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**INTERLIMB DIFFERENCES IN COORDINATION OF UNSUPPORTED REACHING
MOVEMENTS**

A Thesis in
Kinesiology
by
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Abstract

Previous research suggests that interlimb differences in coordination associated with handedness might result from specialized control mechanisms that are subserved by different cerebral hemispheres. Based largely on the results of horizontal plane reaching studies, we have proposed that the hemisphere contralateral to the dominant arm is specialized for predictive control of limb dynamics, while the non-dominant hemisphere is specialized for control of limb impedance. The current study explores interlimb differences in control of 3-D unsupported reaching movements. While the task was presented in the horizontal plane, participant's arms were unsupported and free to move in 3-Dimensions. Results indicated significant dominant arm advantages for both initial direction accuracy and final position accuracy. The dominant arm showed greater excursion along a redundant axis that was perpendicular to the task, and parallel to gravitational forces. In contrast, the non-dominant arm better impeded motion out of the task-plane. Nevertheless, left arm task errors varied substantially more with shoulder rotation excursion than did dominant arm task errors. These findings suggest that the dominant arm controller was able to take advantage of the redundant degrees of freedom of the task, while non-dominant task errors appeared enslaved to motion along the redundant axis. These findings are consistent with a dominant controller that is specialized for intersegmental coordination, and a non-dominant controller that is specialized for impedance control.

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Introduction

Brain lateralization, the division of labor between the cerebral hemispheres, is a well-established feature of the human nervous system that affects a variety of behaviors, ranging from language to handedness. Although lateralized differences are seen in a wide range of functions there have been many attempts to develop an organizational principle that might account for lateralization of the large array of cognitive, perceptual, language, emotional, and motor processes that have been identified. Dien (2008) reviewed five models of laterality that were based on different aspects of information processing. Integrating these models, Dien proposed a general model of laterality that might provide a parsimonious explanation for the large distribution of neurobehavioral findings that characterize neural lateralizations in many different neurobehavioral domains. This model, called the Janus Model, posits that the left hemisphere is specialized for anticipating future scenarios and choosing between them, while the right hemisphere is specialized for responding to online information (Dein, 2008). This idea is similar to the proposal of MacNeilage and Rogers that posits a left hemisphere specialization for well-established patterns of behavior and a right hemisphere specialization for detecting and responding to unexpected stimuli (MacNeilage et al., 2009). MacNeilage and Rogers model is based on lateralizations observed throughout many vertebrate species.

Handedness

While handedness represents one of the most obvious behavioral consequences of brain lateralization, the neural mechanisms that are responsible for this asymmetry remain controversial. Quantification of the differences in coordination between the dominant and non-dominant arms can be traced back to the seminal work of Woodworth, over a century ago (Woodworth, 1899). Woodworth's experiments showed clear advantages in accuracy of dominant hand movements that became more pronounced when participants made rapid, 'ballistic' movements. Such movements were termed 'ballistic' because, similar to projectile motion, once rapid movements were initiated, they were thought to play out without significant corrections. More specifically, Woodworth proposed that for rapid movements made toward targets, the initial phase of motion, prior to peak velocity, is largely ballistic or uncorrected, whereas the deceleration phase utilizes feedback mechanisms to both correct and stop the movement. For rapid upper limb reaching movements, this idea has been well supported by experimental studies that have applied perturbations and assessed response latencies (Brown and Cooke, 1981; Gordon and Ghez, 1987; Gottlieb and Corcos, 1989; Mutha and Sainburg, 2009). These findings have led to a two-phase model of motor control in which the first phase, prior to peak velocity is characterized as open-loop, reflecting anticipatory processes, and the final phase is characterized as largely closed-loop, including on-line corrective processes.

Many later studies have been designed based on that simple two-phase model to try to determine the processes that might be responsible for the differences in coordination and control of the dominant and non-dominant arms. One prominent idea proposed by

Flowers (1975) was that the hemisphere contralateral to the dominant arm might be specialized in processing visual feedback. This was based on the finding that the dominant arm showed reliable advantages in a visually controlled aiming task, in which visual closed-loop processes were thought to dominate. However, the two hands performed symmetrically in rapid tapping tasks, in which open-loop control was thought to dominate. This led to the conclusion that the dominant hand advantage during visually controlled tasks resulted from specialization of its contralateral hemisphere for feedback processing. In contrast to this idea, Annett et al. (1979) found that in a peg-board task more errors occurred and thus more corrections were made with the non-dominant arm. They also found no differences in the “place” time, or the time between entry of the tip of the peg into the hole and release of the peg. This part of the movement was thought to be feedback mediated, which led Annett et al. to conclude that the dominant hand was superior not in feedback processing, but rather in executing an initial plan that did not need as many corrections. This hypothesis has been supported by studies in which visual feedback conditions were manipulated (Roy and Elliott, 1986; Carson et al., 1990). Roy and Elliott (1986) manipulated visual feedback by involving two conditions: one with full vision of the arm and target, and one with only vision of the target, while Carson et al. (1990) used four visual conditions: one with full vision of hand and target, one with vision of only the target, one with vision of only the hand, and one with no vision of hand or target. Although the visual conditions in these studies altered performance, there was no interaction with hand, indicating that the differences between the hands was not affected by visual feedback conditions. Roy and Elliott (1986) concluded that the difference in accuracy between the arms was not a result of differences in processing visual feedback, but instead was due to a right arm/left hemisphere advantage in generating more consistent and accurate initial movement features, through feedforward mechanisms (Roy and Elliott, 1986). In tests of this hypothesis, Roy and Elliott found better right hand accuracy in a condition where lights were turned off ten seconds prior to movement, indicating that the dominant arm/hemisphere system might be more effective using vision through feedforward mechanisms to plan movement (Roy and Elliott, 1989).

The aforementioned studies either manipulated visual feedback to examine the role of closed-loop processes in motor control, or simply viewed motor corrections as largely visually based, with little concern for the role of proprioception. Proprioception is the sense of relative body segment position, orientation, and movement that arises from muscle spindles and Golgi tendon organs. Proprioception is most often tested by position matching tasks, when vision is occluded. The idea that proprioceptive acuity might be more effective for the non-dominant arm was introduced by Roy and MacKenzie (1978) when they revealed an advantage in a thumb position-matching task, findings that were later supported by Riolo-Quinn (1991). A more recent line of research by Brown and colleagues supported a non-dominant advantage in proprioceptive position matching, while indicating a dominant arm advantage in a visual position matching task (Goble and Brown, 2008). For the most part, the reviewed research supports the hypothesis that the dominant hemisphere-limb is specialized for feedforward control mechanisms that use prior visual information, while the non-dominant system might be specialized for online mechanisms that correct movements based largely on proprioception.

