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ABSTRACT

In the work reported in this thesis, I sought to understand how individuals select particular actions when more than one can achieve the task at hand. My approach to studying this degrees-of-freedom problem was to identify body- and task-related features that help constrain the alternatives. The current work addressed the understudied issues of whether and how actions depend on multiple constraints in any given task. Thus, the overarching goal of the present research was to test the notion that individuals select actions with respect to multiple constraints that are cognitively ranked by their values for meeting task demands.

To pursue this idea, I conducted a series of experiments that pertained to the prominent preference to use the right hand for unimanual tasks. This hand preference likely serves as a common constraint, but surprisingly little research has described it in such a fashion. It is perhaps unsurprising, then, that little research has tested the relative priority of hand preference with other known constraints. The experiments reported here were meant to fill this void. The first experiment showed that right-handed people make hand choices that are related to, and may therefore depend upon, interlimb control asymmetries that lead to distinct ways of completing point-to-point reaches. However, choices were not related only to these interlimb sensorimotor performance asymmetries but also depended on other workspace location constraints. These findings support the idea that action choices depend on constraints that are ranked for each task.

The second experiment extended this idea to unimanual object transport tasks. I gave right-handed people choices between moving objects in ways that either satisfied hand preference or the well-known tendency to end transports in comfortable arm postures. This experiment tested three specific hypotheses. One was that hand preference is weighted more heavily than comfort. The associated prediction was that participants would use the right hand even when doing so led to uncomfortable postures. Another hypothesis was that comfort is weighted more heavily than hand preference. The associated prediction was that participants would use whichever hand afforded comfortable ending postures. The third hypothesis was the only logical alternative -- that people do not prioritize hand preference and comfort. This hypothesis predicted that participants would not consistently satisfy hand preference or comfort. The results showed that participants almost always used the hand that afforded comfortable ending postures, suggesting that aiming-related comfort outranks hand preference for the types of object transports I tested.

The third experiment explored the flexibility of this weighting by manipulating task demands. The results showed that the magnitude of this priority can be attenuated by more heavily weighting hand preference. However, the priority is not reversed or eliminated in this case.

The final experiment tested the idea that the priority that comfort has over hand preference also reflects considerations of performance. This hypothesis predicted that comfortable postures would afford better performance at the end of the transport than uncomfortable postures and that the right hand would afford better performance than the left hand. The most important prediction, however, was that the performance advantage of comfortable postures over uncomfortable postures would be greater than the performance advantage of the right over the left. The results bore out these predictions, again supporting the idea that manual action choices depend on hierarchies of constraints that are weighted in accordance with the demands of the task.

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CHAPTER 1

INTRODUCTION

Physical actions let us interact with environments and with others to achieve the goals necessary for our survival. They also constitute the behaviors that make cognition tangible, for it is mainly through study of overt responses that covert cognitive structures and processes are inferred. However, there is a tendency for the cognitive scientists who make such inferences to neglect the way overt responses are planned, produced, and controlled (Rosenbaum, 2005). Indeed, the focus is often on what the final outcomes of those overt responses say about cognition – for example, whether button presses indicate accurate memories or perceptions. In this dissertation, I focus on the final outcomes of physical behaviors, but I also take interest in other properties of those actions – for example, whether and how early states of responses reveal anticipation of later states. My specific aim is to better understand what these properties say about the cognitive structures and processes that underlie human action selection.

Neurologically normal adults and children perform everyday reaching tasks like pressing elevator buttons and turning door knobs with relative ease. However, the ways they use their cognitive and neuromuscular systems to perform these actions are not well understood. In fact, there remain several open questions that are core to the study of human motor control. These questions concern how actions and perceptual inputs are integrated (cf. Woodworth, 1989), how actions are sequenced in time (cf. Lashley, 1951), how actions are learned (cf. Held, 1965), and how particular actions are selected (cf. Bernstein, 1967). This dissertation focuses on the last of these questions – the so-called degrees-of-freedom problem.

This problem arises because the bodies of human an non-human animals alike often afford many more ways of completing most tasks than are necessary (Bernstein, 1967). A classic example in the human domain – the domain in focus here – is performing the task of touching one's own nose. If a neurologically healthy person were asked to perform this action, she would probably solve the problem with little difficulty, using a judicious mixture of shoulder, elbow, and wrist flexion to bring an extended fingertip of her preferred hand to the tip of her nose in one smooth action. However, a moment's reflection reveals the remarkable complexity of the problem that our nose-toucher would have so easily solved.

A degree of freedom represents one way that a given system can independently vary. The nose of our nose-toucher has three degrees of freedom – its x-, y-, z-coordinates in space. Each shoulder has three degrees of freedom, while each elbow and wrist have two (Rosenbaum, 2010). Thus, without even considering the many ways each of her fingers could move, or the 10 different fingers that she could use to touch her nose, we can see that each arm affords many more degrees of freedom than are necessary to specify the desired final position of her fingertip. Moreover, our nose-toucher could move the chosen fingertip with a nearly infinite number of unique timing patterns while following a nearly infinite number of distinct trajectories with either arm. How, then, would she plan for, and arrive at, only one of these options?

Before broaching this question through this literature review, I should note that the degrees-of-freedom problem is a "problem" mainly for motor-control scientists, not for the actors who use their flexible motor control capabilities. While the body's surplus degrees of freedom make it difficult to explain action selection, the flexibility they provide in achieving goals can be quite beneficial. Should an individual be limited by injury, such as a broken arm, or by transient environmental factors, such as a need to carry a bag of groceries with one arm, he or she can press the elevator button with the other arm. And if both arms are full of groceries, the same individual can press with another body part, such as the foot or the knee. It is inevitable, however, that people must pay some cost for having so many options. One such cost is predicted by the Hick-Hyman Law, which states that the time it takes people to make a decision increases by a constant amount with each doubling of the number of options (Hick, 1952; Hyman, 1953). Thus, when planning actions, it should be beneficial for actors – and for motor-control scientists, by extension – to have some of way of constraining the many action alternatives.

Indeed, the principal approach to the degrees of freedom problem has been to look for features of the cognitive and neuromuscular systems, and features of the tasks themselves, that reduce the many alternatives (Bernstein, 1967; Nelson, 1983). These linkages are often denoted as constraints, and behavior is then modeled as optimizations of parameters related to those constraints (Nelson, 1983; Todorov, 2004). Models suggest that people have a rather sophisticated (and probably implicit) knowledge of the biomechanical factors involved in potential actions (e.g., & Cisek, 2011). This general idea will be front and center in Chapter 2. However, before going on to characterize human action planning with optimization-constraint models, I will first present evidence that voluntary actions are planned. In so doing, I will briefly review other approaches that have been developed, though they will be of only passing interest in this dissertation.

Let me first address the issue of action planning. There is no a priori reason to exclude the possibility that behaviors which appear to be planned are actually the result of some stimulus-response associations that arise merely by chance and then get reinforced through experience (Hommel, 2003; Rosenbaum et al., 1990). Evidence from multiple lines of research suggests that this stimulus-response explanation for apparent action planning is incorrect and that humans do plan their actions. Evidence from one line shows that human patients (and lesioned non-humans) can carry out actions with limited afferent information, though such actions tend to be more laborious than normal ones (Lashley, 1917; Rothwell et al., 1982; Taub & Berman, 1968). While the quality of these goal-directed actions is indeed degraded in such feedback-impoverished conditions (Sainburg et al., 1995; 1999), these findings indicate that incoming stimuli are not required for successful actions to be carried out.

A second line of work indicates that response latencies often grow with the complexity of forthcoming actions, suggesting that more planning is required for more complicated tasks (Henry & Rogers, 1960; Klapp, Anderson & Berrian, 1973; Rosenbaum, 1987; Zelaznik & Hahn, 1985). Likewise, extended action sequences often show evidence of anticipation. For example, people say the same words and phonemes differently when different words and phonemes follow (Baars, 1980; Motley, Camden & Baars, 1982). When people reach for objects, they adjust their hand-apertures early in the reach according to the sizes of the target objects (Jeannerod, 1981). And when transporting objects, people tend to use initial grasps that optimize the comfort of later arm postures (Rosenbaum et al., 1990); this last constraint will play a major role in this dissertation and will be more fully unpacked in Chapters 3, 4, and 5.

Yet another line of research supports the idea that actions are planned by showing that individuals anticipate the sensory and environmental consequences of intended actions (Hommel, Müsseler, Aschersleben & Prinz, 2001). Take for example the well-known phenomenon of stimulus-response compatibility. Here, reaction times to imperative stimuli show facilitation when features of those stimuli overlap with the actions to which they correspond (e.g., a left signal for a left-finger response), but they suffer interference that leads to longer responses in the absence of such correspondence (e.g., a left signal for a right-finger response). This phenomenon suggests that features of action goals can be available before those actions commence (Hommel, 1996). Moreover, the notion that “efference copies” of motor commands are used to anticipate sensory consequences of movements has become a core tenet of motor control research. Evidence of such a process comes from a variety of studies, the earliest of which originated in the classic work of von Holst and Mittelstaedt (1950) and Sperry (1950).

It seems clear that people do plan voluntary movements where the term “planning” refers to processes that are driven by a goal and that lead to recruitment of the means to achieve that goal. What remains unclear, however, is what action-related features they plan for. To address this issue, I pursued a constraint-optimization approach. In some ways, this tack is similar to others that have been developed, and in some ways it is different. I therefore briefly review those other approaches next.

There have been three main tacks to studying action selection. The first, proposed by Bernstein (1967), is to identify functional dependencies across and within effectors. The idea is that the influences of one effector’s movement on another, or of one effector component on another within the same effector, may reflect linkages that limit the ways the system can uniquely vary. In turn, the number of factors that must be planned for and controlled may be reduced, and the problem of action selection can be simplified. One can readily experience such a dependency across effectors by attempting the classic party game goal of patting the head while rubbing the stomach. The tendency for both arms to produce either a pat or a rub may reflect a general linkage between the upper limbs in humans (Turvey, 1990). A within-effector linkage can be seen in the tendency for coordination between the wrist and elbow to be better when both are flexed or extended compared to when one is flexed while the other is extended (Kots & Syrovegnin, 1966).

Another tack appeals more specifically to the exploitation of mechanics. The goal here is to understand whether and how individuals rely on mechanical interactions between the body and environment to achieve the desired movement. In these cases, action selection can be simplified because the individual need not plan for direct control of that action feature. A prominent example in humans is normal gait, which can be divided into a stance phase in which one foot is on the ground and a swing phase in which the other foot is off the ground. In the swing phase, individuals can rely on gravity to pull the leg downward. The walker need not directly control that particular movement. The efficacy of this tack is reflected in bipedal robots that exploit gravity to walk down slopes (Collins, Ruina, Tedrake, & Wisse, 2005).

The third tack, which is of primary focus here, rests on the idea that some features of the cognitive and neuromuscular systems naturally help constrain action alternatives. This approach is therefore conceptually similar to the one advocated by Bernstein (1967), which focuses on dependencies within and across effectors that limit the ways movements can vary. In this third tack, researchers ask whether and how constraints are optimized. Optimization can be defined as ensuring that the outputs of one or more functions take on one or more prescribed values such as maxima or minima (Rosenbaum et al., 1990; Todorov, 2004). An example is the well-studied constraint that minimizes jerk, or the time-rate change of acceleration (Flash & Hogan, 1985). Indeed, the postulate that actions are chosen on the basis of minimum jerk can explain why movements tend to display certain features such as smoothness, straight trajectories, and bell-shaped velocity profiles (Morasso, 1981). However, other optimization constraints can also explain action choices. Such constraints entail maximizing comfort (Rosenbaum et al., 1990), and minimizing end-point variance (Harris & Wolpert, 1998), mean-squared torque-change

(Uno, Kawato, & Suzuki, 1989), or distance, time, peak velocity, peak acceleration, and energy (Nelson, 1983).

Each of these constraint-based models has succeeded and failed in accounting for human action selection in various tasks. The energy-based model, for example, is supported by the fact that people tend to avoid circuitous routes in point-to-point reaching tasks (Morasso, 1981). However, the minimum-energy constraint is contradicted when people choose energetically suboptimal actions, such as happens when they make contralateral reaches across the body midline (Mamolo, Roy, Bryden, & Rohr, 2004). Minimum-jerk models, as mentioned above, account for the fact that trajectories are often straight and have bell-shaped velocity profiles (Morasso, 1981). However, it is clear that there are some conditions in which humans under relaxed speed requirements still make curved trajectories during reaching, such as at or near the edges of the workspace (Hollerbach & Atkeson, 1987; Uno, et al., 1989). The torque-change model can explain some of these curvatures, but it has been criticized on the grounds that it does not have a mechanism for changing costs within different levels of control – hand-path, muscle, and motor-command levels – suggesting that minimum torque-change models cannot fully account for the tremendous flexibility commonly observed in the neuromuscular system (Rosenbaum et al., 2001). Finally, the constraint by which individuals adopt initial grasps that afford more comfortable postures at the end of object transports can be violated when people perform actions with conflicting habitual associations. For example, Herbort and Butz (2011) showed that although people adopt inverted initial grasps to turn over an upside down cup, as expected by the comfort constraint, they do not as reliably adopt inverted initial grasps to turn over a cup that is initially upright. As a result, they end such tasks in awkward and uncomfortable postures.

The foregoing review suggests that action selection probably does not depend on a single, invariant cost or constraint. Rather, individuals probably choose actions according to multiple constraints. In turn, this postulate implies the necessity of a mechanism by which those constraints can be prioritized – a constraint hierarchy of multiple constraints that are rank-ordered in accordance with the demands of the task at hand (Rosenbaum et al., 2001).

The notion of the constraint hierarchy has been successfully applied in a model of grasping. According to this model, grasps are chosen with respect to goal postures. The point most germane here is that candidate goal postures are evaluated on the basis of whether they satisfy certain constraints. These constraints are thought to be embedded in a constraint hierarchy, and goal postures are selected on the basis of whether they first satisfy the highest level constraint, then whether they satisfy the next highest level constraint, and so on (Rosenbaum et al., 2001). This general process is called elimination by aspects (cf. Tversky, 1972).

This dissertation investigates whether and how the constraint hierarchy idea applies to action selection when people make hand choices. Thus, the main focus is handedness, which has traditionally been defined as the preference to use one hand rather than the other for many unimanual tasks (Bryden, 1977; Oldfield, 1971). Given this choice-focused description of handedness, it may seem surprising that researchers have been reluctant to formally characterize handedness as a constraint on action selection. This neglect may stem, at least in part, from the fact that it has proven difficult to determine whether and how sensorimotor performance variables underlie the typical right-hand preference found in nearly ninety percent of all humans (Annett, 1972; 1985). It would be difficult to argue that a right-hand choice is optimal without having identified an objective, unique performance advantage for that hand.

The first study reported here links arm selection with reliable sensorimotor performance asymmetries (cf. Sainburg, 2002). This study shows that hand choice is predicted by interlimb asymmetries in the coordination of limb and task dynamics, suggesting that people can make hand selections with respect to such coordination control asymmetries. However, these sensorimotor performance asymmetries are unlikely to fully explain hand choices. Rather, other constraints are also likely to be involved in hand choice, consistent with the constraint-hierarchy hypothesis. I pursue this idea further in subsequent chapters, where I present experiments that tested whether and how the handedness and comfort constraints fit into a putative constraint hierarchy for object transport tasks. I also address whether and how the constraint hierarchy is modulated by task demands. In each chapter, I introduce the specific experiment or experiments and relevant hypotheses, report the resulting data, and discuss their implications. I conclude this thesis with a general discussion.

CHAPTER 2

LINKING THE CONTROL OF LIMB DYNAMICS AND HAND CHOICE

Some of the earliest research on human brain lateralization emphasized a left-hemisphere dominance for motor functions in most humans. For example, Broca (1865) described a left-hemisphere specialization for processes that subserve speech and language, including speech motor control. Liepmann (1905) showed that left-hemisphere damage tends to produce greater movement impairment than does right-hemisphere damage, defining Apraxia as a key example of such impairment; see Allen (1983) and Geschwind (1975) for reviews. However, Sperry and Gazzaniga's seminal research on split-brain patients provided definitive evidence that each hemisphere can be dominant for different neurobehavioral processes; see Gazzaniga (2000a) for a review. While this evidence inspired a departure from Liepmann's view of a comprehensively dominant left hemisphere, this change was only recently incorporated into theories of handedness (Carson 1993; Sainburg 2002).

Indeed, the view that each hemisphere may be specialized for different aspects of motor control has led to the understanding that unilateral hemisphere damage produces unique motor deficits that depend on the side of the lesion (Mutha, Sainburg & Haaland 2011; Haaland & Flaherty, 1984; Mani et al., 2013). Perhaps more importantly, hemisphere-specific deficits also occur in the ipsilesional arm of stroke patients, demonstrating that each hemisphere contributes different processes to control of each arm (Schaefer, Haaland & Sainburg 2007; 2009a).

The evidence that hemispheric asymmetries correspond to performance asymmetries in the arms suggests that these asymmetries might give rise to handedness. However, as mentioned above, handedness is most often described and measured in terms of choice – as a recurring preference for performing select motor tasks with the dominant arm. This view of handedness is supported by the fact that most tasks can be accomplished with either limb, regardless of asymmetries in performance measures. In addition, one clearly can alter one's arm preference for performing a task under different environmental constraints. For example, one might reach for a coffee cup with the non-dominant (left) arm if the table supporting the cup is situated on the left side of one's chair. It is therefore easy to understand why handedness has traditionally been characterized as a preference (Bryden, 1977; Oldfield, 1971), rather than as an asymmetry in performance (Carson, 1993; Sainburg, 2002). However, it remains unclear whether one's choice to use a particular hand in a given task depends in some way on performance asymmetries that result from unique motor control strategies.

There has been surprisingly little previous research that has examined both hand selection and limb performance together in the same study. In one of the few examples, Oliveira, Diedrichsen, Verstynen, Duque, and Ivry (2010) measured performance in terms of simple reaction time of the left and right hands to targets arrayed on a semicircle across the workspace. In these conditions, the participant was told which hand to use and was asked to reach to the target as quickly and accurately as possible when it appeared. In another condition, the same participants were asked to make hand choices to the same targets. Reaction times in the choice condition were longer than in non-choice conditions and were highest near the point where the frequencies of left- and right-hand reaches were most similar. Thus, Oliveira et al. (2012) were able to establish a relation between reaction-time performance and choices in their experimental setup – choices take longer in areas where those choices are more uncertain.

By combining these results with those of the more common studies in which limb selection and limb performance are studied in isolation, one might conclude that the two factors are in fact related. For example, it has been shown repeatedly that right-handers tend to reach the nondominant (left) limb to targets on the left side of the workspace and the dominant (right) limb to targets located on the right side (Bryden, Pryde & Roy 2000; Bryden & Roy, 2006; Gabbard & Helbig, 2004; Gonzalez & Goodale, 2009; Mamolo et al., 2004; Peters, 1996). In addition, studies of interlimb motor performance have shown that reaches with either the left or the right hand to the ipsilateral workspace often show advantages in reaction time, peak velocity, duration, final-position accuracy, and movement trajectory deviations relative to contralateral reaches (Carey, Hargreaves & Goodale, 1996; Carson et al., 1992, 1993; Chua, Carson, Goodman & Elliott, 1992; van Der Staak, 1975; Elliott et al., 1993; Fisk & Goodale, 1985; Ingum & Bjorklund, 1994; Prablanc et al., 1979). Thus, the tendency to avoid reaching across midline with each arm might depend on sensorimotor performance advantages for ipsilateral reaches. It should, however, be noted that the mechanisms that drive these hemispace biases in both preference and performance are controversial. Some researchers have argued that hemispace biases reflect primarily cognitive effects of attention and stimulus-response compatibility (Gabbard & Helbig, 2004; Gabbard, Rabb, & Gentry 1998; Hommel, 1993; Verfaellie & Heilman, 1990) -- a suggestion further supported by the finding that the dominant hand receives more attention during bimanual reaches (Buckingham & Carey, 2009; Peters, 1981). However, others have suggested that hemispace effects result from an intrahemispheric information processing advantage, an argument based on the fact that visual stimuli in each hemispace are initially processed in the hemisphere that controls the limb that is ipsilateral to those stimuli (Bradshaw, Bradshaw, & Nettleton, 1990; Fisk & Goodale, 1985). Thus, while different underlying processes might give rise to the relations between limb selection patterns and limb performance patterns, I hypothesize that limb performance asymmetries associated with handedness can predict limb selection.

A recent study in which both performance and choices were recorded provided some initial support for this idea. Pryzybla et al. (2012) asked right-handed people to reach either the left or right hand to one of 32 possible targets that spanned the entire workspace. Participants showed a common pattern of choices in which they reached the right hand to the right workspace, to the workspace midline, and slightly to the left of midline. However, when visual feedback was removed, the point at which people transitioned from right to left reaches in the left workspace moved closer to midline. The fact that this increase in left-hand reaches in the left workspace corresponded to left-hand performance advantages in final-position accuracy under no-vision conditions suggests that choices were based on based sensorimotor performance asymmetries.

The goal of the current study was to further test this hypothesis in the absence of potential hemifield biases. I first recorded which arm people chose to reach toward different targets and then examined whether those choices were associated with performance asymmetries observed in the same participants. I controlled for hemispace biases in the present study by providing right-handers the choice of limb to each of 8 targets in a center-out reaching task that was symmetrically centered in the workspace. This design allowed me to control for potential visual-spatial biases by assuring symmetry in midline start positions and in the 8 radially arranged targets. There were three targets left of body-midline, two targets on the midline, and three targets right of the midline. However, if both hands started in the same central location within such a center-out design, each arm would be an obstacle for contralateral reaches with the other arm. I eliminated this potential confound by presenting a virtual reality display in which cursors representing left- and right-hand positions were displaced 30 centimeters to the center of the workspace. Because these cursor displacements allowed each hand to remain in a symmetric configuration in its own motor-hemispace, I assured biomechanical symmetry for both the start positions, and for the two midline targets.

Method

Participants

Ten right-handed Penn State undergraduate students (7 males) participated for course credit. I used an 13-item version of the Edinburgh Handedness Inventory (EHI; Oldfield, 1971) to confirm that all participants were right-handed. The mean number of EHI items that participants endorsed as right-limb tasks was 12.70 (SD = .48). The mean height of the participants was 176.28 cm (SD = 10.73 cm). Their mean weight was 76.61 kg (SD = 11.84 kg), and their mean age was 20.50 years (SD = 1.41 years). All participants signed an informed consent form approved by the Pennsylvania State Institutional Review Board.

Apparatus

Figure 1 (panel A) shows the experimental setup. Participants sat in a dentist-type chair and faced a horizontal workspace. An air sled attached to each arm minimized the effects of friction and fatigue as participants moved their arms across the workspace. A splint on each arm immobilized joints distal to the elbow. A mirror, positioned above the workspace, reflected stimuli projected by an overhead 55” high-definition television (Sony Electronics, Inc). The mirror prevented participants from seeing their arms. The stimuli were displayed with custom software written in REAL BASIC (REAL Software, USA).

A six-degree-of-freedom (6-DOF) Flock of Birds (Ascension-Technology, Inc.) magnetic tracking system sampled limb positions and orientations at a rate of 130 Hz. For motion tracking, I digitized the following bony structures in each limb: (1) index fingertip; (2) metacarpal-phalangeal joint; (3) lateral and medial epicondyle of the humerus; and (4) acromion process. Each arm had two 6-DOF sensors securely affixed to it (see Figure 1).

Panel B of Figure 1 shows that a 1.5 cm diameter (d) circular cursor with crosshairs represented the 2-D position of the index fingertip of each hand. The software used the two-dimensional position of the finger to project and update the cursor position at a rate of 60 Hz refresh. Each cursor (d = 1.5 cm) had a medial displacement of 30 cm. The mirror reflected the following stimuli: (1) two cursors; (2) a thermometer-style velocity feedback indicator located at the top of the workspace; (3) a green start circle (d = 2.5 cm) located at the body-midline; and (4) a bullseye-style target (d = 3.5 cm) located 13 cm away from the start circle. In each trial, the target appeared at one of 8 possible positions. A 45° interval separated each possible target.

Procedure

I tested participants in individual sessions. After each participant arrived at the laboratory, s/he signed an informed consent form and filled out demographic and handedness forms. I then set up the participant in the apparatus. The setup process lasted about ten minutes. I gave the participant instructions and asked whether the she or he had any questions. The session began when I was confident that the participant understood the procedure. The entire experiment took approximately one hour.

