THE DYNAMIC DOMINANCE HYPOTHESIS AS A GENERAL THEORY OF HUMAN MOTOR CONTROL

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by

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Abstract

The role of lateralization in the control of human motion is difficult to assess. Laterality of skilled control, or handedness is a readily observable yet incompletely understood facet of human control of the upper extremity. Despite the ease with which hand preference is identified, the specific mechanisms producing these differences in control are difficult to integrate into existing models of control. The Dynamic Dominance hypothesis of human motor control, builds a general theory of human motor control from descriptions of the lateralization of hand and arm control. The Dynamic Dominance hypothesis stipulates that the advantage displayed by the dominant limb is in the anticipation and utilization of the dynamics of movement across multiple segments. Additionally the Dynamic Dominance hypothesis proposes that the non-dominant arm has an advantage for specifying limb postures, which often results in advantages in final position accuracy. Further these advantages are due to the lateralization of neural circuits specialized to regulate different aspects of movement. Importantly, the Dynamic Dominance hypothesis proposes that movement of each arm relies on both contralateral and ipsilateral cortex to supply different aspects of control.

The studies presented in this dissertation explore the generalizability of Dynamic Dominance as a model of control. These studies address three specific limitations of past work. First, since Dynamic Dominance was developed based upon data collected from constrained, planar reaches, we wished to test how well the hypothesis generalized to conditions in which gravity must be accounted for. Second, we tested the feasibility of a simple control model that simulated the discrete contribution of the two proposed hemisphere mechanisms to control to of a single movement. We were particularly interested in the ability of such a model to describe the differences in control observed in dominant and non-dominant arm movements. Finally, we examined predictions of how each hemisphere is activated during unilateral reaching. Based upon the control requirements of the task, we predicted the activity over specific areas of cortex, based
upon Dynamic Dominance. These studies extend our understanding of lateralization of the human motor control system.
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Chapter 1: Introduction

Historically researchers have approached basic motor control, and motor lateralization as separate phenomena. This results from a perspective that the non-dominant system is simply a deficient analog of the dominant system. Recent evidence has suggested that the non-dominant system is in fact specialized for different features than the dominant system, and that both dominant and non-dominant elements act during the control of both arms. The Dynamic Dominance hypothesis is a theory of human motor control that serves to integrate these new perspectives on lateralization with a complete theory of control. In the context of this theory, the lateralization of the motor system provides insights into the mechanism of overall control. The goal of this dissertation is to test specific predictions of the Dynamic Dominance hypothesis for movements made under unsupported conditions, for electrophysiological recruitment, and to formalize the model, computationally.

The rest of this chapter is devoted to a discussion of human motor control during reaching movements, and the lateralization of this control by arm. The next three chapters are formatted as stand-alone manuscripts, which present three studies aimed at exploring human motor lateralization in the context of Dynamic Dominance. The second chapter is devoted to a study that examines the control of dominant and non-dominant arm reaching in an unconstrained environment. This study explores whether the Dynamic Dominance hypothesis, which was formulated primarily using data from studies of planar reaches, generalizes to motions involving free reaching where the effects of gravity may affect motor control. The third chapter is devoted to a study that examines how the two hemisphere controllers might be integrated for unimanual control, in a manner that can simply reproduce the lateralization effects observed in real reaches. We use a series hybrid model to control individual reaches, and the transition between elements determines path kinematics. The fourth chapter is devoted to a study exploring the cortical
electrophysiology that arises during a task that evokes interlimb differences in coordination consistent with the Dynamic Dominance hypothesis. Electroencephalographs are used to measure the cortical potentials over motor areas, and to explore the changes in these potentials with a set of movements that produce coordination asymmetries between the arms.

**Reach Planning**

During the planning of a reaching movement substantial evidence suggests that there are at least three phases to the planning of the reach (Cohen and Anderson 2002; Kawato et al. 1988). The first is transformation of visual information regarding the target of the reach into kinematic information about the desired method of task completion in extrinsic space (Imamizu et al 1998; Rosenbaum 1980). The second is formulation of a kinematic sequence, which maps the extrinsic specification of task onto intrinsic parameters of the effectors utilized to complete the task, such as joint space (Ghez et al. 1989; Kawato 1999). And finally, there is the transformation of this kinematic sequence into the kinetic parameters required to produce the desired kinematics (Kawato et al. 1990). Within the motor cortex there appear to be pools of neurons that subserve these processes, and are active in patterns distinctly correlated with movement kinematics and kinetics (Georgopolous et al. 1986; Grammont and Riehle 2003; Moran and Schwartz 1999; Sergio et al. 2005), although it is not clear that these pools are entirely distinct (Mussa-Ivaldi 1988; Sergio et al. 2005).

This diverse array of processes present a challenge for researchers, as observed kinematic effects may relate to any of these processes. To resolve this researchers have attempted to isolate factors contributing to the planning of movements by varying the extrinsic (Krakauer et al. 2000; Shabbott and Sainburg 2009) and intrinsic (Imamizu et al. 1998; Sarlenga et al. 2009) task requirements, and observing adaptation of the motor system. While much research is directed at all of these facets of motor planning and execution, this dissertation will focus on the translation
of a kinematic plan for movement, into a kinetic representation allowing accurate control of the muscular plant.

**Phases of a Reach**

Woodworth in 1899 first elaborated two mechanisms of motor control that can be temporally dissociated to different phases of a single motion. These mechanisms are: predictive and error correcting control. Woodworth ascribed predictive control to the early movement prior to peak hand velocity, and error correcting processes to the late movement following peak velocity. Many subsequent studies focused on characterizing these processes in more detail (Carlton 1981; Keele and Posner 1968; Shabbott and Sainburg 2008). In its most restricted sense, the predictive phase can only describe the first 100 milliseconds of motion, prior to the effects of movement-dependent reflexes, and feedback related modulation of motor output. While reflexes in human forearm muscles can have muscle activation latencies as low as 25 milliseconds (Eccles and Sherrington 1931; Sherrington 1906), electromechanical delays extend the predictive phase substantially. Additionally, the predictive phase appears to be prolonged by the inhibition of feedback processes during the initial acceleration phase of motion (Fabian et al. 2009; Shapiro et al. 2004). These predictive mechanisms are particularly evident because they tend to account for dynamic contingencies of movement, such as the effects of linked-segment mechanics (Brown et al. 2003; Sainburg et al. 1995) and gravitational loads (Papaxanthis et al. 1998; Papaxanthis et al. 2005).

In cases where there are substantial errors in movement, the predictive phase of motion will rapidly give way to error correcting processes. While movement dependent feedback can influence movements early in the trajectory (Carlton 1981; Johnson et al. 2002; Shabbott and Sainburg 2008; Soechting and Lacquaniti 1983), recent work has focused on the active modulation of position and velocity dependent impedance to stabilize posture at the end of motion (Sainburg et al. 1999; Scheidt and Ghez 2007). This is reflective of the idea that feedback
control of within movement errors is used primarily in the later stages of movement as Woodworth suggested.

**Impedance in Motor Control**

The term impedance is commonly used in motor control to refer to feedback driven regulation of limb state. The popularity of this concept stems largely from the ease with which a common understanding of impedance may be utilized to describe certain aspects of human movement. Unfortunately it is not always explicitly clear what is meant by the terms impedance or stiffness, and in fact the usage of these terms within the field of motor control may be at odds with usage in other fields (Latash and Zatsiorsky 1993). The following paragraphs will attempt to describe the usage of the term impedance within the field of motor control.

Casually, impedance may be thought of as the reaction or resistance of a mechanism to kinematic perturbations. This statement would indicate that impedance might be thought of simply as a load, force or torque, produced by a given mechanism in response to deviations from a desired kinematic path or position. More commonly, however, the term impedance is used to refer to the relation between deviations and the load response of the mechanism (Hogan 1985a). In the motor control literature, the most commonly used model of joint impedance is a second order linear model (Burdet et al. 2006; Hogan 1985b; Zhang et al. 1998), which contains position dependent and velocity dependent terms. This second order linear model is sometimes referred to as the KBI model of impedance due to the common use of the variables K for stiffness, B for velocity dependent damping, and I for inertia (Popescu et al. 2003). This type of model presumes that the positional and velocity dependent terms can accurately be modeled as linear, or at least controlled in such a manner as to appear linear. Such models neglect the well-described nonlinearities in muscle mechanical properties (Evans and Hill 1914; Gordon et al. 1966; Hill 1938; Ramsey and Street 1940), in favor of presenting a simplified model of limb mechanics. Even accepting that the tissue mechanics may be linearized in this fashion, this model is a gross
simplification, as it is known that approximate joint stiffness measures can vary not only within a movement (Burdet et al. 2000; Gomi and Kawato 1997), but can also change in accordance with external factors such as anticipation of a variable perturbation (Franklin et al. 2007; Lametti et al. 2007; Wong et al. 2009), and can even vary with factors of the perturbation itself, such as perturbation length and velocity (Heckman and Rhymer 2008; Lin and Rhymer 2000; Zhang et al. 1998). Further, this formulation of impedance is constant with regard to perturbation frequency, which is at odds with definitions of the term that may be found in electrical engineering or mechanics. Some groups characterizing the damping characteristics of the human arm when exposed to high frequency vibrations have used a complex formulation of the linearized equations to reflect frequency dependence of stiffness and damping in the human arm system (Gurram et al. 1995; van der Helm et al. 2002). However, such considerations are rare in the context of motor control.

In many cases, researchers have been interested in the change in impedance under certain task conditions. In these cases, changes in estimations of linearized limb stiffness and damping are frequently taken as substitutes for changes to the true impedance. Presuming that limb configuration is similar between conditions, this may be acceptable, as the inertia of the limb would not be expected to change. In many cases, researchers have utilized stiffness alone to assess changes in impedance, and neglected the damping and inertial components of impedance (Burdet et al. 2001; Franklin et al. 2004; Osu et al. 2004). While inertial components of impedance will be relatively constant within a small range of limb postures, and might therefore be ignored when attempting to measure changes in impedance, the validity of neglecting damping terms is less clear, as the damping coefficient does co-vary with stiffness in some instances (Zhang et al. 1997).

Also noteworthy are cases where reflex action is distinguished from general impedance elements (Hogan 1984; Vlugt et al. 2002). In general, reflexes are presumed to contribute to limb impedance, and indeed reflexes are known to linearize and smooth the stiffness response of
muscle when compared with deafferented muscle (Heckman and Rymer 2008). This is advantageous for linear formulations of impedance. However, reflexes are most effective when compensating for low frequency perturbations because the latency between stimulus and response can cause undesirable oscillations during high frequency perturbations. Many groups therefore elect to distinguish reflex impedance from the impedance due to muscle tone, tissue properties and inertia (Dewald et al. 1996; van der Helm et al. 2002). Investigation of this distinction reveals that the human motor system significantly modulates impedance in the absence of, or distinctly from, changes in reflex thresholds and/or gains. This modulation of impedance is accomplished by selectively modulating co-contraction during movement (Hogan 1984). The elevated muscle activation during co-contraction serves to increase the stiffness and damping of the contracted muscles. This is particularly advantageous in situations where high frequency perturbations are expected, allowing for more effective resistance to undesirable movements than available utilizing reflexes.

The particular disadvantages of reflexive strategies lead to the question of why the human motor system relies on stretch reflexes rather than simply increasing impedance under all conditions. The primary reason may be the energetic cost associated with constant co-contraction (Franklin et al. 2004). Reflexes, such as the stretch reflex, might only produce muscle activity during perturbations from a set position. Comparatively, co-contraction strategies likely incur a significant elevation in metabolic cost. Given the energetic differences, reflexes may be more adaptive than coactivation if the chance of a perturbation occurring is low, or if the perturbation dynamics are such that there is a low cost associated with waiting for reflexes. In addition to the metabolic costs, constant elevation in muscle activation may cause more rapid fatiguing of muscles. Muscle fatigue, when severe enough, can reduce the ability to co-contract and increase the variability of force output, potentially impacting task success (Missenard et al. 2008).

Whether or not reflexes are included as a fundamental part of the impedance control schema, the human motor system relies heavily on expectations of future perturbation in order to
establish the limb impedance for a given task. Tasks for which a subject has relatively low expectation of being perturbed, or the perturbation is predictable, have low impedance to perturbations (Popescu et al. 2003). In tasks where there is a high incidence of perturbation and perturbation is unpredictable, the human motor system utilizes higher impedance to reduce the effects of perturbations (Franklin et al. 2007; Lametti et al. 2007; Wong et al. 2009). This distinction between the behavior of the human system and theoretically ideal behaviors highlights the trade off between task accuracy and other factors like fatigue and energy expenditure.

While many researchers pose predictive and reflex mechanisms as distinct processes, proponents of the equilibrium point hypothesis (Bizzi et al 1972; Feldman 1986) postulate that the whole movement is under proprioceptive feedback control. This theory provides some conceptual advantages, particularly with regard to the simplicity of the model. Rather than model the limb dynamics in an attempt to predict inertial effects, proponents of the $\lambda$ equilibrium point hypothesis propose that the central nervous system simply generates a sequence of equilibrium states about which proprioceptive reflexes are set. Stretch reflexes in the muscles then drive the limb towards this equilibrium state (Feldman 1986). An alternative formulation of the equilibrium state is termed the $\alpha$ model, in which the system co-contracts the agonist and antagonist muscles, and the ratio of activity in these muscle groups will define an equilibrium state (Bizzi 1978; Polit and Bizzi 1978). The segregation of these two models of equilibrium control corresponds to the distinction made previously of general limb impedance and reflexive impedance.

This model is noteworthy in that it does not require a transition from predictive to error correcting processes. Without specific considerations for limb dynamics present in mechanical models of the limb, the inertial mechanics of motion will drive the limb away from the reference trajectory. Therefore, a special trajectory of reference configurations is constructed to limit the appearance of dynamic effects on the kinematics of the effector. In order to construct the correct reference trajectory to produce a desired motion there must be some mapping from desired
trajectory to the required reference trajectory. It would appear that such a mapping would require
that the central nervous system account for the nonlinearities of the specified impedance, as well
as the expected inertial dynamics, which mitigates much of the perceived simplicity of
equilibrium control models.

**Internal Models**

In contrast to pure impedance models of control, proponents of internal models suggest
that control may be affected by maintaining an internal model of the limb mechanics. Researchers
typically consider two separate elements for the forward and inverse models (Bushan and
Shadmehr 1999; Desmurget and Grafton 2000; Miall and Wolpert 1996; Wolpert and Kawato
1998), expecting that these two features are served by different neural substrates. The appropriate
control is predicted from the desired kinematics by inverting the limb model, while corrections to
observed errors are enabled by forward modeling of the expected state. This scenario allows the
controller to compensate for any dynamics that are predictable by the inverse model. This view of
control is supported by studies demonstrating adaptation to, and aftereffects of, a number of
perturbing fields, such as coriolis force fields (Lackner and Dizio 1994), inertial effects of applied
masses (Sainburg et al. 1999), and visuomotor rotations (Krakauer et al. 2000; Sainburg and
Wang 2002; Wang and Sainburg 2005). These studies show not only adaptation to the
perturbations, but substantial aftereffects, which would not be anticipated from simple changes in
an impedance strategy. These effects suggest that whatever control system is utilized, it
anticipates and compensates for predictable perturbations, such as external force fields or the
inertial dynamics of the limb. Such control appears to rely heavily on sensory information about
limb kinematics in order to maintain proper models of limb mechanics. Indeed, patients without
proprioception are unable to predictively account for the inertial dynamics of the limb (Sainburg
et al. 1993, Sainburg et al. 1995). This degradation in the ability of the nervous system to model
limb state, implies that there is a constantly maintained model of the system, which degrades over
time if not maintained. One interpretation is that this degradation relates to the manner in which these models are updated to reflect new dynamics in healthy individuals, reflecting the normal adaptation of these models based upon proprioceptive feedback.

The output of control based upon internal models lacks any inherent facility for correcting kinematic errors that develop during the course of movement. Instead, when errors are assessed, a new kinematic plan, with associated kinetics must be constructed and implemented to effect a correction to the trajectory (Desmurget and Grafton 2000). Consequently if the human system utilizes such a scheme to produce controlled motion, there must be a transition from the control output of the internal model to an error correcting strategy like impedance control to correct on the fly errors and to stabilize posture at the end of movement. This means that while predictive control based on internal models can explain many aspects of human movement, they likely do not represent a general model of human motor control.

Hybrid Control

While impedance control and internal models are often posed as mutually exclusive solutions to the problem of control, it is feasible to combine the two mechanisms into a single hybrid strategy. Indeed the phases of movement described by Woodworth offer a simple schema for such integration (Woodworth 1899). Woodworth’s description of an initial predictive phase would correspond well to the predictive mechanism based on internal models, whereas the postural phase, with its reliance on feedback, might correspond well to a model equilibrium description of control. This description then formats human motor control as the sequential application of predictive control with closed loop control (Hirayama et al. 1993; Gottlieb 1996; Sainburg et al. 1999; Scheidt and Ghez 2007; Yadav and Sainburg 2011). Such a control model has a number of advantages including the conceptual simplicity of ascribing a discrete form of control to the open and closed loop phases of movement, rather than attempting to formulate a monolithic controller which accounts for both aspects of control.
An alternative mechanism for combining predictive and error correcting control schemes is a model of impedance control wherein the primary motivation for movement is supplied not by the impedance controller as is suggested by equilibrium control strategies, but by an anticipatory control strategy. The impedance of the limb is then specified relative to the desired limb state at any point in the movement, effectively acting only when the movement deviates from the kinematics planned by the anticipatory controller (Hogan 1985a; 1985b; 1985c). Such a scheme has the advantage of only engaging corrective mechanisms when errors in the movement kinematics are present. The disadvantage of such a scheme is that both the predictive and error correcting controllers must be active concurrently. This adds conceptual complexity when compared with the scheme of sequential application of the two control modes. Further, such a scheme does not implicitly account for the observation that reflexes are suppressed early in a movement (Fabian et al. 2009; Shapiro et al. 2004), while this is true by definition in a sequential scheme. In this type of impedance specification it would be feasible to simply stipulate that impedance to deviations from the desired kinematics would be low early in the movement. However, the advantage of this view over the serial scheme is unclear, as the gain on each controller would effectively impose a serial order to control.

**Lateralization of Motor Control**

**Behavioral Lateralization**

The lateralization of skilled control, or handedness is a readily observable yet incompletely understood facet of human control of the upper extremity. Despite the ease with which hand preference is identified, the specific mechanisms producing these differences in control remain difficult to describe. Dominant limb movements tend to display straighter hand paths (Bagesteiro and Sainburg 2002; Sainburg and Kalakanis 2000), as well as more consistency in performance over many trials (Hore et al. 1996; Todor and Kyprie 1980). In contrast to these differences the non-dominant limb tends to display similar (Bagesteiro and Sainburg 2002;
Sainburg and Kalakanis 2000), or even better (Goble et al. 2009; Lenhard and Hoffmann 2007; Wang and Sainburg 2007) final position accuracy than the dominant limb.

Early attempts to describe interlimb differences in control attempted to differentiate planning mechanisms from feedback mediated error correction mechanisms by examining the kinematics of rapid reaching. The reaction time under such paradigms was presumed to reflect the duration of the predictive planning of a movement. The observation of lower reaction times in the non-dominant arm lead to the hypothesis that the non-dominant arm had a particular advantage for planning movements (Carson et al. 1990; Carson 1992; Carson et al. 1995; Elliott et al. 1993). Smaller times spent in the late phase of movement, from peak velocity to end of movement, were presumed to reflect the efficiency of using error information for ongoing control of the movement (Flowers 1975; Carson et al. 1993; Todor and Cisneros 1985). In these studies, the advantage of the dominant limb in utilizing feedback was inferred from the measures of kinematic consistency and path straightness.

In an attempt to test these ideas, some studies limited vision of subject’s movement, which should result in diminished dominant arm accuracy due to its presumed superior feedback control. However, these studies failed to support this prediction (Carson et al. 1990; Roy and Elliott 1986). Further, in primarily ballistic movements, the limb with more adept predictive control should make smaller errors and thus require shorter correction times. In the context of this conclusion, we may describe the dominant limb advantage in kinematics in terms of an advantage in movement planning. Longer reaction times then result from reliance on more sophisticated but slower control schemes, which reflect a dominant limb advantage in planning and predictive control rather than in feedback control, as previously proposed (Annett, et al. 1979; Roy and Elliott 1986).

Given this description of kinematic lateralization it makes sense to describe the kinetic lateralization of control in the context of predictive control of movement. The hypothesis that handedness might be characterized by dominant limb advantages in the predictive planning of
movements, leads to the prediction that the kinematic differences between the limbs will vary with the dynamic complexity of the movement. To accurately generate predictive control, the system must account for the fact that forces generated by the musculature must interact with other internally generated forces, such as those arising from deformation of non-contractile tissues such as ligaments and cartilage, and external forces such as those applied by gravity and interactions with tools. Further, the dynamic effects of motion at each segment, quantified as interaction torques, can substantially impact motion of the other limb segments. While the internal effects of nonmuscular tissues are problematic to assess, measurements of kinematics allow for the reconstruction of the kinetics of movement, and consequently the assessment of these interaction torques. As these effects are due to the velocity and acceleration of segments, they are particularly prominent in rapid movements like ball throwing, that are strongly lateralized tasks (Hore, et al. 1996). These interaction torques can contribute substantially to the total torque at a joint, matching or exceeding the torques contributed by the musculature (Bagesteiro and Sainburg 2002; Hollerbach and Flash 1982; Sainburg and Kalakanis 2000). In studies where the interaction torques are deliberately varied, the non-dominant limb shows deviations in trajectory that vary with the magnitude of the interaction torques (Sainburg and Kalakanis 2000). Further the dominant limb appears to utilize the interaction torques in order to reduce the required contribution from the musculature (Bagesteiro and Sainburg 2002; Sainburg and Kalakanis 2000). These observations are consistent with a dominant limb advantage in predicting and compensating for the inertial dynamics of movement.

Despite the popular view that the non-dominant limb is simply deficient compared to the dominant limb, there are certain cases where it displays substantial performance advantages. When the non-dominant arm is perturbed by an unexpected inertial load, it displays rapid and accurate online movement corrections, resulting in movements that terminate more accurately than those made by the dominant arm. In fact, the dominant arm response is often maladaptive, increasing the overall final position error (Bagesteiro and Sainburg 2003; 2005). In addition, the
non-dominant arm adapts to novel dynamic conditions by increasing limb impedance, while the dominant limb adapts by anticipating the imposed forces and compensating for them before errors are introduced into the movement (Schabowski et al. 2007; Duff and Sainburg 2007). These findings indicate that the non-dominant limb is actually more proficient than the dominant limb in correcting errors, and more prone to utilizing an impedance strategy than the dominant limb. This suggests that the non-dominant limb may be specialized for impedance control when compared with the dominant limb.

Taken as a whole these findings indicate that lateralization in the upper extremity is the result of each limb specializing in a different type of control. The dominant limb appears to be specialized for the anticipatory control of limb dynamics. The advantages displayed by the dominant limb during unperturbed reaching, and steady state adapted reaching, are consistent with this hypothesis. In contrast, the non-dominant limb appears to be specialized for feedback mediated impedance control. This is consistent with a non-dominant limb advantage in correcting errors due to perturbations, as well as the observations of less constrained kinematics during movement.

**Neural Lateralization**

While a plethora of investigative techniques have been employed to measure the differences in kinetics and kinematics of movement across limbs, it is often very difficult to record differences in neural activity simultaneous with these measurements. Techniques such as EEG and fMRI are extremely sensitive to artifacts caused by gross movements such as the elbow and shoulder rotations undertaken as part of a rapid reaching motion. As a consequence most studies measuring lateralization of neural activity during movement focus on fine movements of the fingers and wrist.

