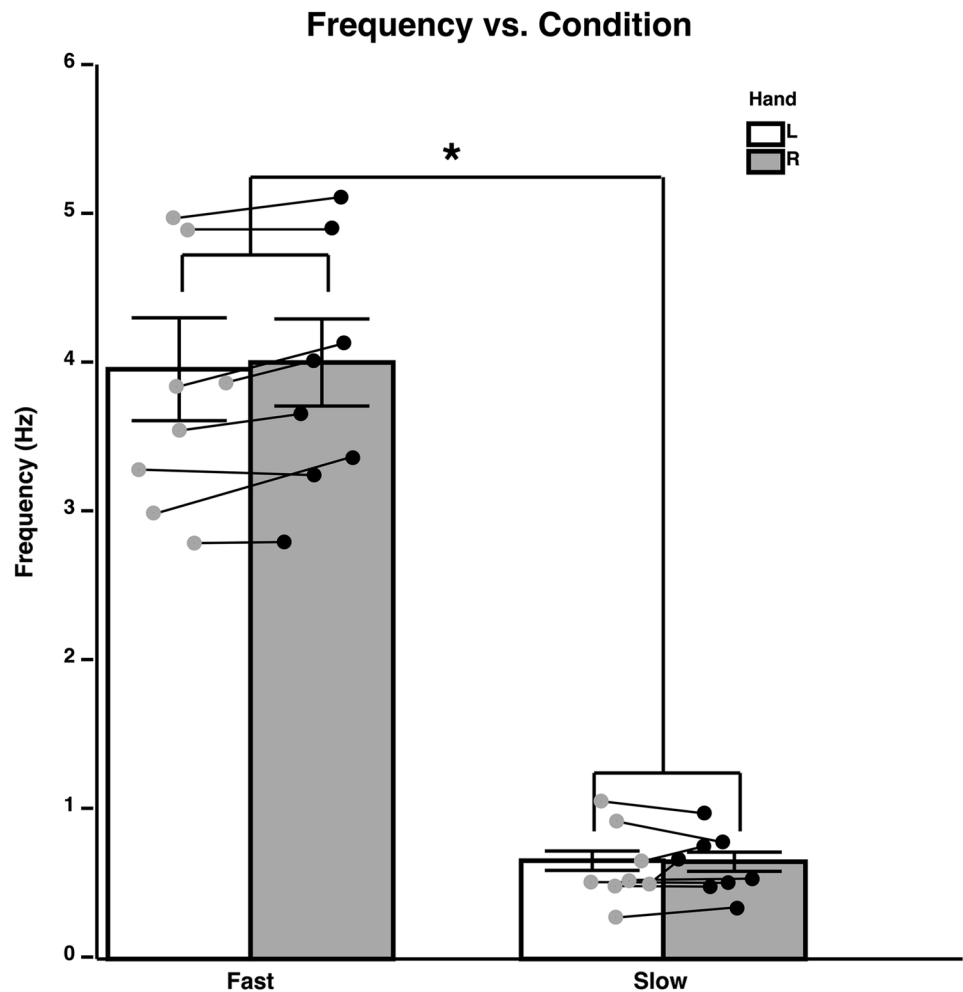


Figure 4 shows the mean \pm SE of the 3D distance moved in each full cycle of motion (up and down movement). As expected, participants made smaller excursions under the fast, as compared with the slow condition. When asked to move as fast as possible, the mean 3D distance of the finger was 14.9 cm (\pm 1.5 cm), while under the slow condition, the finger-tip moved 20 cm (\pm 1.95 cm). Our ANOVA indicated a main effect of condition ($F(1,7) = 8.28$, $p = 0.0237$), but no main effect of hand nor interaction between factors.

As expected, the peak tangential velocity of the finger varied with speed condition, but not with hand (see Fig. 5). We found that participants made movements under the fast conditions with a mean peak velocity of 91.8 cm/s (\pm 5.0 cm/s), and under the slow condition, they moved with a peak velocity of 30.2 cm/s (\pm 2.2 cm/s). Our ANOVA indicated a main effect of condition ($F(1,7) = 231.78$, $p < 0.0001$), but no main effect of hand nor interactions between factors. Thus, Figs. 3, 4, 5 demonstrate that participants were fairly consistent in the speed, distance, and frequency of the hand tangential motion across conditions.