Hemispheric Specialization Requires Bihemispheric Control of Movements

Research on individuals with unilateral brain damage has given more insight into the role of brain lateralization in motor control and coordination. If the two hemispheres are specialized for different aspects of motor control, this would predict that both hemispheres must be recruited to control unilateral movements that exploit these two aspects of control. For example, from the studies listed above, one might conclude that one hemisphere is specialized for open-loop mechanisms and the other for closed-loop mechanisms. It is impossible to conceive of a unilateral movement that would not require both processes. This view leads to the very clear prediction that damage to one hemisphere should produce hemisphere specific motor deficits in both the contralesional arm and the ipsilesional arm. While the motor deficits that result from contralesional hemisphere stroke can be devastating and include complete loss of voluntary control, in the case of plegia, or severe deficits in voluntary movement in the case of paresis, the idea that deficits might also occur in the arm ipsilateral to the brain lesion has also been confirmed. Many studies have found that damage to one hemisphere causes deficits in the ipsilesional arm, (Haaland et al., 1977; Haaland and Delaney, 1981; Fisk and Goodale, 1988; Haaland and Harrington, 1989) and that these deficits are different depending on the side of the damage. Haaland and Harrington (1989) showed that in a simple aiming task done with the ipsilesional arm of both right hemisphere damaged and left hemisphere damaged patients, the left hemisphere damaged group was slower and the initial movement was less accurate than controls. The right hemisphere damaged group was not significantly impaired on any measure. Winstein and Pohl later (1995) supported these findings in an alternating tapping task, showing that left hemisphere damage resulted in deficits in the open-loop components of movement and right hemisphere damage affected the closed-loop components. Haaland et al. (2004b) found a similar distinction between open-loop and closed-loop components as left hemisphere damaged patients suffered deficits in the initial components of movement and right hemisphere damaged patients suffered in final position error. Studies that have applied more detailed kinematic and kinetic analyses have indicated a similar dichotomy. While left hemisphere damage produces ipsilesional deficits in predictive aspects of control that affect trajectory and multi-joint coordination, right hemisphere damage produces deficits in the ability to achieve and stabilize final steady state positions (Schaefer et al., 2007; Schaefer et al., 2009). These studies confirm that each cerebral hemisphere contributes specific processes to the motor control of each arm, and suggest that this asymmetry in neural control might lead to the asymmetry in limb performance that we call handedness.

Research on anatomical and neurophysiological comparisons of the cerebral hemispheres also showed distinct differences. Nudo et al. (1992) used intracortical microstimulation to derive detailed maps of distal forelimb representations in both hemispheres of monkeys. They found that in the hemisphere contralateral to the preferred forelimb, distal representations were greater in number and larger in area, and showed a greater index of spatial complexity (Nudo, et al., 1992). Such asymmetries in neural representation have been supported by studies using magneto-encephalography (Volkmann et al., 1998) and fMRI (Dassonville et al., 1997). Amunts et al. (1996) used

magnetic resonance morphometry to show that the depth of the central sulcus is deeper in the left hemisphere for right-handers and vice versa for left-handers. Brodmann area 4 of the left hemisphere was also shown to have larger neuropil volume, suggesting higher volume of dendrites and synapses and increased connectivity (Amunts et al., 1996). Hammond (2002) suggested that these findings along with others provide evidence that hand representation in the primary motor cortex is greater in the dominant hemisphere and that this hemisphere contains more profuse interconnections, making the dominant hand more dexterous. Haaland et al. (2004a) provided further evidence that the dominant hemisphere contains circuitry for the movements of both limbs using fMRI to show that there was greater ipsilateral activation of the left hemisphere when subjects performed finger sequences using their non-dominant left hands. They also showed that more complex finger sequences recruited left parietal and premotor cortices to a greater extent than simpler sequences, supporting a left-hemisphere role for motor planning (Haaland et al., 2004a).

Dynamic Dominance

Building on this line of research, Sainburg and colleagues have developed a hypothesis that provides a control-theory based explanation for the motor control processes that might underlie handedness. Studies in individuals without nervous system impairments have suggested that the dominant arm shows greater proficiency in predictive control of limb dynamics, including dynamic interactions associated with multiple segment coordination (Sainburg and Kalakanis, 2000; Sainburg, 2002; Sainburg, 2014), but also including predictive control of movement distance when moving only a single segment (Sainburg and Schaefer, 2004). In contrast, the non-dominant controller appears specialized for specifying and achieving steady states and for impeding unexpected perturbations through on-line processes that might control limb impedance (Sainburg, 2002; Yadav and Sainburg, 2014). This hypothesis has been termed 'dynamic dominance'. According to this hypothesis, the dominant hemisphere is able to more accurately predict the dynamic effects of movements through optimization-like processes that might minimize trajectory and energetic costs (Flash and Hogan, 1985; Nakano et al., 1999; Todorov and Jordan, 2002; Nishii and Tani, 2009; Yadav and Sainburg, 2011). It is hypothesized that non-dominant specialization for impedance control does not minimize such costs, but instead insures robustness against unexpected perturbations and conditions in the environment, leading to more stable movements or postures. In a recent test of this hypothesis, participants were exposed to velocity dependent force fields that were unpredictable in amplitude and varied between trials, or that were consistent and predictable between trials. When using the dominant arm, participants performed better in the consistent field, while their non-dominant arm performed better in the inconsistent field. This appeared to support a dominant hemisphere specialization for predictive control and a non-dominant specialization for impedance control (Yadav and Sainburg, 2014). This was one of the first studies to show consistent non-dominant arm superiority for specific aspects of control. The difference in control strategies can also be seen when adapting to novel inertial dynamics. Both arms are able to adapt in final position error, but only the dominant arm improved the initial direction when exposed to novel inertial dynamics over repeated trials, whereas the non-dominant arm was only making corrections for initial

errors (Duff and Sainburg, 2007). Large aftereffects were also seen in the dominant arm but not in the non-dominant arm, indicating a feed-forward predictive control for the dominant hemisphere and impedance control for the non-dominant hemisphere. This is consistent with a study by Schabowsky et al. (2007) that also showed more stability and fewer aftereffects for the non-dominant arm, leading them to conclude that impedance control is relied on for the non-dominant limb.

The specialization of the non-dominant arm for impedance control may also impart advantages when making movements in the absence of visual feedback to a large array of targets. In this case, the non-dominant arm shows greater position accuracy across most of the workspace than the dominant arm (Przybyla et al., 2013). However, when conditions are more predictable, such as when reaching to only three targets over repetitive trials, the dominant and non-dominant arms tend to show equivalent final position accuracy (Sainburg et al., 1999). The dynamic dominance hypothesis has been supported by studies of ipsilesional arm control in right-handed patients with unilateral brain damage (Haaland; Sainburg; etc.). These studies have shown that left hemisphere damage produces deficits in predictive control of distance during single joint movements (Schaefer, Haaland, and Sainburg, 2007), and deficits in direction and interjoint coordination during multijoint movements (Schaefer, Haaland, and Sainburg, 2009). Left hemisphere damage also results in deficits in adapting movement trajectories, but not final positions. In contrast, right hemisphere damage produces deficits in stabilizing the final positions of single joint (Schaefer, Haaland, and Sainburg, 2007) and multijoint movements, and adapting final position accuracies, but not trajectories, over repetitive trials (Schaefer, Haaland, and Sainburg, 2009). We propose that the dynamic dominance hypothesis reflects a more detailed and mechanistic modification of previous open-loop/closed-loop proposals to account for handedness. While the dominant system appears specialized for largely open-loop prediction of limb dynamics, the non-dominant system is specialized for largely closed-loop control of limb impedance.