In fMRI studies movements of the fingers tend to recruit larger areas of M1 cortex in dominant limb movements than non-dominant (Dassonville et al. 1999; Kawashima et al. 1993;
Krings et al 1997) and EMG (Volkmann et al. 1998), however, this is not consistent across all tasks (Baraldi et al. 1999; Janke et al. 1998; Kim et al. 1993). Similarly, when considering the magnitude of signal changes, some studies have reported greater changes during dominant limb movements (Halsey et al. 1979; Kawashima et al. 1993), while others show greater changes during non-dominant movements (Baraldi et al. 1999). Analyses of these findings with regards to the control of motion is further complicated by the fact that it is unclear what processes are reflected in these measures. A greater active area is not necessarily representative of a more diffuse neural pool, as one would expect such sparseness to result in reduced signal to noise ratio and a reduced chance for detecting activity. Similarly greater amplitude in the observed signal could reflect either a more developed pool of neurons acting synchronously on a task, or a less developed pool working harder to compensate for their deficit. Interpreted in the context of the mechanical asymmetries described in the preceding section, the broader area of contralateral M1 that is active during dominant limb motions may be reflective of a more integrated model of the dynamics of the limb. This would be sensible, as accurate predictive control at any given joint would need to be aware of the output at other joints, resulting in less discrete mappings of joints than one would expect from classical mappings of motor cortex described by the homunculi. The greater amplitude of activity observed during dominant motions might reflect the activity in more developed circuits associated with the greater coordination displayed by the dominant limb. This view is supported by studies that observe greater activity amplitude during more complex tasks (Lotze et al. 2000), and lower activity in more skilled individuals (Kristeva 1984). These findings indicate that activity is related to the difficulty of the task as well as the individual subject’s skill in the task, rather than purely reflecting the degree of lateralization of his/her cerebral cortex. As a consequence, it is difficult to draw conclusions regarding lateralization of cortical circuits purely from these data. These data must therefore be measured and interpreted in the context of behavioral studies.

While “knockout” models of motor cortex in humans are not feasible due to ethical
concerns, patients with cortical stroke may serve as an approximation of a knockout group. Studies of unilateral stroke subjects have shed substantial light upon the nature of motor lateralization as well as the structure of unimanual control. In studies of reaching with the arm ipsilateral to the lesion, hemiparetic patients with dominant (left) hemisphere lesions move in a manner consistent with an inability to account for the inertial dynamics of the limb, especially during the early phases of the trajectory (Schaefer et al. 2007; 2009a; 2009b; 2011). Despite this deficit, the final hand position of this group remains accurate, and in some cases even shows advantages over the intact age-matched control group. It is clear then that the right hemisphere is able to effectively control final limb posture, even while failing to predictively account for inertial dynamics. In contrast, hemiparetic subjects with right hemisphere lesions show adept coordination of ipsilesional limb inertial dynamics. These subjects have a tendency to produce fairly straight hand paths. Despite being able to control hand path kinematics quite well, both movement accuracy and precision were deficient relative to both their age-matched controls and left hemisphere damaged patients. Recently these findings have been extended to show similar deficits in the contralesional arms of patients without hemiparesis (Mutha et al. 2011). Further, the location of these control features has been traced to the frontal cortex of right hemisphere damaged patients, and the posterior parietal cortex for left-hemisphere damaged patients. These findings support the hypothesis that performance advantages in the dominant and non-dominant limb reflect the aspects of control that have become lateralized to that arm’s contralateral hemisphere, rather than some difference in peripheral mechanics, or spinal level neural circuitry.

One additional finding of note in these stroke studies was that the deficits in coordination for left hemisphere damage, and error correction for right hemisphere damage, were observed in both the ipsilesional and the contralesional arms of the subjects. Historically control of a limb has been viewed as a primarily contralateral phenomenon (Geschwind 1975; Goldenberg 2003; Liepmann 1905; Taylor and Heilman 1980). This view has been perpetuated due largely to the contralateral preponderance of the descending corticospinal tracts (Brinkman and Kuypers 1972;
Kuypers and Brinkman 1970; Kuypers 1982). The finding that ipsilateral cortex is involved in normal control of the arm forces a new perspective on the control of unimanual reaches. Neural activity associated with control of reaching occurs in both hemispheres and is integrated in healthy subjects. This integration produces movements that both account for the limb dynamics and perform online correction for errors in planning.

**The Dynamic Dominance Hypothesis**

The Dynamic Dominance hypothesis stipulates that the advantage displayed by the dominant limb is in the anticipation and utilization of the dynamics of movement across multiple segments. This is in contrast to earlier theories of lateralization, which proposed dominant advantages in feedback utilization. Similarly the Dynamic Dominance hypothesis proposes that the non-dominant arm has an advantage for the control of postural errors, most notable in the final limb state. These elements of the hypothesis are based upon the observations of mechanical coordination (Bagesteiro and Sainburg 2002; Sainburg and Kalakanis 2000), and error correction (Bagesteiro and Sainburg 2003; 2005) noted previously. Further, these advantages are due to the lateralization of neural circuits specialized to regulate these aspects of movement. The neural circuits primarily involved in prediction and compensation for limb dynamics are located in the posterior parietal cortex that is contralateral to the dominant hand, while the circuits involved in feedback correction of final position are located in the posterior frontal cortex ipsilateral to the dominant hand. This claim derives from the performance studies in stroke subjects (Schaefer et al. 2007; 2009a; 2009b; 2011; Mutha et al. 2011). Finally the Dynamic Dominance hypothesis proposes that movement of each arm will rely on ipsilateral cortex to supply the elements of control for which the contralateral cortex is deficient.

This theory serves to integrate the lateralization of movement into a coherent part of a more general schema for motor control. Since the lateralization inherent in the motor control system is fundamental to the Dynamic Dominance description of control, there is no need for
additional explanation as is the case in the case of most formulations of internal models or impedance strategies. This need for additional explanation commonly results in the assumption that the non-dominant hemisphere is simply a deficient copy of the dominant controller, which neglects the advantages of the non-dominant limb in perturbation correction.
Chapter 2: Dynamic Dominance Persists During Unsupported Reaching

Introduction

Handedness is a readily observable yet incompletely understood facet of human control of the upper extremity. Given the mechanical similarities between the dominant and non-dominant limb, handedness is generally considered to be the result of asymmetries in the neural control of the two limbs. However, the specific mechanisms that give rise to the differences in observed behavior remain controversial.

Early attempts to investigate interlimb differences in control examined kinematic parameters of rapid and brief 'ballistic' movements, in an attempt to differentiate planning mechanisms from feedback mediated error correction mechanisms. Such movements were presumed to be so brief that little to no feedback mediated corrections occurred. Measures such as reaction time, movement time and final accuracy of ballistic movements were presumed to reflect planning of the movement. The distinction between planning and error correcting control schemes in handedness was also reflected in studies investigating the role of precision requirements of rapid reaches under controlled visual feedback conditions (Carson et al. 1993; Elliott, et al. 1994; Flowers 1975; Steingruber 1975; Todor and Cisneros 1985). However, attempts to differentiate the effects of sensory feedback on control of the dominant and non-dominant limbs have provided little coherent insight into the mechanisms that give rise to handedness (Carson, et al. 1990; Carson 1992; Carson et al. 1993; Elliott, et al. 1993; Elliott et al. 1994; Flowers 1975; Roy and Elliott 1986; Roy, et al. 1994; Todor and Cisneros 1985). Manipulations of target information prior to movement onset yielded longer reaction times in the dominant arm than the non-dominant, suggesting some differences in movement planning (Carson et al. 1990; Carson 1992; Carson, et al. 1995; Elliott et al. 1993). Initial hypotheses that
these differences reflected a lateralized advantage in the integration of visual feedback (Flowers 1975) were not supported by studies occluding vision during task execution (Carson et al. 1990; Roy and Elliott 1986), suggesting that the difference may lie in the differential ability of the two hemispheres to plan movements. These differences are difficult to interpret in a manner that grants insight into the mechanisms of control, and it should be stressed that while longer reaction times could reflect inefficient planning, they might also reflect more sophisticated planning that produces better control, at the expense of planning time. Similarly, dominant arm advantages in movement accuracy might be accounted for by multiple mechanisms. For instance, some researchers suggested that the dominant limb has advantages in error correcting mechanisms, resulting in straighter, more accurate, hand paths (Carson et al. 1993; Todor and Cisneros 1985); while others suggested that the dominant limb had an advantage in initial movement planning, rendering less corrections necessary (Annett, et al. 1979; Roy and Elliott 1986).

Taking the approach that handedness might be characterized by interlimb differences in coordination, we previously investigated how each arm coordinated muscle activity and muscle-related torques with non-muscle forces, such as limb interaction torques during movements (Bagesteiro and Sainburg 2002; Sainburg and Kalakanis 2000). The mechanics of the human arm can yield insights into the control strategies that produce specific patterns of behavior. Forces generated by the musculature must interact with other internally generated forces, such as those arising from deformation of non-contractile tissues such as ligaments and cartilage, and external forces such as those applied by gravity and interactions with tools. Further, the dynamic effects of motion at each segment, quantified as interaction torques, can substantially impact motion of the other limb segments. As these effects are due to the velocity and acceleration of segments, they are particularly prominent in rapid movements like ball throwing, that are strongly lateralized tasks (Hore, et al. 1996).

Our previous studies on horizontal plane reaching movements indicated that dominant arm coordination is characterized by efficient coordination of muscle torques with intersegmental
interaction torques, while the non-dominant arm shows less efficient coordination strategies. Our Dynamic Dominance Hypothesis describes the advantage of the dominant limb in predicting the dynamic effects of motion in order to produce efficient movements (Sainburg 2002), and advantages of the non-dominant arm for achieving and maintaining positional stability (Bagesteiro and Sainburg 2003; Duff and Sainburg 2007; Wang and Sainburg 2003). This hypothesis stems from studies demonstrating that the coordination of non-dominant limb movements varies with the dynamic forces arising from the motion of segments. In contrast the kinematics of the dominant limb are relatively unaffected by these forces (Bagesteiro and Sainburg 2002; Sainburg and Kalakanis 2000). This suggests that the dominant controller employs a more sophisticated mechanism to develop the desired output of the muscular plant, one that accounts for dynamic aspects of movement which are not well accounted for in non-dominant arm coordination. While the kinematics of the limbs vary during task execution, the final performance assessed by radial distance from the target position tends to be similar across limbs (Sainburg and Kalakanis 2000; Sainburg 2002; Shabbott and Sainburg 2008), suggesting corrective or postural stabilization mechanisms in the non-dominant limb that are at least as proficient as those in the dominant limb.

Our previous research on handedness was carried out predominantly with reaching movements constrained to the horizontal plane, and with the limb supported in air sleds. This arrangement allowed for the experimental control over limb mechanical requirements, and had the advantage of preventing subject fatigue. However, it is plausible that our findings for horizontal plane movements may not generalize to unsupported movements made in the vertical plane, due to systematic mechanical differences between movement conditions. For example, it has been suggested that the temporal extent of a movement, or the speed, may be altered by simply scaling pre-computed torques that produce the desired path kinematics (Hollerbach and Flash 1982). In this schema, torques are scaled by a factor that varies as the square of the movement velocity. In an environment without gravity such a scaling will produce movements
with similar trajectories, at a variety of velocities. Gravitic torques however, are unaffected by movement velocity, varying only with limb configuration and orientation. Consequently one might expect that a system that takes advantage of such simple scaling must treat gravity specially in order to preserve spatial features of movement paths. Further, in studies of free reaching with the dominant limb, subjects have been shown to take distinctly different paths with and against gravity, despite covering the same space (Gentili, et al. 2007; Papaxanthis, Pozzo, Vinter and Grinshin 1998). While this might be the result of altered kinetic requirements of reversing the direction of movement, removal of gravity disrupts these paths only transiently (Papaxanthis, Pozzo, Popov and McIntyre 1998; Papaxanthis, et al. 2005). The invariance of path to external loading suggests that subjects are using gravity as an orientation, and planning different kinematics based on this reference rather than incompletely compensating for some kinematic difference. Further, the invariance of paths in gravity and non-gravity conditions suggests that gravitic torques are readily separable from internal models of limb kinetics.

In addition to the effect of gravity on the planned kinematics of movement, the motor system must accurately account for gravity in order to execute a desired kinematic plan. Many studies in the dominant limb have shown strong invariant kinematic features of free reaching movements, which are stable against changes in load, and movement speed implying that the dominant limb plans kinematic trajectories in 3d space (Lacquaniti, et al. 1982; Papaxanthis, Pozzo and Stapley 1998; Soechting and Lacquaniti 1981). The reliable execution of consistent movement plans would require a sophisticated model of the limb to compensate for the varied inertial and gravitic effects encountered under various speed and load conditions.

Given the sophistication with which the dominant limb compensates for both gravity and inertial effects, despite the clear mechanical differences in how these effects impact movement, we now ask how the non-dominant limb coordination strategy might account for the effects of gravitic torques. If the forward controller utilized by the dominant limb system treats gravity differently than inertial effects, it is plausible that the non-dominant limb utilizes the same system
to compensate gravity, despite showing deficiencies in anticipation of inertial effects, such as interaction torques.

The purpose of this study is to examine whether the Dynamic Dominance hypothesis that we had developed based on horizontal plane movements can be extended to vertical reaches under more natural movement conditions. To address this, we compare the performance of the dominant and non-dominant arms of subjects while performing rapid, unsupported reaches in a parasagittal plane. Two groups of subjects performed with either the right or left hand. We used a group design, in order to prevent the effects of interlimb transfer that we had previously characterized (Bagesteiro and Sainburg 2005; Sainburg and Wang 2002; Wang and Sainburg 2004a; 2004b). To vary the effects of interaction torques at each segment, a three direction reaching task was utilized with two directions corresponding roughly to single joint movements of the shoulder and elbow and the third representing a combination of movement at both joints. To investigate the coordination of the limbs we compared torques impulses as well as the timing within the movement at which the occurrence of peak torques at the elbow and shoulder occur. We hypothesized that we would see predictable changes in the muscle torque impulse and the relative timing of the net torque in the dominant limb associated with adapting to the changing dynamic inertial loads. We further expected that the non-dominant limb would display errors associated with failure to predict systematic variations in interaction torques. Additionally we expected that the non-dominant limb, as a consequence of utilizing a less sophisticated predictive controller, would show trajectory errors consistent with failure to predict the effects of gravity on the arm. As a consequence of these differences we expected to see that the non-dominant limb displays greater path curvature, and higher errors in initial path direction than the dominant limb.
Materials and Methods

Subjects

All methods utilized in this study were approved by the Pennsylvania State University Institutional Review Board. Twelve neurologically intact right-handed adults, aged from 19 to 25 years old were tested. All subjects were screened for handedness using a modified version of the Edinburgh inventory (Oldfield 1971). All subjects gave informed consent prior to participation. Subjects were randomly assigned to perform with either their dominant (right), or non-dominant (left) hands (n=6 per group).

Apparatus

Subjects were seated, with a mirror placed in the parasagittal plane at the performing shoulder and a LCD screen placed in the parasagittal plane at the non-performing shoulder (Figure 2.1). A cursor displaying finger position, a start circle and a target were displayed on the screen. Cursor movements on the screen were calibrated such that cursor location was veridical to actual finger location. Subjects were instructed to look at the mirror so that the cursor appeared to be at the finger location, while vision of the hand was occluded by the mirror. The wrist and fingers were splinted to restrict the task to two-segment motion. Orientation and position of the upper arm and forearm were collected using a flock of birds 6-DOF movement recording system (Ascension Technology). Sensors were attached to the back of the hand over the palm, and approximately centered on the upper arm. Digital position and orientation of the sensor were collected at 130 Hz. Fingertip, elbow and shoulder locations were computed from the raw sensor data using calibrated points collected using a stylus at bony landmarks prior to the first trial.

Experimental Task

In each trial subjects were shown one of three targets, presented in a pseudorandom sequence. The initial finger position for all three movements was set 15-20cm in front of the
shoulder, with the arm in a configuration that the subject found comfortable. The direction of movement was specified to be -45° (out and down), 0° (horizontally away from the trunk) or 45° (out and up) from the initial position. All targets were displaced from the start position by 50% of the subject’s maximum horizontal reach from the starting location.

To initiate a trial subjects were asked to center the cursor in a starting circle for 300ms, at which time they would receive an auditory cue to begin movement. Upon receiving the cue, subjects were instructed to reach rapidly to the target and stop with the cursor in the center of the target. To encourage subjects to maintain consistent performance, points were awarded for accuracy. To encourage rapid movements, subjects only received points for performance when the fingertip movement was faster than 1.5 m/s. Subjects performed 90 reaches with targets presented in a randomized order, with all subjects receiving trials in the same order. Cursor feedback was removed at the go cue and resumed after the completion of the trial. After completion of the trial, a display of the movement path was presented along with a marker indicating the final finger position. To eliminate learning effects, trials 1-30 were excluded from analysis.

**Kinematic Data**

Finger, elbow and shoulder position data were low pass filtered at 8 Hz using a dual pass 3rd order Butterworth filter. Segment angles were computed from the position data using a moving plane analysis, with the plane defined through the finger, elbow and shoulder (Schneider and Zernicke 1990). Movement start and stop were defined to be the first minima below 5% of the peak in the tangential finger velocity to either side of the main peak in the movement tangential velocity. All further analyses were performed on the data between the movement start and movement stop.

Three measures of hand path accuracy were used: initial direction error, path curvature, and final position error. The initial direction error was defined as the angular deviation between a
vector defining the instructed movement and a vector passing through the initial finger position and the finger position at peak hand velocity (Figure 2.2a). In this measure negative angles indicate that the finger path was directed lower than the actual target, while positive angles indicate that the finger path was aimed higher than the target. Path curvature was defined as the major axis of the finger path divided by the minor axis of the finger path. The final position error was the magnitude of the distance between the finger location at movement end and the target.

**Kinetic Data**

Joint torques were computed using an inverse dynamic analysis of the movement based on the kinematic segment angles. We assume here that the upper limb is composed of two rigid links attached by frictionless spherical joints. The moving plane analysis employed to generate the kinematic joint angles allows planar equations of motion to be utilized to compute the joint torques within the moving plane, thus allowing partitioning of the equations into a few terms (Schneider and Zernicke 1990). Joint torques were partitioned into net torque, interaction torque, muscle torque and gravitational torque (Figure 2.2c-d), with net torque representing the torque driving rotational acceleration of a segment, the interaction torque arising from the velocity and acceleration of the other segment and the muscle torque comprising the residual of the joint torques once the net and interaction torques are accounted for in the homogeneous form of the equations of motion. The muscle torque is the composite of not only agonist and antagonist activity, but also passive tissue properties such as stiffness and damping of the muscle tissues.

Two measures of arm kinetics were used in this study: torque impulse, and the difference in timing of peak net torque onset between the elbow and shoulder. The torque impulse was taken as the integral of the muscle and interaction torques. For this analysis muscle and interaction torques were considered positive if acting in the same direction as net torque, and negative if acting in the opposite direction. The integrals for torque impulse were computed across two ranges: from the initiation of movement up to the time of peak tangential acceleration of the
finger, and from movement start to the end of movement. The range from start to peak acceleration was selected to focus on early differences in control that might reflect differences in prediction of gravitic effects, while the whole movement range reflects previously reported measures of torque impulse that are reflective of the Dynamic Dominance hypothesis (Bagesteiro and Sainburg 2002; Sainburg and Kalakanis 2000). The timing of peak torque onset was taken as the absolute time after movement start at which the peak net torques occurred. The relative timing of elbow and shoulder peak torque was taken as the time at which the peak elbow torque occurred minus the time at which the peak shoulder torque occurred.

Statistics

Right and left hand movements were performed by two different groups (6 subjects each) of right-handers. This was done to eliminate the potential for interlimb transfer effects, which have been well documented for reaching tasks (Sainburg and Wang 2002; Wang and Sainburg 2003). All analyses were performed in the statistical processing software JMP. Measures analyzed in this study were assessed using individual 2X3 mixed factor repeated measures analyses of variance (ANOVAs), with hand (2) and target (3) as the factors, and subjects as the repeated measure. Post hoc tests were performed only in cases where an interaction between main effects was observed. In these cases, Tukey's honest significant difference tests were used to identify specific differences. To assess the relation between relative torque timing and the path kinematics, we performed simple linear regressions on each subject-target case separately for both the 0° and 45° targets. These fits were assessed for significance using an F test where the F statistic of this analysis constitutes the ratio of mean square errors described by the fit to the mean square of errors not described by the fit. Significance indicates a rejection of the null hypothesis that the model does not predict any of the observed variance in the dependent measure. As a second stage of analysis we wished to compare the regressions of left hand subjects to right hand
subjects. For this analysis we converted the slope and intercept of each regression to z-score and performed a repeated measures ANOVA to assess differences in these variables due to hand.

Results

Kinematics

Our targets were designed to require increasing amounts of shoulder motion, as target elevation increased. Figures 2.3a-2.5a depict representative limb paths for movements to each target. Stick figure representations of upper arm, forearm, and hand segments are drawn at every data point, while shoulder, elbow, and finger paths connect these segments. The relative angular dispersion of the upper arm segment reflects the shoulder angular motion for each trial. Note that the upper arm stick figures for both arms remain fairly parallel and closely aligned for the -45° target in figure 2.3a, but shows large angular displacement for the 45° target in figure 2.5a. This increase in required shoulder excursion was related to increased intersegmental coordination requirements across directions, as discussed below.

Final Position Error

While the mean final position error for both hands increased with the target angle (Main effect of Target: F(2,20)=6.39, P<0.01), there was no significant difference between the hands (Main effect of hand: F(1,10)=2.15, P=0.17), or interaction between hand and target (F(2,20)=2.93, P=0.08). Despite this, the dominant and non-dominant arms showed substantial differences in the kinematic patterns to the three targets.

Initial Direction Error

Interlimb differences in initial direction error, summarized in figure 2.6a, were driven by a hand by target interaction (F(2,20)=3.45, P<0.01), wherein the dominant arm produced movements that were, on average, directed on line with the target, while the non-dominant arm showed an increasing undershoot as target elevation increased, from -45 to 45 degrees. There was
also a main effect of hand for direction error ($F_{(1,10)}=4.80, P=0.05$), which was related to the larger errors at the 0 and 45 degree targets. For the example paths in figure 3a, the right and left paths are very similar. Note that this movement involves mostly elbow motion, with little motion about the upper arm, and no wrist motion due to the splinting. In contrast to the -45 degree direction, for the 0 and 45 degree targets shown in figures 2.4a and 2.5a, the left arm direction errors become progressively greater. In contrast to the non-dominant arm, dominant arm direction errors were unaffected by target elevation, displaying finger paths directed towards the target for all directions.

**Path Curvature**

The combination of substantially greater undershoot with similar final errors in the non-dominant hand, explains the increasing curvatures of the non-dominant finger paths across the target elevations (Figures 2.4-2.5a). As summarized in figure 2.6b, the curvature of the non-dominant limb was greater than that of the dominant limb for all target directions (Main effect of hand: $F_{(1,10)}=6.42, P=0.03$). Additionally, for both hands the curvature of the finger path increased as the target angle increased (Main effect of target: $F_{(2,20)}=31.07, P<0.01$), with greatest curvatures for both hands displayed in the 45 degree direction. There was a significant hand by target interaction for curvature (interaction: $F_{(2,20)}=3.50, P=0.05$). This reflected a greater dependence of curvature on target elevation for the left than the right hand.

**Kinetics**

Figures 2.3-2.5b depict the torques at the shoulder and elbow joints, associated with the exemplar reaches in figures 2.3-2.5a.