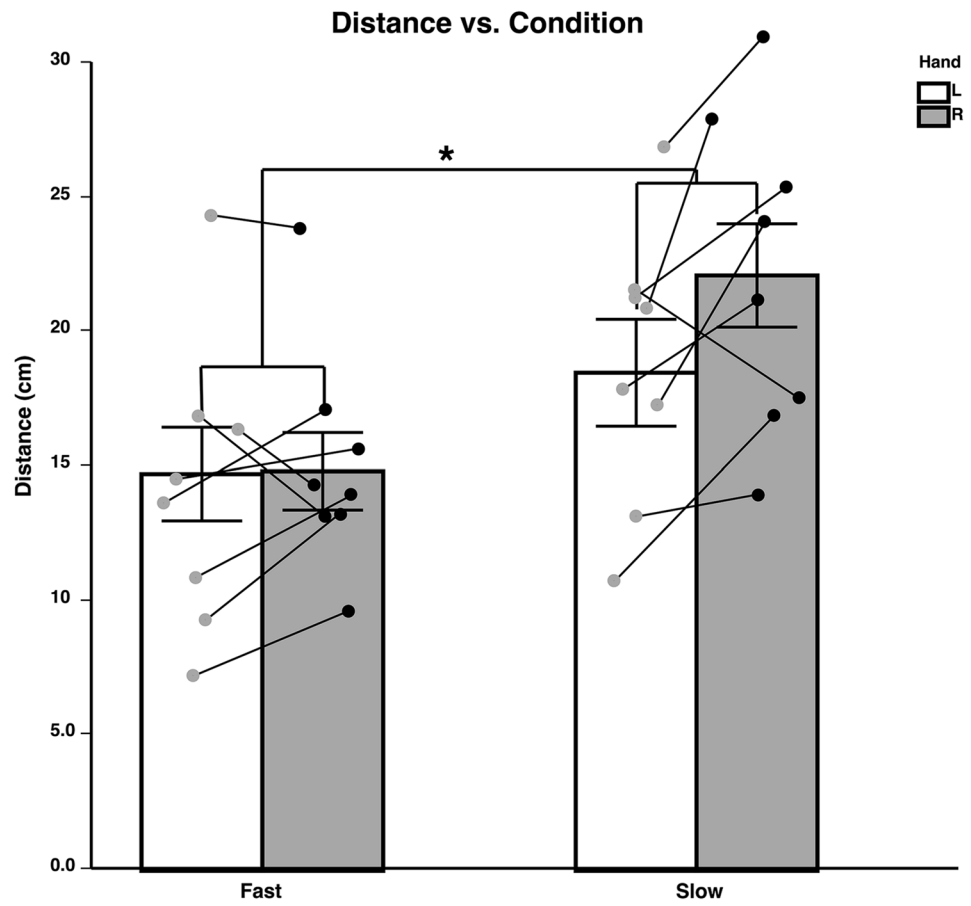
Motion in each degree of freedom

Our analysis of hand motions, as detailed above, demonstrates that all participants performed the task similarly with each hand, as measured in terms of finger motion in 3D space. We now assess how participants produced these hand motions at each degree of freedom at the wrist and forearm: we quantified the change in angle for each full cycle of hand motion.

Wrist ulnar/radial deviation (RUD) was the instructed degree of freedom in this task. As shown in Fig. 6, we found that participants made movements under the fast conditions with a mean RUD displacement of 25.2° (\pm 4.05°), and under the slow condition, the RUD displacement was 54° (\pm 3.45°). There were no significant differences between the hands. Thus, our ANOVA showed a main effect of condition ($F(1,7) = 56.43$, $p < 0.0001$), but no main effect of hand nor interactions between factors.

We quantified movement in non-instructed degrees of freedom as a percentage of motion in the instructed degree of freedom (see “Methods”). Regardless of the instruction

Fig. 4 Distance vs. condition. Participant's mean distance of movement throughout a 1/2 cycle compared in fast and slow conditions with error bars representing SE. Asterisk signifies a significant difference between fast and slow conditions