Purpose of the Study

A significant limitation of the previous studies on handedness is that the reaching movements were almost always performed in the horizontal plane, with the arms supported to reduce the effects of gravity and friction. This allowed control over the effects of intersegmental dynamics, because in this horizontal plane frictionless environment, the non-muscular forces acting on the limb are primarily inertial, including intersegmental interaction torques. In addition, the movements are constrained and do not exhibit the same redundancy available during unconstrained 3-D motion. While this reduction allows one to address specific questions about control and coordination, it does not address how movements are coordinated in a gravitational field or when confronted with redundant degrees of freedom. Previous research has emphasized the role of gravitational forces in planning and execution of movements (Papaxanthis, et al., 2003; Gentili, et al., 2007). Bernstein (1930) observed through hammering movements, that people never produce exactly the same movement between repetitions. Instead, they utilize the redundant degrees of freedom in the musculoskeletal system to reveal infinitely variable solutions to reach the end goal. This redundancy introduces motor abundance (Latash, 2012), which may help to stabilize task performance across multiple trials. This redundancy may elicit

different movement characteristics from constrained movements. Atkeson and Hollerbach (1985) observed substantially more curved hand paths when the arm was performing unconstrained vertical reaches compared to 2-D, constrained horizontal plane reaches. The authors gave three possible explanations as to why there may have been more curved paths in the unconstrained movements: 1) That difficulties in handling gravity in certain directions could result in curved paths, 2) that the vertical plane motions were more natural than horizontal plane movements, and 3) that restricted degrees of freedom in the horizontal movements made them compliant motions, which may be executed under a different control strategy.

The unique dynamic and kinematic properties of 3-D movements accentuate the importance of studying them and comparing them to the extensive findings that have been made on 2-D movements. While previous studies have demonstrated asymmetries in coordination of the dominant and non-dominant arms during natural tasks performed in 3-dimensions, such as throwing (Hore, O'Brien, Watts, 2005), carrying infants (Harris, 2014), and kayak paddling (Rynkiewicz and Starosta, 2011), whether such asymmetries correspond to the coordination asymmetries described by the dynamic dominance hypothesis remains unclear. In this study, participants reached toward targets presented in the horizontal plane but requiring the participants to support their own arms in space. Because the task was presented as a horizontal plane projection of the hand, z-axis displacement of the hand was completely redundant to the task. In this way, we required participants to control their movements in a gravitational field, as well introducing degrees of freedom that were redundant to the task. We compared performance of the dominant and non-dominant arm to see how the differences in control mechanisms between the hemispheres are expressed during performance of a 3-D reaching task.

Experimental Procedures

Participants

Participants were 20 healthy, right-handed adults aged 18-25 years old. All participants were screened for handedness using the Edinburgh Inventory (Oldfield, 1971) and provided informed consent before participation in this study, which was approved by the institutional review board of Penn State University.

Experimental setup

Participants were seated at a 2-D virtual reality workspace in which stimuli from a TV screen were reflected by a mirror, with the participants' arms under the mirror. Figure 1 shows this experimental set-up. Participants' arm movements were tracked at 116 Hz using 6 DOF magnetic sensors (Ascension TrackStar) placed on the wrist and upper arm. Vision of the participants' arms was occluded while position of the hand was provided as a cursor on the screen. Both wrists and fingers were immobilized using a splint, while all degrees of freedom through the shoulder, elbow, and forearm were available.

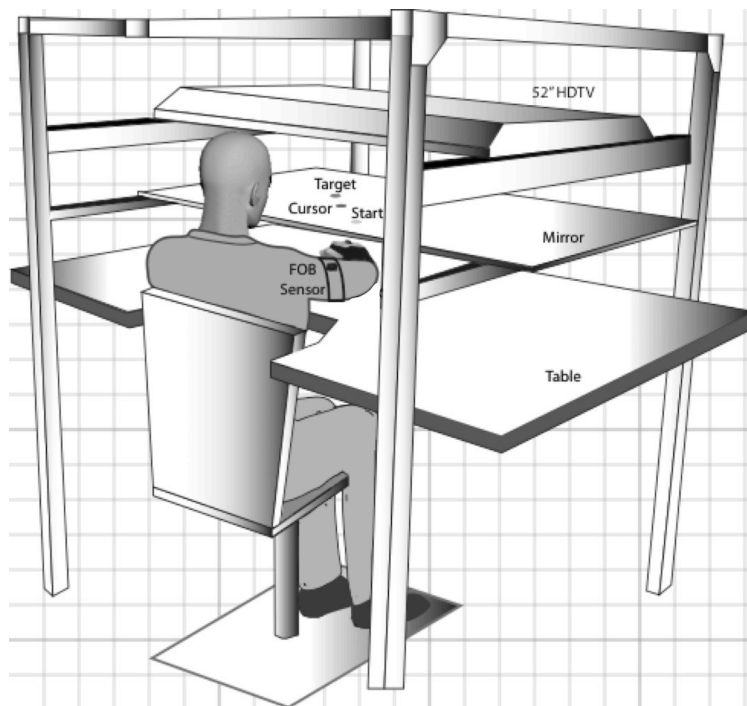


Figure 1- Experimental Set-up: A TV screen was positioned above a mirror, creating a 2-D virtual reality environment.

Experimental Task

The task required multijoint reaches to three different targets. The three targets were made based on the arm segment angles in the horizontal plane and required movements of equal elbow extension (20 degrees), but varying degrees of shoulder flexion. Target 1 required 10 degrees of shoulder flexion, Target 2 required 20 degrees and Target 3 required 30 degrees. Participants reached to these targets, holding their arms above table, and were thus able to move freely in a range of 3-D space. This unconstrained

movement allowed degrees of freedom that were not in the horizontal plane, and thus allowed for a variety of combinations of joint excursions in the 3-D space that result in reaching the targets. For each trial, participants moved the cursor into a starting circle, and waited for 300 milliseconds, at which time an auditory 'go' tone was provided. When the participants moved the cursor outside of the starting circle, the cursor disappeared. Participants were instructed to move quickly and accurately to the target circle, and were given points for motivation. Points were available for all movements made with a peak tangential hand velocity of 0.7 m/s or higher.

Participants performed blocks of 30 reaching movements per arm (10 per target) for a total of 60 trials per participant. Ten of the participants used the right arm first and ten participants used the left arm first, and in order to eliminate any effect of interlimb transfer for this task, only data from the first arm each participant used was included for this study.

Kinematic Analysis

The three-dimensional position of the index finger, elbow, and shoulder were calculated from sensor position and orientation data and elbow and shoulder angles were calculated from these. All kinematic data were low-pass filtered at 8 Hz (3rd order, dual pass Butterworth). The three main measures of task performance for this study were final position error, direction error, and linearity. Final position error was calculated as the distance between the index finger location at movement end and the target position. Direction error was calculated as the angle between the vector from the start to the target circle, and the vector originating at the starting location of the hand and terminating at the point at which the peak tangential hand velocity occurred. Deviation from linearity was assessed in 2-D and 3-D as the minor axis divided by the major axis of the hand path. The major axis was defined as the largest distance between any two points in the path, while the minor axis was defined as the largest distance, perpendicular to the major axis, between any two points in the path (Sainburg, 2002; Sainburg et al., 1993).