**Early Torque Impulse**

As expected by our target design, the amplitude of elbow muscle and interaction torque impulse varied systematically across directions, reflecting the differences in elbow excursions
required with changing target elevation. As a result, for the early impulse we found a main effect of target on elbow muscle and interaction torque impulse ($F_{(1,20)}=155.23, P<0.0001$; $F_{(1,20)}=239.03, P<0.0001$), but no effect of hand ($F_{(1,10)}=0.31, P=0.59; F_{(1,10)}=0.0074, P=0.93$), or interaction between hand and target ($F_{(1,20)}=0.55, P=0.59; F_{(1,20)}=0.79, P=0.47$). At the shoulder a similar main effect of direction was observed ($F_{(1,20)}=85.12, P<0.0001; F_{(1,20)}=17.01, P<0.0001$). Again no main effect of hand was observed for either muscle or interaction torque impulse ($F_{(1,10)}=2.10, P=0.18; F_{(1,10)}<0.0001, P>0.99$), and the interaction torque impulse showed no interaction between hand and target ($F_{(1,20)}=1.79, P=0.19$), however, the shoulder muscle torque impulse did show an interaction between hand and target ($F_{(1,20)}=3.53, P=0.05$). Post hoc testing revealed that the only comparison of hand within target which achieved significance was in the 45° direction. Figure 2.7 shows the shoulder muscle torque impulse across hands and targets, and while no significant difference was found at the 0° target, there is a visible difference between arms consistent with that observed at 45°. This may reflect a difference between hands that scales with the required shoulder joint excursion. Since the 0° direction has lower impulse requirements than the 45° direction, it is possible that in this direction, potential interlimb differences in impulse may be smaller than the intersubject variability of the data. We expect that the elevated muscle torque impulse in the dominant limb may be associated with compensation for gravity, while the relatively lower impulse in the non-dominant limb could result in an initial deficit in elevating the upper arm against gravity. This interpretation is consistent with the observed errors in initial movement direction.

**Total Torque Impulse**

The amplitude of elbow muscle and interaction torque impulse varied systematically across directions, reflecting the differences in elbow excursions required by the different target elevations. Consequently, we observed a main effect of target on elbow muscle and interaction torque impulse ($F_{(1,20)}=155.23, P<0.0001; F_{(1,20)}=239.03, P<0.0001$), but no effect of hand.
(F_{1,10}=0.31, P=0.59; F_{1,10}=0.0074, P=0.93), or interaction between hand and target (F_{1,20}=0.55, P=0.59; F_{1,20}=0.79, P=0.47). Similarly, at the shoulder we observed a main effect of target on shoulder muscle and interaction torque impulse (F_{1,20}=155.23, P<0.0001; F_{1,20}=239.03, P<0.0001), but no effect of hand (F_{1,10}=0.31, P=0.59; F_{1,10}=0.0074, P=0.93), or interaction between hand and target (F_{1,20}=0.55, P=0.59; F_{1,20}=0.79, P=0.47).

**Torque Timing**

Because of the relatively small peak torques for the -45° target, we restricted our analysis of elbow and shoulder torque relationships to only the 0° and 45° targets. We marked the timing of shoulder and elbow net torques with vertical lines in figures 2.4b and 2.5b. Note that for the right arm, elbow torque lags behind shoulder torque, with greater lag for the 45° than the 0° target. In contrast, for the non-dominant left arm, the elbow tended to act earlier relative to the shoulder at each target, even preceding shoulder peak torque in the 0 degree direction (Figure 2.4b). Figure 2.8 shows the mean shoulder-elbow peak torque timing difference across subjects. Note that the left arm difference is smaller, and negative in the zero degree direction, indicating that on average the left arm elbow peak torque either preceded that of the shoulder, or showed reduced lag, relative to that of the right arm. As a result, our ANOVA showed a main effect of hand (F_{1,10}=10.84, P=0.01), and of target direction (F_{1,10}=14.88, P<0.01), but no interaction between hand and target (2 directions) (F_{1,10}=1.75, P=0.22).

We reasoned that the effect of delaying elbow extensor torque relative to shoulder flexor torque in dominant right arm movements, was to elevate the hand toward the targets at movement initiation. In contrast, the more rapid elbow extensor acceleration for the non-dominant left arm countered hand elevation, and resulted in the initial direction undershoot, characterized above. In order to quantitatively examine the relationship between the elbow-shoulder torque timing and the kinematic differences between the hands we regressed the torque timing against initial direction error, for each subject separately. Our simple linear regression within target (Figure
showed a statistically significant correlation between elbow-shoulder torque timing differences and initial direction error ($F_{(1,30)} > 4.17$, $p < 0.05$) for all subjects. The relative timing of elbow and shoulder are clustered around discrete values (Figure 2.9). This is due to the 130Hz frequency of the data digitization, such that the smallest interval that could be resolved was approximately 7.7ms. To assess the effect of hand, intercept and slope for these regressions were converted to z-scores and the left and right fits compared, and subject to ANOVA (2 direction X 2 Hand). No main effect of hands was found in either measure (Slope: $F_{(1,10)} = 0.86$, $p = 0.37$; Intercept: $F_{(1,10)} = 0.59$, $p > 0.46$). Thus, for both hands, initial movement direction was substantially dependent on intersegmental coordination, measured as the timing difference between elbow and shoulder joint net torque profiles. We conclude that the systematic undershoot of left arm movements (exemplified in figures 2.3-2.5a), compared to right arm movements, resulted from poor coordination of timing between shoulder and elbow joint torques.

**Discussion**

In this study, we examined dominant and non-dominant arm coordination during unsupported, sagittal plane reaches. We hypothesized that interlimb differences in kinematics and kinetics should be consistent with the differences shown in previous studies of horizontal plane reaching. Our results showed substantial interlimb differences in coordination, as reflected by initial movement direction and trajectory curvature, such that dominant arm movements showed lower initial direction errors, and were straighter than non-dominant arm movements. The increased initial direction errors of non-dominant arm reaches were associated with lower muscle torque impulses in the non-dominant arm, and poor timing between peak torques at the shoulder and elbow joints, wherein the left arm displayed early elbow extension in relation to shoulder elevation. We conclude that in vertical plane reaching, non-dominant arm intersegmental coordination deficits are similar to the deficits reported previously for horizontal plane movements. In agreement with previous findings, final position accuracy and precision showed
no significant differences between the limbs (Sainburg and Kalakanis 2000; Sainburg 2002; Shabbott and Sainburg 2008).

Previous studies in horizontal plane reaching showed substantial interlimb differences in the magnitudes of muscle torques across movement directions. We showed that dominant arm muscle torques were well coordinated with interaction torques, while non-dominant muscle torques were not (Bagesteiro and Sainburg 2002; Sainburg and Kalakanis 2000). In the current study we did not observe differences in muscle and interaction torque impulses consistent with this previous work. This is very likely a consequence of the fact that we did not design the targets in the current study to require specific joint excursions, as was possible in the more constrained studies done in the horizontal plane. In addition, due to the greater freedom to move the scapula, and to change the plane of motion, we expect greater differences in torque profiles between subjects and trials. Nevertheless, our previous studies revealed that incoordination in muscle torque magnitude resulted in discoordination between segment motions, which gave rise to larger direction errors and greater hand path curvatures, but not greater final position errors, in the non-dominant arm (Bagesteiro and Sainburg 2002; Sainburg and Kalakanis 2000). In this way, the current findings regarding the torque impulse across the entire movement are consistent with our previous horizontal plane studies.

In the current study we introduced an additional measure of impulse calculated between the start of movement and the time at which the finger achieved peak tangential acceleration. In this measure we observed that there was an interaction between target and hand for the muscle impulse. In the case of the 45° target the dominant limb displayed significantly greater muscle torque impulse than the non-dominant limb. Since no differences were observed in the elbow impulse this would drive the elbow to accelerate earlier than the shoulder in the non-dominant limb. This is consistent with the observed kinematics wherein the non-dominant limb showed initial finger paths directed below the target. Because no differences were observed in the early
interaction torque impulse, it is reasonable to attribute this effect to the accurate prediction of gravitic torques in the dominant limb, but not in the non-dominant limb.

The noted differences in early shoulder muscle impulse but not in the early elbow muscle impulse, indicates a shift in the timing of joint acceleration. Indeed in our current study, the coordination of torque events at each joint appears to contribute the consistent interlimb differences in initial direction and movement curvature. It is apparent that the non-dominant limb displays earlier elbow torques relative to shoulder torques when compared to the dominant limb. This means that elbow extension tended to lead shoulder flexion in the non-dominant limb but not the dominant limb. This manifested as an error in direction and resulted in non-dominant paths that were initially directed below the target, a finding consistent with poor prediction of gravitation loads on the segments. Since the magnitude of total shoulder muscle impulse was similar between the two hands, similar shoulder elevation occurred in the non-dominant limb as in the dominant limb, however, this elevation occurred later in the movement. This appeared to be a correction for the initial direction deficit, as reflected by the 'hooks' toward the target shown in figure 2.3-2.5a. This initial direction error followed by late corrections resulted in greater curvatures for non-dominant movements. The deficiencies in non-dominant limb coordination observed here are consistent with the findings of Hore et al. that dominant limb advantages in throwing accuracy are related to better timing of finger extension relative to whole limb movement (Hore, et al. 1996). While our previous studies showed that non-dominant arm deficits in intersegmental coordination arose from poor prediction of interaction torques (Sainburg and Kalakanis 2000), our current findings suggest that prediction of gravitational torques might also be deficient during vertical reaching movements.

The coordination deficits of the non-dominant limb in our current and previous studies suggest that non-dominant system is less adept at predicting gravitational and intersegmental dynamics when specifying early movement trajectories, and that this limb relies more on feedback mechanisms to reach the final position with similar accuracy to the dominant arm. This
finding is consistent with the Dynamic Dominance hypothesis, which predicts dominant limb advantages in predicting task dynamics, but not in the corrective or postural phase of movement (Duff and Sainburg 2007; Shabbott and Sainburg 2008). In the current study, it is apparent that the dominant limb system produces movements that are directed more accurately toward the target than the non-dominant system, reflected in the temporal coordination of the elbow and shoulder torques. In contrast with the early movement errors, the non-dominant system did not show significant difference in final position accuracy. While the difference in initial direction errors precludes a direct comparison of the feedback mediated control during late movement, we may conclude that the error correction based control late in the movement is not substantially impaired in the non-dominant limb when compared with the dominant limb. This again is consistent with the Dynamic Dominance hypothesis, which does not predict deficits in feedback-mediated control in the non-dominant limb.

Several studies have noted the kinematic consistency of the dominant limb during free reaching, noting that hand paths remain invariant despite changes in loading, movement speed or gravity (Gentili, et al. 2007; Lacquaniti, et al. 1982; Papaxanthis, Pozzo, Vinter and Grinshin 1998; Papaxanthis, Pozzo, Popov and McIntyre 1998; Papaxanthis, et al. 2005; Soechting and Lacquaniti 1981). In keeping with these findings our current results in the dominant limb show strong suppression of curvature and direction errors in all movement directions. In contrast we observe that the non-dominant limb displays errors in movement direction and curvature consistent with failure to predict the effects of gravity. This is consistent with the Dynamic Dominance hypothesis, which predicts that the non-dominant limb will rely on a feedback controller, and consequently will not predictively compensate for gravitational or inertial effects. If this theory does explain the performance deficits of the non-dominant limb here then we may expect that non-dominant movements will not display the same kinematic invariances that the dominant limb displays.
Consistent with the current results, some researchers have suggested that movement control may be modeled by a two phase controller specifying first an open-loop plan for movement, followed by a second phase for stabilizing posture in which feedback is utilized to stabilize the limb around the desired configuration (Gottlieb 1996; Hirayama, Kawato and Jordan 1993; Sainburg, et al. 1999; Scheidt and Ghez 2007). It is plausible that the non-dominant limb relies more on the postural control elements, while the dominant arm relies more on the predictive control elements of such a hybrid controller. Since this postural control is derived from configuration errors, joint torques will emerge based on the state of the joint errors without accounting for the activity at other joints, or the effects of gravity (Bizzi 1987; Bizzi and Abend 1983; Bizzi, et al. 1976; Bizzi, et al. 1982; Feldman 1986; Flash 1987; Polit and Bizzi 1979). An earlier transition to the suggested postural phase of movement might result in timing deviations that do not allow the more effective coordination of muscular activity that the dominant limb displays. This would be consistent with the “advantages” in error correction observed in the non-dominant limb responding to unexpected inertial loads (Bagesteiro and Sainburg 2003). In fact, in our current study, both arms showed similar final position errors, while the non-dominant arm showed greater initial errors, indicating greater non-dominant arm reliance on corrective control mechanisms. Although these findings suggest a greater reliance on feedback mediated mechanisms, the differences in initial errors preclude drawing conclusions about the relative efficacy of the dominant and non-dominant corrective schemes.

While our current results cannot conclusively distinguish the specific algorithmic differences that give rise to interlimb differences in coordination, the differences observed here are similar to those shown previously in the horizontal plane movements and provide preliminary evidence that our findings generalize across different planes of motion and across different dynamic environments. Further these findings do indicate at a gross level, greater reliance on predictive mechanisms in the dominant limb, and greater reliance on feedback in the non-dominant limb.
Acknowledgements

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Figure captions

Figure 2.1
Experimental setup, (A) birds eye view and (B) lateral view.

Figure 2.2
Sample movement with associated data. (A) Example of a single left hand movement to the 0° target. Θ indicates the angle of initial direction error. (B) The tangential finger velocity associated with the movement displayed in (A). (C) Elbow torques computed for the movement in (A). The arrow marks the peak net torque, at which time measures of peak torque are taken. (D) Shoulder torques for the movement in (A). The arrow marks peak net torque. The elbow muscle torque is included here as this torque acts symmetrically across the elbow joint and, consequently, must be accounted for at the shoulder. This results in a sign inverted mirror of the elbow muscle torque acting at the shoulder.

Figure 2.3
Sample movements to the -45° target. (A) Movement plots for the right and left arms. Both movements are very straight, however, dominant arm movements tend to be slightly straighter. Initial direction error is similar across hands in this direction. (B) Net torques at the elbow and shoulder joints. Vertical lines denote the time of peak elbow torque incidence.
Figure 2.4
Sample movements to the 0° target. (A) Movement plots for the right and left arms. Both limbs tend to make more curved movements to this target than to the -45° target, however, dominant arm movements still tend to be slightly straighter at this target. The non-dominant hand shows a notable undershoot in the initial direction, while dominant paths tend to be directed at the target or slightly above it. (B) Net torques at the elbow and shoulder joints. Vertical lines denote the time of peak torque incidence.

Figure 2.5
Sample movements to the 45° target. (A) Movement plots for the right and left arms. Movements of both arms display the most curvature to this target, however, dominant arm movements show less differences from the 0° target than the non-dominant. The non-dominant arm shows a notable undershoot in the initial direction, while the dominant paths tend to be directed at the target or slightly above it. (B) Net torques at the elbow and shoulder joints. Vertical lines denote the time of peak torque incidence.

Figure 2.6
Summary of kinematic results. (A) Initial finger path angular deviation from the true target direction. Negative values indicate an undershoot, while positive values indicate aiming higher than the target. (B) Hand path curvature expressed in arbitrary units.

Figure 2.7
Shoulder muscle impulse across hand and direction. Hand differences in muscle impulse increase with target elevation, only becoming statistically significant at the 45° target.
Figure 2.8
Timing difference between elbow and shoulder peak net torque occurrence. Negative values indicate an elbow lead time, while positive values indicate an elbow lag time.

Figure 2.9
Sample regressions describing correlations between torque timing and initial direction error for a right performing subject and a left performing subject.

Figure 2.10
Coordinate system used for kinematic and kinetic analyses. \( J_w \), \( J_e \) and \( J_s \) represent the location of the wrist, elbow and shoulder joints respectively. System \( x\-y\-z \) is the global coordinate system and is fixed with the \( z \) axis aligned with gravity and the subject’s superior-inferior axis. The \( x \) axis is aligned along the subject’s medial-lateral such that the \( x\-z \) plane is parallel to the subject’s coronal plane. The \( y \) axis is parallel to the subject’s anterior-posterior axis such that the \( y\-z \) plane is parallel to the subject’s sagittal plane. System \( x’\-y’\-z’ \) is the local system within which the kinematics and kinetics of the arm movement are described. The system center is located at the elbow center of rotation, and the \( z’ \) axis is the axis about which the elbow rotates. Since the elbow is a planar joint, the \( z’ \) axis is normal to the plane containing the upper arm and forearm segments, which is the \( x’\-y’ \) plane. The \( x’ \) axis is the intersection of the global \( x\-y \) and the local \( x’\-y’ \) planes. The \( y’ \) axis is simply the cross of the \( x’ \) and \( z’ \) axes.
Figure 2.1: Experimental apparatus
Figure 2.2: Sample movement with associated data.

A. Movement Plot

B. Finger Tangential Velocity

C. Elbow Torque

D. Shoulder Torque

<table>
<thead>
<tr>
<th>Net</th>
<th>Shoulder Muscle</th>
<th>Elbow Muscle</th>
<th>Interaction</th>
<th>Gravity</th>
</tr>
</thead>
</table>

- Net: Total force applied to an object
- Shoulder Muscle: Force generated by shoulder muscles
- Elbow Muscle: Force generated by elbow muscles
- Interaction: Interactions between different muscle forces
- Gravity: Effect of gravity on the movement
Figure 2.3: Sample movements to the -45° target.
Figure 2.4: Sample movements to the $0^\circ$ target.
Figure 2.5: Sample movements to the 45° target.
Figure 2.6: Summary of kinematic results.
Figure 2.7: Shoulder muscle impulse.
Figure 2.8: Timing differences.
Figure 2.9: Sample regressions.
Figure 2.10: Coordinate system for kinematic and kinetic analysis.
Appendix 2.1

The equations of inverse dynamics presented here are adapted from Schneider and Zernicke 1990

The following terms are used in this appendix:

- $g'$ = the projection of the acceleration of gravity into the $\hat{y}'$ axis
- $I_e$ = moment of inertia of the forearm-hand unit about it's center of mass
- $I_u$ = moment of inertia of the upper arm about it's center of mass
- $\hat{J}_w$ = the position of the wrist joint in extrinsic space (Room coordinates)
- $\hat{J}_e$ = the position of the elbow joint in extrinsic space (Room coordinates)
- $\hat{J}_s$ = the position of the shoulder joint in extrinsic space (Room coordinates)
- $l_u$ = length of the upper arm segment
- $M_e$ = mass of the forearm-hand unit
- $M_s$ = mass of the upper arm segment
- $r_e$ = distance from the forearm-hand unit center of mass to the elbow joint
- $r_s$ = distance from the upper arm center of mass to the shoulder joint
- $\theta_e$ = angle of the forearm segment relative to the upper arm segment relative to the right horizontal axis
- $\epsilon$ = angle of the upper arm segment relative to the right horizontal axis
- $T_{em}$ = Elbow muscle torque
- $T_{en}$ = Elbow net torque
- $T_{ai}$ = Elbow interaction torque
- $T_{eg}$ = Elbow gravitational torque
- $T_{sm}$ = Shoulder muscle torque
- $T_{sn}$ = Shoulder net torque
- $T_{si}$ = Shoulder interaction torque
- $T_{sg}$ = Shoulder gravitational torque
- $x', y', z'$ = the position of the shoulder joint in the local coordinate system
- $\hat{x}'$ = the right horizontal axis in the local coordinates
- $\hat{y}'$ = the free axis of the local coordinate system
- $\hat{z}'$ = the axis of rotation for the elbow joint

Coordinate transformations:

$\hat{z}'$ is defined as the axis about which the elbow rotates. Modeling the elbow as a pin joint we can conveniently compute this axis at any given time utilizing the cross product of two vectors aligned to the forearm and upper arm segments:

$$\hat{z}' = U([\hat{J}_s - \hat{J}_e] \times [\hat{J}_w - \hat{J}_e])$$  \hspace{1cm} \text{Equation 2.1}

Where the function $U(\vec{v})$ returns a unit vector parallel to $\vec{v}$. The orientation of the $x'$ axis is defined as parallel to the line of intersection between a plane with its normal parallel to $\hat{z}'$, and
the global (x,y) plane, which is aligned perpendicular to the subject’s superior-inferior axis and gravity. This may be computed as the cross of the two plane normal: \( \hat{z}' \) and \( \hat{z} \)

\[
\hat{x}' = \hat{z}' \times \hat{z}
\]

Equation 2.2

\( \hat{x}' \) will be horizontal in the global frame, as it lies within a plane normal to the global vertical axis. We will consequently refer to it as the right horizontal axis of the local system. Given \( \hat{x}' \) and \( \hat{z}' \), the \( \hat{y}' \) axis is simply the cross of the \( \hat{x}' \) and \( \hat{z}' \):

\[
\hat{y}' = \hat{x}' \times \hat{z}'
\]

Equation 2.3

Computing torques in the new frame:

The elbow joint muscle torques are given by:

\[
T_{eM} = T_{eN} - T_{eI} - T_{eg}
\]

Equation 2.4

\( T_{eN} \) and \( T_{eI} \) are given by:

\[
T_{eN} = \left( I_e + m_e r_e^2 \right) \ddot{\theta}_e
\]

Equation 2.5

and

\[
T_{eI} = \begin{bmatrix}
- \left( m_e r_e l_s \cos(\theta_e) + I_e + m_e r_e^2 \right) \dot{\theta}_s \\
- m_e r_e l_s \sin(\theta_e) \dot{\theta}_s^2 \\
+ m_e r_e \sin(\theta_e + \theta_s) \hat{x}' \\
- m_e r_e \cos(\theta_e + \theta_s) \hat{y}'
\end{bmatrix}
\]

Equation 2.6

and the elbow gravitational torque is given by:

\[
T_{eg} = -m_e r_e \cos(\theta_e + \theta_s) g'
\]

Equation 2.7

Similarly shoulder Torques are given by the equation:

\[
T_{sM} = T_{sN} - T_{sI} - T_{sg} + T_{eM}
\]

Equation 2.8

\( T_{eM} \) is given by equation 2.4, and \( T_{sN} \) and \( T_{sI} \) are given by:

\[
T_{sN} = \left( I_s + m_s r_s^2 + m_I l_s^2 + m_e r_e \cos(\theta_e) \right) \ddot{\theta}_s
\]

Equation 2.9

and
\[
T_{sl} = \begin{bmatrix}
-(m_r l_s) \cos(\theta_e) \dot{\theta}_e \\
-(m_r l_s) \sin(\theta_e) \dot{\theta}_e^2 \\
-2m_r l_s \sin(\theta_e) \dot{\theta}_e \dot{\theta}_s \\
-m_r l_s \sin(\theta_e) \dot{\theta}_s^2 \\
+(m_s r_s + m_l l_s) \sin(\theta_s) \ddot{x}_s \\
-(m_s r_s + m_l l_s) \cos(\theta_s) \ddot{y}_s
\end{bmatrix}
\]

Equation 2.10

and the shoulder gravitational torque is:

\[
T_{sg} = -(m_s r_s + m_l l_s) \cos(\theta_s) g'
\]

Equation 2.11

Computing torque impulse:

Torque impulse across the whole movement was computed by simple numerical integration. At the elbow:

\[
I_{eM} = \sum_{i=1}^{n} T_{eM,i} \times \text{sign}(T_{eM,i} T_{eN,i})
\]

Equation 2.12

\[
I_{el} = \sum_{i=1}^{n} T_{el,i} \times \text{sign}(T_{el,i} T_{el,i})
\]

Equation 2.13

where the sign function returns 1 if the operand is positive, and -1 if the operand is negative.