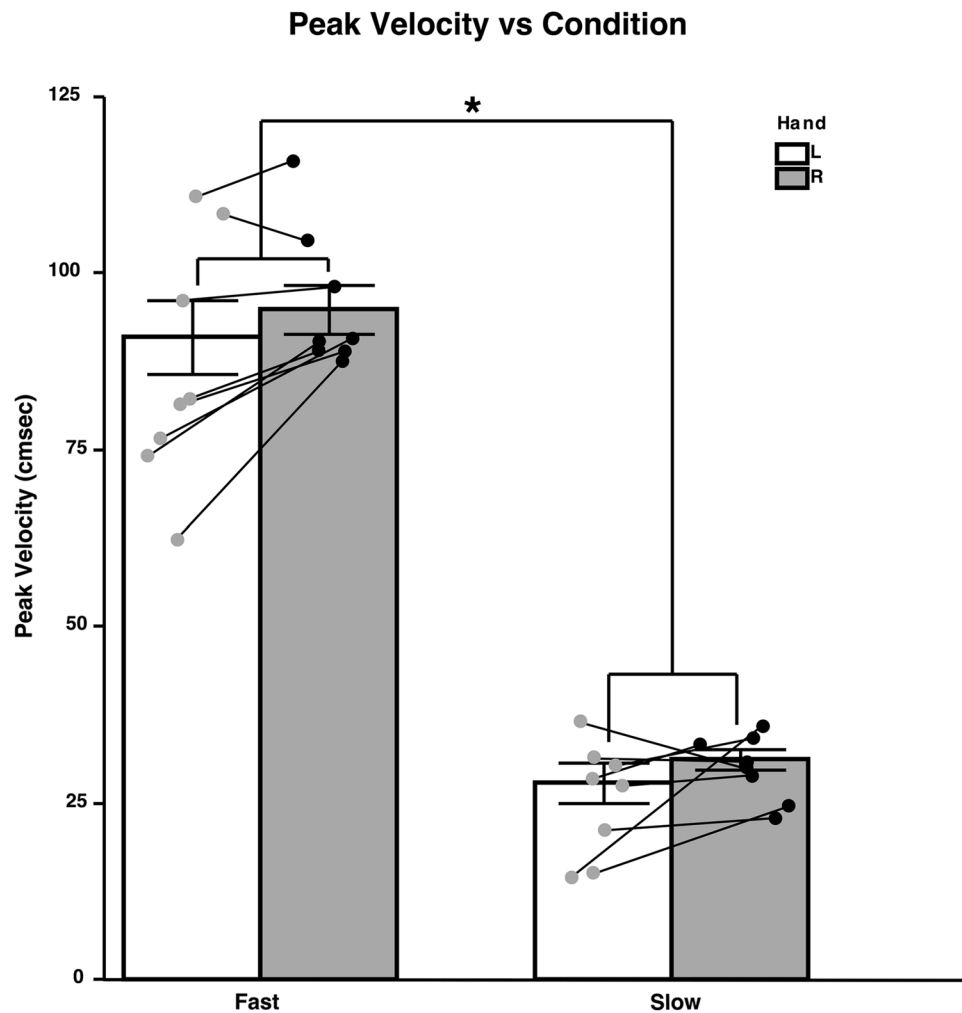
to isolate movements to radial/ulnar deviation, all subjects showed substantial flexion/extension (FE) displacement. Figure 7 shows flexion/extension angle, normalized to the amplitude of the instructed motion (radial/ulnar deviation) to provide a measure of degrees flexion/extension per degree of deviation. Under the slow condition, participants showed flexion/extension excursion that was 40% ($\pm 5.0\%$) that of radial ulnar deviation. However, under the fast condition, flexion/extension displacement was 122% ($\pm 21\%$) that of radial-ulnar deviation displacement. Our ANOVA showed a main effect of condition [$F(1,7) = 19.23, p = 0.0032$]. However, we found no effect for hand, nor interaction between hand and condition. Thus, for both hands, participants showed substantial flexion/extension motion that increased with speed. For reference, non-normalized flexion–extension did not show a main effect of condition [$F(1,7) = 2.7435, p = 0.1416$].

Figure 8 shows that participants also incorporated substantial pronation–supination displacement, and that the relative pronation–supination displacement increased with movement speed. Our ANOVA for normalized (to deviation displacement) pronation–supination angle showed a significant hand by condition interaction [$F(1,7) = 5.12, p = 0.0481$], with more pronation displacement produced

by the left hand as compared to the right hand under the fast condition (TUKEY HSD, $p = 0.0395$) but not under the slow condition (TUKEY HSD, $p = 0.9460$). We found that participants made movements under the fast conditions with a mean relative pronation displacement of 128% ($\pm 28.4\%$) for the left hand and 65.4% ($\pm 18.9\%$) for the right hand, and under the slow condition, the mean relative pronation displacement was 45.0% ($\pm 8.32\%$) for the left hand and 47.9% ($\pm 8.14\%$) for the right hand. Thus, while participants were able to maintain similar pronation/supination displacements with their dominant and non-dominant arms under the slow condition, this was not the case for the fast condition. Under the fast condition, the non-dominant left hand showed nearly twice the displacement in pronation/supination than did the dominant right hand. However, removal of a single participant's data (outlier) in the scatter plot resulted in no significant hand by condition interaction [$F(1,6.818) = 2.0747, p = 0.1941$] for normalized pronation/supination. For reference, non-normalized pronation–supination showed no significant hand by condition interaction [$F(1,7) = 3.6605, p = 0.0973$].