Experimental Design

I used a fully within-subjects design. In two choice conditions, participants could reach either hand to the target. In four non-choice conditions, participants reached a specified hand to the target. In both types of trials, participants were asked to reach the target as quickly and accurately as possible and to minimize their corrective movements. Table 1 describes the progression of all the conditions.

Participants first received practice on 32 choice trials (four choices to each of eight targets) for familiarization with the dissociation between the visual feedback of the cursors and the proprioceptive feedback of the hands. To this end, I also encouraged participants to choose both the left and the right hands during different practice trials. In the second choice-condition, they performed 80 more choice trials. In each of the last four conditions, they made 32 non-choice reaches (four reaches to each of eight targets). I blocked the non-choice trials on the basis of limb and fixed the order of all conditions; participants first performed 32 non-choice trials with the nondominant limb and then 32 non-choice trials with dominant limb. They repeated this sequence once. I randomized the order of target presentation within each condition so that the target location was unpredictable and fixed that order for all participants.

Experimental Task

In order to provide visual stimuli that were symmetric relative to the hand locations and the body midline, we centered the 8-direction center-out task at the body-midline (see Figure 1, Panel B). By displacing the cursor from the hand 30 cm toward the midline, the arms remained geometrically symmetric at the starting position. This design also separated the hands in space so that they could not interfere with each other during the task. In the choice conditions, I asked participants to reach only one cursor to the displayed target in each trial. Each cursor remained visible throughout the trial. In the non-choice conditions, the set-up was the same except that subjects were instructed to reach with either the left or the right hand for a full block of trials.

In the choice conditions, each trial began after participants moved both cursors into the midline start circle and kept them there for 700 milliseconds (msec). Because the target for that trial appeared immediately after the preceding trial, the target was visible while the participants positioned the cursors in the start circle. After the participants held the cursors in the start circle for 700 msec, they received an audiovisual go-cue consisting of a tone and color change of the start circle circumference.

Participants had 1 second to complete each 13 cm-long reach. They completed all reaches well before this time limitation expired. To help ensure maximum tangential hand velocities were similar across targets and across participants, I instructed participants to move as quickly and accurately as possible. I also required them to monitor the velocity feedback indicator, which provided feedback of the maximum velocity following each reach. To motivate participants to be both quick and accurate, I awarded points for accuracy only when the maximum tangential velocity exceeded .8 meters per second. I showed at the top of the screen a running total of earned points.

Participants always had full visual feedback of the cursors. In addition, participants saw a brief feedback display (2 second interval) of the hand-path following each reach. The hand-path display then disappeared and participants began the next trial at their own pace.

The only difference between the choice trials and the non-choice trials was that each non-choice trial began after participants moved only a single cursor into the midline start circle.

Data Processing and Analysis

I processed the data with custom programs written in IgorPro 6.0 (WaveMetrics, Inc). I low-pass filtered the displacement data at 8 Hz with a 3rd-order dual-pass Butterworth filter prior to differentiation to obtain velocity and acceleration profiles. Because there were minor oscillations of the cursors in the start circle, I defined the start of each reach as the first minimum in tangential velocity which was under 8% of the maximum velocity for that trial. Likewise, I defined the end of each reach as the first minimum following peak velocity, which was below 8% of maximum velocity.

Limb Choice Analysis

To assess whether limb choices varied by workspace, I first arcsine-transformed the proportion of right-hand reaches to each target. I did so because the variance of proportions derived from binomial data depends on the values of those proportions. This dependence violates the homogeneity of variance assumptions of traditional inferential statistics. By contrast, the variance of arcsine-transformed proportions is independent of their associated proportion values (Hogg & Craig, 1995). It should be noted that the arcsine transformation yields the inverse sine of the square root of each proportion, which is expressed in radians. Thus, some of the transformed values were greater than 1.

I then grouped targets according to their visual workspace location relative to the body midline and pooled the transformed values accordingly (see Figure 2). Hereafter, the three targets left of the body-midline are simply called “left” targets, the two targets at the midline are called “midline” targets, and the three targets right of the midline are called “right” targets.

Movement Kinematics Analysis

I report three kinematic measures to characterize performance: hand-path deviation from linearity, final-position error, and maximum tangential hand velocity (V_{max}). Previous work has shown that for reaches with similar maximum velocities, linearity deviation and final-position error systematically vary across the arms (Sainburg, 2002; Sainburg & Kalakanis, 2002; Wang & Sainburg, 2007).

I defined hand-path deviation from linearity as the minor axis of the path divided by the major axis of the path. The major axis was the longest distance between any two points on the hand-path, while the minor axis was the longest distance between any point in the hand-path and the major axis, measured perpendicular to the major axis. I computed final-position error as the Euclidean distance between the cursor center (index fingertip) at the end of the reach and the target center.

Movement Dynamics Analysis

Appendix A details the method I used to quantify joint torques. I modeled each limb as a set of three rigid, planar links with 8 degrees of freedom (DOF; see Figure 1 of Appendix A). I then partitioned the equations of motion into three components: (1) net torque, which equaled the sum of muscle and interaction torque components; (2) interaction torque, which reflected the effects of the motion of the other limb segments; and (3) muscle torque, which estimated the rotational forces from muscle contraction. This segmentation of the equations of motion was inspired by Schneider and Zernicke (1990), and has previously been reported by the Movement Neuroscience Lab group (Sainburg et al., 1999). Here I focus on the torques observed during the time interval between reach onset and V_{max} because this interval largely reflects the effects of movement planning processes (Latash 2007; Sainburg et al., 1999).

Statistical Analysis

I analyzed the transformed choice data using a one-way, repeated measures ANOVA with visual workspace (left, midline, and right) as the factor. I performed planned comparisons between nondominant and dominant limb distributions (for choice, kinematic, and dynamic analyses) with paired-samples t-tests and Bonferonni-corrected the significance threshold for multiple comparisons. Bonferonni-corrected alpha was defined as, $\alpha_{Bon} = \alpha / n$, where α was .05 and n was the number of comparisons (Abdi, 2007).

Non-choice data came from conditions in which participants made an equal number of reaches to each target. I analyzed each dependent measure using a 2 X 2 X 2 repeated-measures ANOVA with the following factors: limb (nondominant vs. dominant), target (90° vs. 270°), and non-choice condition order (first vs. second).

Results

Limb Choice

Previous research has shown that right-handers tend to reach the nondominant limb to left targets and the dominant limb to right targets (see Peters, 1996, for review). I therefore expected participants to reach the dominant limb to left targets less often than to right targets. Indeed, a repeated-measures ANOVA on the arcsine-transformed values revealed a significant effect of target location on dominant reaches, $F(2,18) = 42.94$, $p < .001$ (see Figure 2). The size of this effect, estimated by partial eta-squared (η_p^2), was .83. Post-hoc tests confirmed that left targets received fewer dominant reaches (M = .32, SE = .15) than right targets (M = 1.55, SE = .01), t(9) = 7.62, p < .0001.

Previous work has also shown that the tendency for people to reach each limb to its own hemispace is asymmetric, such that people reach the dominant limb to targets in the nondominant (left) space more often than they reach the nondominant limb to targets in the dominant (right) space (Bryden & Roy, 2006; Bryden et al., 2000; Mamolo et al., 2004, 2006; Gabbard & Helbig, 2004; Peters, 1996). Figure 2 shows that participants displayed a similar pattern. There was a trend for the rate of nondominant reaches to left targets (M = 1.25, SE = .15) to be lower than the rate of dominant reaches to right targets, although this trend did not reach statistical significance (M = 1.55, SE = .01), t(9) = 2.04, p = .07.

The main aim of this study was to determine whether limb performance asymmetries can predict limb choices in the absence of hemispace and proximity effects. Thus, I focused on the midline targets because they were equidistant from each hand. Post-hoc tests showed that the midline targets (M = 1.24, SE = .08) received a larger proportion of dominant reaches than left targets, t(9) = 5.74, p < .001, but a lower proportion of dominant reaches than right targets, t(9) = 4.19, p = .002.

If limb choices depended entirely on hemispace effects on performance and preference, then one would expect equal rates of nondominant and dominant reaches to midline targets. I tested these predictions by assessing whether the midline targets received more dominant reaches than would have been expected by chance alone. A one-sample t-test showed that midline targets received an above-chance number of dominant reaches, t(9) = 6.06, p < .001. We observed this effect at both the 90° target ($M = 1.37$, $SE = .07$), $t(9) = 7.94$, $p < .001$, and at the 270° target ($M = 1.10$, $SE = .10$), $t(9) = 3.35$, $p = .009$ ($\alpha_{Bon} = .05/3 = .02$).

Finally, to ensure that these effects were not due to differences across targets in the same visual workspace, I conducted seven pair-wise t-tests -- three for the left targets, one for the midline targets, and three for the right targets. These tests confirmed that there were no significant differences in dominant reaches across left ($ts(9) < 1.54$, $ps > .16$) or right targets ($ts(9) < 1.50$, $ps > .17$). There was a trend suggesting that the 90° midline target received more dominant reaches ($M = 1.37$, $SE = .07$) than the 270° midline target ($M = 1.10$, $SE = .10$), but this effect did not survive the Bonferonni-corrected significance threshold ($\alpha_{Bon} = .05/7 = .007$), $t(9) = 3.35$, $p = .01$. It should be noted that despite this trend, both midline targets received an above-chance number of dominant reaches.

Kinematics

Having confirmed that left targets received mostly nondominant reaches and that right targets received mostly dominant reaches, I asked whether limb performance asymmetries can explain the preponderance of dominant reaches to midline targets. In order to address this issue, I compared movements made under non-choice conditions with the left and right arms. The non-choice conditions were necessary for drawing statistical comparisons, as they allowed me to have equal numbers of observations in each condition of interest.

Below I first detail kinematic differences between nondominant and dominant reaches to each of the two midline targets. I then relate these kinematic results to interlimb differences in dynamic coordination. As seen in Figure 3 (panel A), there was a main effect of limb on linearity deviation, $F(1,9) = 20.40$, $p = .001$, $\eta_p^2 = .70$; nondominant reaches ($M = .15$ au, $SE = .02$ au) displayed greater deviation than dominant reaches (M = .06 au, SE=.01 au).[1] There was also a main effect of order, F(1,9) = 12.04, p=.01, η_p^2 = .57, such that linearity deviation was greater in the first non-choice condition (M=.11 au, SE=.01 au) than in the second (M = .10 au, SE = .01 au). This order effect was the same for each limb and for each target as there were no interactions (Fs < 2.64, ps > .13), so I collapsed across order and performed planned comparisons. These tests confirmed that nondominant linearity deviation was greater (M = .14 au, SE = .02 au) than dominant linearity deviation (M = .07 au, SE = .01 au) to the 90° target, t(9) = 3.82, p=.004. The same pattern between nondominant linearity deviation (M = .15 au, SE = .02 au) and dominant linearity deviation (M = .05 au, SE=.01 au) was seen at the 270° target, t(9) = 4.38, p = .002.

Figure 3 (panel B) shows a main effect of limb on final-position error, F(1,9) = 8.64, p = .02, η_p^2 = .49, such that the nondominant limb (M = 2.50 cm, SE = .20 cm) showed larger final-position errors than the dominant limb (M = 2.00 cm, SE = .20 cm). This is consistent with previous findings for reaching under visual feedback conditions (Carson et al., 1990). There was a main effect of target, F(1,9) = 5.52, p = .04, η_p^2 = .38; reaches to the 270° target (M = 2.00 cm, SE = .20 cm) showed more final-position error than reaches to the 90° target (M = 2.50 cm, SE = .20 cm). There was no main effect of order, and there were no interactions (Fs < 3.28, ps > .10).

I performed planned comparisons which showed no difference between nondominant final-position error (M = 2.67, SE = .27) and dominant final-position error (M = 2.36, SE = .26) at the 270° target, t(9) = 1.38, p = .20. At the 90° target, however, the nondominant limb showed greater final-position error (M = 2.27 cm, SE = .19 cm) than the dominant limb (M = 1.68 cm, SE = .16 cm), t(9) = 5.16, p = .001.

Figure 3 (panel C) confirms that none of these interlimb differences could be attributed to differences in maximum velocity. There was only a main effect of target on maximum velocity, F(1,9) = 7.49, p = .02; reaches were slower to the 90° target (M = .84 m / sec, SE = .03 m / sec) than to the 270° target (M = .88 m / sec, SE = .02 m / sec). There were no other main effects, and there were no interactions (Fs < 3.52, ps > .05).

Inverse Dynamics

The previous sections established that limb choice varied by workspace and that midline workspace received mostly dominant reaches. They also showed that the dominant limb produced straighter hand-paths to midline targets relative to the nondominant limb. By contrast, it was not clear that interlimb differences in final-position accuracy could explain reaches to both midline targets.

These results indicate that asymmetries in rates of nondominant and dominant reaches to midline targets might be attributable to limb performance asymmetries. More specifically, the preponderance of dominant midline target reaches might be attributable to a dominant-limb coordination advantage. This notion is consistent with previous work showing that the dominant limb / hemisphere system appears specialized for the coordination of intersegmental dynamics (Sainburg & Kalakanis, 2000; Sainburg, 2002). Thus, I now examine how the observed asymmetries in linearity deviation related to interlimb differences in dynamic control.

Panels C and D of Figure 4 show representative shoulder and elbow joint torques, respectively. Two torque components contributed to the shoulder (or elbow) net torque: muscle torque and interaction torque (see Method). The torque profiles in Figure 4 show that each limb produced similar peak net torque magnitudes at both the elbow and shoulder. For both limbs, these magnitudes were higher at the shoulders than at the elbows (see y-axis scales) because the shoulders carry greater inertial loads. Overall, there were no significant interlimb differences between absolute peak net torques at the shoulders (Fs < 4.50, ps > .05). There was only a statistical trend for a main effect of limb, F(1,9) = 4.50, p = .06. The dominant limb tended to display slightly greater peak net torques (M = 13.23, SE = 1.10) compared to the nondominant limb (M = 11.59, SE = 1.17). However, this effect did not reach traditional levels of statistical significance. There were also no significant interlimb differences between absolute net torques at the elbows (Fs < 2.51, ps > .15).[2]

Although initial peak net torques were similar across the limbs, closer inspection of peak muscle and peak interaction torques revealed substantial interlimb differences in dynamic coordination. Panel C of Figure 4 shows that the nondominant arm generated smaller shoulder peak muscle torques (M = 6.64 Newton.Meters {N.m}, SE = .63 N.m.) than the dominant arm (M = 8.84 N.m, SE = .85 N.m.). Across subjects, this difference resulted in a main effect of limb, F(1,9) = 35.43, p < .001, η_p^2 = .80. There were no other significant main effects and or interactions (Fs < 4.46, ps > .05).

Figure 4 (panels C and D) shows that shoulder flexion in each limb was accompanied by elbow extension as the hand moved toward the target. However, interaction and muscle torque made different contributions to net torque at the shoulder and at the elbow in each limb. At the nondominant shoulder, interaction and muscle torque made similar contributions to net torque. By contrast, interaction torque at the dominant shoulder contributed less to net torque and muscle torque contributed more.

These asymmetries in shoulder torque components were associated with clear differences in elbow torque components. As shown in Figure 4 (panel D), nondominant elbow muscle torque made a substantial contribution to net torque. By contrast, dominant elbow muscle torque made very little contribution to net torque, as interaction torque arising from motion of the upper arm accounted for most of the net torque and remained near zero throughout the trial. As a result, the dominant elbow displayed very little extensor muscle torque while driving the hand toward the target. Indeed, there was a main effect of limb on peak elbow muscle torque, F(1,9) = 10.08, p = .01, η_p^2 = .58, such that nondominant reaches showed higher peak elbow muscle torques (M = 1.62 N.m., SE = .23 N.m.) than dominant reaches (M = 1.00 N.m., SE = .09 N.m.). There was also a main effect of target, F(1,9) = 40.19, p < .001, η_p^2 = .82; participants generated less elbow muscle torque to reach to the 90° target (M = 1.12 N.m., SE = .14 N.m) than to the 270° target (M = 1.52 N.m., SE = .16 N.m.). There were no other main effects, and there were no interactions (Fs < 3.6, ps > .05).

These results indicate that the coordination patterns displayed by the nondominant and dominant limbs were different. Relative to the dominant limb, coordination of the nondominant limb was characterized by a strategy that generated smaller peak muscle torques at the shoulder and greater peak muscle torques at the elbow. By contrast, coordination of the dominant limb was characterized by greater peak muscle torques at the shoulder, which produced elbow interaction torques that were efficiently coordinated with small elbow muscle torques.

These results are consistent with previous findings that the movement of the shoulder joint creates large interaction torques at the elbow that are proficiently used to reduce muscle torque requirements at the elbow (Kalakanis & Sainburg, 2000). However, nondominant arm movements in the current study were characterized by greater elbow and lower shoulder muscle torques. This strategy resulted in lower interaction torques from the shoulder acting at the elbow, which resulted in greater elbow muscle torque requirements. Furthermore, increases in muscle torques at the nondominant elbow resulted in greater interaction torques at the shoulder, an effect that required active compensation at the shoulder. That is, muscle torques and interaction torques acted “antagonistically,” suggesting that the nondominant arm uses a less efficient coordination strategy than does the dominant arm.

Figure 5 shows that these coordination patterns also characterized reaches to the 270° target, even though those reaches were made in the opposite direction from the 90° target. Both limbs tended to move the hand medial to the 270° target. However, linearity deviation was again greater for the left limb, which generated greater flexor elbow muscle torque.

Figure 6 confirms that the patterns of shoulder and elbow muscle torques were relatively consistent across targets and participants. More specifically, panel A of Figure 6 shows that initial peak muscle torques were smaller at the shoulder of the nondominant arm compared to the shoulder of the dominant arm. Panel B shows that this pattern was reversed at the elbow where peak muscle torques were greater for the nondominant arm compared to the dominant arm.

To further support the idea that interlimb differences in dynamic coordination may have led to interlimb differences in linearity deviation, I analyzed the relation, across participants, between initial peak elbow muscle torque magnitude and linearity for nondominant and dominant reaches. If higher peak elbow muscle torques led to increases in linearity deviation, then one would expect them to be positively correlated with linearity deviation for the nondominant limb but not for the dominant limb. Indeed, magnitudes of nondominant peak elbow muscle torques positively correlated with nondominant linearity deviation at the 90°

target, r(77) = .39, $R^2 = .15$, p = .02, and at the 270° target, r(77) = .37, $R^2 = .14$, p = .03; see Figure 7, panels A and C. By contrast, dominant peak elbow muscle torques did not correlate with dominant linearity deviation at the 90° target, r(78) = .03, $R^2 < .01$, p = .83, or at the 270° target, r(76) = .04, $R^2 < .01$, p = .74; see Figure 7, panels B and D.

The non-zero regression slopes in panels A and C of Figure 7 indicate that nondominant peak elbow muscle torque explained a moderate but significant amount of variance in nondominant linearity deviation at each target. The moderate nature of these relations may be explained by the fact that for each limb, elbow muscle torque contributed less to elbow net torque than did elbow interaction torque. Variations in the shape of the torque profiles also contributes significantly to the relative displacement profiles of the joints, and thus ultimately to hand-path linearity. These points notwithstanding, the non-zero slopes for the nondominant limb contrast the near-zero slopes for the dominant limb (see Figure 7, panels B and D).

Finally, I analyzed the relation between initial peak shoulder muscle torque magnitude and linearity for dominant and nondominant reaches. If interlimb differences in linearity deviation were based on interlimb differences in dynamic coordination across the elbow and shoulder, then linearity deviations should also be more strongly negatively correlated with peak shoulder muscle torques in the dominant arm. I found some support for this prediction, as dominant peak shoulder muscle torques negatively correlated with dominant arm linearity deviation at both the 90° target, r(77) = -.23, $R^2 = .05$, p = .01, and at the 270° target, r(77) = -.24, $R^2 = .06$, p = .04. By contrast, nondominant peak shoulder muscle torques only correlated with nondominant linearity deviation at the 270° target, r(76) = -.30, $R^2 = .09$, p =.01, and not at the 90° target, r(78) = .09, $R^2 < .01$, p = .45.

Discussion

Early research on brain lateralization proposed that the left-hemisphere plays a special role in motor processes (Broca, 1865; Geschwind, 1975; Leipmann, 1905). Later work focusing mainly on higher cognitive and perceptual asymmetries established that both hemispheres are specialized for different functions (Corballis, 1998; Gazzaniga, 2000a; Sperry, 1982). Recent work from the Movement Neuroscience Lab has extended these ideas to the motor system. This work has proposed that the two hemisphere / limb systems are specialized for distinct, but complementary, motor control processes: the dominant system for coordination of limb and task dynamics and the nondominant system for stabilizing position through impedance control mechanisms (Bagesteiro & Sainburg, 2002, 2003; Przybyla et al., 2011; Sainburg, 2002; Sainburg & Kalakanis, 2000; Wang & Sainburg, 2004, 2007). The idea of distinct and complementary control systems was previously proposed by Guiard (1987), who described a similar division of labor between the arms during bimanual actions. This more recent research emphasizes the complementary division of labor between the two hemispheres during unimanual actions (Schaefer et al., 2007). This characterization of handedness provides a unique opportunity to study the link between functional lateralization and the decisions that people make about how to move. In fact, handedness has traditionally been characterized by the arm choices that people make when they approach a given task (Bryden, 1977; Oldfield, 1971). I now ask whether and how limb choice is related to, and may therefore depend upon, sensorimotor asymmetries in dynamic coordination.

To address these questions, I had right-handed participants reach either limb to a single target in an eight-direction center-out task. I centered the task in the workspace so there were three targets left of body-midline, three targets right of midline, and two targets on the midline. I displaced both cursors to a midline start circle so that each limb remained in its own hemispace (see Figure 1). This design assured geometric symmetry between the arms for the midline targets and eliminated potential mechanical conflicts between the limbs.

The main question was whether asymmetries in limb choice for symmetric targets correspond to asymmetries in performance. To address this question, I assessed whether the two midline targets would receive more dominant reaches than would be expected by chance. These targets were equidistant from the actual start locations of each hand and were neither in the left nor right hemispaces. Therefore, if limb selection were dictated solely by a hemispace bias, one would expect an equal distribution of dominant and nondominant reaches. However, data from the choice conditions showed that the midline targets received more dominant than nondominant reaches (see Figure 2). Data from our non-choice conditions clarified the relations between this pattern of limb choice and performance asymmetries. In these conditions, the dominant hand-paths were substantially straighter (see Figure 3, panel A); they reflected more proficient utilization of limb dynamics (shoulder interaction torques), as compared to the nondominant arm (Bagesteiro & Sainburg, 2002, 2003; Sainburg, 2002; Sainburg & Kalakanis, 2000). While both arms had similar initial peak elbow and shoulder net torques, the dominant arm strategy was characterized by higher shoulder muscle torque that drove motion at both the shoulder and elbow joints. Critically, nondominant initial peak elbow muscle torques positively correlated with linearity deviations, whereas no such correlations occurred for the dominant arm (see Figure 7). Together, these findings suggest that in the absence of hemispace effects, sensorimotor asymmetries in dynamic coordination may contribute to limb choice.

As predicted by hemispace biases, left targets received mostly nondominant reaches and right targets received mostly dominant reaches (see Figure 2). My data confirmed a trend for the dominant (right) arm to reach to left targets more than the nondominant (left) limb reached to right targets. Previous research has reported that the distribution of reaches is asymmetric across the workspace, such that right-handers prefer dominant reaches to targets located in the middle of the workspace and to targets just left of the body-midline (Bryden & Roy, 2006; Bryden et al., 2000; Mamolo et al., 2004; Gabbard & Helbig, 2004; Peters, 1996). To the best of my knowledge, however, the current study is the first to show that the dominant limb reaches into contralateral space more than the nondominant arm even when only the visual representation of the hand (i.e., the cursor) moves across the body-midline while the hand does not. This finding suggests a strong influence of vision on the dominant-arm preference.