Statistical Analysis

Our primary hypothesis was that reaching coordination will vary with arm, when reaching unsupported in 3-Dimensions. We used a 3 target (within participant) by 2 hand (group) design (Sainburg, Ghez, Kalakanis, 1999; Bagesteiro and Sainburg, 2002). We predicted that measures of task performance and coordination would depend on both target (within hand) and hand (group). Statistical analysis was done using a 3 X 2 mixed factor ANOVA model. Significant interactions and main effects were subjected to post-hoc analysis using the Student's t test. We used a simple linear regression analysis to assess the relationships between specific variables.

Results

Arm Kinematics

Figure 2a shows typical hand paths from two different subjects to each target for the left and right hands and illustrates arm movement for Target 1 in the horizontal plane. The lines showing the whole arm movements represent stick figures of the arms that are taken every 2 data points (17.2 ms). In the horizontal plane (Figure 2a), the hand paths appear roughly similar between the arms (subjects), while the right arm movements appear slightly more accurate in direction and final position. While the horizontal projections appear largely similar, the frontal plane projections show quite distinct differences between the arms. Figure 2b shows the frontal plane projections of the movements shown in figure 2a. For the left hand, the elbow, wrist and finger show restricted displacement on the Z (vertical axis), indicating that motion remained largely within the horizontal plane. In contrast, the right arm shows greater displacement along the z-axis, most notable by the twisting of the forearm that results in greater hand motion on the z-axis.

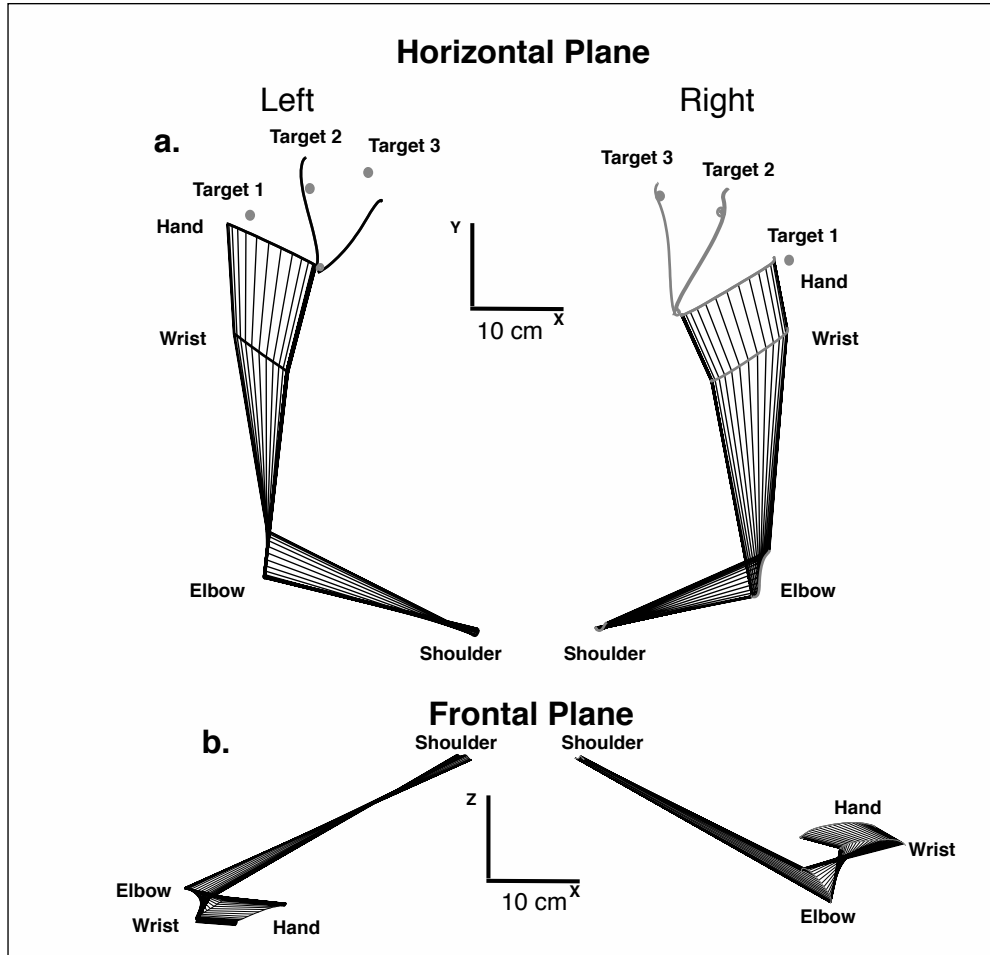


Figure 2- Hand Paths: A) Horizontal plane projection of hand paths from two different subjects for the left and right arm to all targets, as well as whole arm representation of movements to Target 1. B) Projections of the arm into the frontal plane of the same movements to Target 1 shown in A.

Kinematics in the Horizontal Plane:

The bar graphs in Figure 3 a-d show mean \pm SE performance measures in the horizontal plane, reflecting performance in the horizontal task space. Figure 3a shows maximum velocity, which varied systematically with target ($F(2,36)= 23.3644, p< .0001$) but showed no main effect of hand ($F(1,18)= .7613, p= .3944$), nor interactions between hand and target ($F(2,36)= .4124, p= .6651$). We measured horizontal plane linearity as aspect ratio (see methods) shown in Figure 3b. Aspect ratio showed a main effect of target ($F(2,36)= 9.2939, p= .0006$), but not of hand ($F(1,18)= .7273, p= .4050$), nor interactions between target and hand ($F(2,36)= .4060, p= .6693$). Figure 3c shows our measure of final position error, which although consistent across targets ($F(2,36)= .1628, p= .8504$) showed significant effects of hand ($F(1,18)= 7.1025, p= .0158$), such that the left non-dominant arm had significantly higher errors than the right-dominant arm. In our previous study of planar supported movements, such trends did not reach significance (Sainburg et al, 1999). Figure 3d shows how well the initiation of movement was directed toward the target, measured as direction error at the maximum of hand tangential velocity. While there was no effect of target ($F(2,36)= .4489, p= .6418$), the left hand had significantly larger direction errors at peak velocity ($F(1,18)= 5.4351, p= .0316$).