We defined circumduction as the area encompassed by the path of the hand in the frontal plane (cm^2), normalized by the total 3D distance travelled by the hand (cm) in

Fig. 5 Peak velocity vs. condition. Participant’s mean peak velocity throughout a full cycle compared in fast and slow conditions with error bars representing SE. Asterisk signifies a significant difference between fast and slow conditions

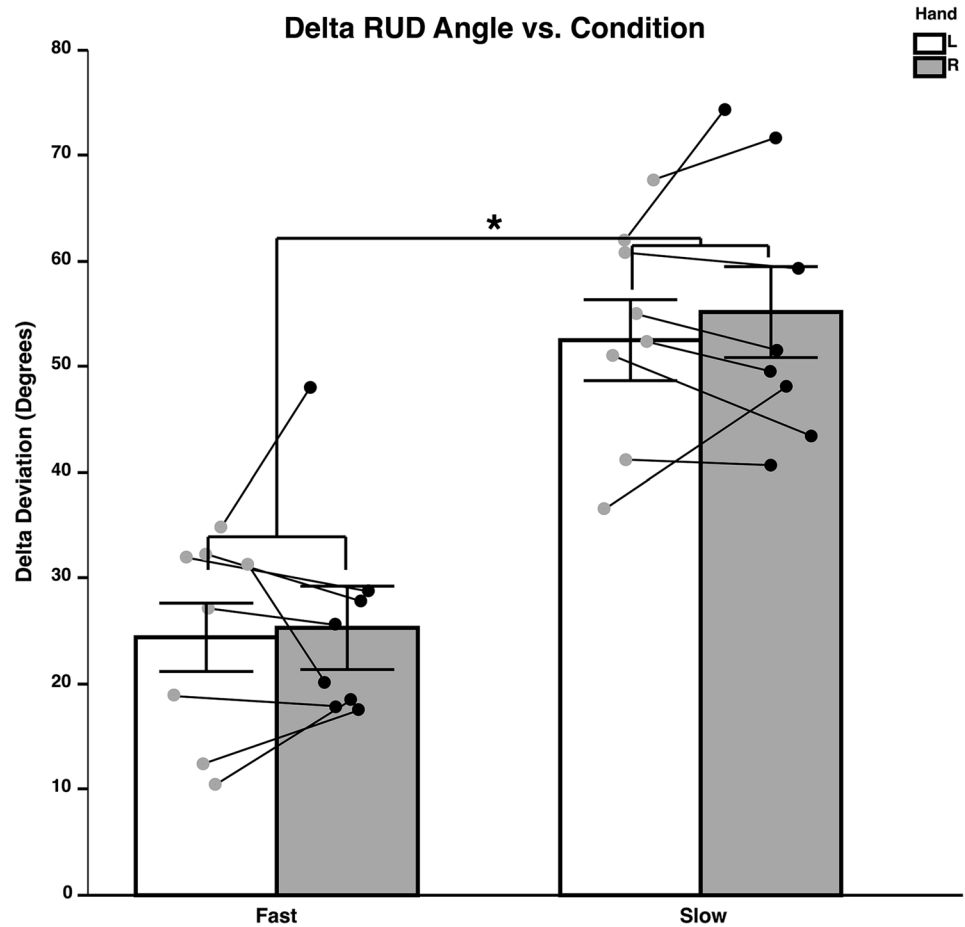


each cycle of motion. This measure reflects coordination between the wrist degrees of freedom, and the units of this measure are cm. Figure 9 shows our measure of circumduction across hands and conditions. This provides a measure that corresponds to the hand-path circularity or linearity, normalized to the amplitude of the motion. Our ANOVA for circumduction showed an interaction between hand and condition ($F(1,7) = 6.01, p = 0.044$ with greater circumduction in the left hand under the fast condition (TUKEY HSD, $p = 0.0159$), but there were no differences in circumduction between conditions for the right hand (TUKEY HSD, $p = 0.5275$). We found that participants made movements under the fast conditions with a mean circumduction of 0.435 cm (± 0.031 cm) for the left hand and 0.341 cm (± 0.0285 cm) for the right hand, and under the slow condition, the mean circumduction was 0.311 cm (± 0.0293 cm) for the left hand and 0.324 cm (± 0.0249 cm) for the right hand.