Consistent with this idea, Przybyla et al. (2012) reported that people choose significantly fewer contralateral reaches with the dominant limb, when visual feedback is not available. Moreover, this decrease appears to be driven by a corresponding change in sensorimotor performance that is consistent with the dynamic dominance hypothesis. This hypothesis states that dominant reaches rely largely on predictive mechanisms that specify mechanically efficient movement patterns. Such predictive control has been shown to depend on visual feedback mechanisms to update predictive mechanisms on a trial-to-trial basis (Sainburg, 2002; Yadav & Sainburg, 2011). Thus, if removing vision decreases the relative proficiency of dominant reaches, and if limb choice depends on sensorimotor asymmetries, then the dominant limb should reach less. The link between limb choice and the dynamic dominance model that has emerged in this study and in the study of Przybyla et al.(2012) has implications for theories of action selection, for our understanding of handedness, and possibly for models of neural lateralization. I address these issues next.

A popular approach to the problem of action selection has been to identify linkages within the neuromuscular system (Bernstein, 1967) and then to model behavior as optimizations performed under those constraints (Nelson, 1983; Todorov, 2004). Using this approach, a number of factors have been suggested to govern action selection; see Rosenbaum et al. (1990) for reviews. Although some 90% of all humans prefer the right limb for most unimanual actions (Annett, 1972; Corballis, 1997; 2003), researchers have been reluctant to formally characterize handedness as an important constraint on action selection. This reluctance, as noted above, has likely been due to the fact that it has proven difficult to establish whether sensorimotor performance asymmetries underlie handedness; see Carson (1993) and Sainburg (2002) for discussions. Indeed, it would be difficult to argue that choosing the dominant arm is optimal without knowing if there is a performance advantage for the dominant arm in that particular instance. A related problem is the paucity of studies that have examined limb choice and sensorimotor asymmetries together in the same experiments.

The current study addresses these issues by assessing both limb choice and limb performance in the same participants and by linking limb choice to a reliable sensorimotor asymmetry in dynamic coordination. However, I do not suggest that asymmetries in dynamic coordination fully explain limb choice. By contrast, I argue that limb choice likely depends upon multiple factors. In the current study, for example, it is clear that limb choice to targets that were visually located to the left and right strongly depended on hemispace biases. But where hemispace biases could not predict limb choice I found evidence for a link between limb choice and dynamic coordination differences. This case was one in which the mechanical requirements for the two possible actions – a dominant or nondominant reach – were symmetric and equivalent. Thus, the current findings suggest that the hemispace bias may act as the most useful constraint on limb choice to lateralized targets, but also because dynamic coordination asymmetries may facilitate action selection in the face of geometric and mechanical symmetry. This perspective is consistent with the idea that action selection in general likely depends on a hierarchy of multiple constraints whose relative priority may depend on task demands (Rosenbaum et al. 2001).

In conclusion, the current results establish a clear relation between sensorimotor asymmetries in dynamic coordination and the decisions people make about how to move. However, I do not argue on the basis of this association that differences in dynamic coordination caused particular patterns of arm choices. My aim in this study was simply to demonstrate a link between arm selection and reliable interlimb performance asymmetries. I can speculate, however, that although the interlimb differences in energetics we observed may be small in the current task, the choices I observed could reflect a well-established strategy based on dynamics. Moreover, that difference could be substantial when stressed by either the need for continuous action (fatigue) or strenuous action (approximating maximal output). The choices observed in this sub-maximal task may reflect such rules that may have been developed to deal with more taxing conditions under the stress of evolutionary adaptation processes. I suggest that limb selection may in fact be driven by a lifetime (ontogenetic) and by many generations (phylogenetic) of movement choices that involve more energetically costly movements, such as those required during tool making, tool use, hunting, and fighting. Indeed, it has recently been verified that interlimb differences in dynamic coordination persist during more stressful vertical reaching movements performed in a gravitational field (Tomlinson & Sainburg, 2012). It will be important for future work to test whether hand choice corresponds to interlimb coordination asymmetries in this and other energetically demanding tasks.

This link between arm selection and arm performance may also have a more general implication for models of neural lateralization. It has been suggested that lateralization of neural function reflects an adaptive “no-cost extension” whereby more cortical tissue can be devoted to expansion of function while restricting control to local circuits -- a factor that is beneficial in terms of both speed and energetics of neural processing (Corballis, 2009; Gazzaniga, 2000a; Tommasi, 2009). Consistent with this view, Sainburg and Eckhardt (2005) have argued that handedness first reflected adaptation at the individual level that resulted from the demand for skilled behavior and later became conserved genetically through the process of natural selection. The current findings emphasize the link between hemispheric specializations in dynamic coordination and action selection, thereby supporting this skill-based evolutionary perspective. Moreover, Gazzaniga (2000a) has pointed out that specialization of a given hemisphere for a particular function implies that the other hemisphere is functionally limited for that function. Thus, a primary benefit of lateralization is that new abilities can emerge over the course of evolution through the expansion of intrahemispheric circuitry, while evolutionarily older abilities are sustained. It follows, then, that lateralization should also underlie the ability to make adaptive behavioral decisions that are based on lateralized skills. Future work can test this idea by asking whether people use the nondominant limb more in tasks that match that arm’s specialization for position stabilization via impedance-based control mechanisms (e.g., Wang & Sainburg, 2007).

Notes

1. Three trials (.94%) were excluded from the linearity analysis because they yielded values that were more than three standard deviations above the mean. Nine trials (2.8%) were excluded from the final-position error analysis, and four trials (1.3%) were excluded from the elbow muscle torque analysis for the same reason.

2. The ANOVAs that yielded these results also included target as a factor. Thus, there were no differences in shoulder or elbow net torque across the two midline targets.

CHAPTER 3

COMFORT TRUMPS HAND PREFERENCE IN OBJECT TRANSPORTS

Experiment 1 showed that hand choices in right-handers can be accounted for by interlimb coordination asymmetries when they cannot be accounted for by other common kinematic measures or by hemifield-related biases. The results also showed that the preference to use the right hand can be modulated by the workspace location of the target. These outcomes therefore support the notion that different task features can differentially weight the hand preference constraint. If the importance of the well-known hand preference constraint can be modulated, then it is also important to test whether other actor-related constraints can be weighted more heavily than hand preference. The experiment reported here tested this possibility in the context of object transport tasks where hand preference could be pitted against another well-known constraint – the tendency for individuals to grasp objects in ways that afford less extreme grasp orientations at the end of object transports.

The first laboratory demonstration of this effect came from Rosenbaum et al. (1990). In each experimental trial, right-handed participants chose either overhand or underhand initial grasps with the right hand to transport a horizontal dowel so that either its left or right end touched a nearby target. When participants touched the target with the left end, they chose underhand initial grasps, presumably so they could perform the target-touch with thumb-up grasps. Likewise, when participants touched the target with the right end, they chose overhand initial grasps which again allowed them to finish the transports in thumb-up orientations. In a subsequent experiment, participants rated the comfort of the possible postures and confirmed that thumb-up orientations were more comfortable than thumb-down orientations.

Rosenbaum et al. (1990) concluded that choices maximized the comfort of the final grasp orientation. Several studies have confirmed that target-positioning comfort is an actor-related goal that constrains manual action selection. However, it is not the sole objective for such action choices. As reviewed above, several others are known, and so a challenge inspired by the constraint-based approach to action selection is to find out which constraints are more important than others. Many experiments that have been done in the Lab for Cognition and Action and elsewhere have pursued this issue by using a simple preference procedure. Participants have been presented with pairs of tasks and have been asked to pick and perform one of the tasks. By using pairs of tasks that differ with respect to well defined features, it has been possible to assess the relative weighting of the features based on the likelihoods of their associated choices. For a review, see Rosenbaum, Chapman, Weigelt, Weiss, and van der Wel (2012).

The present study followed in this tradition and pitted the hand preference and the comfort constraint against each other in a single study. I should note that in one previous study Fischman (1998) showed that right-handers prefer overhand right-hand grasps not only to underhand right-hand grasps, but also to left-hand overhand grasps, and to left-hand underhand grasps when freely selecting grasp and hand for 90 degree rod rotations. However, that finding leaves open the question of which is more important, hand preference or comfort?

Based on how well-known hand preference is, not to mention that nearly ninety percent of humans report a right-hand preference (Annett, 1995), one might expect hand preference to be much more important than aiming-related comfort. In this study, I checked whether that is true.

EXPERIMENT 2A

I asked right-handed participants to make hand or grasp choices. In so doing, I tested three competing hypotheses. One was that hand preference is prioritized over comfort. Based on this hypothesis, I predicted that participants would choose the right hand even for options that led to uncomfortable final postures. The other hypothesis was that comfort is prioritized over hand preference. Based on this hypothesis, I predicted that participants would choose the hand that led to comfortable final postures. The third and final hypothesis was that participants do not prioritize either hand preference or final comfort. Based on this hypothesis, I predicted that participants would essentially choose options at random.

Method

Participants

Sixteen Pennsylvania State University undergraduate students (5 females) participated for course credit. Their mean age was 20.25 years (SD=1.34 years), their mean height was 1.73 m (SD=.10 m), and their mean weight was 71.98 kg (SD=10.83 kg). The participants reported preferring the right hand for an average of 10.41 items (SD=1.18 items) on the 11-item version of the Edinburgh Handedness Inventory (Oldfield, 1971). All participants signed an informed consent form that was approved by the Pennsylvania State Institutional Review Board.

Apparatus, Procedure, and Design

In each trial, the seated participant grasped a light wooden dowel (9.92 g) and transported the left (white) or right (black) end to one of five nearer targets (see Figure 8). At the start of each trial, the dowel rested horizontally on a .15 m-high cradle – high enough so participants could adopt overhand or underhand grasps while taking hold of the dowel. The dowel had a cylindrical shaft with a diameter of .02 m and a length of .31 m. Each end of the dowel had a square base with side lengths of .04 m. The start location of the dowel was centered on the body- and workspace-midline for all trials.

The targets were spaced at 30 degree intervals. The distance between the start location of the dowel and each target was set for each participant to 70% of his or her maximal reach in order to control for potentially different anthropometric features of the participants. This measurement was made from the right acromion process to the tip of the middle finger on the right hand. The square target holes were slightly bigger than the square bases of the dowel, and each base fit snugly into each target so the dowel stood vertically on its own once inserted. We used this setup so the task would require a relatively high degree of precision for the target placement. All items occupied the surface of a .76 m high × 1.51 m wide × .76 m deep table.

The participant began each trial with the left and right hands resting on the left and right home locations, respectively (see Figure 8). After the participant inserted the dowel into the target, he or she released the dowel, letting it stand vertically on its own. The participant briefly returned the hand to its home location and then moved the dowel back to the cradle, always putting the black end on the right side of the cradle. Each movement was self-paced.

In one set of 20 trials, I told each participant which hand to use and which end of the dowel to insert into which target. In each of these hand-specified trials, the participant had the option to choose either an overhand or an underhand initial grasp with the hand specified by the experimenter. One choice led to a comfortable final (thumb-up) posture. The other led to an uncomfortable (thumb-down) final posture. These comfort levels were expected based on previous rating studies and were verified in Experiment 2B, which is reported below. Specifying hand (left or right), end (white or black), and target (A-E) resulted in 20 trials. The dependent measure was the probability, p(TU), pooled over participants, of using an initial grasp that led to a thumb-up final posture.

In another set of 20 trials, the same participants were told which initial grasp to use and which end of the dowel to insert into which target. In these grasp-specified trials, the participant was free to choose either hand. One choice led to a comfortable (thumb-up) posture. The other led to an uncomfortable (thumb-down) posture. There were two initial grasps that were possible (overhand and underhand), two dowel ends (white and black), and five targets (A-E). The dependent measure here was the probability, p(RH), pooled over participants, of choosing the right hand.

The two types of trials, hand-specified and grasp-specified, were mixed and were tested in a different random order for each participant. Each participant experienced each unique trial only once. The experiment took about 20 minutes.

Results

Hand-Specified Trials

Figure 9 shows p(TU) as a function of which hand (left or right) was specified and which dowel end (left / white or right / black) was inserted into the target. Participants almost always chose the grasp that afforded a thumb-up posture at the time of placement in the target. This was equally true for the two hands, as tested with Cochran’s Q non-parametric procedure for related samples (Siegel, 1956). The analysis included all 20 hand-specified trials, each defined by a unique combination of hand, dowel end, and target, Q(19) = 13.97, p > .05.

I confirmed that the p(TU) values did not differ significantly across dowel color or target by computing one Cochran’s Q for the ten p(TU) values from the left hand and another for the ten p(TU) values from the right hand. Participants chose left- and right-hand grasps that led to thumb-up postures regardless of target location, Q(9) = 8.25, p > .05, and regardless of which end of the dowel was brought to the target, Q(9) = 5.49, p > .05.

Grasp-Specified Trials

Figure 10 shows p(RH) as a function of which grasp (overhand or underhand) was specified and which end of the dowel (left / white or right / black) was brought to the target. Participants tended to use the right hand only when doing so afforded a thumb-up final posture – that is, when overhand was specified for the black / right end and when underhand was specified for the left / white end. Participants rarely used the right hand if doing so would have led to a thumb-down final posture – that is, when overhand was specified for the left (white) end or when underhand was specified for the right (black) end. This same pattern held at each target, but the data in Figure 10 were not collapsed across target locations so that these data could be easily compared to the results of experiments reported later in this thesis.

Cochran’s Q showed that p(RH) significantly varied within the 20 grasp-specified trials, Q(19) = 202.90, p < .001. Post-hoc Cochran’s Q analyses confirmed significant differences in p(RH) within the 10 overhand-specified trials, Q(9) = 109.02, p < .001, as well as within the 10 underhand-specified trials, Q(9) = 84.49, p < .001 (see Figure 10). However, post-hoc McNemar tests showed that there were no significant differences in p(RH) between any two targets within a given dowel end color, X^2s ≤ 2.0, ps > .05.

Violations of Comfort

There were a few trials in which participants made choices that led to thumb-down final postures. As shown in Table 2, participants showed a low overall rate of comfort violation (5.4%). Violations were nearly three times more likely in the *grasp-specified* trials (25 trials) than in the *hand-specified* trials (9 trials). This result suggests that specifying the hand that enabled a comfortable final posture may have been more difficult than specifying the grasp that enabled a comfortable final posture. As will be seen later, this interpretation accords with the main conclusion of this study as a whole.

EXPERIMENT 2B

It was important to confirm that the postures I denoted in Experiment 2A as more comfortable (i.e., thumb-up) actually were. Comfort ratings have been obtained in previous studies, and they bear out the idea that thumb-up postures are, in general, more comfortable than thumb-down postures; see Rosenbaum et al. (2012). Still, the postures required in those studies differed from those required here. Therefore, I decided to collect comfort ratings for the postures adopted here, which spanned a wider range than used in earlier studies.

Method

Participants

I obtained comfort ratings from a new group of participants – 13 right-handed Pennsylvania State University undergraduates (10 females), all of whom participated for course credit. Their mean age was 19 years (SD = 1.83 years), their mean height was 1.67 m (SD = .08 m), and their mean weight was 64.41 kg (SD = 12.68 kg). These measures resembled those of the participants in the first experiment. Likewise, this new group reported a right-hand preference with a similar average number of tasks on the Edinburgh Handedness Inventory: 10.54 items (SD = .78 items).

Apparatus, Procedure, and Design

The experimental materials were the same as in Experiment 2B, except that the dowel was only colored white. On each trial, the experimenter placed the dowel into the target so it stood vertically on its own. The experimenter used a pincer grip to move the dowel so as not to bias participant comfort ratings (Wilson & Knoblich, 2005). The experimenter then told the participant which hand to use and which grasp orientation to adopt (thumb-up or thumb-down). Each participant used a power grasp, as before, and held the dowel at each target with each of the four possible postures: left-hand thumb-up; left-hand thumb-down; right-hand thumb-up; right-hand thumb-down.

The participant rated the perceived comfort of the posture he or she adopted using a Likert scale of 1 (least comfortable) to 5 (most comfortable). After saying the rating, the participant returned his or her hand to its home location and waited for the next trial. The participant performed each trial at his or her own pace.

I collected two sets of ratings from each participant. The order of conditions was random for each participant but was the same for both rounds for each participant. At the start of the experiment, we told each participant that he or she would experience each possible posture twice and that he or she should not feel compelled to give the same rating the second time through. As done in previous studies, I told each participant that the first round of ratings was meant to help him or her calibrate the ratings (Rosenbaum et al., 2012). Each participant also rated each initial grasp on the cradled dowel (underhand and overhand with each hand). These trials were mixed with the thumb-up and thumb-down trials, and ratings were likewise obtained a first and then a second time. Altogether, there were 48 within-subject trials. Each rating was self-paced. The experiment took about 15 minutes.

Results

I restricted my analysis of the comfort ratings to the second set of ratings, as has been done in previous research (Rosenbaum et al., 2012). I set my significance threshold, alpha (α), at .05 for all analyses and Bonferroni-corrected alpha for multiple comparisons in post-hoc t-tests. Bonferroni-corrected alpha was defined as, $\alpha_{Bon} = \alpha / n$, where n was the number of multiple comparisons (Abdi, 2007).

For the comfort ratings of the initial grasps on the cradled dowel, I performed a two-way repeated-measures ANOVA with hand (left or right) and grasp (underhand or overhand) as factors. This analysis revealed a main effect of grasp, $F(1,12) = 58.17$, $p < .001$, such that participants rated overhand grasps ($M = 4.19$, $SE = .24$) more comfortable than underhand grasps ($M = 2.08$, $SE = .17$). There were no other significant effects.

For the comfort ratings of the final grasps on the standing dowel, I performed a three-way repeated-measures ANOVA with hand (left or right), thumb orientation (down or up), and target (A-E) as factors (see Figure 11). There was a main effect of thumb orientation, $F(1,12) = 182.55$, $p < .001$, such that participants rated thumb-up postures ($M = 4.48$, $SE = .08$) more comfortable than thumb-down postures ($M = 2.73$, $SE = .16$). There was also a main effect of target, $F(4,48) = 5.89$, $p = .001$, such that rated comfort was greatest for the midline target ($M = 3.79$, $SE = .12$), slightly lower for targets to the immediate left of midline ($M = 3.75$, $SE = .12$) or to the right of midline ($M = 3.71$, $SE = .10$), and lowest for targets to the far left ($M = 3.25$, $SE = .18$) or to the far right ($M = 3.35$, $SE = .19$).

These main effects were qualified by a two-way interaction between thumb orientation and target, $F(4,48) = 7.77$, $p < .001$, such that thumb-up ratings varied with target (Figure 11). Participants perceived comfort of thumb-up postures at midline ($M = 5.00$, $SE = 0.00$) to be higher than comfort of thumb-up postures at targets to the immediate left ($M = 4.65$, $SE = .09$), $t(24) = 3.92$, $p < .001$, or right ($M = 4.61$, $SE = .08$), $t(24) = 3.67$, $p = .001$. In turn, participants rated thumb-up postures at the target just left of midline to be more comfortable than thumb-up postures at the far left ($M = 3.81$, $SE = .18$), $t(24) = 4.29$, $p < .001$, and thumb-up postures at the target just right of midline to be more comfortable than thumb-up postures at the far right ($M = 3.96$, $SE = .20$), $t(24) = 3.04$, $p = .006$. These effects survived the corrected significance threshold, $\alpha_{Bon} = .05 / 4 = .01$. In contrast to thumb-up ratings, however, ratings for thumb-down postures were equally low, statistically speaking, for all targets ($ts < 1.07$, $ps > .29$).

Another two-way interaction between hand and target, $F(4,48) = 17.60$, $p < .001$ showed that participants rated both thumb-up and thumb-down postures for each hand as more comfortable in the ipsilateral workspace than in the contralateral workspace (Figure 12). Comfort declined for each hand the farther it was positioned in the contralateral hemifield. There were no other main effects or interactions.

The finding from that thumb-up postures were more comfortable than thumb-down postures supports the conclusion from Experiment 2A that the grasp and hand choices participants made there were consistent with the goal of reaching comfortable final postures. This outcome accords with previous research establishing the preference for ending comfortably when precise aiming is required (Rosenbaum et al., 2012), as was required here. Insofar as the comfort ratings were as reliable as they were, they reinforce my conclusion that comfort was more important than hand preference in Experiment 2A. The data of Experiment 2B also show that comfort varied in a systematic fashion as a function of where in space the thumb-up and thumb-down postures were adopted. This is the first time this relation has been documented.

General Discussion of Experiments 2A and 2B

In the present pair of experiments, I tested the relative priority of hand preference versus the tendency to end object transports comfortably. I asked right-handed university students to transport the left or right end of a horizontal dowel into a target. In the critical trials, participants chose between a left-hand option that led to a comfortable final posture or a right-hand option that led to an uncomfortable posture. I found that participants did not use the right hand if doing so would have led to an uncomfortable posture. Rather, they chose to end their object transports comfortably at the expense of using the nonpreferred left hand. This outcome suggests that final comfort is more important than hand preference in object transport tasks of the sort studied here.

The comfort ratings supported this conclusion by virtue of their systematic structure. Thumb-down ratings were lower than thumb-up ratings at all targets, confirming a clear mapping between comfort and grasp choice. Thumb-down ratings were equally low for all targets, whereas thumb-up ratings were high at midline and decreased for more lateral targets. Finally, ratings for each hand were high in ipsilateral workspace and decreased for contralateral targets. The reliability of the ratings, not to mention the ease of collecting them, recommends their use in understanding how physical tasks are mentally represented.

The reliability of the comfort ratings bears on my discovery that participants weighted comfort more heavily than hand preference. A priori, participants could have weighted hand preference more heavily than comfort, they could have shown no priority for either constraint, or they could have shown the priority they did for comfort over hand. I did not know before doing this study which outcome I would obtain. Having found the answer, we now have a better understanding of the relative importance of these task constraints for the object manipulation task I studied. Whether and how this ranking generalizes to other tasks, or even to the same general task with different demands remains an important issue. The next experiment addresses this issue and others related to it.

CHAPTER 4

COMFORT TRUMPS HAND PREFERENCE UNDER HIGH DEMANDS

The main results from Experiments 2A and 2B were as follows: (1) right-handed participants chose initial grasps that led to thumb-up final postures; (2) these grasp choices were equally common for both hands; and (3) participants used whichever hand afforded aiming-related final comfort. These outcomes suggest that the preference for thumb-up final grasp orientations was weighted more heavily than preferences for overhand initial grasp orientations or for the right hand. The comfort ratings participants gave in Experiment 2B suggest that these choices were in fact made in the service of reaching comfortable postures. Indeed, participants were willing to adopt less comfortable (underhand) grasps with each hand in order to end the transports in comfortable final postures. Ratings also confirmed that for all targets thumb-up postures were more comfortable than and thumb-down postures.

There are some possible concerns, however, about the conclusion that aiming-related final comfort is more important than hand preference. One is that the transport task I used in Experiment 2A may not have required participants to weight the hand preference constraint sufficiently. After all, participants did not have to do anything especially difficult with either hand, even though the task required a non-trivial degree of precision. Nonetheless, previous research has shown that right-handed children (Hill & Khanem, 2004; Leconte & Fagard, 2004) and adults (Gonzalez & Goodale, 2009; Mamolo et al., 2006) tend to choose the right hand more often when the task is more challenging. This research raises the possibility that the right-handed participants in Experiment 2A might have been willing to use the right hand in thumb-down postures if the task tested there was in fact more challenging.

A related concern is that hand choices may have been overshadowed by the clear differences in comfort that were required – either very comfortable (thumb-up) or very uncomfortable (thumb-down). Said another way, participants may have made hand choices that appeared to be sensitive only to comfort, but that was because the only levels of comfort that were tested were extreme. If this hypothesis were correct, it would still be reasonable to conclude that hand choices are based on aiming-related final comfort, but it would not be reasonable to say with confidence whether people are sensitive to more fine-grained variations of comfort.

A third concern is that while participants were able to choose an option that led to final comfort in every trial of Experiment 2A, they were <u>not</u> able to choose the right hand in every trial. Because I used a within-subjects design in that experiment, participants were always given the chance to achieve final comfort. However, in some trials (grasp-specified), doing so required choosing a hand, and in other trials (hand-specified), doing so required choosing an initial grasp. It is therefore possible that participants in Experiment 2A were biased toward final comfort simply because they had more options that led to final comfort than any other alternative.