Similarly, at the shoulder:

\[
I_{sM} = \sum_{i=1}^{n} T_{sM,i} \times \text{sign}(T_{sM,i} T_{sN,i})
\]

Equation 2.14

\[
I_{sl} = \sum_{i=1}^{n} T_{sl,i} \times \text{sign}(T_{sl,i} T_{sl,i})
\]

Equation 2.15

Computation of the early torque impulse was performed simply by limiting the range of summation to those points prior to the time of peak acceleration

\[
I_{eM} = \sum_{i=1}^{a_{eM}} T_{eM,i} \times \text{sign}(T_{eM,i} T_{eN,i})
\]

Equation 2.16

\[
I_{el} = \sum_{i=1}^{a_{el}} T_{el,i} \times \text{sign}(T_{el,i} T_{el,i})
\]

Equation 2.17

and at the shoulder:
\[ I_{sM} = \sum_{j=1}^{a_{\text{max}}} T_{sM,j} \times \text{sign}(T_{sM,j} \times T_{sN,j}) \]  

Equation 2.18

\[ I_{sI} = \sum_{j=1}^{a_{\text{max}}} T_{sI,j} \times \text{sign}(T_{sI,j} \times T_{sI,j}) \]  

Equation 2.19
Chapter 3: A serial Control Model That Accounts for

Lateralization of Multijoint Reaching Kinematics

Introduction

While lateralization of the human motor system is readily observable in performance characteristics, such as the timing and precision of movements (Carson et al. 1993; Elliott et al. 1994; Flowers 1975; Steingruber 1975; Todor and Cisneros 1985), the underlying neural mechanisms remain poorly understood. The pioneering work of Gazzaniga in split brain patients has provided a model of brain lateralization for language, cognitive, and perceptual functions. This work led to the recognition that brain lateralization is a general optimization process, which expands neural circuits for a given function by reducing redundancy across the hemispheres. Thus, different neurobehavioral functions may be specialized to different hemispheres. For example, language lexicon and syntax are specialized to the left hemisphere, while prosody and emotional content is specialized to the right hemisphere in most individuals (Knecht et al. 2000; Ross and Mesulam 1979; Wada and Rasmussen 1960; Weintraub et al. 1981). In more general terms, different aspects of a given neurobehavioral function can be specialized in different brain hemispheres. However, lateralization of motor functions has not traditionally been viewed from this perspective. Instead, the non-dominant system is typically viewed as a deficient copy of the dominant system. In this context, the non-dominant arm is often described as clumsy, a description that is consistent with kinematic observations of manual performance, in which the non-dominant arm often shows less consistent performance (Hore et al. 1996; Todor and Kyprie 1980), as well as more curved trajectories, and less energetically efficient coordination patterns (Bagesteiro and Sainburg 2002; Sainburg and Kalakanis 2000). Despite these differences, the accuracy of the non-dominant arm can be similar (Bagesteiro and Sainburg 2002; Sainburg and Kalakanis 2000) or better (Goble et al. 2009; Lenhard and Hoffmann 2007; Wang and Sainburg 2008).
than that of the dominant arm, suggesting that this arm is not simply a less skilled counterpart of the dominant arm, but may in fact be utilizing a different control scheme to complete the same task.

Previous research examining responses of the dominant and non-dominant arms to perturbations suggest that the non-dominant arm, rather than simply being deficient, might be specialized for specific aspects of control. When the non-dominant arm is perturbed by an unexpected inertial load during reaching, it displays rapid and accurate online movement corrections. In contrast, the dominant arm response is often maladaptive, increasing the overall error (Bagesteiro and Sainburg 2003; 2005). In addition, research examining adaptation to novel dynamic conditions has shown that the non-dominant arm adapts by increasing limb impedance, while the dominant limb adapts by anticipating the direction and magnitude of the imposed forces (Schabowski et al. 2007). Taken together, these results suggest a non-dominant specialization for stabilizing the limb against unanticipated perturbations, in order to bring the arm to a stable posture at the end of motion. This research suggests that lateralization of the motor control system reflects two distinct specializations, while the predominantly contralateral organization of human motor control suggests that these functions are lateralized to opposite hemispheres.

Whereas the aforementioned studies in healthy subjects have elaborated the mechanisms of motor lateralization, recent studies in patients with unilateral stroke support the hypothesis that these specializations reflect hemispheric asymmetries. Our hemispheric model of motor lateralization predicts that each hemisphere contributes unique processes to control of each limb, and that lesions in one hemisphere should produce specific deficits in both the contralesional and the ipsilesional arms. Studies in the ipsilesional arms of right-and left hemisphere damaged patients with unilateral stroke have confirmed these predictions. Patients with dominant (left) hemisphere lesions show a persistent deficit in the ability to account for the inertial dynamics of the limb during the early trajectory (Schaefer et al. 2007; 2009a; 2009b; 2011). Despite this, final hand position remains accurate, even showing advantages over the intact age-matched control
These results support the idea that the intact, right hemisphere is able to effectively control final limb posture, even while failing to predictively account for inertial dynamics. In contrast, subjects with right hemisphere lesions show adept coordination of limb inertial dynamics, with a tendency to produce fairly straight hand paths. These patients however, tend to show substantial errors in final position accuracy. While they tended to make straight, well coordinated paths, both movement accuracy and precision were deficient, relative to their control group and left hemisphere damaged patients. Recent work has extended these findings to the contralesional arms of patients without hemiparesis (Mutha et al. 2011), and has localized these control processes to the frontal cortex of right hemisphere damaged patients, and the posterior parietal cortex for left-hemisphere damaged patients. These findings support the hypothesis that each limb displays performance advantages that are associated with the aspects of control that have become lateralized to that arm’s contralateral hemisphere, however, it remains unclear how such control mechanisms might be integrated for control of a single limb.

Woodworth in 1899, first elaborated two mechanisms of motor control that can be temporally dissociated to different phases of a single motion: predictive and error correcting control. Many subsequent studies focused on characterizing these processes in more detail (Carlton 1981; Keele and Posner 1968; Shabbott and Sainburg 2008). In its pure form, the purely predictive phase can only describe the first 100 milliseconds of motion, prior to the effects of movement-dependent reflexes. While reflexes can have muscle activation latencies as low as 25 milliseconds, electromechanical delays extend the predictive phase substantially. In addition, a number of studies have indicated that proprioceptive feedback processes may be inhibited through the initial acceleration phase of motion (Fabian et al. 2009; Shapiro et al. 2004) a finding consistent with Woodworth’s initial observations that this predictive phase extends to peak tangential velocity, roughly midway through a reaching movement. Previous research has shown that such predictive mechanisms account for dynamic contingencies to movement, such as the effects of linked-segment mechanics (Brown et al. 2003; Sainburg et al. 1995) and gravitational
loads (Papaxanthis et al. 1998; Papaxanthis et al. 2005). While movement dependent feedback can influence movements early in the trajectory (Carlton 1981; Johnson et al. 2002; Shabbott and Sainburg 2008; Soechting and Lacquaniti 1983), recent work has focused on the active modulation of position and velocity dependent impedance to stabilize posture at the end of motion (Sainburg et al. 1999; Scheidt and Ghez 2007). Thus, two aspects of motor control have been well-characterized: Predictive control that initiates the movement, and closed-loop processes that are used to stabilize the limb at the end of motion.

We have developed a theory of motor lateralization that incorporates the predictive and error correcting aspects of control into a model of hemispheric specialization. Our Dynamic Dominance hypothesis posits that the primary differences between dominant and non-dominant control lie in the ability to predict the dynamic consequences of movement (Sainburg 2002), and the ability to stabilize the limb at the end of movement (Duff and Sainburg 2007; Sainburg 2005). It is known from basic mechanics that the motion of one segment of a kinematic chain imposes forces on the adjacent segments. Studies of human reaching have demonstrated that the torques arising from these interactions frequently match or exceed the net action of muscular torques acting on the same joint (Bagesteiro and Sainburg 2002; Hollerbach and Flash 1982; Sainburg and Kalakanis 2000). Predictive compensation for the kinematic effects of these interaction torques is therefore critical for accurate control of limb kinematics during reaching movements. Studies from our group have demonstrated that the dominant limb is advantaged in coordinating muscle actions with these intersegmental interaction torques. We have shown that the shape of the non-dominant hand path, measured as aspect ratio, varies with the magnitude of these interaction torques (Sainburg and Kalakanis 2000) while dominant arm aspect ratios do not. In fact, the dominant system tends to exploit these interactions in a mechanically efficient manner (Bagesteiro and Sainburg 2002).

We now examine the plausibility of a hypothesized mechanism by which anticipatory and feedback control of the hemispheres might be integrated into a single movement of each arm. We
propose a two stage serial-hybrid control scheme (Sainburg 2002; Yadav and Sainburg 2011), which models control of a single movement as the sequential application of an open-loop controller followed by a closed-loop controller. This idea is consistent with some previous work that has modeled distinct mechanisms to control the ballistic and postural phases of movement (Hirayama et al. 1993; Gottlieb 1996; Sainburg et al. 1999; Scheidt and Ghez 2007). Given the apparent cortical lateralization of control functions, this scheme of control is appealing, as it describes the sequential integration of control, directed primarily by a single hemisphere at a time. According to this model, control of movement arises from two independent control processes with predictive planning specialized to the dominant system, and proprioceptive stabilization of posture lateralized to the non-dominant system. In our model, these two processes are combined in a serial manner, such that the early movement of both arms is controlled by the predictive controller, and the postural phase is controlled by the impedance controller. In this scheme, forward control might generate a straight path without corrections, while feedback control would be driven by inertial dynamics to produce movement curvatures. Due to the contralateral preponderance of ascending and descending fibers it may be reasonable to propose that utilization of ipsilateral cortex incurs some cost. In fact, quite a large body of research has indicated processing costs associated with inter-hemispheric communication (Holtzman and Gazzaniga 1984; Passarotti et al. 2002; Putnam et al. 2008; Ringo et al. 1994). Thus, the contralateral controller for each arm controls more of the movement, presumably due to these processing advantages.

In this study we postulate that the transition dynamics from predictive to feedback control may explain the kinematic differences between the two arms during multi-joint reaching movements. A similar model has previously been rigorously examined for single joint movements (Yadav and Sainburg 2011). We now present a simple hybrid control simulation that reproduces many qualitative effects of multijoint reaching movements, and relies solely on the
transition timing from feed forward to feedback control to adjust movement kinematics. In order to further examine the plausibility of our model, we modeled left and right arm reaching data, using our simulation. With this modeling we examine whether right and left arm movements can be differentiated by the transition dynamics of our model. Our ability to match the model to empirical data does not represent a direct and rigorous test of our hypothesis, but rather, it provides an elaboration of a mechanistic model of motor lateralization and tests the adequacy of this model for explaining coordination differences between the two arms.

Materials and Methods

Forward Simulation

This section presents a description of the modeling methods used in this study. A formulaic description is presented in the appendix. An inverse kinematic model of the upper limb was written in Real Basic (Real Software, Lake Oswego, OR) to compute the interaction torques and driving torques required for a specific desired movement. This model accepted segment lengths and inertias as inputs allowing for the simulation of movements by subjects with a wide range of anthropometry. Arms were modeled as planar two link kinematic chains with fixed shoulder positions. Two distinct controllers were constructed: a forward predictive controller which produced torques that generated a specified hand path, and a feedback controller which generated torques based on the errors in joint angle when the current configuration was compared to an expected time series of joint angles.

In the forward controller, sequences of joint angles were computed from the hand path, and from the angle time series. The desired hand paths used for the predictive controller were simple minimum jerk trajectories (Plamondon et al. 1993). From the joint angle time series, the joint torques computed using the planar equations of inverse dynamics as described by Bagesteiro and Sainburg (2002). With this model it is feasible to segment the net joint torques into
interaction torques derived from the segment motion and muscle torques required to drive the movement. The muscle torques derived from this inverse model are the residual terms of the net and interaction torques, and consequently can be described as the driving torques necessary to produce the prescribed movement. In this framework, the muscle torques produced by the inverse dynamics of the minimum jerk trajectory are taken as the output of a forward controller.

The feedback controller was constructed separately, and derived joint muscle torques based on the errors between the joint angle and the joint angle in a sequence of reference limb configurations. This controller was conceptualized as an equilibrium point type impedance controller (Feldman 1986), where the equilibrium configuration was specified at each joint as a reference angle. Each joint was independently assigned a stiffness value and, for simplicity, both joints were assigned a common viscous-like damping. Stiffness and damping remained constant during each trial. Driving torques at each joint were computed from the error between the current joint angle and the desired angle in the reference sequence. In order to simulate the latency of human feedback circuitry, a delay between error occurrence and torque application was introduced, so that at each time step, the joint error 80ms in the past was used to compute the feedback torque. A further torque impeding movement was computed from the joint angular velocity and viscous-like damping, and added to the stiffness torque to produce the final control torque for the feedback controller. In order to prevent large under-damped oscillations of the hand around the target, an additional viscous-like damping at the end of movement was applied. This ensured that forward simulations of hand path stabilized at a stationary end point within a reasonable movement timeframe.

Values in the literature for stiffness and damping in simple second order models of limb mechanics vary widely. Single joint stiffness may vary from approximately 1Nm/rad (Hayes and Hatze 1977; Konczak et al. 1999) to 350-400Nm/rad (Cannon and Zahalak 1982). Stiffness values measured during movement are typically found well below these maximal stiffnesses
(Bennett et al. 1992; Bennett 1993; Burdet et al. 2000; Gomi and Kawato 1997). Further, elbow stiffness is typically substantially lower than shoulder stiffness (Burdet et al. 2000; Gomi and Kawato 1997). Stiffness selected in this study was constrained to lie between 0 and 50Nm/rad for the elbow, and between 0 and 100Nm/rad for the shoulder. Measures of the damping properties of the human limb are less common in the literature than measures of stiffness, in large part due to the difficulty of dissociating stiffness and damping during motion of the limb. The studies that do report estimates of damping in the limb report low damping rates compared to the apparent stiffness of the limb (Hogan 1989; Konczak et al. 1999). During modeling of empirical data, damping was constrained to lie between 0.5 and 6Nms/rad.

In order to simulate movements a forward solver was constructed to iteratively compute the joint position when given an initial limb configuration and a time series of torques. Validation of the forward solver was performed with forward simulations using the time series of torques produced solely by the inverse model produce perfectly straight minimum jerk hand paths. As the controllers specify only the muscle contribution to the net torque, interaction torques were computed on the fly from the simulated segment motions. To simulate a dual stage control scheme, we assume that the magnitude of joint muscle torques may be the product of the weighted superimposition of the two distinct control schemes (Figure 3.1). The weights on the two controllers were varied throughout the movement, thus modulating the degree to which each controller contributed to the driving torque at any given time. In order to generate sequential application of the forward and feedback controllers, the weights were modeled as sigmoidal functions of time, with the forward controller weight starting at a magnitude of one and falling to zero, and the feedback controller weight starting at a magnitude of zero and rising to one (Figure 3.2). Both weights used the same temporal profile, such that the sum of the two weights was always equal to one. This scheme yields three distinct phases to the simulated movement: Phase 1, the movement is entirely under forward control. During this phase the hand trajectory remains
straight, following the minimum jerk path. Phase 2, the weight on the forward torques begins to fall and the weight on the feedback torques rises, producing a mixture of feed forward and feedback control. During this phase the hand trajectory begins to deviate from the minimum jerk path. The sigmoidal weighting function selected displayed a relatively rapid transition, consequently, this mixed control time is relatively short. Phase 3, the weight on the forward control is effectively zero, while the weight on the feedback torques is effectively one. As a consequence of the pure feedback drive, inertial dynamics act to drive the hand away from the minimum jerk hand path, yielding substantial deviations, followed by hooked corrective movements. We defined the transition time from forward control to feedback control to be the time at which the weights on each controller achieved a value of one half.

In order to evaluate the efficacy of this model in simulating a range of realistic reaching movements, we present here data for a limb based upon the expected anthropometry of a 160lb, 5’10” individual (Winter 1990). Further we establish an arbitrary but realistic set of gains for the feedback controller. The proportional gain of the feedback controller (stiffness) was set at 25Nm/rad for the elbow, and 50Nm/rad for the shoulder. The derivative gain (viscous damping) of both joints was set at 2Nms/rad. We then simulated a series of movements iteratively changing only the transition time. Start location and target for the simulated movements were both directly in front of the shoulder, with movement amplitude of 15cm. Movement time for the minimum jerk trajectory was specified as 300ms, corresponding to a peak finger velocity of approximately 1m/s in the minimum jerk profile.

To compare the simulated hand paths to data from literature, the aspect ratio of the finger path, and the deviation of the initial finger path from the start to target vector were computed. The aspect ratio is simply the minor axis of the movement divided by the major axis of the movement, and has been referred to as linearity or curvature in previous literature. The deviation of the initial finger path was computed as the angle between the target vector and a vector connecting the
initial finger position and the finger position at a relevant point in the movement. To examine the evolution of direction errors we computed the finger vector using both the position at peak finger acceleration, and the finger position at peak velocity. This allows some assessment of the rapidity with which path deviations away from the target are corrected. The path deviation was computed so that medial deviations produced positive angles for both hands, and lateral deviations produced negative angles.

**Modeling Human Data**

**Subjects**

In order to assess this model’s ability to capture the lateralization of arm movements, real movements were modeled with simulation parameters estimated to match the specific subject data. A pool of subjects was recruited to perform real reaching movements with similar kinematics to those present in the preceding simulation section. Four subjects were screened for neurologic and skeletal pathology as well as handedness (Oldfield 1971), and gave informed consent prior to participation. Subjects were healthy university students, neurologically intact and displaying no pathology of the upper limb. All procedures involving participants in this study were approved by the Pennsylvania State University institutional review board.

**Experimental Setup**

Subjects rested their forearms in an air sled apparatus, such that the hand was placed just below the level of the subjects shoulder (Figure 3.3). The air sleds removed the effects of gravity, and maintained a planar movement. To measure the positions of segments in real time, 6DOF electromagnetic sensors (Flock of Birds, Ascension Technologies) were placed on the hand and upper arm segments. The position of the finger, wrist, elbow, and shoulder joints were calibrated relative to the sensors prior to testing. This system allowed collection and processing of joint
locations at 130Hz. A mirror was placed above the subjects arm, obscuring vision of the limb, and reflecting the display of a 55 inch high-resolution LCD monitor placed above the subject’s head. The screen of the monitor reflected in the mirror, allowed subjects to direct their gaze at their hands, and observe the task cues. Data on the joint positions was captured by a custom software package written in Real Basic (Real Software, Lake Oswego, OR) and used to display a cursor representing the location of the subject’s finger on the monitor, and updated at the refresh rate of the screen so as to appear to the subjects in real time. The location of the LCD screen was carefully calibrated such that the reflected position of the cursor was veridical with the true position of the finger.

**Testing**

Movements were directed away from the subject, and both the starting hand location and final target were located 15cm lateral to the body midline, approximately in front of the subjects shoulder. As in the pure simulation movement extent was 15cm directed anteriorly away from the subject. Subjects were instructed to make rapid, accurate movements to the target, stopping as close as possible to the center of the target. Points were awarded for accuracy in order to maintain motivation for task performance. The start and end of movement were identified as the time of the first minima in the tangential finger velocity to either side of the peak that fell below 5% of the peak velocity. Kinematic analysis of subject hand paths, as in the pure simulation was limited to measurements of path aspect ratio, and the deviation of the initial finger path from the target vector. In this case however, the path deviation was computed only at peak finger velocity.

**Modeling**

Modeling real movements required selecting an appropriate minimum jerk path. To simulate the desired torques and reference path based upon the subject’s actual movement, the minimum jerk hand path was taken between the true hand locations at the start and end of
movement. This avoids the assumption that the subjects always planned an accurate trajectory to the target. Since real movements display a substantial tail effect as subjects perform late corrections to final finger position, the minimum jerk time was fixed at 75% of the actual movement time. This forced the initial movement velocity to more closely match the velocity observed in real movements, as real movements in this task showed pronounced skewing of the velocity profiles.

To find stiffness and damping parameters for each subject, a single trial was selected from that subject’s movement set that displayed an exaggerated hooked hand trajectory. Stiffness and damping parameters were fit using a grid search of the available parameter space. Shoulder stiffness was varied in 5Nm/rad steps between 0 and 100Nm/rad, while elbow stiffness was varied in 2.5Nm/rad steps between 0 and 50Nm/rad. Damping was varied in 0.25Nms/rad steps between 1 and 6 Nms/rad. The shift point was varied in steps of 0.05, between 0 and 1. To assess the geometric matching of the hand paths, the empirical and simulation paths were parameterized with 100 equidistant points, such that:

\[
D_{99} = \left\| \overrightarrow{P_n} - \overrightarrow{P_{n-1}} \right\|
\]

Equation 3.1

Where D is the cumulative distance along the finger path, computed as the discrete integral of the point to point distances between adjacent points, and \( P_n \) is the 2D vector from the origin to the \( n^{th} \) point in the trajectory. Once the paths were parameterized, the error was computed simply as the mean square error of the two paths on a per-point basis:

\[
E = \frac{\sum_{n=1}^{100} \left( \overrightarrow{P_{n,empirical}} - \overrightarrow{P_{n,simulated}} \right)^2}{100}
\]

Equation 3.2

The parameters in the search space that minimized E were selected as the parameters with which to model the empirical data. These parameters were then used for all movements that subject
made with either hand. Once the stiffness and damping parameters were selected and the minimum jerk path specified, the kinematics of each simulated movement were varied by adjusting the transition time from forward to reverse control. For every movement the transition time was adjusted in steps of 0.01 and the path error computed according to equation 3.2. The transition point that minimized the error was selected as the transition time.

Statistics

Direct comparisons of hand were made using a one way ANOVA. In the case of empirical data, subjects were included in the model as a random effect. Regressions were compared using a simple F test, where the F statistic was the Mean square error due to lack of fit, divided by the mean square pure error. All statistics are reported with a significance threshold for type 1 error of \( \alpha=0.05 \).

Results

Simulation

The simulations made with representative segment parameters show characteristics strongly resembling those of real reaching movements (Figure 3.4a). At low transition times, there is a pronounced lateral deviation from the minimum jerk path in the early movement, which grows in magnitude between peak acceleration and peak velocity (Figure 3.4b). This appears to be associated with the relatively low inertia elbow extension pivoting the hand about the elbow before shoulder acceleration can compensate for the lateral drift of the hand. These early errors are corrected by a late hook towards the target associated with the comparatively high inertia shoulder motion. As a consequence of this pattern of deviation and corrections, the aspect ratio of the finger path is quite high in simulations with an early transition time (Figure 3.4c). As transition time is increased, the early finger paths tend to follow the minimum jerk trajectory,
producing lower direction errors, eventually decaying to the point where the early movement is essentially linear. As a consequence of the lowered deviations in the early movement, the late movement corrections are also smaller in the late transition time simulations. Predictably this yields progressively lower aspect ratios as transition time is increased. It is worth noting that at no transition time does this simulation produce medially directed deviations in the initial movement direction. This pattern of lateral deviations from the target direction followed by late corrections is similar to the patterns of real subject movements observed under similar target conditions.

**Modeling Empirical Data**

The model was able to fit the real movements well in most cases. Figure 3.5 shows a range of movements from both limbs of a single subject. For the real movements, non-dominant arm movements showed higher aspect ratios and show more laterally directed errors in initial movement direction ($F_{(1,6)}=8.52, P=0.02$) than dominant arm movements (Figure 3.6). In accordance with our expectations those movements displaying large aspect ratios were well fit by early transition times, while movements with small aspect ratios tended to be well fit by later transition times. It is important to note that while the dominant limb modeling showed significantly later transitions ($F_{(1,6)}=5.91, P=0.05$), the models for both arms displayed a range of transition times that overlapped. As most real movements display some curvature of the hand path and deviation in initial direction it is not surprising that the transition time in both arms tends to be well before the midpoint in the movement. While the majority of large deviations were laterally directed, some real movements displayed small medial deviations in initial hand paths. These medial deviations were particularly evident in the dominant arm, and relatively rare in the non-dominant arm.