Discussion

Previous research has indicated that the dominant hemisphere/arm, in right and left handers, shows advantages for intersegmental coordination of visually targeted discrete hand motions incorporating predominantly shoulder and elbow joint motion (Bagasteiro and Sainburg 2002; Przybyla 2011; Yadav and Sainburg 2014). The purpose of this study was to determine whether similar dominant arm advantages for coordination occur during more distal movements of continuous movements that were not visually targeted nor directed. We tested whether instructed dominant arm wrist deviation movements are better isolated to a single instructed degree of freedom for the dominant arm of right-handers. Because of the coupling between degrees of freedom of wrist muscles across forearm pronation/supination and wrist flexion/extension axes, rapid radial/ulnar deviation requires substantial coordination to prevent motion outside of the instructed degree

Fig. 6 Change in radial/ulnar deviation angle. Participant's mean change in RUD throughout a full cycle compared in fast and slow conditions with error bars representing SE. Asterisk signifies a significant difference between fast and slow conditions



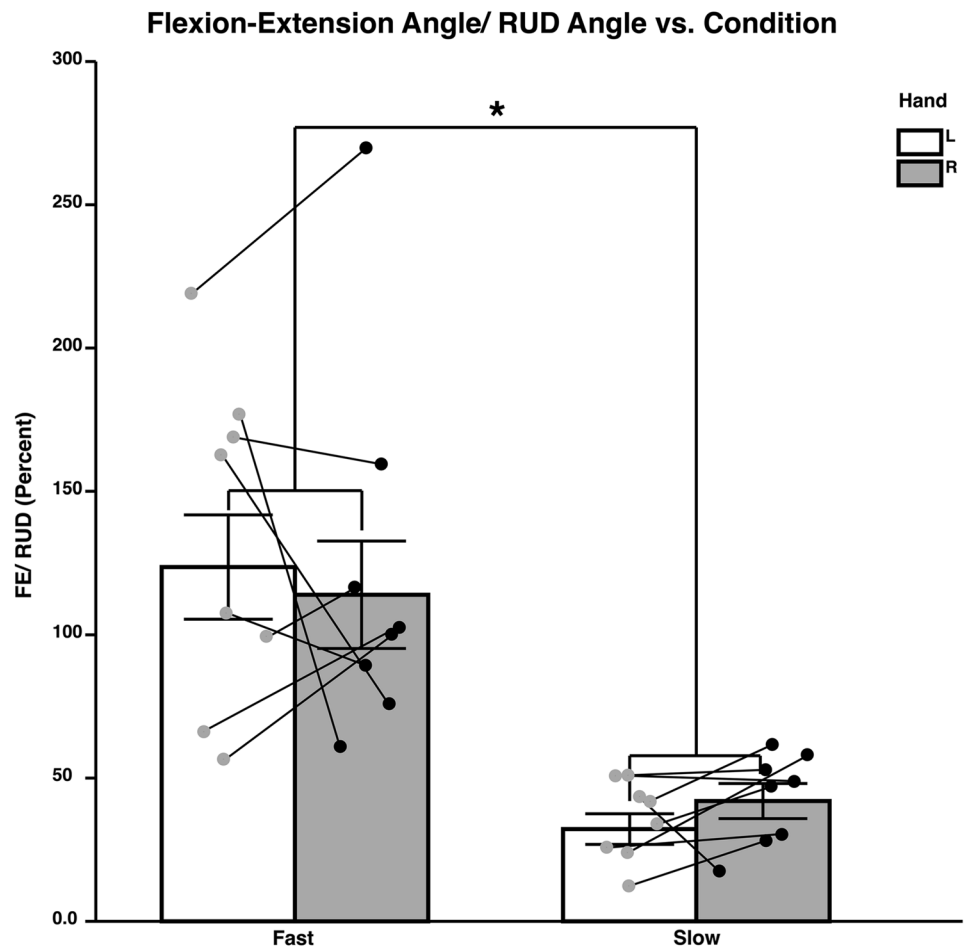
of freedom (Ramsay et al. 2008). We hypothesized that the dominant hemisphere is specialized for predictive control of multi-effector coordination, and thus predicted that the non-dominant arm should show greater motion outside of the instructed degree of freedom, and that this effect should be potentiated by movement speed, when predictive mechanisms are emphasized. Our results indicated that the frequencies and displacements of the hand (finger point), as well as wrist deviation displacements varied similarly across hands under both slow and fast conditions. However, incorporation of uninstructed degrees of freedom was substantial in both flexion/extension and pronation/supination. Most importantly, while both arms showed similar relative displacement of pronation/supination under slow conditions, the non-dominant arm showed nearly twice the relative pronation/supination displacement during rapid movements than that of the dominant arm. It is important to note that upon removal of a single participant in our ANOVA removed the significance of our hand by condition interaction. That being said, it does appear as though the trend remained. Thus, under rapid conditions, when feedforward control was emphasized, the non-dominant arm showed significantly more uninstructed