I addressed these concerns in Experiment 3A by using the same general paradigm as in Experiment 2A, but with a few changes. I addressed the first concern by placing the dowel directly in front of the target at the start of each trial – not always at the workspace and participant midline as in Experiment 2A. Thus, in Experiment 3A I challenged the hand preference constraint more by making it so that achieving a thumb-up final posture with the left hand at the far right target (E) – see Figure 8 – required a far initial reach into the (right) contralateral space. Likewise, achieving a thumb-up final posture with the right hand at the far left target (A) required a far initial reach into the (left) contralateral space. Virtually all previous studies that I know of have shown that right-handed individuals rarely reach the left hand into the far right workspace; see Peters (1996) and Corballis (2003) for reviews. Thus, the alternative explanation for the findings in Experiment 2A, that comfort only outranks hand preference for less demanding tasks, predicted that participants in Experiment 3A would show a bias to use each hand in the ipsilateral (same side) workspace, even when doing so led to uncomfortable final postures.

I addressed the second concern – that hand choices in Experiment 2A were overshadowed by the two extreme final grasp orientations – by testing two new target conditions. In addition to the up-facing target condition (see Figure 13, panels A and B), one of the new target types faced up and to the right (see Figure 13, panels C and D), and the other target type faced up and to the left (see Figure 13, panels E and F). These angled targets were meant to provide more fine-grained variations of the relative final comfort of the left- and right-hand options. Compared to up-facing targets, for example, the orientation of the right-hand thumb-up posture in the right-facing target condition became less similar to the orientation of the left-hand thumb-down posture (see Figure 13, panel C). By contrast, the orientation of the right-hand thumb-down posture in the right-facing target condition became more similar to the orientation of the left-hand thumb-up posture (see Figure 12, panel D). By hypothesis, then, the comfort difference between the right- and left-hand postures shown in panel C would be greater, and the comfort difference between the hands shown in panel D would be smaller.

This situation was mirrored for left-facing targets (see Figure 13, panels E and F), where the orientation of the right-hand thumb-up posture became more similar to the orientation of the left-hand thumb-down posture (see Figure 12, panel E). Again by contrast, the orientation of the right-hand thumb-down posture and became less similar to the orientation of the left-hand thumb-up posture (see Figure 12, Panel F). I expected that the comfort differences between right-and left-hand postures would grow in the less similar cases and shrink in the more similar cases. This setup therefore allowed me to test the hypothesis that hand choices are insensitive to gradations of relative degrees of final comfort. Said another way, this design provided a higher-resolution sample from the putative function relating choices to comfort. Nonetheless, the alternative hypothesis just mentioned predicted that right-handed participants would use the right hand at equal rates across the target-angle conditions.

I addressed the third concern – that the within-subjects design used in Experiment 2A biased participants to pursue final comfort – by using a between-subjects design. Right-handed people participated in either the grasp- or the hand-specified conditions. This design made it impossible for participants to be biased toward aiming-related comfort as a result of having more chances to choose options that led to aiming-related comfort than to choose the right hand. The hypothesis that the priority of final comfort over hand preference seen in Experiment 2A resulted from such a bias predicted that participants in the current study would show no such priority.

The between-subjects design allowed me test the influence task demands in one additional way. Recall that in Experiment 2A, participants moved at a comfortable pace in both the grasp- and hand-specified trials. In the current study, I again asked participants to move at a comfortable pace, but I also asked another grasp-specified group and hand-specified group to move as quickly and accurately as possible. Doing so provided another test of the hypothesis that aiming-related comfort only outranks hand preference for easy tasks. Based on the finding that right-handed people tend to use the right hand more often for more challenging tasks, (Gonzalez & Goodale, 2009; Hill & Khanem, 2004; Leconte & Fagard, 2004, Mamolo et al., 2006), one might expect that right-hand reaches would be more prevalent in the speeded groups.

EXPERIMENT 3A

Method

Participants

Sixty-four healthy, right-handed, undergraduate students from Pennsylvania State University participated for course credit. Their demographic information is shown in Table 3. As in Experiment 2A, their collective preference for the right hand was confirmed with the 11-item version of the Edinburgh Handedness Inventory (Oldfield, 1971). All participants signed an informed consent form that was approved by the Pennsylvania State Institutional Review Board.

Apparatus, Procedure, and Design

In all four groups, the participant sat at the same table used in Experiment 2A and grasped the same light wooden dowel (9.92 g). The dowel rested horizontally on the same cradle at the start of each trial. This time, though, the right platform of the cradle was fitted with a small micro-switch so that the time at which the participant lifted the dowel off the platform could be recorded and used to compute transport times. I was not interested in the recordings made in the current choice groups, however, and the reason is as follows. The fact that participants made choices in the current experiment meant that some conditions would have more transport movement-time observations than others – an undesirable situation for appropriate statistical analyses. Thus, I ran an entirely separate study (Experiment 3C, reported below) in which separate participants made one non-choice transport in each of the conditions offered in the current choice experiment. That design ensured that all conditions had an equal number of observations so that transport-time estimates could be analyzed with appropriate statistical procedures. It should be noted that I did record the transport time in each choice trial of the current experiment so that the materials and the timing of the trials remained as similar as possible across the choice groups (Experiment 3A) and the non-choice groups (Experiment 3C).

Returning to the current study, at the start of each trial, the right (black) end of the dowel rested flat on the small black micro-switch. The participant transported either the left (white) or right (black) end of the dowel to one of five nearer target locations (A-E), just as was done in Experiment 2A. The square target holes were again just slightly bigger (~4.4 cm) than the square bases of the dowel, although the target setup was slightly different compared to Experiment 2A. In that previous experiment, participants saw all five targets at once and were instructed to move the dowel to a specified target in each trial. Those previous targets were also constructed from thin pieces of cardboard so that their heights were approximately 1 cm.

In the current study, participants only saw one target at a time but for consistency were still told which target (A-E) to use in each trial. The experimenter moved the target at the end of each trial to set up for the next trial. The target was fitted with another small black micro-switch and was therefore slightly taller (4.4 cm versus 1 cm) than each of the previous targets. The widths of the new square target holes (~ 4.4 cm) were very similar to the widths of the previous targets.

There were three total target angles. The up-facing angles corresponded to the (flat) target angles used in Experiment 2A. The surfaces of the other two target types – the right- and left-facing targets – formed a 45° internal angle with the flat table surface; see Figure 13. The whole target structure in the angled target conditions was approximately 12 cm high; its base was a square with 16 cm-long sides. Pilot testing helped confirm that the height of the target structure neither induced accidental collisions with the target nor influenced hand or grasp choices.

The locations of the targets were set in the exact same way as in the previous study. Thus, because the anthropometric features of the previous and current participants were very similar (see Table 3), the target locations were also very similar. The initial location of the dowel in each trial was set directly in front of the target, also at a distance of approximately 70% of maximal reach for each participant. Reach was measured in the exact same way as in Experiment 2A. In some rare cases, however, this protocol put the dowel just out of reach for the seated participant. In these cases, the experimenter moved the initial location of the dowel slightly closer to the participant so that it was just inside his or her seated reach envelope.

The participant began each trial with the left and right hands resting on the left and right home locations, respectively (see Figure 8). However, after the participant inserted the dowel into the target, he or she could not release the dowel to let it stand vertically on its own, as participants did in Experiment 2A. The reason was that the dowel would have fallen out of the new angled targets. Thus, participants here placed the dowel into the target long enough and firm enough to depress the micro-switch embedded in the bottom of the target – the switch made an audible click when it was pressed – and then to move the dowel back to the cradle at a speed that was comfortable. To help ensure the participant represented each transport as one discrete task, participants were told that each trial was over as soon as the target micro-switch was pressed. The participant always put the black end of the dowel flat on the black micro-switch located in the right platform of the cradle.

There were four between-subjects groups – two hand-specified groups and two grasp-specified groups. In the hand-specified groups, each participant was again told which hand to use (left or right) and which end of the dowel (left / white or right / black) to insert into which target

(A-E). In each of these hand-specified trials, the participant again had the option to choose either an overhand or an underhand initial grasp with the hand specified by the experimenter. As was the case in the previous experiment, one choice led to a thumb-up final posture while the other choice led to a thumb-down final posture. The thumb-up and thumb-down postures in the new angled targets were, by design, different from those adopted at the up-facing targets. However, I still refer to them here as thumb-up and thumb-down postures, respectively. Specifying hand (left or right), dowel end (left / white or right / black), and target (A-E), resulted in 20 trials. These 20 trials were all presented in a random fashion within each of three target-angle blocks (up-facing, right-facing, and left-facing) for a total of 60 trials. The order of these blocks was also random. The dependent measure was the pooled probability, p(TU), of using an initial grasp that led to a thumb-up final posture.

In one hand-specified group, participants were asked to move the dowel from the cradle to the target at a comfortable speed. In the other hand-specified group, participants were told that it was very important to move the dowel from the cradle to the target as quickly and as accurately as possible, where “accurately” was defined as “...minimizing any contact between the dowel base and the edges of the target.”

In the two grasp-specified groups, participants were again told which initial grasp to use (overhand or underhand) and which end of the dowel (left / white or right / black) to insert into which target (A-E). Here, the participant was free to choose either hand. One choice led to a thumb-up final posture while the other led to a thumb-down final posture. There were two possible initial grasps (overhand or underhand), two dowel ends (left / white or right / black), five targets (A-E), and three target angles (up-facing, right-facing, and left-facing) for a total of

60 possible trials. These trials were presented in the same block-random fashion just described. The dependent measure here was the pooled probability, p(RH), of choosing the right hand.

In one grasp-specified group, participants were asked to move the dowel from the cradle to the target at a comfortable speed. In the other grasp-specified group, participants were told that it was very important that they move the dowel from the cradle to the target as quickly and as accurately as possible. In all groups, each participant experienced each unique trial only once. The experiment took about 40 minutes.

Results and Discussion

Hand-Specified Groups

Figure 14 shows the pooled probability, p(TU), that the hand-specified groups chose initial grasps that led to thumb-up postures in the flat, right-facing, and left-facing target conditions. Left and right panels show data for left- and right-hand conditions, respectively. The data are collapsed across the two hand-specified groups (self-paced and speeded) because, as reported below, there were no statistically significant differences between them.

Participants displayed a clear bias to choose initial grasps that led to thumb-up final postures, especially for the up-facing targets. As shown in row A of Figure 14, p(TU) for each condition with up-facing targets was much higher than the .50 rate that would be expected by chance alone. This pattern held for left-hand trials (.89), for right-hand trials (.88), and for all workspace locations.

Focusing next on the right-facing target conditions shown in row B of Figure 14, overall p(TU) was higher when the left hand was specified (.92) but declined precipitously when the right hand was specified (.68). It is clear that this decline was driven by a decrease in choices that led to thumb-up postures via underhand initial grasps. The mirror-equivalent pattern occurred in the left-facing target condition when the left hand was specified (see row C of Figure 14). Here, overall p(TU) was lower for the left hand (.63) but higher for the right hand (.88). There was no apparent affect of workspace on p(TU) within a given dowel end for any target-angle condition.

To confirm the statistical significance of these results, I subjected the p(TU) data to a mixed-factor logistic regression which treated subject (1-32) as a random variable and trial (1-60), dowel end (left / white or right / black), target (A-E), specified hand (left or right), and target angle (up-facing, right-facing, or left-facing) as fixed within-subjects variables. The logistic regression treated group (self-paced or speeded) as a fixed between-subjects variable.

The following explains why I used logistic regression. It also lays out why I used the specific method of logistic regression I did. I used logistic regression because my outcome variable was a dichotomous choice between either two initial grasps (overhand or underhand) in hand-specified groups or between hand (left or right) in grasp-specified groups. Such variables can violate one or more assumptions of normal linear regression, such as homogeneity of variance and normality (Peng, Lee & Ingersoll, 2002). Traditional logistic regression accounts for these violations by computing odds ratios of the probabilities of one particular outcome type (e.g., successes) to the probabilities of the other outcome type (e.g., failures). These odds ratios are then transformed into logits by computing their natural logs. Then, a simple or multiple linear regression is performed on those logits (Peng et al., 2002).

One problem with this general process is the difficulty of applying it to mixed statistical models – those models that contain both within- and between-subjects variables. This problem is especially salient when, as is normally the case, the subject variable is modeled as a random effect (Hadfield, 2010). This complication stems from the estimation of variance components related to random effects (Snijders, 2005). Indeed, subjects are canonically modeled as levels of a random variable so that researchers can draw conclusions about the population from which those subjects came. Random effects are denoted as such because their variations are clearly subject to chance, just as the selection of subjects in an experiment is often purposely subjected to chance. A difficulty with incorporating a random variable is that it cannot be assumed to have a singular or fixed value but instead must be assumed to potentially take on a number of possible values. Complicating the matter further, each of these values can have its own probability of occurring. Other more typical independent variables, by contrast, are usually modeled as fixed variables because researchers directly manipulate those variables and because the researchers are interested in drawing specific conclusions about any effects they may have (Snijders, 2005).

One approach to this mixed-modeling problem with random and fixed effects in logistic regression is to estimate all the integrals of random effect distributions even though such integrating is technically intractable (Breslow & Clayton, 1993; McCulloch & Searle, 2005). Another strategy is to use a Markovian Chain Monte Carlo (MCMC) method to approximate the random effect integrals (Browne & Draper, 2006).

I therefore addressed this problem by running a MCMC logistic regression on p(TU) that treated the relevant variables as described above – and I ran a similar regression on p(RH) as described below. I used the MCMCglmm function in the programming language of R. The function was developed by Hadfield (2010).

The MCMCglmm function yields a Wald z-value, which is equal to the ratio of β, the estimated coefficient, or slope, for each fixed effect to the standard error, SE, of that estimate (Hadfield, 2010). This value can therefore be negative or positive depending on whether the relevant slope (β) is negative or positive. Finally, the function computes an estimated p-value using the Laplace Approximation for complex integrals (Breslow & Clayton, 1993). This value is denoted here as p_{LA} to distinguish it from the more typical p-value, which is based on the theoretical F distribution and not used in this analysis. The significance threshold was $\alpha = .05$.

Returning to the p(TU) data from the hand-specified groups, the MCMC logistic regression revealed a significant effect of trial (1-60), $\beta = -.03$, $SE = .005$, $z = -7.70$, $p_{LA} < .001$. Even though participants showed a high overall rate of choices that led to thumb-up final postures, the participants were more likely to make decisions that led to thumb-down final postures earlier in the experiment. This outcome was revealed by a separate, significant, and negative correlation between the overall pooled number of choices that led to thumb-down postures and trial number, $r(59) = -.32$, $p < .05$. In turn, this outcome suggests that learning may have contributed to participant decisions.

There was a two-way interaction between hand (left or right) and dowel end (left / white or right / black), $\beta = 9.42$, $SE = 3.05$, $z = 3.09$, $p_{LA} < .05$, such that p(TU) for the left hand, across all other factors, was higher (.91) for the left / white end and lower (.70) for the right / black end. Conversely, p(TU) for the right hand was lower (.71) for the left end and higher (.92) for the right end. This interaction may reflect a preference for overhand initial grasps given that achieving a thumb-up final posture using the left hand to insert the left end of the dowel required an overhand initial grasp. Likewise, achieving a thumb-up final posture using the right hand to insert the right end of the dowel also required an overhand initial grasp. Comfort ratings gathered and reported in Experiment 3B below provide support for this conclusion.

This analysis also revealed a two-way interaction between hand and target angle , $\beta = -.06$, $SE = .02$, $z = -3.63$, $p_{LA} < .001$. The nature of this interaction was noted at the outset of this section, and it can be seen in rows B and C of Figure 14. Here, p(TU) was lower for the right hand (.68) than for the left hand (.91) in the right-facing target conditions. Thus, participants were more willing to adopt overhand initial grasps with the right hand that led to thumb-<u>down</u> postures for the right-facing targets. By contrast, row C shows that p(TU) was higher for the right hand (.88) than for the left hand (.63) in the left-facing condition. This outcome indicates that participants were more willing to adopt overhand initial grasps with the left hand that also led to thumb-<u>down</u> postures for the left-facing targets. It should be noted that in both these cases the thumb-down postures were less extreme than the thumb-down postures at the up-facing targets. Given that the thumb-up postures in these cases would have required potentially less comfortable underhand initial grasps, these outcomes again suggest that participants cared about initial-comfort more in the angled target conditions. Comfort ratings reported in Experiment 3B also bear out this idea. There were no other significant main effects or interactions.

Grasp-Specified Groups

Figure 15 shows the pooled probability, p(RH), that the right hand was chosen as a function of target (A-E) and of which end of the dowel (left / white or right / black) that was inserted. Rows A, B, and C show that the grasp-specified groups tended to choose whichever hand led to a thumb-up posture in the up-, right-, and left-facing target conditions, respectively. The data are collapsed across the two grasp-specified groups because, as reported below, there were no statistically significant differences between them.

Participants again tended to choose whichever hand afforded a thumb-up final posture. Focusing on the flat-target condition (see Figure 15, row A) these outcomes replicate the main finding from Experiment 2A and support the conclusion that final thumb-up grasp orientations are weighted more heavily than hand preference. Another key finding here, however, is that the magnitude of this priority was reduced in ipsilateral workspace. Participants displayed a new willingness use the ipsilateral arm when doing so led to thumb-down final postures. This point notwithstanding, the probability of ending in a thumb-down posture with the ipsilateral hand never exceeded .5 in the up-facing target conditions. These outcomes therefore suggest that challenging hand preference slightly reduced the weighting of the grasp orientation constraint but did not make it less important than hand preference.

Turning now to the angled-target conditions, Figure 15, rows B and C respectively show that overall p(RH) was higher when the target faced to the right (.78) versus when it faced to the left (.48). Finding that p(RH) varied with target angle goes against the hypothesis that people are not sensitive to parametric variations of comfort. By contrast, participants did seem sensitive to variations of relative aiming-related grasp orientations. It should be noted that the new effect of workspace location can also be seen in the data from all three target angle conditions.

In another MCMC logistic regression, I subjected the p(RH) data to a mixed factor logistic regression which treated subject (1-32) as a random variable and trial (1-60), target (A-E), and target angle (up-facing, right-facing, or left-facing) as within-subjects fixed variables. Note that I did not include dowel end (left / white or right / black) or initial grasp (overhand or underhand) as separate variables. The reason is that I experimentally manipulated which dowel end was inserted with which initial grasp in order to ultimately manipulate thumb-up or thumb-down final-postures. Note also that it was always the case in the grasp-specified groups that when the left-hand option ended in a thumb-up posture, the right-hand option ended in a thumb-down posture, and vice versa. Thus, I was able in this analysis to reduce the dimensions of the regression by computing a conglomerate variable of dowel end and initial grasp. This variable indicated whether the right-hand option was the thumb-up option (no or yes). The regression treated this variable as a fixed within-subjects factor. Group (self-paced or speeded) was treated as a between-subject fixed variable.

This MCMC logistic regression revealed another significant effect of trial (1-32), $\beta = -.01$, SE = .004, $z = -2.90$, $p_{LA} < .05$, indicating that participants in the grasp-specified groups also tended to make decisions that led to thumb-down final postures earlier in the experiment. This finding was confirmed by another significant negative correlation between the pooled number of choices that led to thumb-down postures and trial, $r(59) = -.57$, $p < .001$.

As expected from inspection of Figure 15, there was a clear main effect for target, $\beta = .98$, SE = .19, $z = 5.27$, $p_{LA} < .0001$, such that p(RH) was highest for target E (.72), second highest for target D (.69), third highest for target C (.64), fourth highest for target B (.53), and lowest for target A (.47). There was a main effect for target angle, $\beta = .04$, SE = .005, $z = 8.76$, $p_{LA} < .0001$, such that p(RH) was highest in the right-facing condition (.78), second highest in the up-facing condition (.58), and lowest in the left-facing condition (.47). Finally, there was a main effect such that p(RH) was highest for the right-hand thumb-up options (.87) versus the right-hand thumb-down options (.34), $\beta = 4.89$, SE = .65, $z = 7.54$, $p_{LA} < .0001$.

There was another two-way interaction between target and target angle, $\beta = -.006$, $SE = .001$, $z = -3.65$, $p_{LA} < .001$. The effect of target location on right hand usage appeared to be more severe for the left-facing targets, suggesting that the more extreme thumb-down final grasp orientation for the right hand was especially disfavored as the target moved farther into the left workspace (see Figure 15, row C). There was also a two-way interaction between target angle and right-hand thumb-up options, $\beta = -.03$, $SE = .006$, $z = -4.07$, $p_{LA} < .0001$. This interaction can be seen in row B of Figure 15 where p(RH) was much higher in both thumb-up and thumb-down positions for the right-facing targets.

These two-way interactions were qualified by a three-way interaction between target, target angle, and right-hand thumb-up options, $\beta = .009$, $SE = .003$, $z = 2.74$, $p_{LA} < .001$. This three-way interaction can be interpreted as follows. The two-way interaction by which the effect of right-hand thumb-up options was attenuated in right-facing target conditions and facilitated in left-facing conditions depended on target location. This pattern is plotted in Figure 16, which shows that while the overall difference in p(RH) between right-thumb-up and right-thumb-down options did not change across targets in the right-facing target conditions, it did change in the up-facing and left-facing target conditions. Furthermore, the difference in p(RH) between right-thumb-up and right-thumb-down options grew for targets farther to the left. These outcomes are consistent with the fact that right-hand thumb-down postures were especially disfavored as the target moved farther into the contralateral (left) workspace. There were no other significant main effects or interactions.

Individual-posture Analysis

The foregoing analyses were concerned with the effects of the various experimental manipulations on the probability, p(TU), of thumb-up final grasps and on the probability, p(RH), of right-hand choices within experimental groups. The main results of those analyses were that participants tended to make choices that afforded thumb-up final postures and that this tendency was modulated by various task-related factors. To increase confidence in the conclusion that choices depended on experimental manipulations, it was important to show that there were no apriori biases for any of the four general postures: right-hand thumb-up, right-hand thumb-down, left-hand thumb-up, and left hand thumb-down. Said another way, it was critical to show that the probability that each of these postures was chosen did not remain constant across the hand-specified and grasp-specified groups.

I addressed this issue by performing four additional MCMC logistic regressions, one for each of the probabilities just mentioned. Each regression incorporated data from participants in all four experimental groups and treated subject as a random variable. Target and target angle were treated as within-subjects fixed variables. A critical component of these analyses was that each included a between-subjects variable indicating whether the relevant probability came from the hand- or grasp-specified choice groups.

I hypothesized that if the choices made in the hand- and grasp-specified groups were not the result of some default bias for each final posture, then each regression should reveal either a main effect of choice group (hand- or grasp specified) or an interaction effect involving the choice-group factor. In this context, I was therefore only interested in determining whether there were effects of choice-group. I did not have any specific hypotheses about the nature of those effects, per se, and therefore do not report the nature of those effects below.

A MCMC logistic regression on the overall probability, p(RTU), that participants chose options that led to right-hand thumb-up final postures revealed a main effect of choice-group, $\beta = 5.57$, $SE = .95$, $z = 5.91$, $p_{LA} < .001$. There were also a couple two-way interactions – one between target and choice-group, $\beta = -.88$, $SE = .31$, $z = -2.84$, $p_{LA} < .01$, and one between target angle and choice-group, $\beta = -.04$, $SE = .009$, $z = -4.55$, $p_{LA} < .001$.

A separate MCMC logistic regression on the overall probability, p(RTD), that participants chose options that led to right-hand thumb-down final postures also revealed a main effect of choice-group, $\beta = 3.30$, $SE = 1.12$, $z = 2.96$, $p_{LA} < .01$. There was a two-way interaction between target and choice-group, $\beta = -.94$, $SE = .29$, $z = -3.29$, $p_{LA} < .001$, and another between target angle and choice-group, $\beta = -.03$, $SE = .009$, $z = -3.09$, $p_{LA} < .01$.

Another separate MCMC logistic regression on the overall probability, p(LTU), that participants chose options that led to left-hand thumb-up postures showed a significant main effect of choice-group, $\beta = -7.21$, $SE = 1.03$, $z = -6.97$, $p_{LA} < .001$. This analysis also revealed a two-way interaction between target and choice-group, $\beta = .87$, $SE = .26$, $z = 3.35$, $p_{LA} < .001$, and between target angle and choice-group, $\beta = .08$, $SE = .01$, $z = 8.00$, $p_{LA} < .001$. Finally, there was also a three-way interaction between target, target angle, and choice-group, $\beta = -.01$, $SE = .002$, $z = -2.062$, $p_{LA} < .05$.