In our model, transition time is the primary variable controlling the aspect ratio of the movement. It should therefore be the case that the aspect ratio of real movements is correlated
with the fit transition time. When we fit transition time to hand path aspect ratio, both hands display significant trends of decreased transition time with increased path aspect ratio (left: $F_{(1,30)}=7.39$, $P=0.011$, right: $F_{(1,30)}=18.63$, $P<0.001$) (Figure 3.7). This common correlation suggests a common mechanism producing lateral deviations in both hands, however, the slope of the relation is different indicating that hand influences the correlation. One effect that may explain this difference was dominant hand movements directed medial to the target early in the movement trajectory. Simulated movements could only be directed at the target via the minimum jerk trajectory, or with lateral deviations induced via feedback control. Consequently movements with medially directed initial deviations were best modeled by simulated movements with very straight paths and late transitions. Figure 3.5 shows several examples of this type of movement in the dominant arm condition. These late transition times are easily distinguished from the majority of observed points. This difference in transition times, combined with the clustering of these datum around low aspect ratio movements leads to skewing of the regression for the dominant arm (Figure 3.7). As the majority of these movements were observed in the dominant arm, the regression for the dominant arm displayed a more pronounced slope than that of the non-dominant arm. This effect is the primary cause of the large dissociation in regressions of the transition time by the path aspect ratio between the two arms. Despite this, the difference in the mean aspect ratio for each hand does suggest that early transitions will remain associated with non-dominant arm movements even after this effect is corrected.

**Discussion**

In this study we examine the transition time of a serial model for the control of reaching movements, with the premise that the transition time in our model may account for the major interlimb differences associated with dominant and non-dominant arm reaching movements. The idea that a movement may be composed of two phases, a feed forward or ballistic phase, and a feedback or postural phase is certainly not novel (Woodworth 1899). However, the premise that
the differences in movement kinematics within and across the arms might arise from the transition dynamics between these two control phases has not yet been tested for multi-joint movements. A previous study has rigorously tested this hypothesis for single-joint movements (Yadav and Sainburg 2011). The purpose of this study is to test the plausibility of this model for multi-joint movements. Our findings indicate that by varying the transition time from forward to feedback control we can vary the path deviation and the aspect ratio of simulated arm movements. These metrics are common measures that reliably distinguish dominant from non-dominant arm movements. Thus, a transition variable that controls both of these metrics is a good candidate for distinguishing the fundamental difference between dominant and non-dominant arm coordination.

Our findings indicate that transition times between the predictive and feedback control mechanisms are later for the dominant arm, suggest a greater reliance on predictive control. We speculate that the costs associated with accessing the ipsilateral hemisphere might result in the preferential use of contralateral cortex for the majority of the movement. Consequently we suggest that the change in transition times might be associated with the cost of utilizing the ipsilateral hemispheres. In the dominant arm, the transition is late, in order to avoid recruiting ipsilateral control. In the non-dominant arm, however, the transition is early, allowing termination of ipsilateral forward control, early in movement. It is unclear from this study what form these costs might take, however, increased latency for ipsilateral control, and degradation in the quality of control are both plausible candidates. In a previous study, our group (Yadav and Sainburg 2011) rigorously tested a more elaborate, but conceptually similar, hybrid control model for single-joint movements. In that study, the coefficients that accounted for both the predictive and impedance controllers, as well as the transition time were adjusted to optimally fit the movements of the dominant and non-dominant arms. In that study, the hybrid control scheme was characterized by five “open” parameters that could be altered to fit the model to subject’s movements. Our results indicated that the predictive mechanisms did not differ between the arms
and that joint stiffness and viscosity parameters fell within reported physiological ranges. More importantly, we showed that the one parameter that consistently differentiated dominant and non-dominant coordination was the time of switch between the two controllers. Our current findings provide an initial test of the extension of these control principles to multiple joint motions.

As a model for the lateralization of motor control in the arms, the transition time is an appealing variable, as it matches well with previous studies examining the cortical lateralization of control functions. Work in subjects with cortical lesions provides evidence that ipsilateral arm function after stroke displays characteristics of either pure predictive or pure feedback control, depending on the damaged hemisphere (Schaefer et al. 2007). In right handed subjects, lesions to the dominant (left) hemisphere produce movements in the non-dominant arm that display the characteristics of a pure feedback controller. Movements remained characteristically swayed by the segment dynamics even after prolonged adaptation times. In contrast non-dominant (right) hemisphere lesions produce movements in the dominant arm that do not display adjustments in hand path during the late movement that would be characteristic of a feedback controller. This stroke data suggests that each hemisphere is specialized for one phase of control, and that both hemispheres contribute to single arm movements. This meshes well with the model proposed in the current study of a controller which utilizes the controller most specialized for each sub-phase of a movement. The idea that unimanual control may draw on ipsilateral cortex is further supported by imaging studies which have shown greater lateralization of cortical potentials early in the movement for the dominant hand and later in the movement for the non-dominant hand (Grünewald et al. 1979). In this context, greater lateralization of cortical potentials suggests a greater reliance on contralateral cortex, rather than bi-cortical activation.

While the use of a model using the equations of motion for a two-link chain might imply that the current findings are contingent on the existence of internal models in the central nervous system. Proponents of the equilibrium point hypothesis (Feldman 1986) postulate that the whole
movement is under feedback control. In this context, a special trajectory of reference configurations is constructed to limit the appearance of dynamic effects on the effector kinematics. In the case of the current experiment it is sufficient to say that the early movement, prior to initiation of postural stabilization, constitutes movement along a planned trajectory, without ascribing a specific mechanism to the controller that accomplishes this. For the sake of computation we construct our model using a predictive controller that solves inverse limb dynamics in order to produce the correct joint torques to generate a desired movement. Although we used an inverse dynamical model of control was utilized for our forward controller, an equilibrium trajectory would serve equally well in this model. Consequently the findings of the current work are not necessarily contingent upon the specific predictive mechanisms employed by the central nervous system.

While the current work makes no direct addition to the debate on internal models, it does suggest the existence of a predictive controller, which accounts for dynamic effects early in the movement. Given that the inertial dynamics of the early movement appear to be anticipated, the premise that the control system is capable of predicting the inertial dynamics of movement, rather than using sequence of memorized reference trajectories, seems quite reasonable. Consequently one might take this as evidence that the neural system contains a model of the limb mechanics that it utilizes to generate this prediction. This view is supported by studies demonstrating adaptation to, and aftereffects of, a number of perturbing fields, such as coriolis force fields (Lackner and Dizio 1994), inertial effects of applied masses (Sainburg et al. 1999), and visuomotor rotations (Krakauer et al 2000; Sainburg and Wang 2002; Wang and Sainburg 2005). These effects suggest that whatever control system is utilized, it anticipates and compensates for predictable perturbations, such as external force fields or the inertial dynamics of the limb. It is important to note that, while this model treats the dominant controller as an open-loop controller, the concept of a purely open or closed loop control structure in the central nervous system is
suspect. Feedback from previous reaches is certainly used to adapt the predictive estimation of
dynamic effects and consequently the movement plan. Similarly some groups have suggested that
rapid correction of errors may rely on forward models of the limb to predict the future limb state
and correct for errors without suffering the effects of latency in the nervous system. Consequently
it is more appropriate to consider the dominant proficiency with the prediction and compensation
for the dynamic effects of movement, while the non-dominant system proficiency is with the
correction of within trial errors, and stabilization of posture around the desired configuration.

The model presented here to explain the differential control of dominant and non-dominant
arm movements is a deliberately simplified model based on well-established theories of motor
control. Here the postural controller utilizes constant stiffness and damping factors to control the
movement. This of course is a gross simplification, as it is known that joint stiffness can vary not
only within a movement (Burdet et al. 2000; Gomi and Kawato 1997), but can also change in
accordance with external factors such as anticipation of a variable perturbation (Franklin et al.
2007; Lametti et al. 2007; Wong et al. 2009). Further the length tension relations of the soft
tissues are decidedly nonlinear, particularly in the muscles, potentially limiting the utility of
linear spring models for large positional errors such as those observed here. Additionally the use
here of minimum jerk trajectories for the forward control scheme does not account for medial
deviations in initial hand path from the direct path between start and target. It seems likely that
the forward controller is in fact utilizing a more sophisticated schema to plan movements, such as
minimum torque change (Kawato et al. 1990; Nakano et al. 1999) or minimum energy (Alexander
1997). The model as presented here represents an ideally simplified version of a two-stage
controller, wherein all variance is derived from changes in a single parameter. Another feature
of the current formulation of the control model is its reliance on a discrete linear movement
pattern for the predictive control element. This would seem to suggest that in cases where the task
goals evolve over the course of the motion, as in the case of a moving target, would be handled
poorly by late transitions. In the case of the predictive controller, the system must assess the new
target location, and construct a novel kinematic trajectory, taking into account the current limb kinematics, and then transform this new kinematic sequence into a series of muscle torques. In contrast the positional controller merely needs to update the reference configuration for the limb in the final intended state. Consequently, if the dissociation of transition time by hand is a feature of control lateralization, we may expect a non-dominant hand advantage in cases where the target changes after movement initiation. In a study of exactly those conditions comparing healthy controls to patients with ischemic lesions, Schaefer et al. showed that patients with damage to the right hemisphere showed prolonged delays prior to the initiation of the corrective movement, and patients with left hemisphere lesions began corrective movements without ceasing the movement of their hand (Schaefer et al. 2011). In contrast, healthy controls displayed movements where the hand velocity dropped to zero and the corrective movement was initiated with a short latency. This latency did not vary across hands. The increased correction latency displayed in subjects with right hemisphere infarcts suggests that healthy subjects were utilizing error correcting circuitry localized in the right cortex. When this system was disrupted, secondary movements were delayed as the predictive controller in the left cortex was recruited to create a novel movement plan for the corrective motion. In cases of left hemisphere damage where the predictive control was disrupted, the entire movement relies upon the error correcting controller in the intact right hemisphere. Consequently the transition from the original desired final configuration to the new one is more rapid, occurring prior to the cessation of the original motion.

Another similar case which may extend the current model are motions where the intended action consists of a sequence of movements, such as the case where one might be required to reach to a glass, lift it, and transport it to a new location. Certainly with the appropriate control such a task could be modeled as a continuous movement, however, the disparate requirements of the different phases of motion suggest that a segmenting strategy might be more likely, at least with the dominant arm. Conversely, one might expect that the non-dominant arm would be less
likely to parse a movement into segments, as all control problems look equally difficult to an equilibrium controller.

A final case that might alter the application of the model presented here are actions wherein the goal of the movement must be accomplished during the dynamic phase of motion rather than the stable postural phase. An example of such a task would be ball throwing, where the ball release is during the peak of hand velocity rather than at a stable posture. The simulations presented here suggest that both limbs transition to feedback strategies early in a movement, prior to the time of peak hand velocity. In cases where the dynamics must remain constrained, the transition time would need to be delayed in order to restrain deviations in the movement kinematics. The dramatic performance difference in tasks like throwing may reflect an inability of the non-dominant hand to appropriately delay the transition time.

Despite the gross nature of the simplifications undertaken in this model, simulated hand paths display many qualitative similarities to observed movements. The real movements showed primarily lateral deviations, which are in keeping with the simulation, which only produced lateral deviations to the initial path. Further the range of aspect ratios observed in real movements was well covered by the range produced by the simulation. Additionally the qualitative shape of high aspect ratio movements, with a late hook towards the target, was well matched by the simulation. The robust nature of the effects of changing the transition time on movement kinematics is especially encouraging, as one would expect the predictive power of such a simulation to only improve as more elaborate models of forward control are integrated.

The models of subject data in this experiment are very encouraging, as the transition time appears to be a particularly apt variable for proscribing a wide range of arm kinematics. Further, this variable appears to be capable of capturing many of the kinematic differences observed between dominant and non-dominant arm reaches. The ability to capture common kinematic
features of movement, despite the simplicity of the model is very encouraging. Further, the fact that the control described in this model is readily localized in the dominant and non-dominant hemispheres lends additional credibility to this model. By focusing here on the single parameter of transition time we highlight the power of this variable to explain the lateralization of the upper extremity in a manner consistent with the Dynamic Dominance hypothesis. Particularly the Dominant limb advantage in prediction and utilization of interaction torques appears to result from spending more time in a predictive phase of movement than the non-dominant system. A complication of the simple nature of this model is the inability of simulated movements to fit some movements observed in subject data. The poor matching of model to empirical finger paths associated with medially directed initial movement errors appear primarily in the dominant arm. This may indicate a dissociation of the type or quality of forward plan in addition to the timing of transition between the two controllers. This is also consistent with the Dynamic Dominance hypothesis, which predicts an advantage in dominant limb prediction of movement dynamics, and consequently better control of the ballistic phase of movement. Whereas it is possible that these effects and not the transition time are the cause of the lateralization of the hand kinematics, the model and simulation presented here appear to robustly describe the kinematic lateralization observed in real arm movements without the inclusion of such a degradation in forward control. This hypothesis can be explored more rigorously by exploiting a more elaborate version of this model that employs a more rigorous fitting technique, based on optimization (Yadav and Sainburg 2011). This would allow us to test whether the quality of the predictive and impedance controllers hypothesized here would vary between the limbs. In addition, in our current study, our predictive controller was based on a minimum jerk trajectory that described straight and smooth movement initiations. However, our actual movements tended to be more curved during movement initiation than our simulations. It is plausible that these curvatures might reflect optimization algorithms that minimize costs related to task performance, energetics, and signal-dependent noise (Flash and Hogan 1985; Liu and Todorov 2007; Nakano et al. 1999; Nishii and
Taniai 2009; Todorov and Jordan 2002; Bays and Wolpert 2007). Further research is necessary to test these alternatives.

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**Figure Captions**

Figure 3.1.

Block diagram of movement simulation. Sigmoidal curves indicate weighting functions. Torques from the two controllers are weighted by the current output of the sigmoidal weighting function, and summed to produce the driving torques of the movement. Following this the forward integrator is used to generate the simulated hand path.

Figure 3.2.

Examples of transition dynamics for the weighting function of the forward dynamic controller. The transition curve for three transition times: 20%, 50% and 80% of the minimum jerk movement time.

Figure 3.3.

Schematic of experimental setup. (A) Horizontal view (B) Bird’s eye view. In this view the hands are shown for schematic purposes. During actual experiments, vision of the hands and arms was occluded. In this figure occlusion is represented by the greyed out portions of the subject’s limbs, and the air sleds. The LCD screen is not shown in the bird’s eye view.

Figure 3.4.
(A) Hand paths produced by a sequence of transition points. Paths produced by extremely early shifts produce movements with extreme lateral swings, followed by late corrections. Late transitions produce primarily straight movements with late curves associated with transition to postural stabilization. (B) Direction deviation from the minimum jerk trajectory computed at peak finger acceleration and peak finger velocity. Positive errors indicate laterally directed deviations of the finger path from the minimum jerk trajectory. Direction deviation decreases as transition time increases, with direction error at peak velocity consistently larger than at peak acceleration. (C) Finger path aspect ratio plotted against the transition time. As transition time increases the aspect ratio decreases, reflecting a less curved movement path.

Figure 3.5.

Examples of finger trajectories from a single subject fit by the model. Actual finger paths are in grey, and simulated finger paths in black. Movements with a range of transition times are presented for each arm.

Figure 3.6

Mean kinematics from empirical data. (A) The mean aspect ratio of real movements by hand. (B) The mean angular deviation of real movements from a vector connecting the start and target location. Positive values indicate a laterally directed initial finger path.

Figure 3.7.

Transition point as a function of hand path aspect ratio. In both right and left hands the transition time is significantly correlated with the aspect ratio of the hand path to be fit. Dominant limb movements tend to display lower aspect ratio, and higher transition times. Extreme transition times in the right hand primarily reflect inability to accurately fit movements with medially directed early reaches.
Figure 3.1:
Figure 3.2: Examples of transition dynamics

Transition dynamics for 20%, 50% and 80% of movement

Fraction of trial time
Figure 3.3: Schematic of experimental setup

A

LCD Monitor
Mirror
Air Sled
Table

B

Target
Finger Cursor
Air Sleds
Start Circle
Figure 3.4: Simulation kinematics
Figure 3.5: Example finger trajectories
Figure 3.6: Mean kinematics from empirical data
Figure 3.7: Transition point as a function of hand path aspect ratio
Appendix 3.1

In this appendix the following notations are utilized:

- $B$ = viscous like damping of the elbow and shoulder
- $I_s$ = moment of inertia of the upper arm
- $I_e$ = moment of inertia of the forearm
- $K_e$ = Rotary stiffness of the elbow
- $K_s$ = Rotary stiffness of the shoulder
- $l_e$ = length of the forearm segment
- $l_s$ = length of the upper arm segment
- $m_s$ = masses of the upper arm
- $m_e$ = mass of the forearm
- $r_s$ = distance from the shoulder joint to the center of mass of the upper arm
- $r_e$ = distance from the elbow joint to the center of mass of the forearm
- $S_R(t)$ = a rising sigmoidal function which weights the input of the feedback control
- $S_F(t)$ = a falling sigmoidal function which weights the input of the forward control
- $\Delta t$ = Time step. In all computations presented in this study $\Delta t$ is 0.0005s.
- $T_{EN}$ = the elbow net torque
- $T_{SN}$ = the shoulder net torque
- $T_{EM}$ = the elbow muscle torque
- $T_{SM}$ = the shoulder muscle torque
- $T_{EI}$ = the elbow interaction torque
- $T_{SI}$ = the shoulder interaction torque
- $\theta_s$ = orientation of upper arm relative to the global frame
- $\theta_e$ = orientation of the forearm relative to the upper arm
- $\theta_{EF}$ = orientation of upper arm relative to the global frame in the desired final state
- $\theta_{F}$ = orientation of the forearm relative to the upper arm in the desired final state
- $x$ = the position of the shoulder joint in the x axis of the global reference frame
- $y$ = the position of the elbow joint in the y axis of the global reference frame

To approximate a minimum jerk trajectory the following equation was utilized:

$$P(t) = \begin{bmatrix} -1.1425 \times 10^{-4} + 2.1231 \times 10^{-5} \times t \\ -4.447 \times 10^{-7} \times t^2 + 1.1628 \times 10^{-8} \times t^3 \\ -1.1307 \times 10^{-11} \times t^4 - 9.9837 \times 10^{-17} \times t^5 \\ -1.5527 \times 10^{-17} \times t^6 + 2.9055 \times 10^{-20} \times t^7 \\ -1.2326 \times 10^{-23} \times t^8 \end{bmatrix}$$

Equation: 3.3

In equation 3.3, $P(t)$ ranges from 0 to 1 as $t$ ranges from 0 to 1000. $P(t)$ is scaled by the desired movement magnitude in each planar axis to produce the time series of position in each axis:
\[ x(t) = P(t)(x_{r1000} - x_{r0}) + x_{r0} \]
\[ y(t) = P(t)(y_{r1000} - y_{r0}) + y_{r0} \]  

Equation 3.4

Equation 3.3, approximates a minimum jerk trajectory with a slight asymmetry that accounts for the modestly extended tail in the velocity profiles of Plamondon et al.’s original data.

Derivations of the equations used to compute inverse dynamics appear in Bagesteiro and Sainburg (2002), however, only the final form of the equations is presented here. The elbow joint muscle torques are given by:

\[ T_{eM} = T_{eN} - T_{el} \]  

Equation 3.5

\[ T_{eN} = (I_e + m_e r_e^2) \ddot{\theta}_e \]  

Equations 3.6

and

\[ T_{el} = -(l_e m_e r_e \cos(\theta_e) + I_e + m_e r_e^2) \ddot{\theta}_e - l_e m_e r_e \sin(\theta_e) \dot{\theta}_e^2 \]  

Equations 3.7

Similarly shoulder torques are given by the equation:

\[ T_{sM} = T_{sN} - T_{sl} + T_{eM} \]  

Equation 3.8

\[ T_{eM} \]  

is given by equation 3.5, and \[ T_{sN} \]  

and \[ T_{sl} \]  

are given by:

\[ T_{sN} = (I_s + m_s r_s^2 + m_s l_s^2 + m_s l_s r_s \cos(\theta_s)) \ddot{\theta}_s \]  

Equations 3.9

and

\[ T_{sl} = -m_e r_e \left( l_e \cos(\theta_e) \ddot{\theta}_e + l_s \sin(\theta_e) \dot{\theta}_e^2 + 2l_s \sin(\theta_e) \dot{\theta}_s \dot{\theta}_e + l_s \sin(\theta_e) \dot{\theta}_s^2 \right) \]  

Equations 3.10

Feedback control is driven by a simple stiffness and damping control law. At the elbow the feedback torque \[ T_{ef} \]  

is given by:

\[ T_{ef}(t) = K(\theta_e(t - 80) - \theta_{ef}) + B(\dot{\theta}_e(t - 80)) \]  

Equation 3.11
In this equation the feedback driven torque is derived from the position and velocity at a time 80ms prior to the time of torque application. Similarly for the shoulder feedback torque \( T_{sF} \):

\[
T_{sF}(t) = K\left(\theta_s(t-80) - \theta_{sF}\right) + B\left(\dot{\theta}_s(t-80)\right)
\]

Equation 3.12

To simulate a movement these control outputs are combined according to the following law to produce simulated muscle torques, \( T_{sM} \) and \( T_{eM} \), acting at the shoulder and elbow:

\[
T_{sM}(t) = T_{eM}(t)S_F(t) + T_{eF}(t)S_R(t)
\]

Equation 3.13

\[
T_{sM}(t) = T_{sM}(t)S_F(t) + T_{sF}(t)S_R(t)
\]

Equation 3.14

Having computed these terms, the joint acceleration is solved by substituting equations 3.6 and 3.7 into equation 3.5, and equations 3.9 into equation 3.10 into equation 3.8 and rearranging for the joint accelerations. This gives the following:

\[
\ddot{\theta}_e = \frac{\left[\text{Acos}\left(\theta_e\right)(2T_{eM}-T_{sM}) + I_e(T_{eM}-T_{sM}) + \left(I_s+m_rI_r^2\right)T_{eM}\right] - A\left(I_s+m_rI_r^2\right)\sin(\theta_e)\dot{\theta}_e^2 - A^2\sin(\theta_e)\cos(\theta_e)(\dot{\theta}_e + \dot{\theta}_s)^2}{\left(I_s+m_rI_r^2\right)I_e - \left(\text{Acos}\left(\theta_e\right)\right)^2}
\]

Equation 3.15

\[
\ddot{\theta}_s = \frac{\left[I_e(T_{sM}-T_{eM}) - \text{Acos}\left(\theta_e\right)T_{eM} + A^2\sin(\theta_e)\cos(\theta_e)\dot{\theta}_s^2\right] + AI_e\sin(\theta_e)(\dot{\theta}_e + \dot{\theta}_s)^2}{\left(I_s+m_rI_r^2\right)I_e - \left(\text{Acos}\left(\theta_e\right)\right)^2}
\]

Equation 3.16

Where:

\[
A = m_rI_r\theta_e
\]

Equation 3.17

Given these joint accelerations, the joint angles are then solved by simple discrete integration. At the elbow:

\[
\dot{\theta}_e(t + \Delta t) = \dot{\theta}_e(t) + \ddot{\theta}_e(t)\Delta t
\]

\[
\theta_e(t + \Delta t) = \theta_e(t) + \dot{\theta}_e(t)\Delta t
\]

Equation 3.18
And similarly at the shoulder:

\[ \dot{\theta}_s(t + \Delta t) = \dot{\theta}_s(t) + \ddot{\theta}_s(t) \Delta t \]
\[ \theta_s(t + \Delta t) = \theta_s(t) + \dot{\theta}_s(t) \Delta t \]

Equation 3.19

In all computations presented in this study, \( \Delta t \) is 0.0005s.
Chapter 4: Lateralized Cortical Potentials During Whole Arm Movements Reflect the activity of Dynamic Control Processes

Introduction

Lateralization of the human motor system is well recognized but poorly understood. Kinetic studies of the mechanisms of movement lateralization suggest differential specialization of the motor cortex in the right and left hemispheres. Based upon studies of arm mechanics during reaching, our group has formulated a Dynamic Dominance hypothesis, which describes the lateralization of control. In this hypothesis the dominant arm is specialized at anticipating and compensating for predictable forces, including those inertial forces resulting from the motion of the arm (Sainburg 2002), while the non-dominant arm is specialized for correcting perturbations and stabilizing posture (Bagesteiro and Sainburg 2003; 2005). This hypothesis arises from the fact that the dominant limb produces similarly straight, accurate movements regardless of the dynamic requirements of the task. In contrast, non-dominant arm movements vary with the task, growing more curved as the inertial dynamics grow more pronounced (Sainburg and Kalakanis 2000). While it appears to lack the faculties to anticipate the inertial dynamics of motions, the non-dominant limb appears to show an advantage in correcting errors due to unexpected perturbations of the arm (Bagesteiro and Sainburg 2003; 2005).