displacement, suggesting less-effective isolation of motion to the instructed degree of freedom. These results support our hypothesis of dominant hemisphere/limb specialization for multi-degree of freedom coordination at the wrist and forearm, when the movements are continuous and do not involve visual targeting nor guidance.

The ability to constrain out of plane motions during the slow condition, in both arms, may have been accomplished through both predictive and feedback mediated mechanisms. The slow movements allowed time for the recruitment of feedback mechanisms as a strategy to isolate the movement to the instructed degree of freedom (Mutha et al. 2013; Yadav and Sainburg 2014). The increase in pronation/supination under the fast condition, especially for the non-dominant left hand, however, implies a difference in ability between arms/hemispheres to coordinate the instructed motion when an emphasis is placed on predictive mechanisms. The increase in circumduction in the left hand would support this explanation as well.

In this study, we exploited the redundancy and coupling between the muscles that move the wrist. All muscles of the forearm and wrist have moment arms across multiple degrees of freedom (coupling) and each degree of freedom

Fig. 7 Normalized FE angle/ RUD angle. Participant’s mean change in flexion–extension angle divided by the change in RUD angle throughout a full cycle compared in fast and slow conditions with error bars representing SE. Asterisk signifies a significant difference between fast and slow conditions



is acted upon by many muscles (redundancy) (Ramsay et al. 2008). In our task, participants were instructed to move the wrist along one degree of freedom, while the other three degrees of freedom were free to move. We found that participants produced substantial motion along uninstructed degrees of freedom, and that this motion increased with instructed speed condition. While both hands showed similar incorporation of flexion and extension, pronation/supination displacement under fast conditions was significantly higher for the non-dominant left wrist. These findings indicate that the coordination of the redundant and coupled muscle actions at the wrist was more effective in the dominant than the non-dominant arm under fast movement conditions. It is worth noting that due to the continuous movement nature of this task, we did not observe non-dominant arm advantages.