A fourth and final separate MCMC logistic regression on the overall probability, p(LTD), that participants chose options that led to left-hand thumb-down postures showed a main effect of choice-group, $\beta = -1.69$, $SE = .85$, $z = -1.99$, $p_{LA} < .05$. There was also a two-way interaction between target and choice-group, $\beta = .94$, $SE = .29$, $z = 3.27$, $p_{LA} < .01$.

Taken together, these results indicate that the probabilities of each of the four posture options depended on the choice context. These outcomes therefore suggest that there was no particular bias for one or more of the four general postures.

EXPERIMENT 3B

It was again critical to test whether and how perceived comfort related to the grasp orientations I manipulated in the previous choice experiment. This need was especially salient in the present case because I had hypothesized that graded degrees of relative comfort correspond to graded probabilities of choices. By design, many of the postures required in Experiment 3A were quite different from those required in Experiment 2A. I therefore collected comfort ratings for the various postures adopted in Experiment 3A, which spanned a much wider range than those used in previous studies both in this thesis and elsewhere (Rosenbaum et al., 2012).

Method

Participants

Comfort ratings were obtained from four separate groups each consisting of 12 right-handed Pennsylvania State University undergraduates. All subjects participated in exchange for course credit. One group was tested on initial grasp comfort ratings. The other three groups were formed on the basis of target angle, as described in more detail below. The demographic information of these participants is shown in Table 4. These measures resembled those of the participants in Experiment 3A.

Apparatus, Procedure, and Design

The experimental materials were identical to those used in Experiment 3A with the exception that the dowel was only colored white. On each trial, the experimenter placed the dowel into the target. However, the angled targets in Experiment 3A precluded the dowel from standing on its own as it did in the previous comfort rating study (Experiment 2B). Thus, for all trials, the experimenter used a pincer grip on the very top of the dowel to move it so as not to bias participant comfort ratings (Wilson & Knoblich, 2005) and held the dowel in place. The experimenter then asked the participant to adopt a specific grasp (thumb-up or thumb-down) with a specific hand (left or right). Because more target angles were tested in Experiment 3A, there were many more conditions compared to Experiments 2A and 2B. In Experiment 2B, each participant reported 48 ratings – two for each of the hand (left or right), grasp orientation (thumb-down or thumb-up) and target (A-E) combinations and two for each of the four possible initial grasps (overhand and underhand with each hand). To keep the number of ratings similar in the current study, I asked participants to give two ratings for each of the hand, grasp-orientation, and target combinations within only one of the three target angle conditions (up-facing, right-facing, and left-facing). Thus, three separate groups of 12 participants rated 20 unique postures twice for a total of 40 trials. I asked a separate group of 12 participants give ratings of initial comfort. There were also 40 trials in this group – two for each underhand and overhand grasp with each hand at each of the five initial dowel locations. Everything else about the procedure of the experiment was identical to Experiment 2B.

Results and Discussion

I restricted my analysis of the comfort ratings to the second round, as I did in Experiment 2B and has been done in previous studies (Rosenbaum et al., 2012). Alpha (α) was again set to .05.

I ran a three-way repeated-measures ANOVA on the comfort ratings of initial grasps with hand (left or right) and grasp (overhand or underhand) and location (A-E) as within- subjects factors. I use the term “location” here to remind the reader that the initial location of the dowel was always directly in front of each target but that this location should not be confused with the actual target position, per se.

This analysis revealed significant main effects of hand, F(1,11) = 18.41, p < .01, grasp, F(1,11) = 54.35, p < .001, and location, F(4,44) = 54.65, p < .001. Participants rated left-hand grasps (M = 3.50, SE = .16) slightly less comfortable than right-hand ones (M = 3.74, SE = .14), and underhand grasps (M = 3.19, SE = .16) less comfortable than overhand ones (M = 4.05, SE = .15). Participants also rated the midline initial location as more comfortable (M = 4.71, SE = .07) than the location to the immediate left (M = 4.13, SE = .14) and the location to the immediate right (M = 4.06, SE = .13) of midline. The locations to the far left (M = 2.44, SE = .25) and to the far right (M = 2.77, SE = .27) were rated least comfortable. There was also a two-way interaction between hand and location, F(4,44) = 14.14, p < .01, such that the attenuating effect of more lateralized locations on comfort was less severe for the left hand in left locations and for the right in right locations; see Figure 17.

I performed a separate mixed-model ANOVA on the comfort ratings of final grasps with hand (left or right), thumb orientation (down or up), and target (A-E) as within-subject factors.

The between-group factor was target angle (up-facing, right-facing, left-facing). There was a main effect of thumb orientation, F(1,33) = 211.46, p < .001, such that participants rated thumb-up postures (M = 4.27, SE = .08) more comfortable than thumb-down ones (M = 2.90, SE = .11). There was also a main effect of target, F(4,48) = 5.89, p = .001, such that comfort was greatest for the midline target (M = 3.96, SE = .08), slightly lower for targets to the immediate left of midline (M = 3.83, SE = .10) or to the right of midline (M = 3.73, SE = .08), and lowest for targets to the far left (M = 3.28, SE = .11) or to the far right (M = 3.16, SE = .11).

There was a hand by group interaction, F(2,33) = 68.78, p < .001, such that left-hand grasps were rated more comfortable (M = 4.06, SE = .14) than right-hand grasps (M = 3.15, SE = .16) for left-facing targets, whereas left-hand grasps were rated less comfortable (M = 2.98, SE = .14) than right-hand grasps (M = 4.00, SE = .16) for right-facing targets. Grasps made with the left hand (M = 3.70, SE = .14) and with the right-hand (M = 3.70, SE = .16) were rated equally comfortable for up-facing targets.

There was also a two-way interaction between hand and target, F(4,132) = 29.71, p < .01. Left-hand grasps were more comfortable for targets in ipsilateral space, A (M = 3.61, SE = .11), B (M = 3.97, SE = .01), C (M = 3.96 , SE = .01), but tended to be less comfortable for targets in contralateral space, D (M = 3.58, SE = .11) and E (M = 2.71, SE = .13). Right-hand grasps were more comfortable for targets in ipsilateral space, E (M = 3.61, SE = .12), D (M = 3.89, SE = .10), C (M = 3.97 , SE = .10) but less comfortable in contralateral space, B (M = 3.68, SE = .13), A (M = 2.94, SE = .14).

The ANOVA also revealed a three-way interaction between hand, group, and orientation F(2,33) = 88.21, p < .001. The nature of this interaction is shown in Figure 18. The overall difference between thumb-up and thumb-down postures was similar for both hands at the up-facing targets. However, left-hand thumb-up and thumb-down postures were more similar for the left-facing targets than right-hand thumb-up and thumb-down postures. The mirror-equivalent pattern is seen for the right-facing targets. These outcomes importantly confirm that the target-angle manipulation succeeded in making the relative comfort of the thumb-up and thumb-down postures across and within the hands more similar in some cases and less similar in others.

A three-way interaction between hand, target, and group, $F(8,132) = 3.04$, $p < .05$, showed that the hand by target interaction pattern – that both left- and right-hand grasps tended to be more comfortable at targets in ipsilateral space and less comfortable for targets in contralateral space – slightly differed across the target-angle groups. More specifically, the ratings for the left hand in the right-facing group were lower than the left-hand ratings for the up- or left-facing groups. The ratings for the right hand in the left-facing group were lower than the left-hand ratings for the up- or right-facing groups.

Another three-way interaction between hand, grasp orientation, and target, $F(4,132) = 19.53$, $p < .001$, showed that, across target-angles, thumb-up postures for each hand declined in contralateral workspace. This decline was more severe for the thumb-up postures than for the thumb-down postures. However, there was also a four-way interaction between hand, grasp orientation, target, and target-angle group, $F(8,132) = 2.704$, $p < .01$. Figure 19 helps clarify the nature of this higher-order interaction, which can be interpreted as follows. The three-way interaction between hand, grasp orientation, and target just described changed in the different target-angle groups. As can be seen in Figure 19, row A, the comfort for thumb-up and thumb-down postures for both hands depended on target for the up-facing targets in that they tended to decline as the target moved from ipsilateral space to contralateral space. However, the comfort for left-hand thumb-down postures was similarly low for all targets in the right-facing target condition, and the comfort for right-hand thumb-down postures was similarly low for all targets in the left-facing target condition.

These comfort ratings confirm that the gradations of hand choices in the previous experiment generally corresponded to gradations of relative comfort across the left- and right-hand options. The comfort ratings of the right hand relative to the left hand decreased in the left-facing target group – this was the same condition that led to a decrease in right-hand reaches – and the comfort ratings of the left hand relative to the right hand decreased in the left-facing target group – this was the same condition that led to an increase in right-hand reaches. To make this point more concrete, Figure 20 shows the difference of the mean comfort rating between left and right hand options as a function of target and target-angle group. Panel A, for example, shows that the biggest differences in comfort occurred between the far ipsilateral thumb-up postures and far contralateral thumb-down postures. However, panel B shows that this difference was attenuated for the far ipsilateral left thumb-up versus right thumb-down posture in the right-facing group. One can also see in panel B that the differences between the comfort for left thumb-up and right-thumb-down hovered around zero for all targets. By contrast, the differences between the left thumb-down and right thumb-up postures grew farther from zero, especially relative to the up-facing condition (panel A). One can see a mirror-equivalent pattern for the left-facing targets in panel C. In that condition, the comfort differences between the left thumb-up postures and right thumb-down postures noticeably increased for all targets, whereas the differences between left thumb-down and right thumb-up postures were much closer to zero.

EXPERIMENT 3C

The comfort ratings in Experiment 3B showed that thumb-down postures at up-facing targets and at targets that were angled away from the hand that adopted those postures were less comfortable than thumb-up postures at the same target locations. In these cases, participants in Experiment 3A tended to choose options that led to thumb-up postures over options that led to thumb-down postures. However, when targets were angled toward the hand that adopted the thumb-down posture, participants in Experiment 3A showed a weaker preference for thumb-up postures. Experiment 3B confirmed that in these cases the relative comfort of the options was more similar. Taken together, then, the results from Experiment 3A and 3B suggest that the most important constraint brought to bear on decisions was related to aiming-related final comfort. In other words, participants avoided final postures that forced the wrist, elbow, and shoulder joints farther toward the limits of the their ranges of motion.

By hypothesis, however, these more extreme arm postures take longer to achieve. It therefore remains possible that participants made decisions on the basis of minimizing total movement time, or on the basis of minimizing some factor related to total movement time, rather than maximizing comfort, per se. To address this possibility, I invited two separate groups of participants to transport the dowel in each of the possible conditions found in Experiment 3A, and I recorded their transport movement times. If participants in Experiment 3A made choices with the goal of minimizing total movement time instead of maximizing comfort, then there should be a closer correspondence between hand- and grasp-choice probabilities and movement times than between those choice probabilities and final comfort.

Method

Participants

Two separate groups of 32 healthy, right-handed Pennsylvania State undergraduate students participated for course credit. One group only made overhand initial grasps and the other only made underhand initial grasps. The demographic information for the 3 males and 13 females in the overhand group was as follows. Their average height was 169.86 cm (SD = 9.81 cm). Their average weight was 61.42 kg (SD = 8.80 kg), and the average number of Edinburgh Handedness Inventory (EHI) items they endorsed as right-hand items was 10.06 items (SD = 1.95 items).

The demographic information for the 3 males and 13 females in the underhand group was as follows. Their average height was 166.37 cm (SD = 8.30 cm). Their average weight was 61.55 kg (SD = 8.40 kg), and the average number of EHI items they endorsed as right-hand items was 10.81 items (SD = .40 items). Not only were the measures from each of these two groups similar, but these measures were similar to those of the participants in the previous experiments.

Apparatus, Procedure, and Design

The experimental materials were identical to those used in Experiments 3A and 3B. In the current experiment, the left end of the dowel was white and the right end of the dowel was black, just as in Experiment 3A. As was the case in each of the previous two experiments, the right cradle platform and the base of the target each was fit with a small black micro-switch. The switches recorded movement times with a sampling frequency of 125 HZ.

On each trial, the experimenter told the participant whether to use an overhand or underhand initial grasp, and which end of the dowel (left / white or right / black) to insert into which target

(A-E); see Figure 8. Participants performed one object transport in each of the possible conditions presented in Experiment 3A. Combining the two dowel ends, the two hands, the five targets, and the three target angles yielded 60 unique trials for each initial grasp specification (overhand or underhand). To keep the trial number low in order to help avoid fatiguing the participants, I formed two separate groups. As mentioned above, one group only made overhand initial grasps and the other only made underhand initial grasps. The trials were again blocked on the basis of target angle. The order of the trials was random within each block. The order of the blocks was also random.

Results and Discussion

On the transport movement times I ran a mixed model repeated measures ANOVA with hand (left or right), dowel end (left / white or right / black), target angle (up-facing, right-facing, or left-facing), and target (A-E) as within-subjects factors. Initial grasp (overhand or underhand) was a between-subjects factor.

This analysis revealed main effects for hand, F(1,30) = 33.23, p < .001, for target angle, F(2,60) = 25.82, p < .001, and for target, F(4,120) = 5.62, p < .001. Each of these main effects was qualified by a couple two-way interactions. The first was between hand and target angle, F(2,60) = 16.34, such that the biggest difference between the two hands occurred for the right-facing targets where the left hand was noticeably slower (M = 1765.04 msec, SE = 70.00 msec) than the right hand (M = 1516.65 msec, SE = 45.71 msec). This finding may reflect an aiming-related performance advantage for the right hand, as the left hand did not have a similar advantage over the right hand for the left-facing targets. For left-facing targets, movement times for the left hand (M = 1661.16 msec, SE = 59.23 msec) and for the right hand (1631.82 msec, SE

= 56.42 msec) were essentially identical. There was also a slight disadvantage for the left hand (M = 1515.38 msec, SE = 52.51 msec) relative to the right hand (M = 1407.68 msec, SE = 39.81 msec) at the up-facing targets.

A two-way interaction between hand and target, F(4,120) = 4.40, p < .001, showed that left-hand movement times were lowest for the midline targets (M = 1595.95 msec, SE = 55.26 msec), higher for the targets immediately to the left (M = 1625.46 sec, SE = 59.71 msec) and to the right of midline (M = 1618.13 msec, SE = 55.92 msec), and highest for the targets to the far left of midline (M = 1717.25 msec, SE = 71.92 msec) and far right of midline (M = 1679.12 msec, SE = 64.66 msec). Right-hand times were more similar across targets: A (M = 1482.12 msec, SE = 48.14 msec), B (M = 1501.46 msec, SE = 48.40 msec), C (M = 1456.79 msec, SE = 45.72 msec), D (M = 1559.00 msec, SE = 46.99 msec), and E (M = 1594.21 msec, SE = 48.96 msec).

These interactions were qualified by a three-way interaction between hand, dowel end, and grasp, F(1,30) = 45.56, p < .001. Transports that started with left-hand underhand grasps were slower to insert the left / white end of the dowel than the right / black end, but transports that started with right-hand underhand grasps were quicker to insert the left / white end compared to the right / black end. This pattern was mirrored for the overhand grasps, though the time differences between transporting the left and right ends of the dowel with the left and right hands were smaller with overhand grasps; see Figure 21.

There was another three-way interaction between dowel end, target-angle, and target, F(8,240) = 11.44, p < .001. Figure 22 shows that for all target locations, transports to left-facing and right-facing targets took longer than to up-facing targets. Times were slightly higher for left-facing targets in the far left workspace when the right end of the dowel was inserted.

Finally, there was another three-way interaction between dowel end, target-angle, and grasp, F(2,60) = 2.14, $p < .05$. As can be seen in Figure 23, transports that started with overhand grasps were slower to insert the left / white end into left-facing targets but slower to insert the right / black end into right-facing targets. By contrast, transports that started with underhand grasps were faster to insert the left / white end into the left-facing targets but slower to insert the right / black end into right-facing targets. Whereas overhand transports were equally fast to put the left / white and right / black ends into the up-facing targets, underhand transports were slightly slower to insert the left / white end into the up-facing targets.

Overall, the foregoing analysis of movement times revealed some evidence that more extreme thumb-down postures do in fact take longer. This pattern can be seen in Figure 24, which shows the mean movement time in each condition for the overhand group. For the up-facing targets (row A) nearly all the left / white – end down conditions – those conditions in which the thumb pointed up at the end of the transport – showed a movement-time advantage over the left / black – end down conditions – those conditions in which the thumb pointed down at transport end. The mirror-equivalent pattern can be seen for the right hand – so long as it is appreciated that for the right hand it was the left / white – end down conditions that led to thumb-down final postures.

Figure 25 shows that the overall pattern just described was even clearer in the case of underhand initial grasps. However, there were many instances in both the overhand and underhand groups where it was not entirely clear that less extreme thumb-up postures provided a meaningful movement-time advantage over more extreme thumb-down postures.

To clarify the relations between the choices participants made in Experiment 3A, the comfort ratings participants gave in Experiment 3B, and the movement times participants produced in Experiment 3C, I created and considered models that included either one, two, or all three of these variables and asked how well those models predicted hand and grasp choices. Those models and their results are reported in the next section.

Modeling

I created models that were based on the Luce Choice Axiom, which will be hereafter called the LCA (Luce, 1977). The LCA has been used to study the determinants of choices in several fields such as psychology, sociology, and economics (Luce, 1977).

The LCA states that the probability, p(i), of a given item, i, being chosen from a set of alternatives, j, is given by

$$p(i) = W_i / \Sigma_j W_j \qquad (1)$$

where W is some salient property of the item in question. Thus, the LCA provides an elegant way to evaluate whether and how certain features of the task-options given here were meaningful to participants. One can do so simply by testing different values of w in equation 1 above. Furthermore, this simple method provides a critical comparison for testing the hypothesis that participants based their action choices on the relative weighting of that salient feature for both options. The null hypothesis in this case is that participants based their action choices on some salient factor of just one of the alternatives.

To address these issues, I considered a set of models that included the following candidates for the w factor: final comfort, initial comfort, and movement time. I tested one model for each candidate and one for each possible additive combination of the candidates. This section outlines this process for the two separate sets of choices in Experiment 3A – one is from the grasp-specified / hand-choice group and one is from the hand-specified / grasp-choice group – and reports the relevant findings in two separate parts.

Grasp-specified Hand-Choice Group

I first asked whether there was a systematic relation between the probability, p(RH), that the right hand was chosen in Experiment 3A and each candidate. Figure 26 shows p(RH) plotted as a function of the mean final comfort of the right hand (panel A), mean initial comfort of the right hand (panel B), and mean movement time of the right hand (panel C). The data in each panel are fit with a logistic function given by

$$\hat{y} = 1 / (1 + e^{-(x-a)/|b|}) \tag{2}$$

where e is the base of the natural logarithm, x is an empirical measurement, and a and b are empirical constants. More specifically, a is the x-coordinate of the inflection point of the best fitting logistic curve at $y = .5$, and b is a best-fitting scaling factor. Because I required that the maximum and minimum predicted y-values ($\hat{y}$) be 1 and 0, respectively, each best fitting logistic function had only two free parameters, a and b. The fits were based on least-squares regressions.

As can be seen in Figure 26, the mean final comfort of the right hand option in each of the 60 hand-choice conditions offered in Experiment 3A explained approximately 66 percent of the variance in p(RH). By contrast, the mean initial comfort of the right hand option in each condition explained only 4 percent of the variance in p(RH), and the mean movement time for the right hand did not explain any of the variance in p(RH). Note that the negative R^2 value associated with the movement-time candidate indicates a very poor fit; it means that the sum of squared deviations between the observed and predicted y-values was greater than the sum of squared deviations between the observed y-values and the mean y-value. Overall, these outcomes are consistent with the conclusion I drew earlier – that participants in Experiment 3A weighted the comfort of the possible final postures more heavily than initial comfort or hand preference.

The foregoing analysis showed that p(RH) increased as the comfort of the final posture of the right-hand option increased. However, it said nothing about whether and how p(RH) increased as a function of the relative final comfort of the right- and left-hand options. To explore this possibility, and to explore the possibility that p(RH) was also related to the relative initial comfort of both options, I computed the p(RH) predicted by the LCA for each candidate and each possible additive combination of the candidates and fit the observed p(RH) to these values. Because comfort and movement time were measured on different scales, I normalized measures for each candidate before computing the LCA model predictions.

Table 5 shows the results of this analysis and the non-LCA fits just described. The best-fitting model said that participants made hand-choices on the basis of the ratio of right-hand final comfort to the sum of right- and left-hand final comfort. As can be seen in Figure 27, this LCA model accounted for approximately 86 percent of the variance in p(RH). This outcome supports the hypothesis that participants considered and compared the final comfort of both options for each decision. It goes against the hypothesis that participants only considered the final comfort of the right hand. Additional support for this claim comes from a closer comparison of the data and fit shown in Figure 26 (panel A) with the data and fit shown in Figure 27. Of particular interest, the slope in the former case was noticeably shallower (.30) than the slope in the latter case (3.53). This comparison suggests that choices were not only better predicted by the LCA model of relative final comfort, but also that choices more sensitive to the relative comfort.

Hand-specified Grasp-Choice Group

I again asked whether there was a systematic relation between choices and each candidate. Here, I addressed the probability, p(TU), that participants in Experiment 3A chose an initial grasp that led to a thumb-up final posture. Figure 28 shows p(RH) plotted as a function of the mean final comfort of the right hand (panel A), mean initial comfort of the right hand (panel B), and mean movement time of the right hand (panel C).

Table 6 shows the results of this analysis and the non-LCA fits for the grasp-choice groups. The best-fitting model said that participants made grasp-choices based on the ratio of the sum of the final and initial comfort of the thumb-up option to the sum of the final and initial comfort of both the thumb-up and thumb-down options. Figure 28 shows that this LCA model accounted for approximately 63 percent of the variance in p(TU). This finding accords with the hypothesis that participants in the grasp-choice group considered and compared the final and initial comfort of both options for each decision. This conclusion makes sense because grasp-choice participants were allowed to choose initial grasps.

General Discussion of Experiments 3A, 3B, and 3C

Experiment 2 provided evidence that participants tended to make hand and grasp choices with the goal of ending the object transports in comfortable, thumb-up postures. In turn, I tentatively concluded that final grasp orientations were weighted more heavily than both initial grasp orientations and hand preference. However, I had some concerns about the validity of this conclusion. First, it was possible that the object manipulation task I used may not have required participants to weight hand preference sufficiently. Thus, one could argue that the right-handers in Experiment 2A would have used the right hand in thumb-down postures more if the task tested there was in fact more challenging to the hand preference constraint.

Second, it was possible that hand choices may have been overshadowed by the extreme differences in comfort that were required – either very comfortable (thumb-up) or very uncomfortable (thumb-down). Thus, it was unclear whether participants would have been sensitive to more fine-grained variations of comfort and of the relative comfort across the available options.

A third and final concern was that while participants were able to choose an option that led to final comfort in every trial in Experiment 2A, they did not always have the option to choose the right hand. Because in some of the trials (grasp-specified) choosing an option that led to final comfort required choosing a hand and in some of the trials (hand-specified), but doing so required choosing an initial grasp, it was possible that participants in Experiment 2A were biased toward final comfort.

Experiment 3A was intended to use the same general paradigm as Experiment 2A to address these concerns. In Experiment 3A, the initial location of the dowel was placed directly in front of the target in each trial. This manipulation challenged the hand preference constraint by placing the entire task in one hemifield or another (except for the midline target), and by making the more lateralized target and tasks much closer to the nearer hand. I hypothesized that if the priority of final comfort over hand preference seen in Experiment 2A was an artifact of a task that did not weight hand preference sufficiently, then the right-handed participants in Experiment 3A would show a new willingness to use the nearer hand in thumb-down postures, especially for the more lateralized task locations. This hypothesis also predicted that the priority of final comfort over hand preference would be eliminated or reversed for the lateralized task locations. I also addressed this concern by testing two additional groups – one for the grasp-specified and one for the hand-specified groups – who made choices under the instruction to move as quickly and accurately as possible. The hypothesis just mentioned predicted that this grasp-specified group would use the right hand more than the self-paced grasp-specified group.

Participants in Experiment 3A also transported the left or right end of the dowel to three different types of targets, each angled either up, to the left, or to the right. These target angles provided more fine-grained variations of comfort by in some cases increasing the extremeness of one option relative to the other (and relative to the same orientation at the up-facing targets), or by in other cases decreasing the extremeness of one option relative to the other (and relative to the same orientation at the up-facing targets). I hypothesized that if the choices in Experiment 2A were collectively an artifact of the very different thumb-up and thumb-down postures I offered, and if people are not sensitive to more parametric variations of relative degrees of final comfort, then participants in Experiment 3A would use the right hand at equal rates across theses different target-angle conditions.