While substantial behavioral evidence exists to support this Dynamic Dominance hypothesis, relatively little information exists regarding the neural substrates responsible for this lateralization. Data from patients with unilateral strokes encompassing the motor areas have provided evidence for the localization of lateralized motor control mechanisms. In data from our group (Schaefer et al. 2007; 2009a; 2009b; 2011; Mutha et al. 2011), right hand dominant stroke patients with left hemisphere cortical damage, when moving with the nonparetic left arm, display deficits in producing smooth or straight movements, but no deficits in achieving a desired final
position. In contrast, patients with right hemisphere cortical damage, moving with the nonparetic right arm, show no deficit in producing straight movements, but do not display online corrections for errors in the direction of initial movement, resulting in larger final position errors than in control subjects. In contrast to the classical view that movements are controlled through contralateral cortical mechanisms, these findings indicate that ipsilateral cortex contributes substantially to normal reaching movements.

Computational simulation studies (Yadav and Sainburg 2011; Chapter 2) suggest that the differences in hand kinematics for single reaching movements are well reproduced by a sequential control model. Initial motor output is modeled with an open-loop controller using an inverse dynamic model of the limb mechanics, in order to produce a desired hand trajectory. Later movement is controlled by an error correcting process that specifies impedance about a specified trajectory. In this model, lateralization of hand kinematics arises due to differences in the timing of the transition from forward to feedback control. Dominant hand movements are modeled well by late transitions to an impedance control scheme, while non-dominant movements are best modeled by an early transition. The theoretical premise for using the transfer time of control to explain the lateralization of hand kinematics derives from the costs of interhemispheric communication (Holtzman and Gazzaniga 1984; Passarotti et al. 2002; Putnam et al. 2008; Ringo et al. 1994). If movement of a single limb relies on both cortices, we might expect a greater reliance on the controller of the contralateral hemisphere, since we know that the contralateral hemisphere directly innervates the spinal cord for control for any movement. When considering a sequential ballistic and postural control scheme, this would indicate that the dominant limb would spend more time in the predictive phase, while the non-dominant limb would transition comparatively rapidly to the postural phase. This is also compatible with early work on lateralization that examined the portion of movement time spent during deceleration and observed that the post deceleration period was prolonged in the non-dominant limb (Roy and Kalbfleisch 1994).
While the kinematics of upper limb motor lateralization have been well described, and substantial investigation has been directed at the underlying mechanics (Bagesteiro and Sainburg 2002; Sainburg and Kalakanis 2000; Wang and Sainburg 2007), there is little literature describing neural activation correlated with these mechanics. In large part, this is due to the difficulty in restricting the motion artifacts created by such gross arm movements. In this study, we investigate the cortical mechanisms of human motor lateralization by using direct measures of changes in cortical activations associated with upper limb movement. EEG provides an ideal method for investigating the cortical activity during rapid reaching movements, since EEG signals have high temporal fidelity with cortical activity. Indeed a number of movement related potentials have been described in the literature (Deecke et al. 1969; Grünewald-Zuberbier and Grünwald 1978).

Prior to the initiation of finger and wrist movements there are well characterized negative deflections of the recorded cortical potential. In the case of self paced movements these potentials are generally referred to as bereitschaftspotential (Kornhuber and Deecke 1965; Shibasaki and Hallett 2006), whereas in the case of cued movements they are referred to as the readiness potential (RP), or contingent negative variation (CNV) of the cortical potential (Rohrbaugh et al. 1976; Walter et al 1964). These potentials are generally thought to reflect the cortical activity associated with planning and initiation of movement (Kutas and Donchin 1980). The amplitude of the readiness potential is enhanced by attentiveness (McCallum and Walter 1968). This enhancement presumably reflects the increase in cortical activity associated with performance of a more demanding task. Movement initiation is typically heralded by a spike in the cerebral potentials usually called the motor potential (MP) (Deecke et al 1969). During movement there is a secondary potential, which may appear to be a continuation of the premotor potentials, that is sometimes referred to the movement monitoring potential (MMP) (Grünwald and Grünwald-Zuberbier 1983; Grünwald et al 1983). The RP, MP, and MMP are all known to scale with the rate of force production in isometric finger tasks (Slobounov and Ray 1998; Slobounov et al. 1998). It is plausible then that these potentials will scale with the dynamics of a task requiring
gross arm movements, as there are some similarities between the dynamics of force production and motion.

An additional mode of analysis is to take the difference between the ipsilateral and contralateral recordings over motor areas. In the case of studies examining changes in the pre-movement potentials the resulting signal is usually referred to as the lateralized readiness potential (LRP) (Eimer 1998). The LRP is known to scale with the cognitive difficulty in planning, including which hand to utilize, and go-nogo cuing (Kopp 1996; Rohrbaugh et al. 1976), presumably reflecting the increases in cortical activation associated with task planning.

Studies of the slow movement related potentials observed during wrist movement indicate that these potentials may reflect some underlying lateralization of the control system used to effect those movements. Grünewald et. al. Showed in self paced hand movements a lateralization of the N1 pre-movement potential in the dominant right hand, and much weaker lateralization in the non-dominant left hand (Grünewald et al. 1979). In both cases the contralateral recording displayed the largest deflection from the resting potential. In the MP potential the difference was clearer, with the dominant arm hand movements showing a notable lateralization, and the non-dominant hand movements displaying no lateralization of MP potential. Following movement completion this trend in lateralization reversed, such that the non-dominant hand displayed notable lateralization of the slow signal, with the contralateral sites displaying mild negativity, and ipsilateral sites displaying no notable potentials. In contrast the dominant limb showed no lateralization, with both hemispheres showing no notable potentials.

These results are certainly indicative of the effects we would expect based upon the Dynamic Dominance hypothesis. During early movement the non-dominant limb must rely upon the cortical structures in the dominant cortex to supply control of limb dynamics. Consequently we expect that lateralization of the cerebral potentials will be less pronounced than in dominant limb reaches. In contrast, late in the movement the dominant arm must recruit non-dominant cortex to supply control of impedance regulation to stabilize posture about the desired
configuration. Consequently we would expect less lateralization of the cerebral potentials in the later phase of dominant arm reaches than non-dominant. While these results are consistent with the Dynamic Dominance hypothesis, the dynamic difficulty of small hand motions is likely to be different than those encountered in rapid, whole arm, movements. Since the dynamic load is quite different in these cases the applicability of these results to whole arm motions is not clear.

In this study we record broad electrical activity of the left and right cortices under controlled reaching conditions. To test our conceptual model of control, we reproduced reaching conditions in which our model of control predicts specific patterns of cortical activity (Bagesteiro and Sainburg 2002), and observed the cortical EEG response. We expect to see a strong contralateral preponderance in the late LRP during dominant arm movement preparation. We expect this lateralization of potentials to continue through both the MP and early MMP. We then expect this contralateral preponderance to abate in the late MMP as postural stabilization strategies take effect, recruiting ipsilateral hemisphere activity. In contrast, we expect that non-dominant limb movements will display weaker LRPs, which then strengthen during the MMP as reliance on ipsilateral involvement for forward movement control shifts to contralateral circuits specializing in feedback postural stabilization. The observed EEG activity should provide initial validation, or evidence against, of our control model.

Materials and Methods

Subjects

All methods utilized in this study were approved by the Pennsylvania State University Institutional Review Board. Twelve neurologically intact right handed adults, aged from 19 to 25 years old were tested. All subjects were screened for handedness using a modified version of the Edinburgh inventory (Oldfield 1971). All subjects gave informed consent prior to participation. Subjects were randomly assigned to perform with either their dominant (right), or non-dominant (left) hands (n=6 per group).
Experimental Task:

The design of the task in this study attempted to reproduce a task previously established in our lab group to produce strongly lateralized movements (Bagesteiro and Sainburg 2002). This mechanical lateralization is associated with the differences in our theorized control strategies, and consequently should result from lateralization of cortical activity. Figure 4.1 shows the experimental apparatus utilized in this experiment. Subjects were seated in front of the kinematic acquisition apparatus with arms positioned above a horizontal support surface. The subject’s arms rested in air sleds, just below shoulder level. This reduces the effects of friction and gravity on the movements, allowing subjects to perform a large number of trial movements without fatiguing. Interposed between the subject's eyes and hands was a mirror. A cursor representing finger position and circles representing start and end locations were projected onto the mirror by a 55” LCD television monitor placed above the subjects head. The position of the LCD screen is carefully calibrated so that the reflected cursor position appears to the subject to be veridical with their finger position. Location of the finger was sampled in real time using a Flock of Birds electromagnetic six degree of freedom sensor system, with sensors placed at the center of the hand and upper arm segments. Joint center position data was collected at 130hz using a custom written computer program written in Real Basic (Real Software, Lake Oswego, OR) for the Macintosh computer.

In each trial subjects were presented with a starting circle 2cm in diameter located 15cm lateral to the body midline. The same computer uses real time readings of the finger position to provide a low latency cursor over the subject’s finger location, allowing subjects to place their finger at the designated starting location. Targets were presented in three movement directions form the initial finger location: 45°, lateral and away from the trunk; 90°, directly away from the trunk; and 135°, medial and away from the trunk, and movement amplitude was 15cm. In order to motivate subjects to make accurate and fast movements, points were awarded if a movement is
faster than 0.8m/s, and on a graded scale based on accuracy. If a subject’s final finger position was within 3cm of the target position they received 1 point, within 2cm they received 3 points, and within 1cm they received 10 points.

To begin a trial subjects were instructed to move the cursor into the circle indicating the starting finger location. Subjects were required to hold their finger in this position for 5s at which point an audible cue was given indicating the beginning of the trial. Subjects were then instructed to perform a rapid reaching movement attempting to stop with their finger at the indicated target position. The target direction was randomized across the three target directions. Subjects performed 300 movements with a single hand, 100 reaches to each target. Each subject performed with only one hand in order to eliminate the confounding effect of asymmetric transfer of learning (Bagesteiro and Sainburg 2005; Sainburg and Wang 2002; Wang and Sainburg 2004a; 2004b). Kinematic data from the fingertip were saved and used to confirm that the current task indeed stressed the lateralization of the motor system. The aspect ratio of the finger path, early path deviation, and final position error were all compute for this purpose. The aspect ratio was taken simply as the minor axis of the finger path, divided by the major axis. The initial path deviation was taken as the angle between a vector connecting the start circle with the target circle and a vector connecting the starting finger location with the finger location at peak velocity. The final position error was the Euclidean distance between the finger and the target at the end of movement. The start and end of movement were defined as the first minima in the velocity profile to either side of the peak that fell below 5% of the peak velocity.

EEG

EEG data was collected using a 19 channel montage using standard 10:20 electrode placement (Jasper 1958), connected to a Synamp amplifier and software (Compumedics Neuroscan, Charlotte NC). Electrodes are passive silver-silver chloride ring electrodes coupled to the scalp with conductive gel. EEG data was collected continuously at 2KHz for each channel.
during a testing session. To synchronize the EEG data to trial kinematics, a trigger pulse was produced by the computer recording the joint kinematics at the time the subject’s finger left the start circle. This event was logged by the EEG amplifier, allowing the EEG data to be synchronized to the kinematics of each movement. All analyses of the EEG data were performed using the EEGLAB toolbox for MatLab (Mathworks, Natick MA), which provides a suite of well verified functions for the processing and analysis of EEG signals (Delorme and Makeig 2004).

In order to ensure that noise from the kinematic collection system did not contaminate the data a simple bucket test was performed to estimate the spectral content of the noise introduced by the Flock of Birds system. These tests found that, while this system does produce substantial noise in the EEG data, this noise is tightly constrained at the collection frequency of 130hz and it’s higher harmonics. We additionally noted substantial peaks at 60Hz and higher harmonics, presumably associated with the building electric system. In order to eliminate this contamination we low pass filtered the EEG data at 30Hz. Not only does this eliminate the noise from the collection system and building power, but also serves to reduce possible EMG artifact associated with muscle activity (Bilodeau et al. 1990; 1991).

After filtering the continuous EEG was blocked into epochs around the trigger events. Each epoch ran from 3 seconds prior to the trigger, to 1 second post trigger. Movements in this study lasted between 400ms and 500ms, so 1 second post trigger was sufficient to easily capture all of the cortical potentials associated with movement generation. In order to reduce the effects of artifacts in the signal EEG data were decomposed using an independent component analysis (ICA) to isolate signals within the electrode space. This analysis makes isolation of certain noise sources such as ocular artifact very easy (Delorme et al. 2007). Components associated with clear noise sources were eliminated from the signal. Following this trials were scanned using EEGLAB’s automatic facilities to identify bad trials based upon the peak values, standard deviation of potentials, kurtosis, and spectral power. These facilities are known for the high reliability detection of artifacts, especially when utilized on the decomposed signals form ICA
rather than the raw signals (Delorme et al. 2007). After automatic trial identification, the remaining trials were scanned manually for abnormal activity.

While previous work has utilized ICA to identify and remove motion artifacts relating to gait from EEG data (Gwin et al. 2010), this method is appropriate only if the motion artifact is uncorrelated with the signals of interest, which is not the case here. Consequently we took every precaution to reduce the motion artifacts in this study as much as possible. Subjects were seated in a chair with a four-point harness designed to restrain the subject’s torso against the chair. Further, each subject wore a cervical collar for the duration of testing, which restrained movement of the subject’s head relative to the chair. These constraints served to limit much of the motion that might produce artifacts in the EEG.

The lateralized potential was computed by re-referencing the contralateral electrode to the ipsilateral electrode. For this study we elected to examine data from the P3 and P4 electrodes, as our previous work in stroke patients indicates that the parietal cortex is the primary locus for predictive, predictive control (Mutha et al. 2011). To produce the event related potential, epochs were averaged across all accepted trials within each subject to approximate the true event related signal.

Results

In the kinematics, both hand groups behaved in a manner consistent with our previous work. Subject finger paths showed substantially greater aspect ratios in non-dominant arm movements than in dominant arm movements ($F_{(1,12)}=5.30, p=0.04$) (Figure 4.2a), which reflected greater curvatures for the non-dominant arm. While there was not a significant effect of hand on the initial direction of movement, there was a strong trend ($F_{(1,12)}=4.17, p=0.07$) for more laterally directed errors in the non-dominant hand (Figure 4.2b). Despite these differences there were no significant differences ($F_{(1,12)}=1.78, p=0.21$) in the final accuracy of the hands (Figure 4.2c). This is consistent with the effects observed previously in our reference studies (Bagesteiro and

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Sainburg 2002; Sainburg and Kalakanis 2000), indicating that the current task does indeed represent a good discriminator of lateralization in the motor system.

In the event related potentials, clear lateralization was evident in the signals recovered from dominant arm movements (Figure 4.3b), but not for non-dominant movements (Figure 4.3a). Interestingly the observed lateralization peaked well after the initiation of movement, rather than before movement. In the current study lateralized potentials during dominant arm movements were evident with a peak 145ms after the trigger event. To compare the strength of lateralization, the magnitude of the lateralized potential was measured at 145ms post trigger. To compare the effects of hand on the lateralized potential we performed a 2 hand by 3 target repeated measures ANOVA. Subjects were included as a random effect, and nested within hand. This comparison showed a main effect of hand ($F_{(1,12)}=4.72$, $p=0.05$) and target direction ($F_{(1,12)}=4.95$, $p=0.03$), but the interaction between target direction and hand was not significant ($F_{(1,12)}=2.52$, $p=0.12$). As we expect that the amplitude of the lateralized potential in dominant limb movements will scale with the task demands, and that this drives the main effect of target direction, we performed a further one way ANOVA on target direction within the hand performing groups. In this sub-group there was a significant effect of target direction ($F_{(1,6)}=11.85$, $p=0.01$), while the same analysis in the left hand group showed no significant effect ($F_{(1,6)}=0.14$, $p=0.71$).

**Discussion**

In these data we observe a strong lateralization of the MMP cortical potential in dominant limb movements. In contrast, non-dominant limb movements showed very little lateralization of cortical potential during any phase of motion. The magnitude of the lateralized cortical potential is associated with the differential recruitment of cortex, and larger potentials appear to reflect increased activity in contralateral cortex. The lack of lateralization in cortical potentials during non-dominant arm movements is consistent with symmetric activations of cortex and with the
idea that the non-dominant arm recruits ipsilateral cortex to support dynamic control of the movement. In dominant arm movements the strong lateralization is reflective of contralateral activity without associated activations in the ipsilateral cortex. In contrast to our predictions, we did not observe a reversal of this trend in the late potentials. Non-dominant limb movements did not show stronger lateralization of cortical potentials in the late MMP. This is likely due to the selection of electrodes used for the analysis presented in this experiment. We focused on the P3 and P4 electrodes, as we anticipated that these would recover the activity over areas of cortex known to be involved in dynamic processing for the dominant limb (Schaefer et al. 2007; 2009a; 2009b; 2011; Mutha et al. 2011). Since the areas associated with feedback mediated correction of the final finger position would be expected in the frontal cortex, the lack of strong lateralization in the MMP for non-dominant movements late in movement is unsurprising. While previous work has noted a transition to stronger lateralization late in the movement for non-dominant finger motions (Grünewald et al. 1979) this work averaged the potentials in P3 and C3 electrodes and those in P4 and C4 electrodes. Consequently the previous work might distribute effects that are in fact localized on the anterior-posterior axis.

In addition to the primary effect of hand on the lateralization of cortical potentials, there was a main effect of target, driven primarily by the cortical lateralization observed during dominant arm movements. This effect appears to follow the interaction dynamics at the elbow. While the lateralized cortical motor potentials are known to vary with the difficulty of motor planning and attention (Rohrbaugh et al. 1976, McCallum and Walter 1968), it is not clear from the past literature whether the dynamic requirements of the task should be considered as an index of the difficulty in planning a task. While some evidence exists that load state is represented in the bereitschaftspotential, the magnitude of load was not represented (Kristeva et al 2000). In fact some recent evidence from isometric tasks has suggested that the LRP reflects simply the lateralized nature of the execution mechanism, and consequently varies with the arm but not task.
In contrast, and consistent with the current findings, notable effects of load amplitude and rate of loading have been observed in the movement monitoring potential (Slobounov and Ray 1998), and an additional study noted effects of rate of force production on all phases of the motor potential, including the readiness potential (Slobounov et al. 1998). The current results in the context of Dynamic Dominance suggest that the cortical lateralization of the control of limb dynamics does play a role in the lateralization of cortical potentials, but only during the movement monitoring phase. In this context changes in the direction of movement that tend to increase interaction torques at the elbow, also tend to recruit additional contralateral cortex in dominant arm movements. This appears to indicate that the more medial directions with increased elbow interaction torques stress the motor system more, causing increases in cortical recruitment. Why these potentials should not increase during the pre-movement phase is not immediately apparent, as one might expect that these effects would be similar to those observed for changes in the rate of force production (Slobounov et al. 1998).

In contrast, the same movement directions produce no changes in the lateralized cortical potential during non-dominant arm movements. In this case it appears that any increases in cortical recruitment are symmetric. This is consistent with the premise that the non-dominant arm must recruit ipsilateral cortex to supplement the activity of the contralateral cortex in dynamically demanding scenarios.

These findings appear to support the Dynamic Dominance Hypothesis. First the finding that lateralized cortical potentials scale with the dynamics requirements of the task indicates that these dynamics do indeed act as stressors for the motor system. This is consistent with evidence from mechanical studies of the non-dominant limb showing that dynamic errors increase with these same dynamics (Bagisteiro and Sainburg 2002; Sainburg and Kalakanis 2000), and is fundamental to the Dynamic Dominance hypothesis. If increased dynamic requirements of a task were not stressors for the neural circuits responsible for dynamic planning, then these dynamics
would do little to differentiate the dominant and non-dominant hemispheres. Secondly the observation that the non-dominant arm movements do not show any notable lateralization of the cortical signals is consistent with the hypothesis that the non-dominant arm is symmetrically recruiting both contralateral and ipsilateral cortex to complete these tasks. An alternative hypothesis would be that the non-dominant arm simply does not recruit cortex near the P3 and P4 electrodes. This hypothesis would also be a sensible hypothesis as we did not observe the late lateralization that one would expect from the recruitment of non-dominant cortex in the role of controlling postural stabilization. This is not surprising as we would expect that the cortical circuits involved in this task are localized near the C4 electrode rather than the P4 electrode, and consequently were not examined in the course of this analysis. While it might be suggested that the lack of lateralized signal results from a simple lack of activity in both the ipsilateral and contralateral hemispheres, this is contrary to evidence from stroke subjects suggesting ipsilateral contribution to the control of unimanual movements. Stroke patients with left parietal damage showed deficits in the constraint of task dynamics with their ipsilesional hand (Schaefer et al. 2007; 2009a; 2009b; 2011; Mutha et al. 2011), suggesting that the current findings do not reflect a simple lack of relevant activity during non-dominant arm movements. Some additional studies that stress the feedback stabilization portion of the human control system may be beneficial in showing potentials that scale with task during non-dominant reaches.

While these results are consistent with the Dynamic Dominance Hypothesis in many respects, and are certainly very encouraging, there are a number of potential caveats that must be addressed. In our methods we attempted to limit the impact of motion artifact on the recorded signal with some success. The cervical collar and torso restraint system did manage to restrict most movement, however, there was some play in all of these elements. While some motion artifact was clearly evident in the observed signals, there is no reason to suspect that this artifact would be asymmetric with regards to its effect on cortical signals. One additional critique of the
current findings is that we have examined a differential signal rather than the direct signals from either the P3 or P4 electrodes. While this does limit our ability to draw conclusions about the direct recruitment of cortex in these areas, this method offers some advantages. The Dynamic Dominance hypothesis makes specific claims about how dominant and non-dominant limbs recruit bilateral cortex. The current analysis allows for a convenient single metric to examine these effects. Finally the lateralized potentials observed here did not develop until approximately the time that motion began. This is at odds with literature showing the development of lateralization during the readiness phase prior to movement initiation. While this may appear surprising, some previous work has indicated that premotor potentials in a CNV task can be segregated into an early and late potential if the inter-stimulus interval is long enough (Rohrbaugh et al. 1976) By giving subjects a full five seconds without distractions between setting of posture and gaze and the initiation of motion, the current methods may have allowed for this sort of separation in the response. Consequently the early wave of the CNV may have occurred closer to the initiation of the trial at -5s, well outside the range of the -3 to 1s trial window. Further, as reaction time was not emphasized in this paradigm, the secondary pre movement peak may have been de-emphasized. Further, the magnitude of the CNV is known to be related to attentiveness (McCallum and Walter 1968). In the current study the task was a relatively simple movement, and it is possible that subjects did not remain fully attentive, resulting in lower overall CNV, and consequently reduced LRPs.

While these issues certainly warrant additional exploration, the current results certainly seem to suggest that at least some of the cortical processes predicted by the Dynamic Dominance hypothesis are indeed present during reaching control in healthy subjects. Further explorations of these effects with higher density EEG arrays would certainly be instructive, as to the localization of activity during these reaches. Further a paradigm which emphasizes planning at a restricted
time in each trial might be warranted to see if the lateralization of motor potentials observed here for the dominant hand also occur during movement planning.