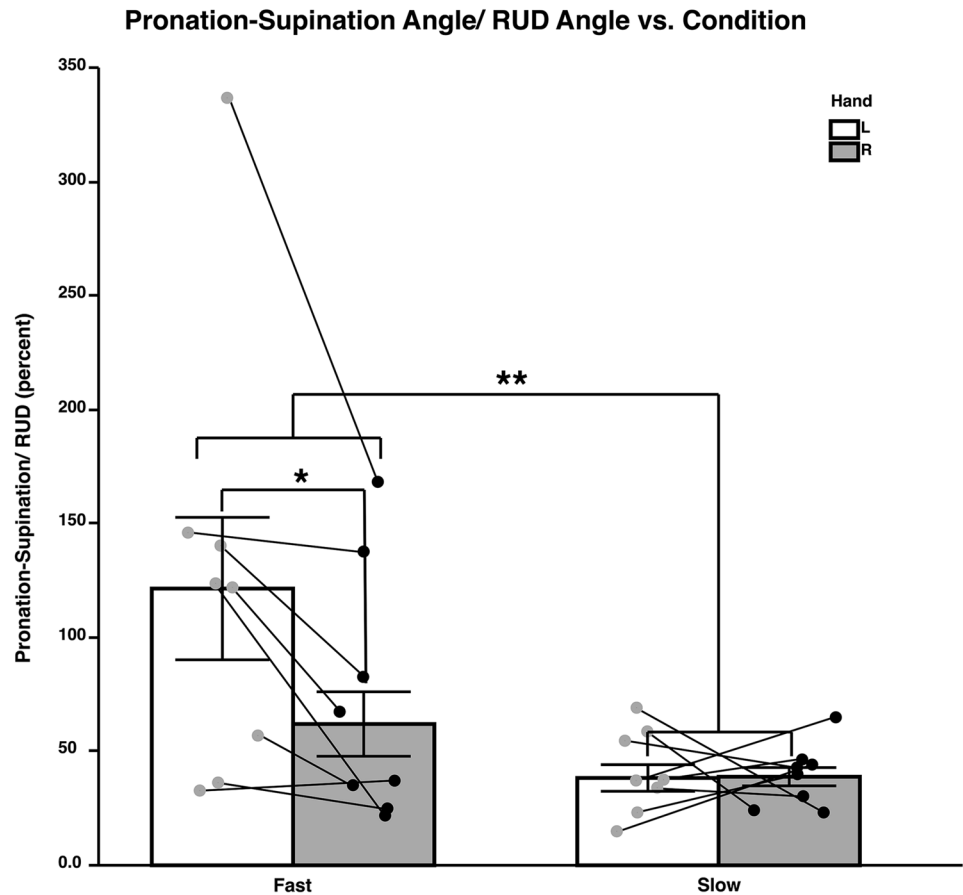
We conclude that inter-degree-of-freedom coordination is a fundamental specialization of the dominant limb controller. It is plausible that many components of activities of daily living that are preferentially performed by the dominant arm might require, and thus practice, coordination of the dominant wrist muscles more than those components of tasks

performed by the non-dominant arm. For example, twisting a doorknob and turning a key in a lock. However, the specific coordination required for this task is not a common component of activities of daily living, nor were participants familiar or practiced with this task. Whether the advantages in coordination demonstrated by the dominant arm controller are developed through ontogenetic or phylogenetic processes remains unclear, but there is ample evidence that handedness evolved over phylogeny (Hopkins 2013; Rogers and Andrew 2008; Sainburg and Eckhardt 2005), and that genetics plays a significant role in the expression of handedness (Annett et al. 1979; Bryden et al. 1997; Armour et al. 2014).

Handedness and task complexity

An interesting feature of the task employed in this study is that it is simple, continuous, and likely involves little cognitive resources. This task requires a continuous back-and-forth motion of the wrist that is not required to conform to external speed nor visually targeting and thus accuracy requirements. Yet, our findings indicate substantial inter-limb differences in coordination. This brings into question