Finally, I addressed the concern that the within-subjects design I used in Experiment 2A biased participants toward final comfort by using a between-subjects design in Experiment 3A. I reasoned that if the priority of final comfort over hand preference shown in Experiment 2A was due to this type of within-subject biasing, then participants in Experiment 3A would show no such priority.

Regarding the first concern, Experiment 3A provided some evidence that placing the initial location of the dowel in front of the target instead of on the midline did weight hand preference more heavily. Right-handed participants were more willing in Experiment 3A compared to Experiment 2A to use the ipsilateral hand when it led to a thumb-down posture, especially for the far lateralized targets in the up-facing target conditions. In these conditions, the hand-choice groups were also more willing to use the right hand in ipsilateral thumb-down postures than they were to use the left hand in ipsilateral thumb-down postures. However, the probability of using the left or right hand in a thumb-down posture never exceeded .50. Taken together, these results suggest that hand preference was in fact weighted more heavily in Experiment 3A but that the priority of thumb-up of final postures over hand preference was neither eliminated nor reversed.

One can ask, however, whether this explanation holds for the right-facing and left-facing targets where the overall probability of the right-hand being chosen noticeably increased and decreased, respectively. A way of addressing this question is to ask whether the increased willingness to use the right-hand in thumb-down final postures in the right-facing target conditions and the increased willingness to use the left-hand in thumb-down final postures in the left-facing target conditions corresponded to changes in thumb-down postural comfort. This tack might also help explain why the probability, p(TU), that initial grasps were chosen in the hand-specified groups that led to thumb-up final postures was generally high across all the up-facing targets but decreased for right-hand grasps across the right-facing targets and decreased for left-hand grasps across the left-facing targets.

The comfort ratings gathered from separate groups of right-handed participants helped clarify these interactions. Those ratings showed that when thumb-down postures were chosen more often, those thumb-down postures were more comfortable than the thumb-down postures in the up-facing targets. These outcomes helped assuage the second concern – that people are not sensitive to parametric variations of comfort – by showing that these different degrees of comfort predicted gradations of hand and grasp-choices. This finding also addresses the third concern, which proposed that the within-subjects design in Experiment 2A biased participants toward final comfort. That alternative hypothesis can be ruled out because the correspondence between choices and final comfort persisted despite the fact that a between-subjects design was used in Experiment 3A.

Experiment 3C addressed the possibility that the more extreme joint angles associated with less comfortable postures did not lead to a situation in which choices depended on the longer movement times that it took to enter those more extreme postures rather than on the lower levels of comfort they afforded. An analysis of the transport times revealed a series of interesting interactions, but did not reveal a clear answer to this question. I pursued a clearer answer by developing a series of models, most of which were based on the Luce Choice Axiom (LCA). The model that best agreed with hand choices in the grasp-specified groups was a LCA-based model, which said that participants made hand choices on the basis of relative comfort of the left- and right-hand options. This model was able to account for nearly 86 percent of the variance in hand choices; see Figure 26.

The story differed slightly for the hand-specified grasp groups, where the model that best agreed with grasp choices said that participants made choices on the basis both final and initial comfort. This model accounted for approximately 63 percent of the variance; see Figure 29. That this model was able to account for this much variance can be considered quite good given how little overall variance there was in grasp choices – the probability, p(TU), that grasps were chosen that led to thumb-up postures was quite high, especially for the up-facing targets. Indeed, the little variance that was present in p(TU) came from the left- and right-facing target conditions. In turn, this observation can be taken to validate one of the original motivations for the target angle manipulation – to provide more parametric samplings of the putative function underlying the grasp and hand choices made in this experimental setup.

In sum, I can more confidently conclude at this point that the best predictor of both hand and grasp choices in the current object transport task paradigm is the comfort of final postures. Indeed, the final comfort constraint appears to consistently outrank the prominent hand preference constraint. Moreover, the findings of Experiments 3A, 3B, and 3C and my modeling of these empirical results allow me reject the above-mentioned alternative explanations. Thus, I can draw three main conclusions: First, comfort trumps hand preference in terms of constraint weightings for hand choice, at least for the types of tasks I studied. Second, the fact that this ranking persisted when task demands drew out the differences between the hands suggests that this ranking may be a general principle of manual action selection and control. Third and finally, right-handed people seem to make choices on the basis of considerable sensitivity to relative degrees of comfort.

Despite the importance of final comfort shown in the previous two experiments, I also found evidence that uncomfortable final postures required longer movement times. The results and modeling from Experiment 3C cast doubt on the idea that performance, as measured by overall transport times, was the main basis for the decisions that were made in Experiment 3A. However, it remains possible that thumb-up final postures are important both because they tend to be more comfortable but also because they tend to afford better control, and hence better performance. Given that the main finding reported above was that the final comfort constraint outranks the hand preference constraint, this possibility leads to a question about how the potential relative performance advantage of comfortable postures versus uncomfortable postures compares to the performance advantage of the right hand over the left.

Thus, the last experiment reported in this thesis, which is presented in the next chapter, represents a return to the issue with which I opened: How do sensorimotor asymmetries contribute to the choice of limb? More specifically, I ask in the next section about whether and how the relative priority of final comfort over hand preference maps onto a similar relative performance advantage of final grasp orientation relative to those afforded by the right hand.

CHAPTER 5

PERFORMANCE EFFECTS OF COMFORT AND HAND

I have argued here that multiple constraints can be brought to bear on the choices people make about how to move and that people deal with this problem by rank-ordering the constraints for each task. In the context of object transport tasks, I have provided evidence that the choices right-handed people make indicate that they tend to more highly prioritize ending transports in thumb-up grasp orientations compared to using the preferred hand. This chapter specifically addresses the hypothesis that this constraint hierarchy is also formed in accordance with the performance ability that these constraints afford. If this idea is correct, then in the context of the object transport task used here the performance advantage afforded by thumb-up relative to thumb-down final postures should be greater than the advantage afforded by the right hand relative to the left.

Stepping back for a moment, it is important to note that the question of whether and how the tendency to end transports in thumb-up postures is driven by considerations of the movement quality they afford is still very much open. This hypothesis has been dubbed as the “precision hypothesis,” and has received surprisingly scant attention in the literature. Below I briefly review this corpus of work.

Thumb-down postures require high degrees of forearm pronation and wrist flexion. Thus, there is relatively indirect evidence for the precision hypothesis, which comes from biomechanical studies showing that intermediate joint angles, relative to extreme angles, generally afford more force production and better control (Huxley, 1974; McMahon, 1984; Rothwell, 1987; Rossetti, Meckler, & Prablanc, 1994). However, a few direct tests of the precision hypothesis have provided evidence that comfortable postures do in fact afford better performance than uncomfortable postures.

Rosenbaum, Heugten, and Caldwell (1996) had participants oscillate their forearms through different ranges of pronation and supination in a handle rotation task. The ranges of motion were set in accordance with studies that have confirmed the tendency to end transports in thumb-up postures. Participants performed the rotation task in a standing position while keeping the elbow stationary. Consistent with the precision hypothesis, oscillation frequencies were highest in the middle of the pronation-supination range – an effect that held for the preferred hand whether that hand was the left or the right. Because this mid-range was representative of comfortable ending postures, the authors took these findings to suggest that the tendency to end transports in comfortable postures "…stemmed from an expectation that movements can be made more quickly in the middle of the pronation-supination range that at either extreme" (p.59).

Short and Cauraugh (1999) had participants stand in front of a vertical array of wall-mounted targets. The task was simply to place a dot in the middle of each target with either a comfortable or uncomfortable grasp. Indeed, the mean spatial accuracy was higher for comfortable grasps, suggesting that end-state comfort is based on the desire to achieve greater precision.

Solnik et al. (2013) asked standing right-handed individuals to repeatedly adopt thumb-up, thumb-down, thumb-left, or thumb-right postures in a frontal plane with the right hand. After participants adopted a posture, they held that posture for a short period and tried to accurately point to a target in that plane. The authors collected comfort ratings and joint configuration angles during these steady-state periods. The main finding of the study was that less comfortable postures (thumb-down and thumb-right) had higher joint-configuration variance than did more comfortable postures (thumb-up and thumb-left). This outcome indicates that more extreme joint configurations associated with uncomfortable postures also lead to poorer precision.

These tests of the precision hypothesis are few in number and may be unrepresentative of the table-top reaching tasks often used to demonstrate the comfort constraint. The just-mentioned oscillation-study by Rosenbaum et al.(1996), for example, required participants to maintain a stationary elbow position while rotating the forearm. By contrast, uncomfortable thumb-down postures detailed in the original study of end-state comfort by Rosenbaum et al. (1990), and in many later studies required non-trivial degrees of rotation *and* translation of the elbow; see Rosenbaum et al. (2012) for review. Especially important for the current proposal is the fact that neither of these studies, nor any other study to the best of my knowledge, has tested the relative precision of comfortable and uncomfortable postures for the preferred and non-preferred hands.

This question is especially interesting given the reliable interlimb performance asymmetries in coordination detailed in Chapter 2 of this thesis and elsewhere; see Mutha, Haaland, and Sainburg (2012) for review. Moreover, it should be noted that these asymmetries have been shown to persist in unsupported, 3-dimensionsional tasks (Tomlinson & Sainburg, 2012). Thus, the experiment reported next tested whether the relative performance advantages afforded by satisfying the comfort and hand preference constraints map onto the hand choices reported in previous experiments.

My specific hypotheses were as follows. First, if the comfort constraint arises from considerations of movement quality, then more comfortable (thumb-up) postures should yield quicker and more consistent reaches relative to uncomfortable (thumb-down) postures. Second, if satisfying the comfort constraint has a greater impact on performance than does satisfying hand preference, the performance benefit, as indexed by a statistical effect size measure, afforded by thumb-up postures over thumb-down postures should be greater than the benefit afforded by right- verses left-hand use. To test these hypotheses, I asked right-handed individuals to make a series of reciprocal tapping movements between two targets with thumb-up and thumb-down postures with the left and right hand.

Method

Participants

Fifteen right-handed, healthy Penn State undergraduate students participated for course credit. Their mean height, weight, and handedness scores were 171.53 cm (SD = 10.98 cm), 68.07 kg (SD = 13.10 kg), and 10.13 items (SD = 1.25 items), respectively. All participants read and signed an informed consent form approved by the Penn State Institutional Review Board.

Apparatus, Procedure, and Design

The experimental materials were identical to those used in Experiments 2A-B and 3A-C. However, there were two targets used in the current experiment. Each target was identical to the other and was fitted with a small micro-switch. The switches recorded movement times with a sampling frequency of 125 HZ.

I adopted the same general task setup as in Experiment 2A (see Figure 8) and only used up-facing targets. The far target was placed at the same midline location as the initial start location of the dowel in Experiment 2A and was held constant for all trials and across all participants. The reason I used this setup instead of the one from Experiment 3A-C was twofold. First, pilot testing showed that participants struggled to insert the dowel fully when the far target was placed where the initial location of the dowel was placed in Experiment 3A – directly in front of the nearer target at a distance approximately equal to 70 percent of maximal reach. This problem meant that they could not reliably close micro-switch in the far target, especially for the more lateralized target locations. The second reason was related to the first. The problem here was that when angled targets were placed where the initial location of the dowel was placed in Experiment 3A, especially at the lateralized locations, pilot participants reported difficulty in seeing the targets.

In the current experiment participants were therefore instructed to move back and forth between two up-facing targets – one was at a constant midline location as described above and one that was set at 70 percent of maximal reach as in Experiment 2A – as quickly and as accurately as possible. Participants were told to minimize the contact between the base of the dowel and the edges of the target and were asked to avoid counting the number of taps. They continued to move back and forth until the experimenter said, “Stop.” Each participant tapped 12 times, creating 12 inter-target time intervals on each trial. The dowel stood vertically in the home target at the beginning of each trial.

One orange piece of tape was set along the left and right side of the each target hole. There was a corresponding piece of tape placed along the left and right side of dowel base. This manipulation increased experimental control by constraining the rotation of the dowel between targets. The participants were free to rotate the base of the dowel during the transport if they so desired, but they were asked to insert the dowel into the target so that the pieces of tape on the target and on the dowel aligned.

The participants replaced the dowel to its vertical position at the end of each trial. Participants were told at the start of each trial which grasp to use. There were 4 possible grasps: (1) thumb-up with the left hand; (2) thumb-up with the right hand; (3) thumb-down with the left hand; and (4) thumb-down with the right hand. Participants were told to grasp the dowel fully and firmly, much like they would grasp a tennis racquet, regardless of the posture that was specified for that trial. Combining these 4 possible grasps with five targets (A-E) resulted in 20 unique trials. These trials were tested in a block-random order, such that all 20 unique combinations of grasp, hand, and target were presented randomly within the first block and then again in the same order in a second block. Thus, there were 40 within-subject trials / conditions for each participant. The experiment lasted approximately 30 minutes.

Results and Discussion

This results section has two parts. Each corresponds to one of the two measures of performance quality I computed – movement time and coefficient of variation. Coefficient of variation, calculated on a trial-by-trial basis, was used as a normalized measure of consistency; it was defined as the ratio of the interval standard deviation to the interval mean.

Movement Times

Figure 30 shows mean inter-target movement times plotted as function of target (A-E) and grasp orientation (thumb-up or thumb-down) for the left and right hands. A four-way repeated measures ANOVA with grasp orientation (thumb-up or thumb-down), hand (left or right), block (first or second), and target (A-E) revealed a main effect for grasp orientation, $F(1,14) = 80.70$, $p < .001$, $\eta_p^2 = .85$, and for hand, $F(1,14) = 26.47$, $p < .001$, $\eta_p^2 = .65$. Thumb-up grasps yielded shorter movement times ($M = 1109.03$ msec, $SE = 41.78$ msec) compared to thumb-up grasps ($M = 1258.47$ msec, $SE = 41.36$ msec). The right hand showed shorter times ($M = 1126.17$ msec, $SE = 42.28$ msec) compared to the left hand ($M = 1241.32$ msec, $SE = 42.20$ msec). There were no other main effects or interactions.

Coefficient of Variation

A four-way repeated measures ANOVA on coefficients of variation with grasp orientation (thumb-up or thumb-down), hand (left or right), block (first or second), and target (A-E) as factors yielded only a main effect of grasp orientation, $F(1,14) = 7.207$, $p < .05$, $\eta_p^2 = .34$. Transports that were performed with thumb-up postures displayed more consistent inter-target movement times ($M = .13$ au, $SE = .01$ au) than transports that were performed with thumb-down postures ($M = .150$ au, $SE = .007$ au); see Figure 31. There were no other effects.

General Discussion

This experiment tested the precision hypothesis – the idea that the preference for final comfort also reflects considerations of performance. This hypothesis predicted that thumb-up postures would show performance advantages over thumb-down postures. Consistent with the hypothesis, the participants generated shorter and more consistent reciprocal tapping times with thumb-up grasps than with thumb-down grasps.

A central question in this experiment was whether these measures of movement quality would map onto the constraint hierarchy revealed in Experiments 2A and 3A – where final comfort was shown to be more important for action choices than hand preference. In connection with this question, it is noteworthy that the effect of grasp orientation on movement times ($\eta_p^2 = .85$) was approximately 47 percent greater than the effect of hand ($\eta_p^2 = .58$). This finding suggests that, at least for the task setup used in this thesis, grasp orientation has a greater impact on performance than does using the right hand. That there was an effect of grasp orientation on the consistency of movements, but not an effect of hand, also supports this conclusion.

A more exploratory question was whether any performance advantage of thumb-up postures depends on which arm is used. Given that the dominant hemisphere in right-handers appears to be specialized for coordination of limb and task dynamics (Sainburg, 2002), it was a priori possible that the dominant limb would better compensate for the more extreme joint angles associated with thumb-down postures. Such an effect may have resulted in a smaller difference between thumb-up and thumb-down postures for the right arm relative to the left arm. However, my data do not bear out that prediction. Although I found a movement-time advantage for the right hand, I did not find evidence for an interactive effect of hand and grasp orientation on movement time or on coefficient of variation. I therefore take these results to suggest that thumb-up grasps afford a consistent movement-time advantage across the hands.

It is also interesting that the right-hand advantage in movement time did not depend in an interactive way on target location. This pattern of results may be somewhat surprising given the long history of research showing that each arm tends to perform best in its own hemifield (Carey, et al., 1996; Carson et al. 1990, 1992,1993; Chua et al.; van Der Staak, 1975; Elliot et al.; Fisk & Goodale, 1985; Flowers, 1975; Ingum & Bjorklund, 1994; Levin, 1996; Prablanc et al., 1979). One possible explanation for the present pattern of results is that the task I used was simply too difficult to allow the hemifield effects to emerge. This explanation remains possible, but it is clear that overall performance did not suffer from a floor effect via extreme task difficulty. If a floor effect existed in the current experiment, then one would not have expected such robust main effects of grasp orientation and of the right hand. Moreover, the effect size, as estimated by partial-eta squared (η_p^2), was rather large for both grasp orientation (.85) and for hand (.58). Thus, it does not seem likely that my task was too difficult for hemifield effects to emerge.

A more likely reason for why target location had no effect in the current experiment was that the distance to be covered was the same for all target locations. The aforementioned evidence for the superior performance of ipsilateral reaches largely comes from studies in which participants reached each hand to a given hemifield from a start location in its own hemifield. Thus, each hand had to cover more distance to reach into contralateral space. It is more likely that hemifield effects would emerge in this situation, as opposed to the experimental setup I used here, because velocities tend to positively scale with movement amplitude (Gordon & Ghez, 1994), and because faster movements tend to entail more spatial error (Fitts, 1954).

In conclusion, the main finding from the current experiment is a pattern of reciprocal tapping performance that links the constraint hierarchy seen in Experiments 2A and 3A to a flexible ability to meet task demands. This finding suggests that the rather surprising hierarchy in which comfort sits above hand preference makes sense in terms of the performance advantages that satisfying each constraint affords. This and related issues will be unpacked more in the general discussion found in the next and final chapter.

CHAPTER 6

GENERAL DISCUSSION

This final chapter reviews the problem of action selection and the approaches used to study it. It recaps the aims, methods, and results of the current studies, and it discusses the implications of the present findings for various topics. These topics include the roles constraints play in action selection, the nature of handedness, and the usefulness of simple choice methods. The section concludes with some speculation about how these findings might be applied in related fields.

My aim in this thesis was to understand how people select actions. Bernstein (1967) noted that action selection reflects a deep problem in that individuals must choose particular actions from several alternatives that could achieve the task at hand. Three tacks have been taken to study how individuals solve this problem. In the first, researchers look for linkages across and within effectors. The idea is that coupling can limit the factors that need to be controlled. There is evidence for coupling in both the temporal (e.g., Kelso, Southard & Goodman, 1979) and spatial (e.g., Franz, Zelaznik & McCabe, 1991) domains of action control. However, if coupling were the main means of solving the problem, one would expect linkages to be more fixed and stable than flexible and transient. These predictions are not borne out by research. It has been shown instead that coupling can be attenuated, especially when perceptual task features are simplified during bimanual movements (Diedrichsen, Hazeltine, Kennerley & Ivry, 2001; Mechsner, Kerzel, Knoblich & Prinz, 2001). Finding that coupling can come and go suggests that other means are used for action selection.

Another tack is to study whether and how individuals exploit mechanics. There is evidence that individuals exploit mechanics. During gait, for instance, human adults let gravity pull each leg downward in its swing phase and thereby obviate the need to control that particular movement (Alexander, 1984; Collins et al., 2005). However, it remains doubtful that mechanics alone explain the vast action repertoires shown from one context to the next (Rosenbaum, 2010).

Constraints

The third tack is to look for task- and actor-related features that constrain action alternatives. In this approach, researchers often model action as optimizations of parameters related to proposed constraints (Nelson, 1983). Research suggests several factors which may be optimized, including deviation from midrange joint angles (Rosenbaum et al., 1990), mean-squared jerk (Hogan, 1984), mean-squared torque (Uno et al., 1989), and others (Nelson, 1983).

By this way of thinking, however, one need not subscribe to the view that there is a sole optimization-constraint that governs action. Instead, one can postulate that several constraints are brought to bear on each task and what distinguishes the influence of each constraint in each task is some weighting factor (Rosenbaum et al., 2001). This may be an inescapable conclusion given that no optimization-constraint mentioned above has been able to explain behavior in all tested contexts. However, a question arises about how this multiple-constraint view explains behavior when constraints whose influences have been identified in some tasks cannot be found in others. How can one say that the unidentified constraints are still brought to bear on the task?

One way to answer this question is to say that the putative weights associated with certain constraints are set to zero, or to a value that is functionally equivalent to zero, for that task. This perspective alleviates the concern that one must seek to identify all the constraints that could possibly influence behavior. If many or most potential constraints get zero weights, identifying them becomes a moot point. Furthermore, the perspective implies that individuals may set up default constraint hierarchies for given classes of tasks and adjust these hierarchies in relation to the demands of each particular situation. If priorities can be mapped out, it then becomes critical to know the factors that contribute to them. I pursued these goals in this thesis, focusing on handedness because it is a well-known, but still poorly understood, constraint on manual action selection. I found that handedness is embedded in constraint hierarchies for reaching actions but that it is not the most important constraint on hand choice.

In Experiment 1, I showed that hand choice is predicted by, and may therefore depend upon, interlimb performance asymmetries during point-to-point reaching. When the target was located on the workspace midline or to its right, participants showed a strong preference for the dominant (right) hand. However, when the target was left of midline, participants showed a strong preference for the nondominant (left) hand. These findings suggest that handedness is the most important constraint for midline targets. Whether the factors that govern hand choice are driven by cognitive processes, such as attention (Verfaellie & Heilman, 1990) or stimulus-response compatibility (Hommel, 1993), or by intrahemispheric information processing biases (Fiske & Goodale, 1985), is not of specific interest here. Of great interest is the finding that workspace location, or unidentified factors related to workspace location, modulate handedness. These findings therefore support the idea that multiple constraints contribute to hand choice.

Another outcome from Experiment 1 was that hand choices for midline targets were related to dynamic coordination asymmetries. This result suggests that interlimb differences in dynamic control provide the basis for the hand preference constraint in those locations. The findings of Experiment 1 therefore link interlimb preference and performance asymmetries and suggest that constraints are weighted according to their ability to meet task demands.

These outcomes have a number of implications. One is that they add to growing evidence that one factor that differentiates the two hemisphere / arm systems is the ability to coordinate dynamics involved with reaching (Mutha, Haaland & Sainburg, 2013; Sainburg, 2002). Another is that they also link the preference- and performance-based views of handedness. The debate about whether handedness should be characterized mainly in terms of preference or performance remains a contentious issue in the field of motor control (Carson, 1993). The present findings reflect a step towards uniting these views and reaffirms that action selection accounts for intrinsic limb features like anisotropies and inertial properties (Cos et al., 2011). The alternative to the latter suggestion, of course, is that motor planning is based on kinematics and that dynamics are essentially just means to those kinematic ends (Soechting & Flanders, 1999). This controversy has a long history in motor control research (Cos et al., 2011; Hogan, 1984; Soechting & Flanders, 1998; Uno et al., 1989). My hope is that the data reported in this thesis make a meaningful contribution to this discussion.

In Experiments 2A and 2B, I tested the possibility that another constraint could be weighted more heavily than hand preference. To test for this possibility, I asked right-handed participants to make hand-based or grasp-based choices in a two-alternative forced-choice paradigm. In critical trials, the setup pitted hand preference against the tendency to end transports thumb-up (Rosenbaum et al., 1990; Rosenbaum et al., 2012). Participants chose between one option that led to a thumb-down (uncomfortable) posture with the preferred (right) hand and one that led to a thumb-up (comfortable) posture with the non-preferred (left) hand. Participants consistently chose whichever hand led to a thumb-up posture, suggesting that the grasp-orientation constraint outranked hand preference in this task. Experiment 2B showed that the tendency to end thumb-up was strongly and positively correlated with perceived comfort. This outcome indicates that people prefer thumb-up final postures because those postures are more comfortable than thumb-down postures.