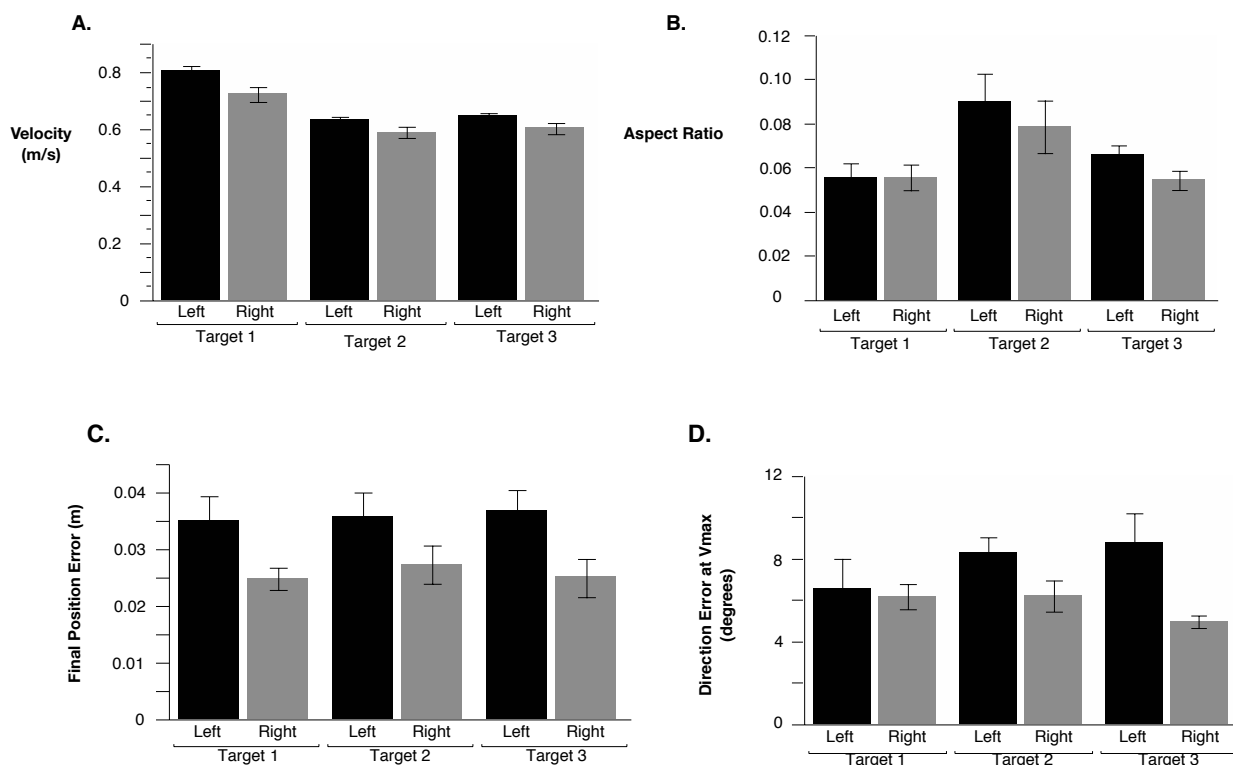


Figure 3- 2-D Hand Kinematic Measures: Mean and \pm SE bars across all subjects, shown for both target and hand for A) Peak Velocity, B) Aspect ratio (linearity), C) Final Position Error, D) Direction Error at Peak Velocity.

Kinematics Out of the Horizontal Plane

The task presented in this study provided feedback about the projection of hand motion within the horizontal plane, and task success depended completely on the projection of motion within this task space. However, we did not constrain the arm within this plane. Instead, participants were required to hold their arm above the tabletop, and the arm was free to move along the z-axis. Thus, movement in the z-axis was redundant to the task. A successful hand position within the target, for example, could be achieved by an infinite range of positions along the z-axis.

We examined whether movements outside of the horizontal plane and thus redundant to the task, were different between the arms (groups). Figure 4a shows the displacement on the z-axis for the hand-path, from the beginning to the end of movement. We found a main effect of hand, such that right hand z-displacement was greater ($F(1,18)=8.2126$, $p=.0103$), and a main effect of target ($F(2,36)=86.3551$, $p<.0001$) but this effect was similar for both hands such that there were no interactions between hand and target ($F(2,36)=1.5777$, $p=.2204$).

We next examined the joint kinematics that gave rise to this arm-difference in z-displacement. In this minimally constrained task (wrists splinted) with the upper arms abducted above 45° and the elbow close to 90° , shoulder roll (internal/external rotation) and shoulder elevation (abduction/adduction) can substantially contribute to hand motion along the z-axis. Figures 4b and 4c show shoulder roll and elevation displacement, respectively, for the three targets and two arms. For shoulder roll (figure 4b), the relationship to hand and target appears similar to the z-axis displacement relationship shown in figure 4a. The right hand showed greater external rotation for targets 1 and 2, while target 3 showed less difference between the hands in internal rotation displacement. In support of this, ANOVA showed a main effect of hand ($F(1,18)=4.6024$, $p=.0458$), a main effect of target ($F(2,36)=250.5701$, $p<.0001$), as well as the interaction between hand and target ($F(2,36)=4.2807$, $p=.0215$). This interaction is reflected by the larger change across targets for the right, as compared to the left arm. In contrast to shoulder roll measures, Shoulder elevation (Figure 4c) showed a starkly different pattern across targets and hands than did z-displacement and shoulder roll. While the amount of shoulder adduction increased across targets (Main effect of target: $F(2,36)=21.1824$, $p<.0001$), no main effect of hand ($F(2,36)=2.6017$, $p=.1241$), nor interactions ($F(2,36)=1.8229$, $p=.1762$) were seen.

The similarity in the pattern of shoulder roll displacement across hands and targets (figure 4b) and z-axis displacement (figure 4a) is striking, leading us to examine the relationship between these measures, through linear correlation analysis. Figure 5a and 5b show these linear correlations for the dependence of z-axis displacement on shoulder roll (figure 5a) and shoulder elevation (figure 5b). Each point in Figures 5a and 5b reflects the mean of one subject for one of the targets, with the right arm subjects shown as gray "X" and the left arm subjects with the black dots. Our correlation analysis indicated a strong dependence of z-displacement on shoulder roll in both the left ($R^2=.70$), and the right ($R^2=$

.83) arms. In contrast, there was very little correlation between z-displacement with shoulder elevation in the left ($R^2 = .10$), or the right arms ($R^2 = .014$). We conclude that hand displacement on the z-axis, reflecting out-of-horizontal plane motion, was largely a result of shoulder roll for both hands.

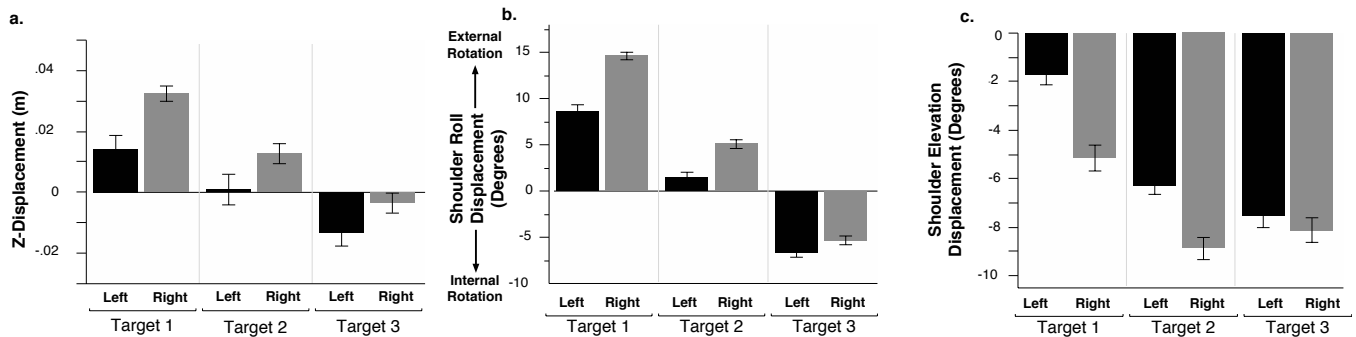


Figure 4- Redundant Axis Movement: Mean and \pm SE bars across all subjects, shown for both target and hand for A) Displacement in the z-axis, B) Shoulder roll displacement, C) Shoulder elevation displacement.