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Figure Captions

Figure 4.1.

Schematic of experimental setup. (A) Horizontal view (B) Bird’s eye view. In this view the hands are shown for schematic purposes. During actual experiments, vision of the hands and arms was occluded. In this figure occlusion is represented by the greyed out portions of the subject’s limbs, and the air sleds. The LCD screen is not shown in the bird’s eye view.

Figure 4.2.

Kinematic measures of movement by target direction and hand. Target direction is labeled for Lateral (Lat. ), Anterior (Ant. ), and Medial (Med. ) directed movements. (A) Movement aspect ratio. (B) Direction deviation. Negative deviations indicate movements directed lateral to the targets, while positive deviations indicate movements directed medial to the target. (C) Final position error.

Figure 4.3.

Event related lateralized potentials. These potentials are smoothed at 4hz for presentation. (A) Potentials recorded for non-dominant, left arm, movements. (B) Potentials recorded for dominant, right arm, movements.
Figure 4.4.

Amplitude of the lateralized motor potential at 145ms post cue.
Figure 4.1: Experimental apparatus

A

LCD Monitor
Mirror
Air Sled
Table

B

Target
Finger Cursor
Air Sleds
Start Circle
Figure 4.2: Kinematics
Figure 4.3: Event related potentials

(A) Lateralized Motor Potential (mV) vs. Trial Time (s)

(B) Lateralized Motor Potential (mV) vs. Trial Time (s)

Legend:
- lateral
- anterior
- medial
Figure 4.4: Amplitude of the lateralized potential at 145ms
Chapter 5: Summary and General Discussion

The works presented in this dissertation represent several tests of the Dynamic Dominance hypothesis as a general control strategy, rather than a description of lateralization. The theory of dynamic dominance presents testable hypotheses about many facets of motor control. The studies presented in this document address a spectrum of hypotheses from the level of dynamic analysis to cortical activity. With these studies we were interested in addressing three specific limitations of past work. First we wanted to examine the Dynamic Dominance in a context of free reaching. Dynamic Dominance was developed based upon data collected from constrained, planar reaches. Despite this limitation in the original data set, the hypothesis predicts that the kinematic and kinetic effects observed in planar cases will also be present in unconstrained reaching where gravity must be accounted for. Second we wished to test the feasibility of a simple control model simulating the discrete contribution of predicting and error correcting control from the hemispheres. Dynamic dominance suggests that one variable which regulates effector kinematics may be the time of transition from predictive control to error correcting postural stabilization. We were particularly interested in the ability of such a model to describe the differences in control observed in dominant and non-dominant arm movements. Finally dynamic dominance suggests specific patterns of cortical activity during a unimanual reach. Based upon the control requirements of the task we felt that we could predict the activity over specific areas of cortex based upon the integration of ipsilateral control predicted by Dynamic Dominance. These studies test specific predictions raised by the dynamic dominance hypothesis, and extend our understanding of control lateralization in the human motor system, as well as the manner in which general control is composed.

The study presented in the second chapter tests the general predictions of dynamic dominance regarding the generalization of kinematic and kinetic lateralization observed in horizontal plane reaching studies, to parasagittal reaches. Based upon prior work in supported
reaching we tested the prediction that the dominant arm would show hand paths with more accurate initial direction and lower aspect ratios than the non-dominant hand, but no substantial difference in final position error. We also tested the additional prediction that these differences would be the result of the non-dominant hand failing to predict the effects of interaction torques and gravity during the movement.

In the second chapter, both the magnitude of the muscle torque impulse, and the coordination of torque events at each joint appear to contribute the consistent interlimb differences in initial direction and movement curvature. While the finding that the torque impulse is improperly scaled in the non-dominant arm is consistent with previous literature (Bagesteiro and Sainburg 2002; Sainburg and Kalakanis 2000) the findings of improper synchronization of the torques at the elbow and shoulder represents a novel description of the discoordination evident in the non-dominant arm movements. In the data presented in the second chapter, it is apparent that the dominant limb system produces movements that are directed more accurately toward the target than the non-dominant system, reflecting the temporal coordination of the elbow and shoulder torques. In contrast with the early movement errors, the non-dominant system did not show significant difference in final position accuracy. These results further indicate that the inability of the non-dominant limb to account for dynamic factors extends to the anticipation of gravity. Consequently we might attribute the motor system’s special representation of gravity (Gentili, et al 2007; Papaxanthis, Pozzo, Vinter & Grinshin 1998; Papaxanthis, Pozzo, Popov & McIntyre 1998; Papaxanthis, et al. 2005) specifically to the dominant limb controller.

The coordination deficits of the non-dominant limb our current and previous studies suggest are reflective of the Dynamic Dominance hypothesis in that non-dominant system is less adept at predicting gravitational and intersegmental dynamics when specifying early movement trajectories, and that this limb relies more on feedback mechanisms to reach the final position with similar accuracy to the dominant arm (Duff and Sainburg 2007; Shabbott and Sainburg 2008).
Several studies have noted the kinematic consistency of the dominant limb during free reaching, noting that hand paths remain invariant despite changes in loading, movement speed or gravity (Gentili, et al. 2007; Lacquaniti, et al. 1982; Papaxanthis, Pozzo, Vinter & Grinshin 1998; Papaxanthis, Pozzo, Popov & McIntyre 1998; Soechting & Lacquaniti 1981). Inconsistent with these studies, which observed consistent, straight, movements of the dominant arm, our results show that the non-dominant arm displays errors in movement direction and curvature consistent with failure to predict the effects of gravity. We expect then that the non-dominant limb, should not display the same invariances as the dominant limb with regards to the effects of gravity. This is easily explained as a reliance on postural control mechanisms in the non-dominant limb, which will only act after errors have developed.

In the third chapter we tested the prediction based upon dynamic dominance that the time of transition from predictive control to postural control represents a variable that may be utilized to adjust movement kinematics. We presented a model of a two phase controller specifying first an open-loop plan for movement, followed by a second phase for stabilizing posture in which feedback is utilized to correct deviations in the current limb configuration from the desired configuration (Gottlieb 1996; Hirayama, et al. 1993; Sainburg, et al. 1999; Scheidt and Ghez 2007). In this model the limbs are differentiated by the time at which they transition from open-loop control to closed loop control. It is likely that qualitative differences exist in the predictive phase of real movements, however, many of the qualitative characteristics of real movements of the dominant and non-dominant arms are described by this model. Since closed loop control in this model is derived from configuration errors, joint torques will emerge based on the state of the joint errors without accounting for the activity at other joints, or the effects of gravity (Bizzi 1987; Bizzi and Abend 1983; Bizzi, et al. 1976; Bizzi, et al. 1982; Feldman 1986; Flash 1987; Polit and Bizzi 1979). We find that the differences between dominant and non-dominant arms may be modeled simply by the transition from open-looped control to closed-loop control. An earlier transition to the suggested postural phase of movement might result in the timing
deviations observed in chapter 2, that do not allow the more effective coordination of muscular activity that the dominant limb displays. This would be consistent with the “advantages” in error correction observed in the non-dominant limb responding to unexpected inertial loads (Bagesteiro and Sainburg 2003; 2005).

While the model we present is mathematical in nature, and thus contains no explicit localization for the open-loop and closed-loop control structures, past work strongly suggests certain areas of the nervous system. Further the concept of a purely open or closed loop control structure in the central nervous system is suspect. Feedback from previous reaches is certainly used to adapt the predictive estimation of dynamic effects and consequently the movement plan. Similarly some groups have suggested that rapid correction of errors may rely on forward models of the limb to predict the future limb state and correct for errors without suffering the effects of latency in the nervous system. Consequently it is more appropriate to consider the dominant proficiency with the prediction and compensation for the dynamic effects of movement, while the non-dominant system proficiency is with the correction of within trial errors, and stabilization of posture around the desired configuration.

The studies of stroke subjects from our group provide strong evidence for placing the anticipatory control of forward dynamics in the anterior parietal lobe, contralateral to the dominant, while the control of feedback mediated error correction is localized to the posterior frontal lobe ipsilateral to the dominant arm (Schaefer et al. 2007; 2009a; 2009b; 2011; Mutha et al. 2011). With this localization, the model we present explicitly requires ipsilateral cortical involvement in all arm movements. While this is contrary to some early suggestions of contralateral dominance (Brinkman and Kuypers 1972; Geschwind 1975; Goldenberg 2003; Kuypers 1982; Kuypers and Brinkman 1970; Liepmann 1905; Taylor and Heilman 1980), many studies have noted ipsilateral activity during unilateral control, both in animals (Cisek et al. 2003; Tanji et al. 1988), and in humans (Baraldi et. al. 1999; Dassonville et al. 1998; Janke et al. 1998; Kawashima et al. 1998; Kim et al. 1993). We find then, that the Dynamic Dominance hypothesis
suggests bilateral activity in motor cortex during even unilateral movements, and that this activity is only lateralized based upon the phase of the movement involved.

In chapter 4 we present a test of the hypotheses developed in the preceding chapters regarding the lateralization of activity in the motor cortex during simple reaches. Based upon the Dynamic Dominance hypothesis we expect that the non-dominant arm will need to recruit resources from dominant cortex in order to control the dynamics of motion. We expected that this would result in less lateralization during the RP phase of motion. Instead what we found was that there was no lateralization evident during the pre-movement phase, and only following movement onset was lateralization of the cortical potential truly evident. Once lateralization developed during the MMP, the patterns we observed were consistent with the hypothesis that the non-dominant arm must recruit ipsilateral cortex, displaying no consistent lateralization, while the dominant arm was able to complete the task utilizing primarily contralateral resources, resulting in notable lateralization. Particularly encouraging was the finding that dominant arm lateralization of the MMP scaled with the dynamic requirements of the task, with higher interaction torques at the elbow corresponding to greater lateralization of the cortical potential. These findings are consistent with previous work that noted changes in the MMP with changes in the rate of isometric force production (Slobounov and Ray 1998; Slobounov et al. 1998). These findings indicate that the source of lateralization may be in the execution of the motor plan, rather than the planning, which in this study appeared to recruit symmetric resources.

**Clinical Implications**

The Dynamic Dominance Hypothesis ascribes a specialization for specific features of control to the dominant and non-dominant hemispheres. In healthy individuals these specializations served to stabilize different aspects of the same movement, recruiting ipsilateral cortex to support the features for which the contralateral cortex is less skilled. This formulation of control explicitly recognizes the contribution of ipsilateral cortex to movement. The existence of
these contributions is supported by a great deal of evidence in animals (Cisek et al. 2003; Tanji et al. 1988), and in humans (Baraldi et al. 1999; Dassonville et al. 1998; Kawashima et al. 1998; Kim et al. 1993; Janke et al. 1998).

Individuals that have suffered unilateral stroke can exhibit deficits in motor control ranging from mild impairments of the contralesional limb, to hemiparesis in the contralesional limb. In these subjects there appears to be a deficit in only one of these features of control (Schaefer et al. 2007; 2009a; 2009b; 2011; Mutha et al. 2011). Hemiparetic subjects are typically forced to rely on the ipsilesional arm, as deficits in the contralesional arm severely impede normal control. Despite the fact that the ipsilesional arm is typically seen as the good arm, the loss of ipsilateral contributions to the control of that limb does affect performance. These effects can reduce a subject’s ability to compensate for the loss of function in their more affected limb. In higher functioning patients, milder deficits may be evident in contralesional limb. These deficits are persistent (Chestnut and Haaland 2008), and may impact the performance of normal tasks (Desrosiers et al. 1996; Sunderland et al. 2000; Wetter et al. 2005).

The Dynamic Dominance description of motor control can shed light on the nature of the specific deficits that a patient will face. Rather than rely on clinical scores, which can rate the severity of a deficit, but not the cause, the Dynamic Dominance hypothesis provides a description of the deficits in relation to the hemisphere where damage occurred. Lesions contralateral to the dominant hand will tend to produce deficits in the coordination of muscles against inertial dynamics, and against predictable external forces such as gravity. Lesions ipsilateral to the dominant hand will produce deficits in the ability to correct errors within a movement, and will be unstable when presented with perturbations. This information may allow therapists to design tasks that stress these control features, thus enabling neural plasticity to mitigate some of the deficit.
Future Directions

While the current studies certainly expand upon the Dynamic Dominance hypothesis, it is still a first assessment of the systems actually utilized by the central nervous system. The specification of the open-loop and closed loop controllers that the Dynamic Dominance hypothesis ascribes to the dominant and non-dominant hemispheres are intentionally left vague, as it is not clear what form these strategies take. In the case of the second study presented here, it is clear that the minimum jerk formulation for the ideal trajectory does not reflect the schema utilized by the nervous system. The exploration of alternative optimizations, such as minimum torque change (Kawato et al. 1990; Nakano et al. 1999) or minimum energy (Alexander 1997), may be avenues of further research. Additionally the model presented in chapter 2, relied on the very crude method of manual selection to estimate the desired parameters from real movements. More elaborate methods such as those employed by Yadav and Sainburg for single joint movements are certainly warranted in the multi-joint movements examined here (Yadav and Sainburg 2011).

The Dynamic Dominance model of control integrates information from both studies of mechanics and studies of the impact of cortical lesions to infer an integrated physiological schema for control. In the third study presented here we explored some of the predictions that the Dynamic Dominance hypothesis makes regarding neural activity during movement. In this study we examined lateralization of the cortical potentials during whole arm movements. While the observations from the MMP were consistent with the lateralization patterns that we anticipated, we did not show these patterns in either the RP, or the MP, as would be suggested by previous work with isometric tasks (Slobounov and Ray 1998; Slobounov et al. 1998). These discrepancies certainly warrant additional investigation. Further, the spectral content of EEG signals is known to change in relation to motor task performance (Pfurtscheller 1981; Pfurtscheller et al. 1996). It may be worth exploring these effects in the context of our whole arm movements.
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Appendix: Dynamic Dominance Persists During Unsupported Reaching
RESEARCH ARTICLE
Dynamic Dominance Persists During Unsupported Reaching
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ABSTRACT. Previous studies examining lateralization of arm movements focused on supported movements in the horizontal plane, removing the effects of gravity. The authors hypothesized that interlimb differences in free reaching would be consistent with the differences shown during supported reaching. Kinematic and kinetic data were collected for the forearm and upper arm segments in a 3-direction reaching task. Results showed lateralization of coordination, reflected by initial movement direction and trajectory curvature. The nondominant arm showed increased initial direction errors, and path curvature associated with a timing deficit between elbow and shoulder peak torques. These coordination deficits did not disrupt final position accuracy. The authors conclude that nondominant arm coordination deficits are similar to those reported previously for horizontal plane movements.

Keywords: dynamic dominance, handedness, lateralization, motor control

Handedness is a readily observable yet incompletely understood facet of human control of the upper extremity. Given the mechanical similarities between the dominant and nondominant limb, handedness is generally considered to be the result of asymmetries in the neural control of the two limbs. However, the specific mechanisms that give rise to the differences in observed behavior remain controversial.

Early attempts to investigate interlimb differences in control examined kinematic parameters of rapid and brief ballistic movements in an attempt to differentiate planning mechanisms from feedback-mediated error-correction mechanisms. Such movements were presumed to be so brief that little to no feedback-mediated corrections occurred. Measures such as reaction time, movement time, and final accuracy of ballistic movements were presumed to reflect open-loop planning of the movement. The distinction between open- and closed-loop control schemes in handedness was also reflected in studies investigating the role of precision requirements of rapid reaches under controlled visual feedback conditions (Carson, Goodman, Chua, & Elliott, 1993; Elliott, Chua, & Pollock, 1994; Flowers, 1975; Steingruber, 1975; Todor & Cisneros, 1985). However, attempts to differentiate the effects of sensory feedback on control of the dominant and nondominant limbs have provided little coherent insight into the mechanisms that give rise to handedness (Carson, 1992; Carson, Chua, Elliott, & Goodman, 1990; Carson et al., 1993; Elliott et al., 1994; Elliott et al., 1993; Flowers; Roy & Elliott, 1986; Roy, Kalbfleisch, & Elliott, 1994; Todor & Cisneros). Manipulations of target information prior to movement onset yielded longer reaction times in the dominant arm than in the nondominant arm, suggesting some differences in movement planning (Carson, 1992; Carson et al., 1990; Carson, Chua, Goodman, Byblow, & Elliott, 1995; Elliott et al., 1993). Initial hypotheses that these differences reflected a lateralized advantage in the integration of visual feedback (Flowers, 1975) were not supported by studies occluding vision during task execution (Carson et al., 1990; Roy & Elliott, 1986), suggesting that the difference may lie in the differential ability of the two hemispheres to plan movements. These differences are difficult to interpret in a manner that grants insight into the mechanisms of control, and it should be stressed that although longer reaction times could reflect inefficient planning, they might also reflect more sophisticated planning that produces better control, at the expense of planning time. Similarly, dominant arm advantages in movement accuracy might be accounted for by multiple mechanisms. For example, some researchers suggested that the dominant limb has advantages in error-correcting mechanisms, resulting in straighter, more accurate, hand paths (Carson et al., 1993; Todor & Cisneros, 1985), whereas others suggested that the nondominant limb had an advantage in initial movement planning, rendering less corrections necessary (Annett, Annett, & Hudson, 1979; Roy & Elliott, 1986).

Taking the approach that handedness may be characterized by interlimb differences in coordination, we previously investigated how each arm coordinated muscle activity and muscle-related torques with nonmuscle forces, such as limb interaction torques during movements (Bagesteiro & Sainburg, 2002; Sainburg & Kalakanis, 2000). The mechanics of the human arm can yield insights into the control strategies that produce specific patterns of behavior. Forces generated by the musculature must interact with other internally generated forces, such as those arising from deformation of noncontractile tissues such as ligaments and cartilage, and external forces such as those applied by gravity and interactions with tools. Further, the dynamic effects of motion at each segment, quantified as interaction torques, can substantially impact motion of the other limb segments. As these effects are due to the velocity and acceleration of segments, they are particularly prominent in rapid movements such as ball throwing, which are strongly lateralized tasks (Hore, Watts, Tweed, & Miller, 1996).

Our previous studies on horizontal plane reaching movements indicated that dominant arm coordination is characterized by efficient coordination of muscle torques with intersegmental interaction torques, while the nondominant arm shows less efficient coordination strategies. Our dynamic dominance hypothesis describes the advantage of the dominant limb in predicting the dynamic effects of motion to produce efficient movements (Sainburg, 2002), and
advantages of the nondominant arm for achieving and maintaining positional stability (Bagesteiro & Sainburg, 2003; Duff & Sainburg, 2007; Wang & Sainburg, 2003). This hypothesis stems from studies demonstrating that the coordination of nondominant limb movements varies with the dynamic forces arising from the motion of segments. In contrast, the kinematics of the dominant limb are relatively unaffected by these forces (Bagesteiro & Sainburg, 2002; Sainburg & Kalakanis, 2000). This suggests that the dominant controller employs a more sophisticated mechanism to develop the desired output of the muscular plant, one that accounts for dynamic aspects of movement that are not well accounted for in nondominant arm coordination. Although the kinematics of the limbs vary during task execution, the final performance assessed by radial distance from the target position tends to be similar across limbs (Sainburg; Sainburg & Kalakanis; Shabbott & Sainburg, 2008), suggesting corrective or postural stabilization mechanisms in the nondominant limb that are at least as proficient as those in the dominant limb.

Our previous research on handedness was carried out predominantly with reaching movements constrained to the horizontal plane, and with the limb supported in air sleds. This arrangement allowed for the experimental control over limb mechanical requirements, and had the advantage of preventing subject fatigue. However, it is plausible that our findings for horizontal plane movements may not generalize to unsupported movements made in the vertical plane, due to systematic mechanical differences between movement conditions. For example, it has been suggested that the temporal extent of a movement, or the speed, may be altered by simply scaling precomputed torques that produce the desired path kinematics (Hollerbach & Flash, 1982). In this schema, torques are scaled by a factor that varies as the square of the movement velocity. In an environment without gravity such a scaling produces movements with similar trajectories, at a variety of velocities. However, gravitic torques are unaffected by movement velocity, varying only with limb configuration and orientation. Consequently it may be expected that a system that takes advantage of such simple scaling must treat gravity specially to preserve spatial features of movement paths. Further, in studies of free reaching with the nondominant limb, subjects have been shown to take distinctly different paths with and against gravity, despite covering the same space (Gentili, Cahouet, & Papaxanthis, 2007; Papaxanthis, Pozzo, Vinter, & Grinshin, 1998). Although this might be the result of altered kinetic requirements of reversing the direction of movement, removal of gravity disrupts these paths only transiently (Papaxanthis, Pozzo, & McIntyre, 2005; Papaxanthis, Pozzo, Popov, & McIntyre, 1998). The invariance of path to external loading suggests that subjects are using gravity as an orientation, and planning different kinematics based on this reference rather than incompletely compensating for some kinematic difference. Further, the invariance of paths in gravity and nongravity conditions suggest that gravitic torques are readily separable from internal models of limb kinetics.

In addition to the effect of gravity on the planned kinematics of movement, the motor system must accurately account for gravity to execute a desired kinematic plan. Many studies in the dominant limb have shown strong invariant kinematic features of free reaching movements, which are stable against changes in load, and movement speed implying that the dominant limb plans kinematic trajectories in 3D space (Atkeson & Hollerbach, 1985; Lacquaniti, Soechting, & Terzuolo, 1982; Papaxanthis, Pozzo, & Stapley, 1998; Soechting & Lacquaniti, 1981) The reliable execution of consistent movement plans would require a sophisticated model of the limb to compensate for the varied inertial and gravitic effects encountered under various speed and load conditions.

Given the sophistication with which the dominant limb compensates for gravity and inertial effects, despite the clear mechanical differences in how these effects impact movement, we now ask how the nondominant limb coordination strategy may account for the effects of gravitic torques. If the forward controller utilized by the dominant limb system treats gravity differently than inertial effects, it is plausible that the nondominant limb utilizes the same system to compensate gravity, despite showing deficiencies in anticipation of inertial effects, such as interaction torques.

The purpose of this study is to examine whether the dynamic dominance hypothesis that we developed based on horizontal plane movements can be extended to vertical reaches under more natural movement conditions. To address this, we compared the performance of the dominant and nondominant arms of subjects while performing rapid, unsupported reaches in a parasagittal plane. Two groups of subjects performed with either the right or left hand. We used a group design to prevent the effects of interlimb transfer that we had previously characterized (Bagesteiro & Sainburg, 2005; Sainburg & Wang, 2002; Wang & Sainburg, 2004a, 2004b). To vary the effects of interaction torques at each segment, a three-direction reaching task was utilized, with two directions corresponding roughly to single joint movements of the shoulder and elbow and the third representing a combination of movement at both joints. To investigate the coordination of the limbs we compared torques impulses as well as the timing within the movement at which the occurrence of peak torques at the elbow and shoulder occur. We hypothesized that we would see predictable changes in the muscle torque impulse and the relative timing of the net torque in the dominant limb associated with adapting to the changing dynamic inertial loads. We further expected that the nondominant limb would display errors associated with failure to predict systematic variations in interaction torques. Additionally we expected that the nondominant limb, as a consequence of utilizing a less sophisticated predictive controller, would show trajectory errors consistent with failure to predict the effects of gravity on the arm. As a consequence of these differences we expected to see the nondominant limb display greater path curvature and higher errors in initial path direction than the dominant limb.
Methods

Subjects

All methods utilized in this study were approved by the Pennsylvania State University Institutional Review Board. Twelve neurologically intact right-handed adults, aged from 19 to 25 years old were tested. All subjects were screened for handedness using a modified version of the Edinburgh inventory (Oldfield, 1971). All subjects gave informed consent prior to participation. Subjects were randomly assigned to perform with either their dominant (right), or nondominant (left) hands (n = 6 per group).