In Experiment 3A, I addressed a series of concerns about the conclusions just offered. The principal concern was that the task used in Experiment 2A did not sufficiently challenge hand preference. However, Experiment 3A showed that participants still preferred to end in a comfortable posture when hand preference was challenged more. While the magnitude of the priority was attenuated, showing that the experimental manipulation was effective at tapping into the variable of interest, the priority for comfort was neither reversed nor eliminated. This finding suggests that the priority of thumb-up final orientations over handedness may reflect a default hierarchy that right-handed individuals use in object transport tasks.

Future work can provide additional tests of this idea by asking right-handed individuals to make hand and grasp choices in tasks that challenge either the left-hand specialization for stabilization (e.g., Wang & Sainburg, 2007) or the right-hand specialization for trajectory control (e.g., Mutha et al., 2013) at the target location. It may also be useful to test left-handed people because they show reduced asymmetries in dynamic control (Przybyla, Good & Sainburg, 2012). In both cases, the extent to which sensorimotor asymmetries contribute to the constraint hierarchy should be reflected in the relation between the degree of performance asymmetry and the magnitude of the relative priority of comfort and hand preference.

Experiments 3A and 3B also confirmed that grasp and hand choices are sensitive to more fine-grained variations in the relative comfort of the alternatives. Experiment 3C showed that uncomfortable postures, which required more extreme joint angles, tended to require longer times than less extreme joint angles. However, a series of models based on the Luce Choice Axiom (Luce, 1977) let me reject the idea that choices in Experiment 3A were based on movement times, per se, or on some other unidentified variable related to movement times.

Though choices did not seem to depend on transport times, in Experiment 4 I showed that comfortable postures afforded a time-based performance advantage over uncomfortable postures. Thumb-up postures led to quicker and more consistent reciprocal tapping than did thumb-down postures – an advantage that was greater than the one afforded by the right hand over the left. These outcomes further support the idea that constraint hierarchies are formed in order to help individuals sufficiently meet task demands. This last point may have a deep implication for the basis of the grasp-orientation constraint.

Just as there is a potentially dichotomous view of handedness – that it is based on either preference or performance – there is a potentially dichotomous view of the grasp-orientation constraint (Rosenbaum et al., 1990). One might suppose, for example, that the tendency to end transports in thumb-up postures is driven by comfort. This conclusion is reasonable given the tight relations between thumb-up postures and comfort ratings. However, one might also suppose that the constraint does not reflect consideration of comfort, per se, but instead reflects consideration of performance advantages that comfortable postures afford. The latter idea – the so-called *precision hypothesis* – is important because it implies that meeting task demands is more critical than being comfortable. In turn, this hypothesis may have more general implications for the determinants of higher-order planning.

Higher-order planning contrasts with first-order planning. First-order planning happens when individuals plan to grasp objects with respect to the observed, current properties of the objects. A well-known example is that the opening between the thumb and forefinger increases linearly with object size and is usually widest in the second half of the reach (Jeannerod, 1984). Higher-order planning occurs when individuals plan to grasp objects with respect to how those objects can be used to meet subsequent task demands. Finding that people grasp horizontal bars with whichever hand or initial grasp affords a thumb-up position at the target exemplifies higher-order planning. The current findings therefore suggest that hand and grasp choices reflect sensitivity to precision advantages that will be used to meet task demands downstream of the original grasp.

One need not subscribe, however, to either a comfort- or performance-based view of the grasp-orientation constraint. One can instead suppose that the constraint allows individuals to satisfice with respect to both comfort *and* precision. Though this view is supported by the present findings, it should be noted that I did not set out to determine whether the tendency to end in thumb-up postures is based on either comfort or precision. I simply intended to show that final grasp comfort increases with precision and that advantages afforded by comfortable (thumb-up) postures are greater than advantages afforded by the dominant (right) hand.

This conservative perspective is justified at this stage in the literature because it remains unclear how best to relate preference and performance. For example, if one choice affords performance that is half as costly as another, should the first be chosen twice as often as the second? As Coelho and Rosenbaum (2013) noted, uncertainty about how to answer this question makes it difficult to determine the extent to which hand and grasp choices reflect consideration of the performance advantages they afford. A useful method for studying the determinants of the grasp-orientation constraint may be to dissociate options that lead to thumb-up or thumb-down final postures. The idea is to have participants choose between an option that affords lower final comfort but higher precision and another that affords higher final comfort but lower precision. Having participants choose one or the other may help identify the determinants of the constraint. Indeed, this general method is analogous to the one I used at the constraint-level to tease apart the relative priority of grasp orientation and hand preference.

It may turn out that the grasp-orientation constraint is ultimately based on control and not on comfort. However, the current literature does not provide a definitive answer to this question (Rosenbaum et al., 2012), so I suggest that one need not yet suppose that the grasp-orientation constraint is about one of these factors or the other. Having made this point, I follow up with a similar suggestion about handedness.

Handedness

The question of whether handedness reflects preferences (McManus, Murray, Doyle & Baron-Cohen, 1992) or performance asymmetries (Annett, 1995; Sainburg, 2002) may reflect an unnecessary dichotomy that has arisen as an artifact of studying one or the other in isolation (Coelho, Przybyla, Yadav & Sainburg, 2013). Without testing both preference and performance in the same task, it is even more difficult to relate the two. This is an especially salient problem within the constraint hierarchy approach because each hierarchy can depend on specific task features. Thus, future research should take pains to assess both preference and performance.

A more satisfying characterization of handedness may come through first appreciating that hand choices are probably based, at least to some extent, on interlimb performance differences. It is encouraging to be able to make this suggestion with some confidence given that researchers have only recently been able to map out reliable sensorimotor performance asymmetries (Sainburg, 2002; Mutha et al., 2012; 2013). Second, one might then set out to understand whether and how these performance differences result in different weightings of hand preference in different tasks or classes of tasks.

Understandable concerns can be raised about this suggestion, however. First, one can ask the chicken-or-the-egg question about whether hand preference asymmetries lead to performance asymmetries, or vice versa. This remains a difficult question because preference and performance asymmetries so clearly covary (Annett, 1995; Sainburg, 2002). Moreover, the answer to this question has implications for the origin of handedness, which has been attributed to evolutionary responses to social pressures for cooperation (Vallortigara and Rogers, 2005), to co-evolution of brain areas for language and gesture (Corballis, 2003), and to modeling of others (Hepper, Wells, & Lynch, 2005). A promising hypothesis on this front – and one that is supported by the results of Experiment 1 – is that handedness reflects an adaptation for skilled behavior that later became conserved genetically through natural selection (Sainburg & Eckhardt, 2005).

It should be noted that the main goal of this thesis was to determine the relative priority of the studied constraints, not to reveal the phylogenic or ontogenetic origins of the constraints. Thus, suggestions about the roots of the hand preference and grasp-orientation constraints are speculative. Still, it seems reasonable to suggest from an evolutionary perspective that action selection pertaining to both constraints takes into account related biomechanical control variables. One reason is that different actions can achieve the same tasks, sometimes with very different energetic and metabolic costs. It therefore makes sense that humans evolved the capacity to consider those costs. Furthermore, decisions about motor responses likely have an evolutionarily longer history than decisions about symbolic responses (Cos et al., 2011). These points notwithstanding, it is not necessarily the case that mechanisms of motor decisions are mutually exclusive with those of cognitive decisions. Indeed, the overarching theme of this thesis is that making decisions about how to move relies on a tight coupling between cognition and action. In support of this view, there is evidence suggesting that perceptual-motor and cognitive skill are more similar than dissimilar (cf. Rosenbaum, Carson & Gilmore, 2001), that neural correlates of physical actions are activated when people engage in cognitive simulations those actions (cf. Guillot & Collet, 2005), and that abilities to make abstract decisions developed from abilities to make motor decisions (cf. Calvin, 1994).

Returning to the idea that handedness reflects a composite of preference and performance, another potential concern is as follows. It begs the question about what can explain hand choice when reliable performance asymmetries cannot. In response to this question, one might suggest that some nontrivial part of hand choice is a simple response bias for the preferred hand. Evidence to support this idea comes from Coelho and Rosenbaum (2013), who used a signal-detection approach to suggest that response bias does contribute to hand choice. We gave right-handed adults a choice between a reciprocal-tapping task whose inter-target distance and location remained constant across trials and another task whose inter-target distance and location varied. For some groups the constant task could only be performed with the left hand whereas the varied task could only performed with the right hand; for other groups this situation was reversed. We reasoned that if hand choice only reflected response bias for the right hand, then participants would choose the right hand equally as often regardless of whether the right-hand task was constant or varied. This prediction was only supported for groups that did not have to lean far to reach the constant task. When participants leaned far for the constant task, they chose the right-hand task more when it was variable. Because the cost of leaning and reaching is higher for the left hand (Rosenbaum, 2008), we argued that both bias and sensitivity contribute to hand choice.

Saying that bias contributes to hand choice need not imply irrationality on the part of decision maker. In fact, having a bias to use the right hand may lead to efficiency in the action selection process, as alluded to above and as suggested, more generally, for other types of choices (Simon, 1956). With regard to hand choices, if there is a default strategy to use the right hand, it may be cognitively efficient to keep choosing that hand unless other factors militate against doing so. An obvious mitigating factor might be fatigue. If the right hand gets used repeatedly, it might become tired and unable to reach effectively. In light of the current studies, another interesting factor may be workspace location. From a satisficing perspective, for example, one could explain the common tendency for right-handed people to grasp left-located objects with the nondominant (left) hand; see Mamolo et al (2004; 2006). The nondominant (left) hand may not always be optimal in terms of performance, depending on which cost function is considered, but the left hand may be good enough to get the job done. Here, workspace location can be said to reweight the hand preference constraint and to mitigate against the bias to use the right hand. This view places priority on understanding which task- and actor-related factors draw on sensitivity to performance asymmetries because these factors may lead to plan modifications via reprioritization of constraints.

The point just mentioned bears on a larger one. The putative flexibility in the organization of constraint hierarchies for different tasks is not borne of theoretical convenience. Rather, it is a core postulate of the constraint hierarchy approach that although there may be a default hierarchy for a given class of tasks, there may also be a unique hierarchy for each specific task. Indeed, the constraint hierarchy approach has roots in a computational model of motor planning which says that the hierarchy not only helps reduce action alternatives and aid successful task completion, but also that the hierarchy defines the task to be performed (Rosenbaum et al., 2001, p.714). This suggestion highlights the possibility that one way to understand how people mentally represent tasks is to test for the task- and actor-related features that people care about when they make action choices.

A concrete example of the usefulness of this approach is the case in which individuals satisfy multiple constraints at the same time. In critical trials of Experiments 2A and 3A, for instance, hand preference and final comfort were pitted against each other so participants had to satisfy either one or the other. Because there was a clear preference for final comfort, and because there were noticeable effects of handedness, it was concluded that both constraints were considered but were weighted differently. Taken together, these findings provide a useful comparison for the case in which these constraints are <u>not</u> pitted against each other. Such a case comes from the trials in which participants used the right hand to end in a thumb-up posture.

In a similar vein, Fischman (1998) showed that when right-handed individuals were only told to transport either end of a horizontal dowel to a flat target with a 90° rotation, participants preferred overhand right-hand grasps over underhand right-hand grasps, over left-hand overhand grasps, and over left-hand underhand grasps. In other words, when participants could use the preferred hand (right) *and* the preferred initial grasp (overhand), *and* end in the preferred orientation (thumb-up), they did so.

In response to these findings, one could suggest that the weightings (or relative importance) of the initial-grasp, final-grasp, and hand preference constraints were equal. Note that this conclusion would be very different from the one that might be drawn under the alternative view that there is a sole governing constraint. Under the latter view, one might be tempted to ignore the zero- or near-zero weighting of handedness and comfort and therefore overlook a critical comparison condition for when the priority of these constraints changes.

In the case that multiple constraints seem to be satisfied, the putative constraint hierarchy may look less like a hierarchy, per se, and more like a heterarchy in which constraints share the same weighting. In a hierarchical structure there is always an uppermost constraint. It is still fair, however, to invoke the hierarchical view here because, by hypothesis, there is likely to be a higher-ranked but unidentified constraint atop the hierarchy. This suggestion may therefore help motivate researchers to empirically map out constraint hierarchies for different tasks, as I have tried to do here for object transport tasks. The simplicity of the preference method I have used to this end, coupled with the orderly data it yielded, bodes well for the future use of the method to identify constraint hierarchies and also to understand whether and how various factors influence their composition.

A final set of remarks connects the current findings to applied and theoretical problems in related fields. These fields have to do with rehabilitation of neuromuscular impairment, robotics, and human factors.

Implications for Related Fields

Perhaps the most salient type of neuromuscular damage comes from stroke. Strokes are cerebrovascular accidents that lead to neural tissue damage and loss of sensorimotor function. The primary mechanism of action is a disturbance of blood supply to the brain. About 700,000 people experience at least one stroke each year, and a significant portion of the healthcare cost is due to rehabilitation (Wolf et al., 2006). The most typical sensorimotor impairment in unilateral stroke is hemiparesis – a moderate-to-severe weakening of the contralateral limbs. In turn, stroke patients perform many unimanual tasks with the ipsilesional arm, as the contralesional arm suffers the most impairment (Sainburg & Duff, 2006). However, ipsilesional motor deficits are often nontrivial and consistent with the dynamic dominance hypothesis of motor lateralization (cf Sainburg, 2002). Unilateral left-hemisphere damage in right-handers leads to trajectory errors of the nondominant (left) limb, whereas right-hemisphere damage leads to final position errors of the dominant (right) limb (Schaefer et al., 2007; 2009a).

Several rehabilitation therapies have been pursued, including bilateral training, electrical stimulation, robot-assisted reaching, and splinting (Langhorne, Bernhardt, & Kwakkel, 2011).

One of the most effective therapies is constraint-induced therapy (CIT); see Wolf et al. (2006) for review. Patients undergoing CIT are led through several practice sessions on specific motor tasks with the contralesional arm. A key to CIT is that the ipsilesional, less-impaired arm is often restrained (Wolf et al., 2006). The idea behind this approach is that obstructing the use of the less-impaired arm forces patients to overcome the bias against using the contralesional arm. This bias is termed "learned nonuse" to reflect that learning contributes to the bias and that the impaired limb can often still achieve several tasks (Taub, 1980; Taub, Uswatte & Pidikiti, 1999).

How can the findings of this thesis be applied to CIT? One way is to build on the idea that patients underestimate what they can do with the impaired limb. Patients may learn to pay little attention to that limb and may therefore benefit from a version of CIT in which the less-impaired limb is not entirely immobilized. Instead of immobilizing the limb, a device could be developed that makes it difficult for the less-impaired limb to perform common tasks, such as brushing teeth or holding cups. Given the current findings that (a) healthy right-handed individuals use whichever hand affords postural comfort and (b) those individuals seem to consider the relative comfort of the given options, one might predict that hemiparetic stroke patients would be motivated to use the contralesional limb more when the ipsilesional limb is harder to use. There is precedence for this general approach in stroke, especially in the context of gait modification (Aruin, Rao, Sharma & Chaudhuri, 2012). Here, contralesional motor impairments of the lower limb lead to detrimental reliance on the less-impaired leg to support body weight. Researchers have been able to induce stroke patients to distribute body weight evenly by compelling such distribution through the insertion of a simple orthotic wedge into the shoe on the contralesional foot (Aruin, et al., 2012). Perhaps a similarly simple device could be applied to the contralesional hand as described above.

A final point is that if the impaired arm is the arm that the patient considered dominant pre-stroke, then promoting the use of that impaired limb, especially in tasks focused on dynamic coordination, might promote the conversion of the nondominant (ipsilesional) controller into a dominant controller (Sainburg & Duff, 2006). When they proposed this idea, Sainburg and Duff (2006) emphasized that researchers should pursue it with caution because it was not yet known whether the nondominant controller could be retrained as a dominant controller (p.312). However, the feasibility of developing such a protocol is buttressed by recent computational modeling of interlimb asymmetries in dynamic coordination. Yadav and Sainburg (2011) characterized interlimb dynamic control asymmetries with a serial hybrid model in which both the dominant and nondominant hemisphere / limb systems commence unimanual reaches via predictive forward-modeling mechanisms and terminate reaches via impedance-based mechanisms. The difference between the limbs was the time at which each system switched from predictive to impedance-based control, with the dominant system switching significantly later than the nondominant system. The output of the computational model agreed with observed experimental data. The point most germane to the current discussion is that the model says that both systems rely on the same underlying processes – a feature one would expect if it were possible to retrain the nondominant system as the dominant controller.

Another applied implication of the current findings concerns human factors. In this field, the goal is to inform hardware and software designs about the cognitive and physical limitations and capabilities of human operators in human-machine interfaces. As mentioned above, the more traditional view of handedness is that one hemisphere / limb system is dominant and favored for all or most tasks and the other system is generally disfavored. This model would have predicted in the studies presented above that right-handed participants would predominantly use the right hand even when doing so led to uncomfortable or imprecise final postures. Indeed, it has been suggested that the willingness to use the dominant hand for awkward tasks reflects the very essence of handedness (Bryden, Singh, Steenhuis & Clarkson, 1994; Gabbard & Rabb, 2000). The findings presented in this thesis go against this traditional model, however, and suggest instead that right-handed individuals avoid using the right hand in uncomfortable, awkward, and hard-to-control postures. As a result, human factors engineers should not assume that critical human-machine interface points are best placed in reach of the dominant hand regardless of whether those locations require thumb-up or thumb-down postures. The current findings indicate not only that such interface placements might lead to discomfort for the operator but also that such placements might work against efficient control and performance.

Finally, the current findings can inform the field of robotics, where a major aim of ongoing work is to allow robots to emulate natural action planning (e.g., Allen, Timcenko, Yoshimi, & Michelman, 1993; Clark, 1999). Humanoid robots have made great strides in recent years. However, when they do perform human-like motor tasks, such as opening bottles and pouring water, robots still move rather laboriously. And still, some tasks that even young children can achieve with relative ease, such as folding laundry and climbing trees, are out of reach for robots. One reason may be that human-like motor performance requires human-like autonomous planning. An important sub-goal for designing robots, therefore, is to understand how humans represent tasks so that the robots can develop internal models of the environment. Though progress has been made on this front, prescribed inputs and outputs are still needed in many cases for robots to approach human-like performance (Clark, 1999). The current approach to mapping out the constraints and their weightings which define tasks might be used to help robots operate more autonomously in various environments. More research is needed to understand whether and how actor- and task-specific profiles predict reliable constraint hierarchies in various tasks. Then researchers can begin to develop algorithms by which robots can use information about its own features and sensory information about the environment to develop internal models similar to those presumably used by autonomous humans.

In closing, my hope is that this thesis, and the aims, methods, findings, and conclusions contained therein, make a meaningful contribution to the field of motor control. As a cognitive psychologist, I recognize that cognitive scientists have historically made fewer contributions to motor control than scientists from other disciplines, such as kinesiology, neuroscience, and biomechanics (Rosenbaum 2005). This thesis takes a primarily psychological perspective on motor control. However, within that perspective there is a clear appreciation for interdisciplinary work that spans the multiple levels of analysis needed to more fully understand how individuals solve the complex problem of action selection.

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Appendix A

Inverse Dynamics Method

Each limb was modeled as a serial three-link manipulator with eight degrees of freedom (DOF). The eight DOFs came from three translational joints and five rotational joints. The first three translational (x-,y-, and z-) DOFs at the shoulder described movement of the shoulder that resulted from movement of the trunk. The next three DOFs at the shoulder corresponded to shoulder rotation. The first two DOFs at shoulder defined the orientation of the plane containing the shoulder, elbow, and wrist joints; the third described the orientation of the upper arm in this plane. The last two DOFs were intersegment joint angles at the elbow and wrist. Pronation, wrist flexion, and wrist extension were not included in the model because the wrist was immobilized and movement was only allowed in the horizontal plane. These features of the experiment made negligible the dynamic effects at the elbow and at the shoulder arising from pronation, wriest flexion, or wrist extension.

In the Appendix Figure (panel A), i = 1, 2,3 represent the three links corresponding to upper arm, forearm, and hand, respectively. The terms m_i, I_{xi}, I_{yi}, and I_{zi} represent masses and moments of inertia of each limb; we computed these variables with the method described in Zatsiorsky (2002). The terms l_i and r_i represent the length and center of mass location for i^{th} link, respectively.

As shown in the Appendix Figure (panel B), the configuration of the limb model in generalized coordinates, q, was described as follows:

$$q = [x_s\ y_s\ z_s\ \Theta_{s,elv}\ \Theta_{s,roll}\ \Theta_s\ \Theta_e\ \Theta_w]^T \tag{1}$$

A screw theory-based approach was used to compute these joint angles and joint torques from the position data of the Flock of Birds motion sensors. Screw theory describes motion of a rigid body as rotation about an axis and translation along that axis (Ball, 1876). When combined with Lie algebra, screw theory provides tools that can be used to derive equations of motions for complex mechanical systems. In turn, these equations can be used to study mechanical properties of the system and to develop control algorithms (Murray, Li & Sastry, 1994). The related inverse kinematics and inverse dynamics method are represented below. The joint angles and derived equations of motion were computed using screw theory as follows:

First, a velocity twist was described. For a purely rotational or a revolute joint, the velocity twist is defined by the orientation of the screw axis and a point on the screw axis by

$$\hat{\xi} = [-(\omega \times r)\ \omega]^T \tag{2}$$

where w is the unit vector along axis of rotation, and r is any point on the screw axis -- the axis of rotation. For example, the velocity twist corresponding to the elbow joint is given by

$$\hat{\xi}_e = [-([0\ 0\ 1]^T \times [l_1\ 00\ ])[0\ 0\ 1]]^T = [0\ \ -l_1\ 0\ 0\ 0\ 1]^T \tag{3}$$

For a purely translational or prismatic joint, the velocity twist is defined as the direction of movement:

$$\hat{\xi} = [h\ 0]^T \tag{4}$$

where h is the unit vector along the direction of motion. For example, the velocity twist corresponding to translation degree of freedom along x axis is given by

$$\hat{\xi}_x = [1\ 0\ 0\ 0\ 0\ 0]^T \tag{5}$$

Therefore, the matrix of twists defining the arm model in panel B of the Appendix Figure is

$$\hat{\xi} = \left[\hat{\xi}_{x_s}\ \hat{\xi}_{y_s}\ \hat{\xi}_{z_s}\ \hat{\xi}_{\Theta_{s,elv}}\ \hat{\xi}_{\Theta_{s,roll}}\ \hat{\xi}_{\Theta_s}\ \hat{\xi}_{\Theta_e}\ \hat{\xi}_{\Theta_w}\right] \tag{6}$$

Second, the inverse kinematics were computed. To obtain equations for forward kinematics using screw theory, the velocity twists that defined the mechanical system were needed (Eq. 6) in addition to the forward kinematic map in zero configuration,

$$g(0) = [I_{3\times3}\ [(l_1 + l_2 + l_3)\ 0\ 0]^T_{3\times1}; 0_{1\times3}\ 1_{1\times1}] \tag{7}$$

where I_{3X3} is the 3 dimensional identity matrix.

Then the forward kinematics were computed as

$$g(q) = e^{\hat{\xi}_{\Theta_w}} e^{\hat{\xi}_{\Theta_e}} e^{\hat{\xi}_{\Theta_s}} e^{\hat{\xi}_{\Theta_{s,roll}}} e^{\hat{\xi}_{\Theta_{s,elv}}} e^{\hat{\xi}_{z_s}} e^{\hat{\xi}_{y_s}} e^{\hat{\xi}_{x_s}} g(0) \tag{8}$$

where the matrix exponents were computed as described in Murray et al. (1994). Once the forward kinematic mapping between joint angles and marker positions was available, then the inverse kinematics were computed using analytical methods, when possible, or by using Newton Raphson root solving methods.

Third, the inverse dynamics were computed. The joint torques that generated movement were calculated using the joint angles computed in the previous step. They were computed first by deriving equations of motion for the arm model in panel B of the Appendix Figure. The general form of the equations of motion of the arm model in a zero-gravity condition is

$$M\left(q\right)\ddot{q}+C\left(q,\dot{q}\right)=\tau \tag{9}$$

where M is the mass-inertia matrix of the human arm and C is the matrix corresponding to Coriolis and centrifugal contributions from movement of joints. The M and C matrices for the arm model were then computed.