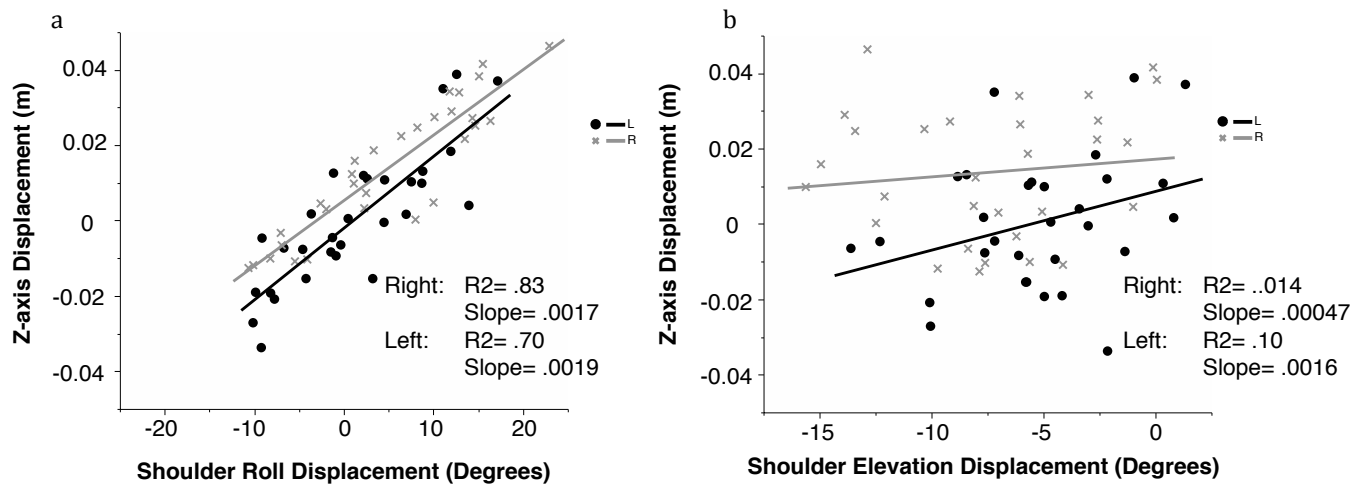


Figure 5- Shoulder Movements vs. Z-axis Displacement: Linear correlations shown for by left non-dominant (black) and right dominant (gray) arms of A) z-axis displacement vs. shoulder roll displacement, and B) z-axis displacement vs. shoulder elevation displacement. Points represent means of one subject to one target, with non-dominant left being represented by black dots and dominant right being represented by a gray X.

Because shoulder roll was significantly different between the arms and also appeared to be largely responsible for z-axis, or out-of-plane motion of the hand, we asked whether this displacement might be responsible for the difference between right and left arm accuracy. The effect of shoulder roll displacement on the task hand movement within the horizontal plane (task-space), is shown in figure 6a and 6b. The relationship between

shoulder roll displacement and final position errors in the plane are shown in the X-axis component of final position errors (6a) and Y-axis components of final position errors (6b). Whereas the dependence of Y-axis errors on shoulder roll is small (left: $R^2 = .063$, right: $R^2 = .13$), task error along the X-axis was substantially affected by shoulder roll, and this correlation was greater for the left than the right arm (left: $R^2 = .70$, right: $R^2 = .25$). Most importantly, however, the slope was substantially smaller for the right than the left arm, indicating a smaller dependence of x-axis error on shoulder roll for the right than the left arm. Thus for every 1 degree of shoulder roll, an x-axis error of 2.6 mm occurred for the left and 0.85 mm for the right arm. Interestingly, the right-arm showed greater shoulder roll displacement than the left arm (Figure 4b), while this displacement was associated with lower task errors. This suggests that left non-dominant arm control is less effective at coordinating redundant out-of-task degrees of freedom than the right dominant-arm, and as a result task errors become enslaved to these motions.

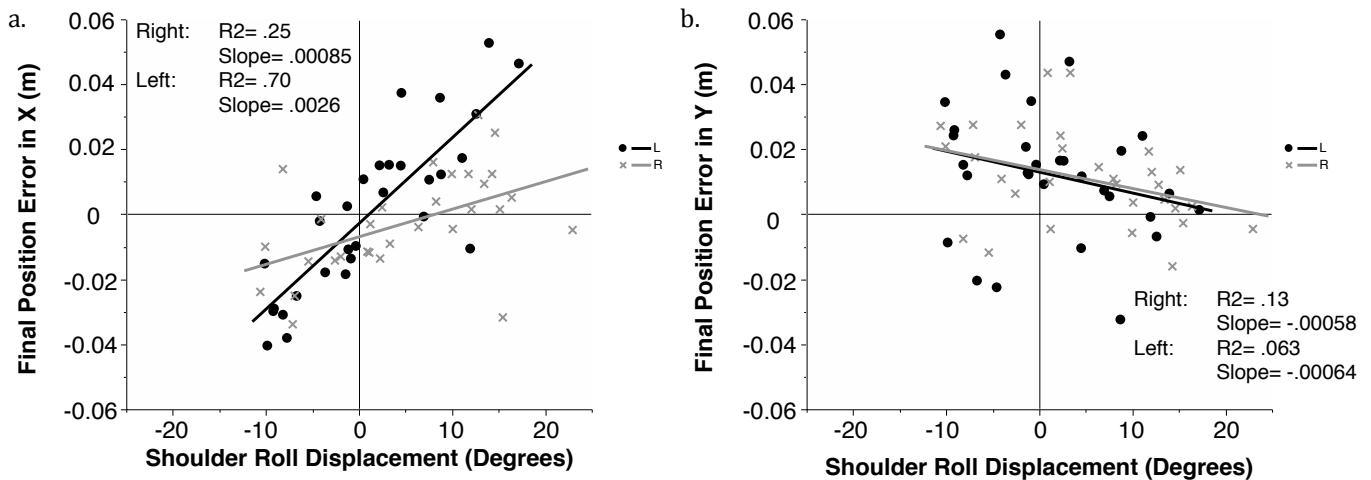


Figure 6- Shoulder Roll vs. X and Y Error: Linear correlations split by non-dominant left (black) and dominant right (gray) arms of A) Final position error in the x-axis vs. shoulder roll displacement, and B) Final position error in the y-axis vs. shoulder roll displacement. Points represent means of one subject to one target, with left being represented by black dots and right being represented by a gray X.