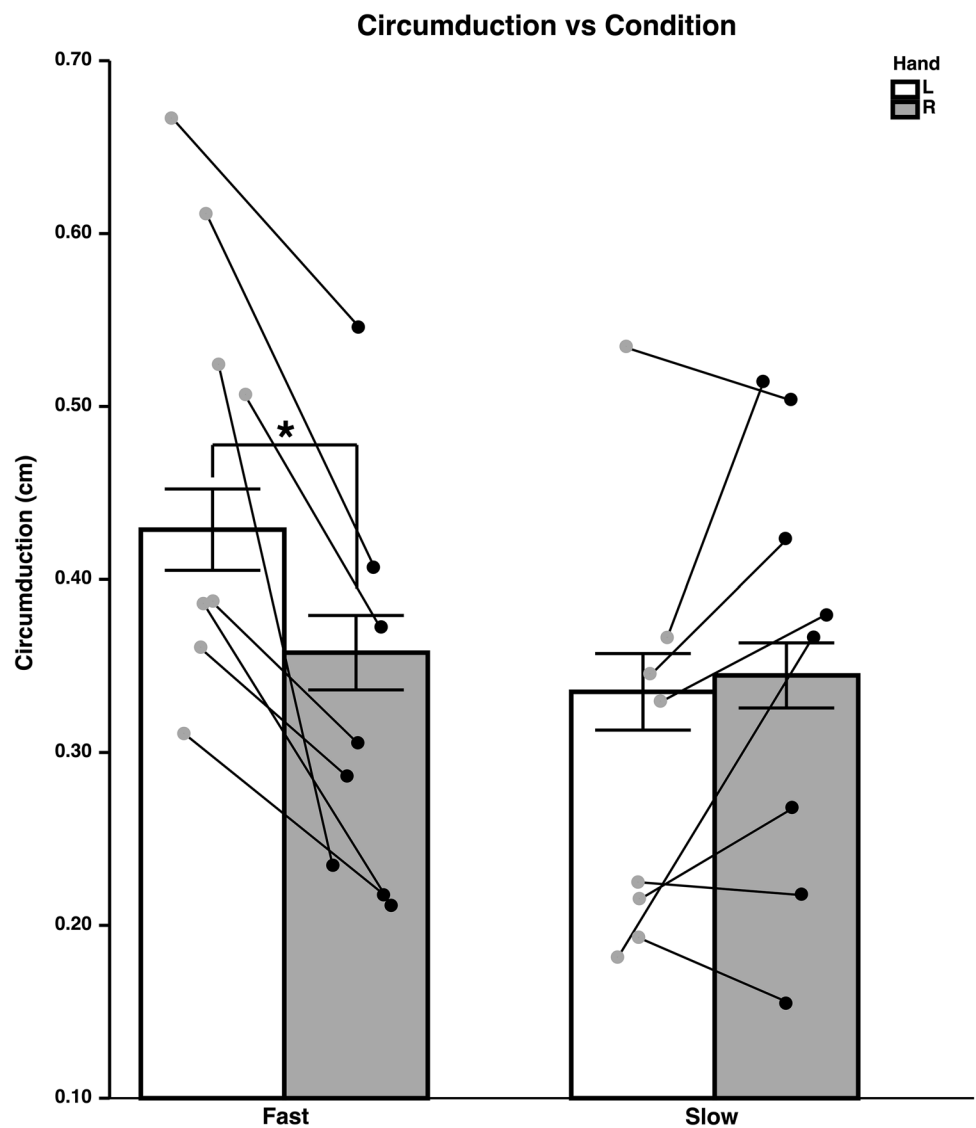
Fig. 8 Normalized pronation/supination angle/RUD angle. Participant's mean change in pronation-supination angle divided by the change in RUD angle throughout a full cycle compared in fast and slow conditions with error bars representing SE. Asterisk signifies a significant difference between the left and right hand during fast trials. Double asterisk signifies a significant difference between fast and slow conditions



whether handedness should be considered a specialization of the dominant system for sensorimotor skill, only during performance of complex tasks. Indeed, previous research has suggested that hand-preference depends on the complexity or skill-requirement of a task; for review, see Brydan (2015). For example, an individual will tend to reach for an object with the dominant hand more often if one intends to manipulate, rather than simply pick up the object. It has been suggested that this might reflect a dominant arm bias for movements that recruit distal musculature (Liederman and Healey 1986), an idea that was challenged by Steenhuis and Brydan (1989), which examined hand preference for distal tasks that required complex manipulation and skill (i.e., writing, throwing, sewing) vs distal tasks that do not require skill such as picking up small objects. That study differentiated the role of task complexity, regardless of distal requirements.

One of the problems with interpreting this line of research is the question of what factors define “skilled” or “complex” behaviors. It has been suggested that complex tasks involve multiple steps (Bryden 2015) and recruit greater cognitive resources. It should be noted that studies examining neural activation through imaging of the brain during motor behaviors (i.e., fMRI) have also supported the idea that activation patterns for dominant vs non-dominant arm movements are more asymmetric during performance of ‘complex’ or skilled tasks vs ‘simple’ motor tasks. Shmuelof et al. (2012) operationally defined motor skill learning as a change in the speed-accuracy tradeoff function, suggesting that skill can be defined by this relationship, an idea supported by much earlier literature (Wickelgren 1977). While this line of research suggests that motor control asymmetries depend on the complexity or skill requirement of a task, the simple repetitive movements

Fig. 9 Circumduction. Participant’s mean area encompassed by the hand path in the frontal plane divided by the 3D distance travelled throughout a full cycle compared in fast and slow conditions with error bars representing SE. Asterisk signifies a significant interaction between hand and condition



studied here did not incorporate these aspects of skill or complexity, yet our findings indicated substantial interlimb differences in coordination. We propose, instead that hand dominance is best reflected by the degree to which a task requires predictive mechanisms that account for biomechanical factors, such as redundant and coupled muscle actions across multiple degrees of freedom.

We conclude that inter-degree-of-freedom coordination at the wrist, measured as the ability to isolate motion to a single instructed degree of freedom, is substantially better coordinated for the dominant arm. These results support the extension of the dynamic dominance hypothesis to include a

dominant system advantage for inter-effector coordination, regardless of whether the task is visually targeted, visually guided, discrete or continuous.

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