Apparatus

Subjects were seated, with a mirror placed in the parasagittal plane at the performing shoulder and a LCD screen placed in the parasagittal plane at the nonperforming shoulder (Figure 1). A cursor displaying finger position, a start circle and a target were displayed on the screen. Cursor movements on the screen were calibrated such that cursor location was veridical to actual finger location. Subjects were instructed to look at the mirror so that the cursor appeared to be at the finger location, while vision of the hand was occluded by the mirror. The wrist and fingers were splinted to restrict the task to two segment motion. Orientation and position of the upper arm and forearm were collected using a flock of birds six degrees of freedom movement recording system (Ascension Technology, Burlington, VT). Sensors were attached to the back of the hand over the palm, and approximately centered on the upper arm. Digital position and orientation of the sensor were collected at 130 Hz. Fingertip, elbow, and shoulder locations were computed from the raw sensor data using calibrated points collected using a stylus at bony landmarks prior to the first trial.

Experimental Task

In each trial subjects were shown one of three targets, presented in a pseudorandom sequence. The initial finger position for all three movements was set 15–20 cm in front of the shoulder, with the arm in a configuration that the subject found comfortable. The direction of movement was specified to be −45° (out and down), 0° (horizontally away from the trunk), or 45° (out and up) from the initial position. All targets were displaced from the start position by 50% of the subject’s maximum horizontal reach from the starting location.

To initiate a trial subjects were asked to center the cursor in a starting circle for 300 ms, at which time they would receive an auditory cue to begin movement. Upon receiving the cue, subjects were instructed to reach rapidly to the target and stop with the cursor in the center of the target. To encourage subjects to maintain consistent performance, points were awarded for accuracy. To encourage rapid movements, subjects only received points for performance when the fingertip movement was faster than 1.5 m/s. Subjects

FIGURE 1. Experimental setup: (A) birds-eye view, (B) lateral view.
performed 90 reaches with targets presented in a randomized order, with all subjects receiving trials in the same order. Cursor feedback was removed at the “go” cue and resumed after the completion of the trial. After completion of the trial, a display of the movement path was presented along with a marker indicating the final finger position. To eliminate learning effects, trials 1–30 were excluded from analysis.

Kinematic Data

Finger, elbow, and shoulder position data were low pass filtered at 8 Hz using a dual pass third-order Butterworth filter. Segment angles were computed from the position data using a moving plane analysis, with the plane defined through the finger, elbow, and shoulder (Schneider & Zernicke, 1990). Movement start and stop were defined to be the first minima below 5% of the peak in the tangential finger velocity to either side of the main peak in the movement tangential velocity. All further analyses were performed on the data between the movement start and movement stop.

Three measures of hand path accuracy were used: initial direction error, path curvature, and final position error. The initial direction error was defined as the angular deviation between a vector defining the instructed movement and a vector passing through the initial finger position and the finger position at peak hand velocity (Figure 2A). In this measure negative angles indicate that the finger path was directed lower than the actual target, while positive angles indicate that the finger path was aimed higher than the target. Path curvature was defined as the major axis of the finger path divided by the minor axis of the finger path. The final position error was the magnitude of the distance between the finger location at movement end and the target.

Kinetic Data

Joint torques were computed using an inverse dynamic analysis of the movement based on the kinematic segment angles. We assume here that the upper limb is composed of two rigid links attached by frictionless spherical joints. The moving plane analysis employed to generate the kinematic joint angles allows planar equations of motion to be utilized to compute the joint torques within the moving plane, thus allowing partitioning of the equations into a few terms (Schneider & Zernicke, 1990). Joint torques were partitioned into net torque, interaction torque, and muscle torque and gravitational torque (Figures 2C and 2D), with net torque representing the torque driving rotational acceleration of a segment, the interaction torque arising from the velocity and acceleration of the other segment and the muscle torque comprising the residual of the joint torques once the net interaction torques are accounted for in the homogeneous form of the equations of motion. The muscle torque is the composite of not only agonist and antagonist activity, but also passive tissue properties such as stiffness and damping of the muscle tissues.

Two measures of arm kinetics were used in this study: torque impulse, and the difference in timing of peak net torque onset between the elbow and shoulder. The torque impulse was taken as the integral of the muscle and interaction torques. For this analysis muscle and interaction torques were considered positive if acting in the same direction as net torque, and negative if acting in the opposite direction. The integrals for torque impulse were computed across two ranges: from the initiation of movement up to the time of peak tangential acceleration of the finger, and from movement start to the end of movement. The range from start to peak acceleration was selected to focus on early differences in control that might reflect differences in prediction of gravitic effects, while the whole movement range reflects previously reported measures of torque impulse that are reflective of the dynamic dominance hypothesis (Bagesteiro & Sainburg, 2002; Sainburg & Kalakanis, 2000). The timing of peak torque onset was taken as the absolute time after movement start at which the peak net torques occurred. The relative timing of elbow and shoulder peak torque was taken as the time at which the peak elbow torque occurred minus the time at which the peak shoulder torque occurred.

Statistics

Right and left hand movements were performed by two different groups (6 subjects each) of right-handed individuals. This was done to eliminate the potential for inter-limb transfer effects, which have been well documented for reaching tasks (Sainburg & Wang, 2002; Wang & Sainburg, 2003). All analyses were performed in the statistical processing software JMP (SAS Institute Inc., Cary, NC). Measures analyzed in this study were assessed using individual 2 Hand × 3 Target mixed factor repeated measures analyses of variance (ANOVAs), with subjects as the repeated measure. Post hoc tests were performed only in cases in which an interaction between main effects was observed. In these cases, Tukey’s honest significant difference tests were used to identify specific differences. To assess the relation between relative torque timing and the path kinematics, we performed simple linear regressions on each subject–target case separately for both the 0° and 45° targets. These fits were assessed for significance using an $F$ test in which the $F$ statistic of this analysis constitutes the ratio of mean square errors described by the fit to the mean square of errors not described by the fit. Significance indicates a rejection of the null hypothesis that the model does not predict any of the observed variance in the dependent measure. As a second-stage of analysis we wished to compare the regressions of left-hand subjects to right-hand subjects. For this analysis we converted the slope and intercept of each regression to a $z$ score and performed a repeated measures ANOVA to assess differences in these variables due to hand.
Results

Kinematics

Our targets were designed to require increasing amounts of shoulder motion, as target elevation increased. Figures 3A, 4A, and 5A depict representative limb paths for movements to each target. Stick figure representations of upper arm, forearm, and hand segments are drawn at every data point, while shoulder, elbow, and finger paths connect these segments. The relative angular dispersion of the upper arm segment reflects the shoulder angular motion for each trial. Note that the upper arm stick figures for both arms remain fairly parallel and closely aligned for the −45° target in Figure 3A.

FIGURE 2. Sample movement with associated data. (A) Example of a single left hand movement to the 0° target. θ indicates the angle of initial direction error. (B) The tangential finger velocity associated with the movement displayed in (A). (C) Elbow torques computed for the movement in (A). The arrow marks the peak net torque, at which time measures of peak torque are taken. (D) Shoulder torques for the movement in (A). The arrow marks peak net torque. The elbow muscle torque is included here as this torque acts symmetrically across the elbow joint and, consequently, must be accounted for at the shoulder. This results in a sign inverted mirror of the elbow muscle torque acting at the shoulder.
but shows large angular displacement for the 45° target in Figure 5A. This increase in required shoulder excursion was related to increased intersegmental coordination requirements across directions, as discussed subsequently.

**Final Position Error**

Although the mean final position error for both hands increased with the target angle (main effect of target), $F(2, 20) = 6.39, p < .01$, there was neither a significant difference between the hands (main effect of hand), $F(1, 10) = 2.15, p = .17$, nor an interaction between hand and target, $F(2, 20) = 2.93, p = .08$. Despite this, the dominant and nondominant arms showed substantial differences in the kinematic patterns to the three targets.

**Initial Direction Error**

Interlimb differences in initial direction error, summarized in Figure 6A, were driven by a hand by target interaction, $F(2, 20) = 3.45, p < .01$, wherein the dominant arm produced movements that were, on average, directed on line with the target, while the nondominant arm showed an increasing undershoot as target elevation increased, from –45° to 45°. There was also a main effect of hand for direction error, $F(1, 10) = 4.80, p = .05$, which was related to the larger errors at the 0° and 45° targets. For the example paths in Figure 3A, the right and left paths are very similar. Note that this movement involves mostly elbow motion, with little motion about the upper arm, and no wrist motion due to the splinting. In contrast to the –45° direction, for the 0° and 45° targets
FIGURE 4. Sample movements to the 0° target. (A) Movement plots for the right and left arms. Both limbs tend to make more curved movements to this target than to the −45° target, however, dominant arm movements still tend to be slightly straighter at this target. The non-dominant hand shows a notable undershoot in the initial direction, while dominant paths tend to be directed at the target or slightly above it. (B) Net torques at the elbow and shoulder joints. Vertical lines denote the time of peak torque incidence.

shown in Figures 4A and 5A, the left arm direction errors become progressively greater. In contrast to the nondominant arm, dominant arm direction errors were unaffected by target elevation, displaying finger paths directed toward the target for all directions.

Path Curvature

The combination of substantially greater undershoot with similar final errors in the nondominant hand explains the increasing curvatures of the nondominant finger paths across the target elevations (Figures 4–5A). As summarized in Figure 6B, the curvature of the nondominant limb was greater than that of the dominant limb for all target directions (main effect of hand), $F(1, 10) = 6.42, p = .03$. Additionally, for both hands the curvature of the finger path increased as the target angle increased (main effect of target), $F(2, 20) = 31.07, p < .01$, with greatest curvatures for both hands displayed in the 45° direction. There was a significant hand by target interaction for curvature, $F(2, 20) = 3.50, p = .05$. This reflected a greater dependence of curvature on target elevation for the left hand than the right hand.

Kinetics

Figures 3–5B depict the torques at the shoulder and elbow joints, associated with the exemplar reaches in Figures 3–5A.
FIGURE 5. Sample movements to the 45° target. (A) Movement plots for the right and left arms. Movements of both arms display the most curvature to this target, however, dominant arm movements show less differences from the 0° target than the non-dominant. The non-dominant arm shows a notable undershoot in the initial direction, while the dominant paths tend to be directed at the target or slightly above it. (B) Net torques at the elbow and shoulder joints. Vertical lines denote the time of peak torque incidence.

Early Torque Impulse

As expected by our target design, the amplitude of elbow muscle and interaction torque impulse varied systematically across directions, reflecting the differences in elbow excursions required with changing target elevation. As a result, for the early impulse we found a main effect of target on elbow muscle, $F(1, 20) = 155.23, p < .0001$ and interaction torque impulse, $F(1, 20) = 239.03, p < .0001$. No effect of hand was observed for elbow muscle, $F(1, 10) = 0.31, p = .59$, or interaction impulse, $F(1, 10) = 0.0074, p = .93$, and no interaction between hand and target was found for elbow muscle, $F(1, 20) = 0.55, p = .59$; or interaction torque impulse, $F(1, 20) = 0.79, p = .47$. At the shoulder a similar main effect of direction was observed, for muscle, $F(1, 20) = 85.12, p < .0001$; and interaction torque impulse, $F(1, 20) = 17.01, p < .0001$. Again, no main effect of hand was observed for either shoulder muscle, $F(1, 10) = 2.10, p = .18$, or interaction torque impulse, $F(1, 10) < 0.0001, p > .99$, and the interaction torque impulse showed no interaction of hand and target, $F(1, 20) = 1.79, p = .19$; however, the muscle torque > impulse did show an interaction between hand and target, $F(1, 20) = 3.53, p = .05$. Post hoc testing revealed that the only comparison of hand within target which achieved significance was in the 45° direction. Figure 7 shows the shoulder muscle torque impulse across hands and targets, and although no significant difference was found
at the 0° target, there is a visible difference between arms consistent with that observed at 45°. This may reflect a difference between hands that scales with the required shoulder joint excursion. Because the 0° direction had lower impulse requirements than the 45° direction, it is possible that in this direction, potential interlimb differences in impulse may be smaller than the intersubject variability of the data. We expect that the elevated muscle torque impulse in the dominant limb may be associated with compensation for gravity, whereas the relatively lower impulse in the nondominant limb could result in an initial deficit in elevating the upper arm against gravity. This interpretation is consistent with the observed errors in initial movement direction.

**Total Torque Impulse**

The amplitude of elbow muscle and interaction torque impulse varied systematically across directions, reflecting the differences in elbow excursions required by the different target elevations. Consequently, we observed a main effect of target on elbow muscle, $F(1, 20) = 155.23, p < .0001$, and interaction torque impulse, $F(1, 20) = 239.03, p < .0001$, but no effect of hand on elbow muscle torque impulse, $F(1, 10) = 0.31, p = .59$; or interaction torque impulse, $F(1, 10) = 0.0074, p = .93$. Nor was there an interaction between hand and target, for elbow muscle, $F(1, 20) = 0.55, p = .59$; or interaction torque impulse, $F(1, 20) = 0.79, p = .47$. Similarly, at the shoulder we observed a main effect of target on shoulder muscle, $F(1, 20) = 155.23, p < .0001$, and interaction torque impulse, $F(1, 20) = 239.03, p < .0001$, but no effect of hand for shoulder muscle, $F(1, 10) = 0.31, p = .59$; or interaction torque impulse, $F(1, 10) = 0.0074, p = .93$. There was no interaction between hand and target for shoulder muscle, $F(1, 20) = 0.55, p = .59$; or interaction torque impulse, $F(1, 20) = 0.79, p = .47$.

**Torque Timing**

Because of the relatively small peak torques for the –45° target, we restricted our analysis of elbow and shoulder torque relationships to only the 0° and 45° targets. We marked the timing of shoulder and elbow net torques with vertical lines in Figures 4B and 5B. Note that for the right arm, elbow torque lags behind shoulder torque, with greater lag for the 45° than for the 0° target. In contrast, for the nondominant left arm, the elbow tended to act earlier relative to the shoulder at each target, even preceding shoulder peak torque in the 0° direction (Figure 4B). Figure 8 shows the mean shoulder-elbow peak torque timing difference across subjects. Note
that the left arm difference is smaller, and negative in the 0° direction, indicating that on average the left arm elbow peak torque either preceded that of the shoulder, or showed reduced lag, relative to that of the right arm. As a result, our ANOVA showed a main effect of hand, $F(1, 10) = 10.84$, $p = .01$, and target direction, $F(1, 10) = 14.88$, $p < .01$, but no interaction between hand and target (2 directions), $F(1, 10) = 1.75$, $p = .22$.

We reasoned that the effect of delaying elbow extensor torque relative to shoulder flexor torque in dominant right arm movements was to elevate the hand toward the targets at movement initiation. In contrast, the more rapid elbow extensor acceleration for the nondominant left arm countered hand elevation, and resulted in the initial direction undershoot, characterized previously. To quantitatively examine the relationship between the elbow–shoulder torque timing and the kinematic differences between the hands we regressed the torque timing against initial direction error, for each subject separately. Our simple linear regression within target (Figure 9), showed a statistically significant correlation between elbow–shoulder torque timing differences and initial direction error, $F(1, 30) > 4.17$, $p < .05$, for all subjects. The relative timing of elbow and shoulder are clustered around discrete values (Figure 9). This is due to the 130 Hz frequency of the data digitization, such that the smallest interval that could be resolved was approximately 7.7 ms. To assess the effect of hand, intercept and slope for these regressions were converted to $z$ scores and the left and right fits and subjected to a 2 Direction $\times$ 2 Hand ANOVA. No main effect of hand was found in either measure, slope, $F(1, 10) = 0.86$, $p = .37$; intercept, $F(1, 10) = 0.59$, $p > .46$. Thus, for both hands, initial movement direction was substantially dependent on intersegmental coordination, measured as the timing difference between elbow and shoulder joint net torque profiles. We conclude that the systematic undershoot of left arm movements (exemplified in Figures 3–5A), compared with right arm movements resulted from poor coordination of timing between shoulder and elbow joint torques.

**Discussion**

In this study, we examined dominant and nondominant arm coordination during unsupported, sagittal plane reaches. We hypothesized that interlimb differences in kinematics and kinetics would be consistent with the differences shown in previous studies of horizontal plane reaching. Our results showed substantial interlimb differences in coordination, as reflected by initial movement direction and trajectory curvature, such that dominant arm movements showed lower initial direction errors, and were straighter than nondominant arm movements. The increased initial direction errors of nondominant arm reaches were associated with lower muscle torque impulses in the nondominant arm, and poor timing between peak torques at the shoulder and elbow joints, wherein the left arm displayed early elbow extension in relation to shoulder elevation. We conclude that in vertical plane reaching, nondominant arm intersegmental coordination deficits are similar to the deficits reported previously for horizontal plane movements. In agreement with previous findings, final position accuracy and precision showed no significant differences between the limbs (Sainburg, 2002; Sainburg & Kalakanis, 2000; Shabbott & Sainburg, 2008).

Previous studies in horizontal plane reaching showed substantial interlimb differences in the magnitudes of muscle torques across movement directions. We showed that dominant arm muscle torques were well coordinated with interaction torques, whereas nondominant muscle torques were not (Bagsteito & Sainburg, 2002; Sainburg & Kalakanis, 2000). In the present study we did not observe differences in muscle and interaction torque impulses consistent with this previous work. This is very likely a consequence of the fact that we did not design the targets in the present study to require specific joint excursions, as was possible in the more constrained studies done in the horizontal plane. In addition, due to the greater freedom to move the scapula, and to change the plane of motion, we expected greater differences in torque profiles between subjects and trials. Nevertheless, our previous studies revealed that incoordination in muscle torque magnitude resulted in discoordination between segment motions, which gave rise to larger direction errors and greater hand path curvatures, but not greater final position errors, in the nondominant arm (Bagsteito & Sainburg, 2002; Sainburg & Kalakanis, 2000). In this way, the present findings regarding the torque impulse across the entire movement are consistent with our previous horizontal plane studies.

In the present study we introduced an additional measure of impulse calculated between the start of movement and the time at which the finger achieved peak tangential
acceleration. In this measure we observed that there was an interaction between target and hand for the muscle impulse. In the case of the 45° target the dominant limb displayed significantly greater muscle torque impulse than the nondominant limb. Because no differences were observed in the elbow impulse this would drive the elbow to accelerate earlier than the shoulder in the nondominant limb. This is consistent with the observed kinematics wherein the nondominant limb showed initial finger paths directed below the target. Because no differences were observed in the early interaction torque impulse, it is reasonable to attribute this effect to the accurate prediction of gravitocentric torques in the dominant limb, but not in the nondominant limb.

The noted differences in early shoulder muscle impulse but not in the early elbow muscle impulse indicates a shift in the timing of joint acceleration. Indeed in the present study, the coordination of torque events at each joint appear to have contributed the consistent interlimb differences in initial direction and movement curvature. It is apparent that the nondominant limb displays earlier elbow torques relative to shoulder torques when compared with the dominant limb. This means that elbow extension tended to lead shoulder flexion in the nondominant limb but not the dominant limb. This manifested as an error in direction and resulted in nondominant paths that were initially directed below the target, a finding consistent with poor prediction of gravitation loads on the segments. Because the magnitude of total shoulder muscle impulse was similar between the two hands, similar shoulder elevation occurred in the nondominant limb as in the dominant limb. However, this elevation occurred later in the movement. This appeared to be a correction for the initial direction deficit, as reflected by the hooks toward the target, as shown in Figures 3–5A. This initial direction error followed by late corrections resulted in greater curvatures for nondominant movements. The deficiencies in nondominant limb coordination observed here are consistent with the findings of Hore et al. (1996) that dominant limb advantages in throwing accuracy are related to better timing of finger extension relative to whole-limb movement. Although our previous studies showed that nondominant arm deficits in intersegmental coordination arose from poor prediction of interaction torques (Sainburg & Kalakanis, 2000), our present findings suggest that prediction of gravitational torques may also be deficient during vertical reaching movements.

The coordination deficits of the nondominant limb in our present and previous studies suggest that nondominant system is less adept at predicting gravitational and intersegmental dynamics when specifying early movement trajectories, and that this limb relies more on feedback mechanisms to reach the final position with similar accuracy to the dominant arm. This finding is consistent with the dynamic dominance hypothesis, which predicts dominant limb advantages in predicting task dynamics, but not in the corrective or postural phase of movement (Duff & Sainburg, 2007; Shabbott & Sainburg, 2008). In the present study, it is apparent that the dominant limb system produces movements that are directed more accurately toward the target than the nondominant system, reflected in the temporal coordination of the elbow and

**FIGURE 9.** Sample regressions describing correlations between torque timing and initial direction error for a right performing subject and a left performing subject.
shoulder torques. In contrast with the early movement errors, the nondominant system did not show significant difference in final position accuracy. Although the difference in initial direction errors precludes a direct comparison of the feedback-mediated control during late movement, we may conclude that the error correction–based control late in the movement is not substantially impaired in the nondominant limb when compared with the dominant limb. This again is consistent with the dynamic dominance hypothesis, which does not predict deficits in feedback-mediated control in the nondominant limb.

Several studies have noted the kinematic consistency of the dominant limb during free reaching, noting that hand paths remain invariant despite changes in loading, movement speed, or gravity (Gentili et al., 2007; Lacquaniti et al., 1982; Papaxanthis, Pozzo, & McIntyre, 1998; Papaxanthis, Pozzo, & Stapley, 1998; Soechting & Lacquaniti, 1981). In keeping with these findings, the present results in the dominant limb show strong suppression of curvature and direction errors in all movement directions. In contrast, we observed that the nondominant limb displays errors in movement direction and curvature consistent with failure to predict the effects of gravity. This is consistent with the dynamic dominance hypothesis, which predicts that the nondominant limb relies on a feedback controller, and consequently will not predictively compensate for gravitational or inertial effects. If this theory does explain the performance deficits of the nondominant limb here then we may expect that nondominant movements will not display the same kinematic invariances that the dominant limb displays.

Consistent with the present results, some researchers have suggested that movement control may be modeled by a two-phase controller specifying first an open-loop plan for movement, followed by a second phase for stabilizing posture in which feedback is utilized to stabilize the limb around the desired configuration (Gottlieb, 1996; Hirayama, Kawato, & Jordan, 1993; Sainburg, Ghez, & Kalakanis, 1999; Scheidt & Ghez, 2007). It is plausible that the nondominant limb relies more on the postural control elements, whereas the dominant arm relies more on the predictive control elements of such a hybrid controller. Because this postural control is derived from configuration errors, joint torques will emerge based on the state of the joint errors without accounting for the activity at other joints, or the effects of gravity (Bizzi, 1987; Bizzi & Abend, 1983; Bizzi, Accornero, Chapple, & Hogan, 1982; Bizzi, Polit, & Morasso, 1976; Feldman, 1986; Flash, 1987; Polit & Bizzi, 1979). A previous transition to the suggested postural phase of movement may result in timing deviations that do not allow the more effective coordination of muscular activity that the dominant limb displays. This would be consistent with the advantages in error correction observed in the nondominant limb responding to unexpected inertial loads (Bagesteiro & Sainburg, 2003). In fact, in the present study, both arms showed similar final position errors, whereas the nondominant arm showed greater initial errors, indicating greater nondominant arm reliance on corrective control mechanisms. Although these findings suggest a greater reliance on feedback-mediated mechanisms, the differences in initial errors preclude drawing conclusions about the relative efficacy of the dominant and nondominant corrective schemes.

Although the present results cannot conclusively distinguish the specific algorithmic differences that give rise to interlimb differences in coordination, the differences observed here are similar to those shown previously in the horizontal plane movements and provide preliminary evidence that our findings generalize across different planes of motion and across different dynamic environments. Further, these findings do indicate at a gross level greater reliance on predictive mechanisms in the dominant limb and greater reliance on feedback in the nondominant limb.

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