Discussion

Summary

In this study, we compared dominant and non-dominant coordination during minimally constrained, 3-D reaching movements to multiple directions. Although the task was presented in the horizontal plane, the arms were unconstrained in space, such that any motion perpendicular to the task-plane (z-axis displacement in our coordinate system) was redundant to the task. Our results showed that dominant arm task performance was significantly more accurate in terms of initial direction errors and final position errors. However, hand path curvature was not significantly different between the arms. Previous studies of supported horizontal plane movements have reported more accurate initial directions and straighter trajectories for the dominant arm, but also similar final position accuracies between the arms (Sainburg and Kalakanis, 2000; Bagesteiro and Sainburg, 2002). Thus, our current findings for 3-D movements contrast with those findings in terms of straightness and final position errors. In terms of redundant axis motion, dominant arm movements showed greater displacements along the redundant z-axis, than did non-dominant arm movements. This z-axis motion primarily resulted from shoulder roll displacement (rotation along the long axis of the humerus). While this rotation was more constrained for the non-dominant arm, components of final position error were highly correlated with shoulder roll for the non-dominant, but not the dominant arm. We conclude that non-dominant arm movements restricted motion along the z-axis in order to constrain final position errors, while dominant arm coordination was able to take advantage of the redundant axis motion without affecting final position errors. Thus, out-of-task motion was better coordinated by the dominant arm to maintain task accuracy, while the out-of-plane motion was constrained by the non-dominant arm, and yet led to greater task errors. These findings are consistent with the proposition of a dominant controller that accounts for limb and environmental dynamics, and a non-dominant controller that stiffens to impede the effects of such dynamics on limb motion.

Interlimb differences in predictive control

We measured initial direction at the peak in tangential hand velocity. This parameter is an early trajectory measure that is thought to reflect movement preparation (Flash and Hogan, 1985; Atkeson and Hollerbach, 1985; Berardelli et al., 1996; Sainburg, Ghez, and Kalakanis, 1999). In previous studies of horizontal plane reaching movements to multiple directions, dominant arm movements consistently show substantially lower initial direction errors than non-dominant arm movements, one of the findings that has led to the idea that the dominant hemisphere is specialized for predictive control mechanisms (Sainburg and Kalakanis, 2000; Bagesteiro and Sainburg, 2002). In fact, in those planar studies, this error varied with the amplitude of interaction torques between the elbow and shoulder for the non-dominant but the dominant arm. Similarly, early trajectory errors have been reported to be larger for the non-dominant arm in studies of 3-D motion (Hore, et al., 1996; Pigeon et al., 2013; Gray et al., 2006), and in the case of reach and turn movements, those errors were shown to vary with the amplitude of coriolis torques produced at the shoulder and elbow by trunk rotation (Pigeon et al., 2013). The idea that

this type of predictive control might be associated with dominant hemisphere contributions to arm coordination has been supported by studies of ipsilesional arm movements in right-handed stroke patients with left- and right- hemisphere damage. For example, Schaefer et al., (2009) showed that lesions to the left, but not the right hemisphere produced greater variance in initial movement direction in the left, non-paretic, arm of left-hemisphere damaged but not the right non-paretic arm of patients with right-hemisphere damage. They concluded that predictive mechanisms responsible for specifying initial trajectory direction for both arms were disrupted by left, but not by right hemisphere damage. Similarly, Haaland et al. (1989) reported ipsilesional (non-paretic arm) deficits in the initial accuracy of movements for left but not right hemisphere damage, and Winstein and Pohl (1995) reported ipsilesional deficits in the timing of the initial phase of motion, prior to peak velocity, in left but not right hemisphere damaged patients. Schaefer et al. (2009) and Mutha et al. (2011) showed that left hemisphere, but not right hemisphere damage impedes adaptation in initial movement direction, when participants are exposed to distorted visual feedback, in which the direction of cursor motion is rotated relative to the direction of hand motion (visuomotor rotation). Thus, the current findings, indicating a dominant arm advantage in initial direction of the hand-path is consistent with previous research indicating a dominant arm advantage for specifying initial trajectory parameters.

However, in our current study, this initial direction advantage was not associated with an advantage in movement straightness. It has previously been reported that non-dominant arm hand paths during pointing movements are often more curved, and that these curvatures vary with intersegmental dynamics, including inertial interaction torques (Sainburg and Kalakanis, 2000; Bagesteiro and Sainburg, 2002) as well as Coriolis torques due to motion of the trunk (Pigeon et al., 2013). Thus, the often straighter movements of the dominant arm have been shown to reflect coordination strategies that take account of limb dynamics. It should be stressed that previous studies of dominant arm movements have shown a tendency toward straight hand paths for the movements that are supported in the 2-D horizontal plane, suggesting that this is an important feature of planar reaching movements (Flash and Hogan, 1985; Morasso, 1981). Flash and Hogan (1985) proposed that the controller optimizes movement smoothness, or minimizes the magnitude of jerk. Other studies have associated similar straight trajectories in the horizontal plane with other optimized parameters, such as energy (Nishii and Tani, 2009), work (Yadav and Sainburg, 2011), and torque change (Nakano et al., 1999). However, there have also been a number of studies that reported that hand paths tend to be more curved when the arm is not supported and constrained in the horizontal plane (Atkeson and Hollerbach 1985; Desmurget et al., 1997; Lacquaniti et al., 1986). Desmurget et al. directly compared dominant arm constrained and unconstrained movements in a reaching task and found that the unconstrained movements had significantly more path curvature. However, when participants were specifically instructed to move in a straight line, the paths were significantly straighter (Desmurget et al., 1997), suggesting that the increased curvature in unconstrained conditions was a preference. Lacquaniti et al. had subjects follow a straight-line path to targets during unconstrained movements, also demonstrating the ability to make straight movements when instructed. They suggested that path straightness is unlikely to be an output of optimizations under 3-D conditions, in which gravitational

torques and additional degrees of freedom are available (Lacquaniti et al., 1986). This might explain why large differences in path curvature have previously been reported for reaching movements constrained and supported in the horizontal plane, but were not evident in the 3-D unconstrained reaching movements reported here.

A major factor in controlling 3-D unconstrained, as compared to supported horizontal plane movements is gravitational torques. Even the kinematics of single joint movements have been shown to depend on gravitational torques (Gentili et al., 2007; Papaxanthis et al., 2003). In unconstrained multijoint reaching movements made by rhesus monkeys, the effects of gravitational torques dominated the trajectories (Jindrich et al., 2011). Thus, during movements made in a gravitational field, exploitation of gravitational torques can become an advantage to a controller that is able to predict dynamics. Such control might exploit optimization-like algorithms to minimize costs such as energy, jerk, work, and/or task performance errors (Flash and Hogan, 1985; Nakano et al., 1999; Todorov and Jordan, 2002; Nishii and Tani, 2009; Yadav and Sainburg, 2011). In horizontal plane reaches, straight movements are made because they are optimal according to such cost functions. We suggest that the reduced straightness of the dominant arm in the current unconstrained task may reflect control that takes advantage of gravitational torques and the additional degrees of freedom. Further research is necessary to examine whether differences in trajectory are predicted by optimization simulations for 3-D unconstrained as compared with movements supported and constrained to the horizontal plane. However, our findings that the dominant hand path shows greater excursion along the redundant degree of freedom, yet less task error associated with this excursion is consistent with this hypothesis.

Interlimb differences in coordination of redundant degrees of freedom

This task was projected into the horizontal plane, but allowed movement perpendicular to this plane, creating a purely redundant axis. Interestingly, the dominant arm showed greater excursion along this axis during movements than did the non-dominant arm. At first glance, this suggests that the non-dominant arm was better able to maintain planar motion and thus better adapt to the task. However, the non-dominant arm made greater task errors. We showed that the excursion along the z-axis was primarily due to shoulder roll displacement, or rotation of the humerus along its long axis. Because of orientation of the shoulder elevation angle (about 45° below the horizontal) and the flexed elbow angle, shoulder roll predominantly influenced x-axis and not y-axis excursion of the hand. Final position errors along this axis showed a higher dependence on shoulder roll for the non-dominant arm than for the dominant arm. Thus, the dominant arm showed greater shoulder roll excursion, but final position errors showed a reduced dependence on this excursion compared with the non-dominant arm. This suggests a difference in how redundant degrees of freedom are coordinated between the arms. While the non-dominant arm likely stiffens to reduce excursion along potentially redundant degrees of freedom, the dominant arm utilizes greater excursion along task-irrelevant degrees of freedom.

One perspective that might shed light on these interlimb differences in excursion along the redundant z-axis and associated relationship to task errors is the uncontrolled

manifold hypothesis. According to this idea, redundancy in the motor system is viewed as a positive feature that allows variance without affecting task performance (Scholz and Schoner, 1999; Latash, Scholz, Schoner, 2002). Variance that does not affect task performance is said to be within an uncontrolled manifold because the controller need not be concerned with variations that do not produce performance errors (V_{UCM}). According to the principle of motor abundance, proposed by Latash (2012), good variance is variance that does not produce task errors. This is achieved by co-variation between elemental or controlled variables, such as muscles or musculoskeletal degrees of freedom. The advantage of this 'good' variance is that it allows stability of performance over repetitions of a movement, as well as robustness to unexpected perturbations and variations in movement conditions. Dounskaia and Wang (2014) saw a similar advantage in motor abundance when comparing constrained and unconstrained movements. When making center-out movements to random directions, there was a wider range of directional preferences when movements were unconstrained and allowed to exploit redundant degrees of freedom. They also found that passive torque contributions were higher at these preferred directions, providing further support that redundant movement is part of a more effective control strategy (Dounskaia and Wang, 2014). Freitas and Scholz (2009) reported differences in how dominant and non-dominant arm joint motions are coupled within the uncontrolled manifold. Right-handed participants reached to the same target under two conditions: 1) final location was certain or 2) there was a 66% probability that its position could jump to a new position. The results indicated that both arms increased motor abundance, or variance in the uncontrolled manifold, under the uncertain conditions. However, the non-dominant arm showed higher hand path variability, which was associated with lower ability to decouple movements in joint space. Although we did not apply uncontrolled manifold analysis in the current study, our findings that the non-dominant arm was less able to decouple shoulder roll from task errors suggests a similar deficit in coordination.

From another point of view, the greater ability of the dominant arm to take advantage of redundant degrees of freedom in order to produce accurate movements has been reported in other 3-D movement conditions. For example, Hore et al. (2005) studied dominant and non-dominant arm overhand throwing motions under different instructed speed conditions. Joint excursions in dominant arm throws were found to vary significantly when throw speed was changed, while non-dominant arm joint excursions were similar at all speeds (Hore, O'Brien, Watts, 2005). The non-dominant arm strategy was seen as a simple scaling technique that was less effective in generating fast and accurate throws, while the dominant arm strategy was able to exploit interaction torques at the higher speeds. In a related study, Gray et al. (2007) found, in recreational baseball players, that overarm throws with the dominant arm exploited interaction torques to a greater extent than did throws with the non-dominant arm. They proposed a greater dominant arm ability to predictively compensate for these self-generated interactions.

In the current study, shoulder joint motions for the dominant and non-dominant arms were quite different, with the dominant arm showing greater excursions that were less associated with task errors. In contrast, the non-dominant arm showed substantially less excursion along the redundant degree of freedom (z-axis). We expect that the non-

dominant arm stiffened, impeding the interaction and gravitational forces that might produce accelerations along this axis, largely through co-contraction. Indeed previous research has indicated that non-dominant arm reaching motions are produced with greater coactivation of antagonist muscles than dominant arm movements (Bagesteiro and Sainburg, 2002). Heuer reported similar effects in a finger-tapping task, in which the non-dominant hand showed significantly greater co-contraction (Heuer, 2007). In both cases, this coactivation was associated with greater task errors and variability, presumably associated with less-accurate prediction of limb dynamic interactions. In the current study, we expect that reduced excursion along the z-axis was associated with greater coactivation of non-dominant arm shoulder muscles. It is plausible that the increased excursions of the dominant arm were associated with exploitation of non-muscular dynamics, including gravitational and interaction torques. However, more research is required to specifically test these predictions.

Conclusions

We compared dominant and non-dominant coordination during a multidirection reaching task that was presented in the horizontal plane, while the arm was unsupported and moved in 3-D space. Motion perpendicular to the task-plane (z-axis) was redundant to the task. Within the task plane, the dominant arm showed lower initial direction error, measured at peak tangential hand velocity. This is consistent with previous research, suggesting the dominant controller is specialized for predictive control mechanisms that account for limb and environmental dynamics. However, both arms showed similar hand path curvatures, while the dominant arm had substantially better final position accuracies, findings that are not consistent with previous studies of planar reaching movements. We suggest that the greater hand path curvatures for the dominant arm during 3-D motion may be related to differences in optimal solutions, when gravity and additional degrees of freedom are available. Indeed, previous studies have reported similar differences in hand-path curvatures during 3-D movements (Atkeson and Hollerbach, 1985; Desmurget et al., 1997; Lacquaniti et al., 1986). We also showed that components of task error were highly correlated with non-dominant arm shoulder roll, which produced hand excursions along the redundant z-axis. This was not the case for the dominant arm, which better dissociated task errors from shoulder roll excursion. We suggest that the lower redundant axis excursion of the non-dominant arm may reflect stiffening through coactivation and modulation of reflexes (Bagesteiro and Sainburg, 2002; Mutha and Sainburg, 2009). Non-dominant arm excursions along the z-axis, therefore, are likely to reflect errors in control. In contrast, the larger dominant arm excursions along the redundant axis are dissociated from task errors and might reflect a control strategy that takes advantage of gravitational torques and the additional degrees of freedom available in this minimally constrained task. These findings are consistent with the proposition of a dominant controller that is better adapted for predictive mechanisms, including specifying movement direction and accounting for limb and environmental dynamics, and a non-dominant controller that stiffens to impede the effects of such dynamics on limb motion.

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