Computing equations of motions for complex mechanical systems is straightforward with this screw theory-based approach in conjunction with methods from Lie Algebra (Murray et al). To derive equations of motion using screw theory, the velocity twist that defined the pose of the center of mass of each link was needed. For example, in the model of human arm in panel B of the Appendix Figure, the twists that defined movement of the center of mass and forward dynamics in zero configuration of the fore arm are given by

$$\hat{\xi}_{fore\ arm}=\left[\hat{\xi}_{x_s}\ \hat{\xi}_{y_s}\ \hat{\xi}_{z_s}\ \hat{\xi}_{\Theta_{s,elv}}\ \hat{\xi}_{\Theta_{s,roll}}\ \hat{\xi}_{\Theta_s}\ \hat{\xi}_{\Theta_e}\right] \tag{10}$$

and

$$g(0)_{fore\ arm}=[I_{3\times 3}\ [(l_1+r_2)\ 0\ 0]^T_{3\times 1};0_{1\times 3}\ 1_{1\times 1}] \tag{11}$$

The twists and forward kinematics in zero-configuration for other links were computed in a similar manner. Then these formulations were used to compute M and C in Eq. 9.

To compute M, the mass-inertia matrix was computed first. The kinetic energy of the arm model in the Appendix Figure is

$$KE = \frac{1}{2}\sum_{i=1}^{3} V_i^T M_i V_i = \frac{1}{2}\sum_{i=1}^{3} \dot{q}^T J_{b,i}^T M_i J_{b,i} \dot{q} = \frac{1}{2}\dot{q}^T \underbrace{\left(\sum_{i=1}^{3} J_{b,i}^T M_i J_{b,i}\right)}_{M(q)} \dot{q}, \tag{12}$$

where J_b is the body Jacobian of the mechanical system. Note that there are different types of manipulator Jacobian for different applications. The body Jacobian used here was defined in Murray et al. The mass-inertia matrix was then simply M(q) in Eq. 12.

To calculate C, the matrix corresponding to Coriolis and centrifugal terms from M using Christoffel Symbols was computed as

$$C_{i,j} = \sum_{k=1}^{8} \Gamma_{i,j,k}\dot{q}_k = \frac{1}{2}\sum_{k=1}^{8}\left(\frac{\partial M_{i,j}}{\partial q_k} + \frac{\partial M_{i,k}}{\partial q_j} - \frac{\partial M_{k,j}}{\partial q_i}\right)\dot{q}_k \tag{13}$$

Fourth, the joint torques were partitioned into interaction, muscle and net torques.

Muscle torque was defined as the torques injected into the mechanical system at the joints

$$\tau_{i,muscle} = \tau_i. \tag{14}$$

Net torque was defined as the joint torques corresponding to the acceleration of the ith joint

$$\tau_{net} = M(q)D_i\ddot{q} \tag{15}$$

where $D_{j,k} = 1$, if j=k=i else $D_{j,k} = 0$.

Once the net and muscle torques were obtained, the interaction torques were computed. Noting that $\tau_{i,net} = \tau_{i,muscle} + \tau_{i,interaction}$, was rewritten in Eq. 8 as

$$\tau_{net} + \left(M\left(q\right)\ddot{q} + C\left(q,\dot{q}\right) - \tau_{net}\right) = \tau_{muscle} \tag{16}$$

Rearranging terms in Eq. 16, the interaction torques were obtained.

$$\tau_{net} = \tau_{muscle} + \underbrace{-\left(M\left(q\right)\ddot{q} + C\left(q,\dot{q}\right) - \tau_{net}\right)}_{\tau_{interaction}} \tag{17}$$

Equations 14, 15, and 17 gave muscle, net, and interaction torques, respectively, for the human arm model described in the Appendix Figure.

Appendix B

Figures and Tables

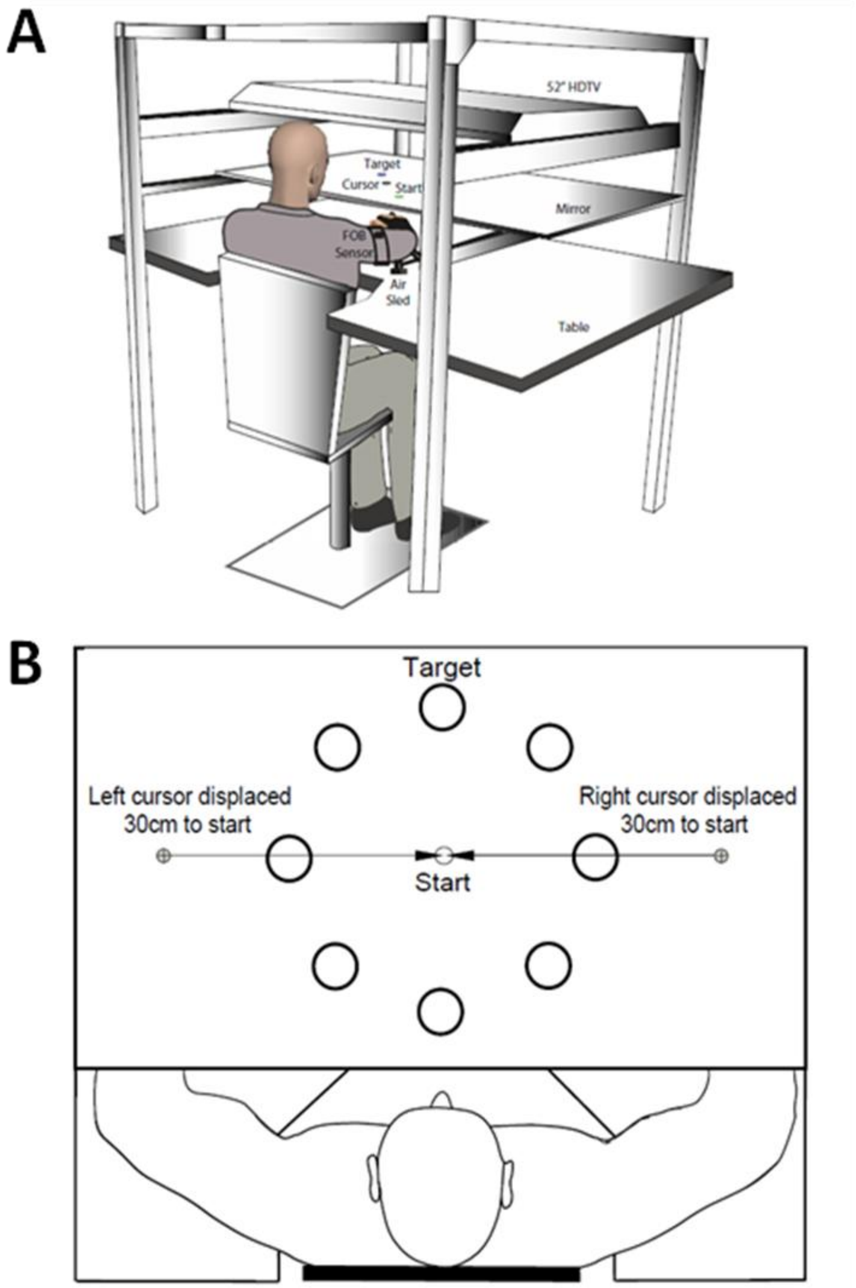


Figure 1. Schematics of the experimental apparatus (panel A) and task (panel B). The distance between the start circle (d = 2.5cm) and each target (d = 3.5 cm) was 13 cm. Only one target was visible in each trial. There were eight potential targets that were spaced at 45° intervals.

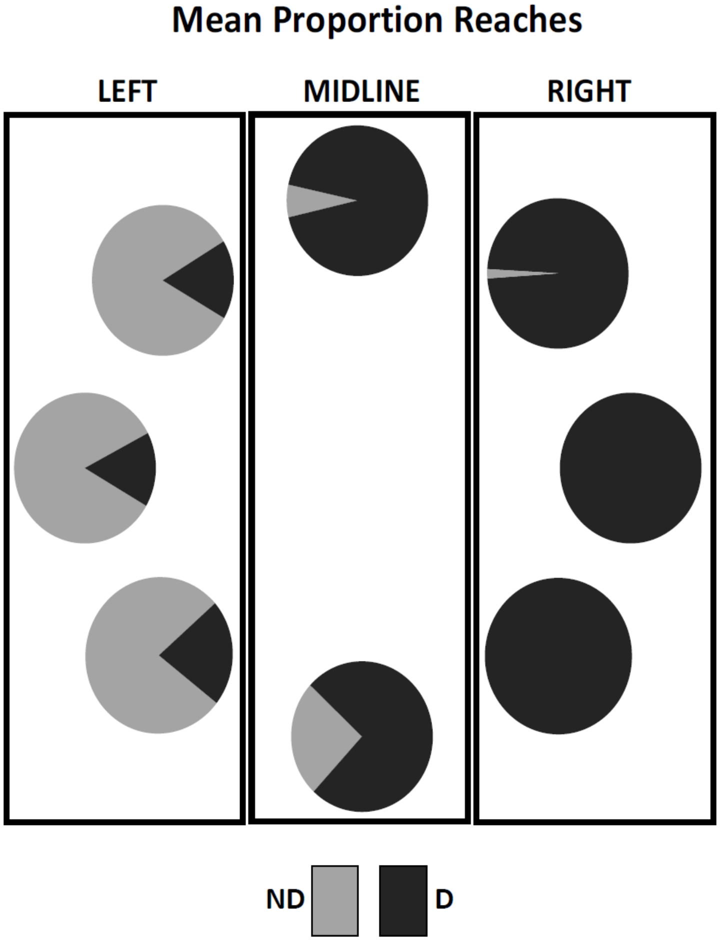


Figure 2. Mean proportions of nondominant (ND) and dominant (D) reaches to each target. Means were computed across participants (N = 10). Rectangles show how targets were grouped into the left workspace, midline workspace, and right workspace.

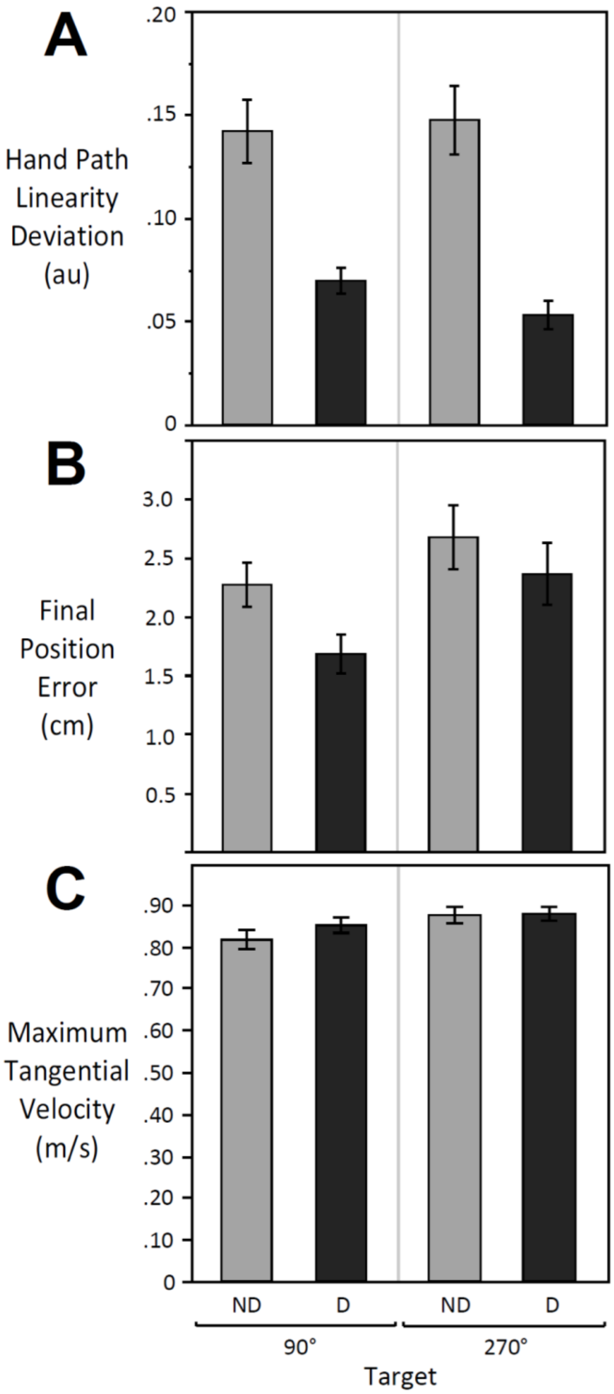


Figure 3. Mean hand-path deviation from linearity (minor axis divided by major axis), final position error (absolute distance between the center of the target and the center of the cursor), and maximum tangential hand velocity as a function of nondominant (ND) and dominant (D) limbs, and midline targets (90° and 270°). Error bars represent ± one standard error of the mean.

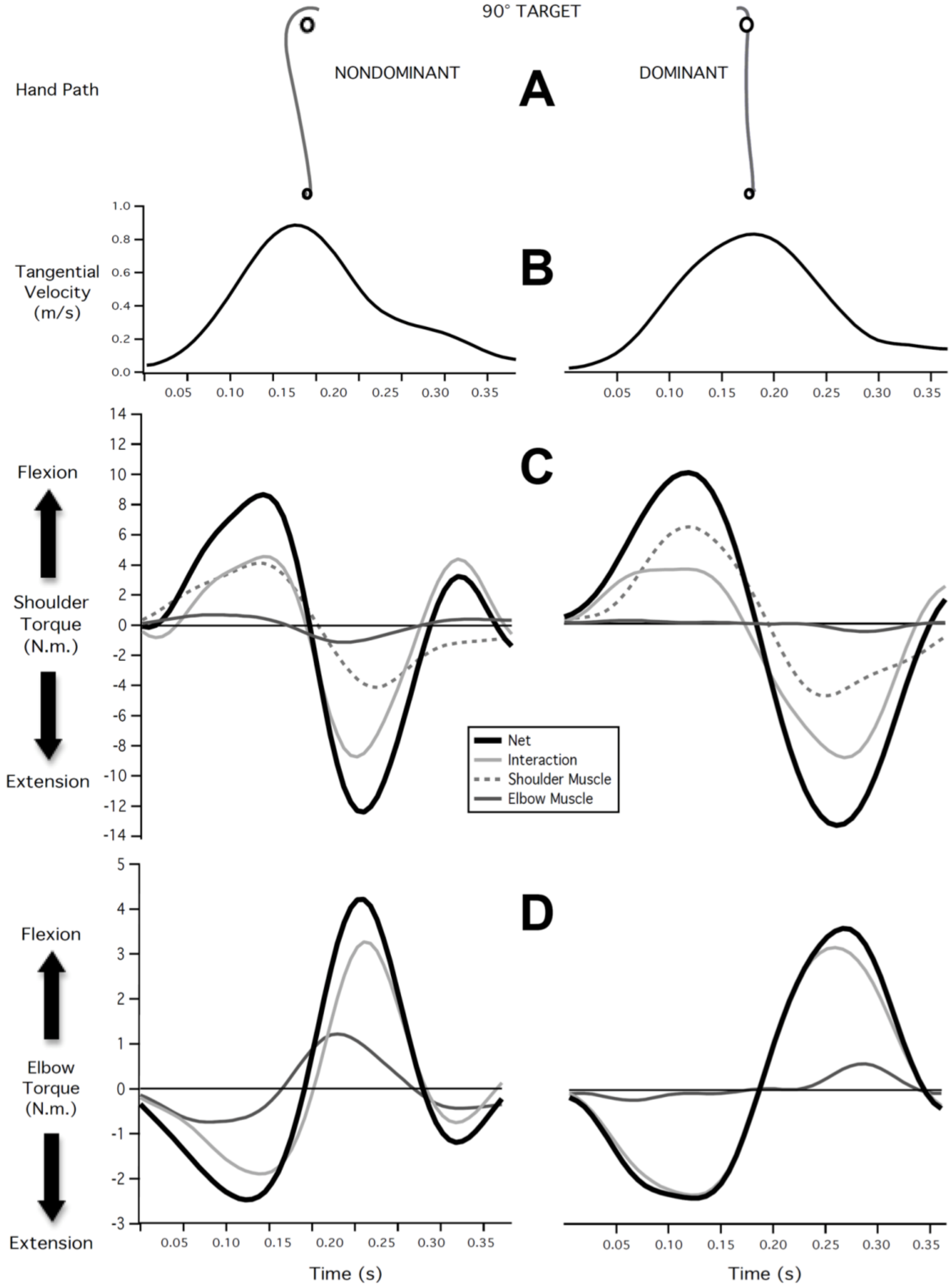


Figure 4. Representative hand paths for each limb (panel A), tangential hand velocity profiles (panel B), shoulder torque components (panel C), and elbow torque components (panel D) toward the 90° target. Example data were taken from the same participant. Torque components include net torque (thick black line), interaction torque (solid, light-gray line), elbow muscle torque (solid, dark-gray line), and shoulder muscle torque (dashed gray line). Elbow muscle torque is equal in amplitude but opposite in sign at the elbow and shoulder.

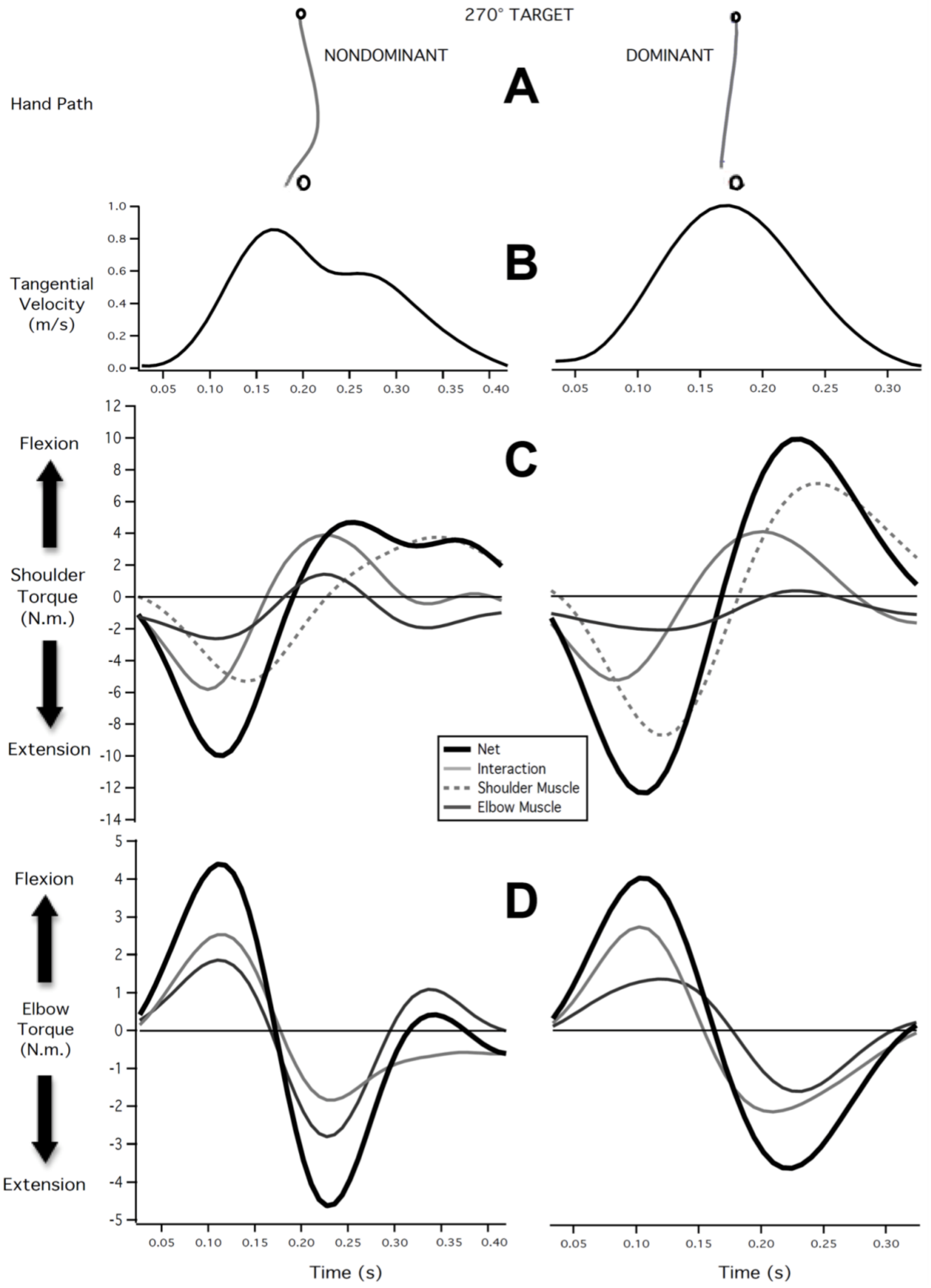


Figure 5. Representative hand paths for each limb (panel A), tangential hand velocity profiles (panel B), shoulder torque components (panel C), and elbow torque components (panel D) toward the 270° target. Example data were taken from the same participant; these data and previous example data (Figure 4) came from different participants. The signs of the torque components are the opposite those shown in Figure 4 because movements to the 270° target were made in the opposite direction.

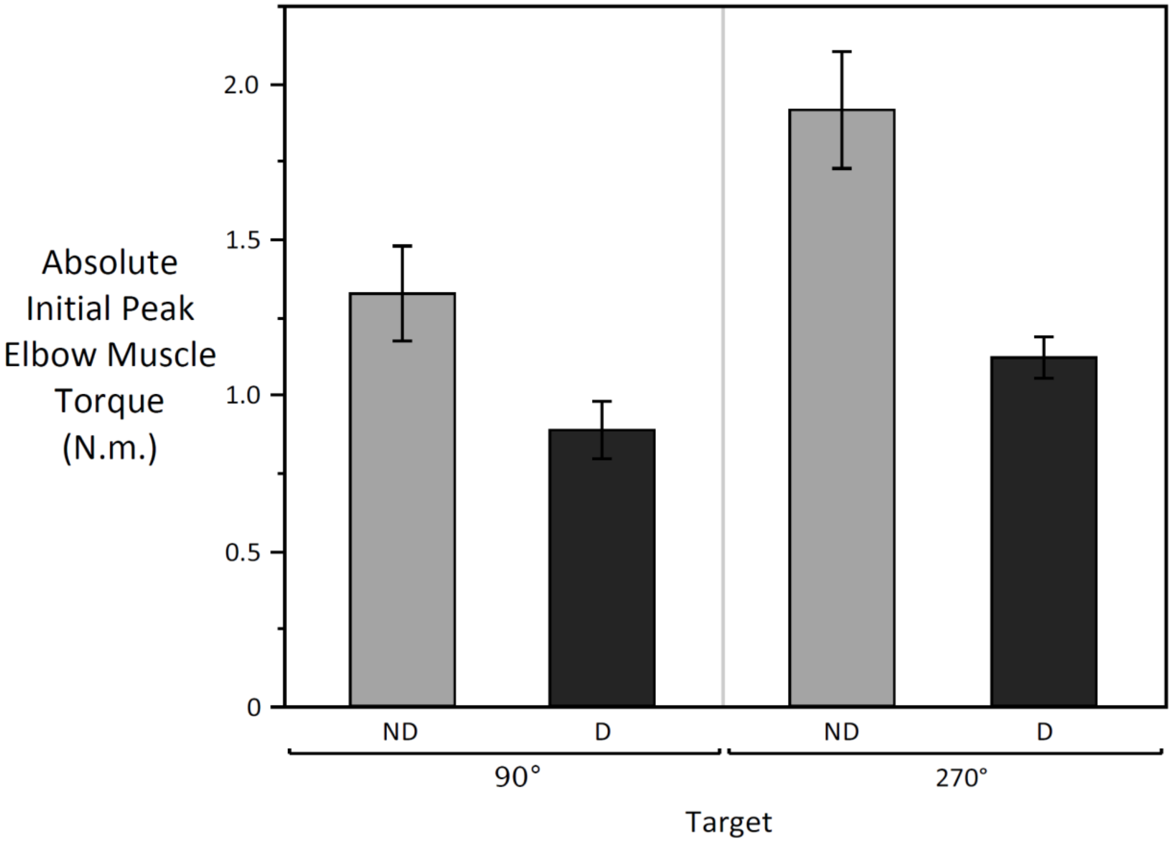


Figure 6. Mean absolute initial peak shoulder (panel A) and elbow (panel B) muscle torque, averaged across subjects. Data are plotted as a function of nondominant (ND) and dominant (D) limbs and midline targets (90° and 270°). Error bars represent ± one standard error of the mean.

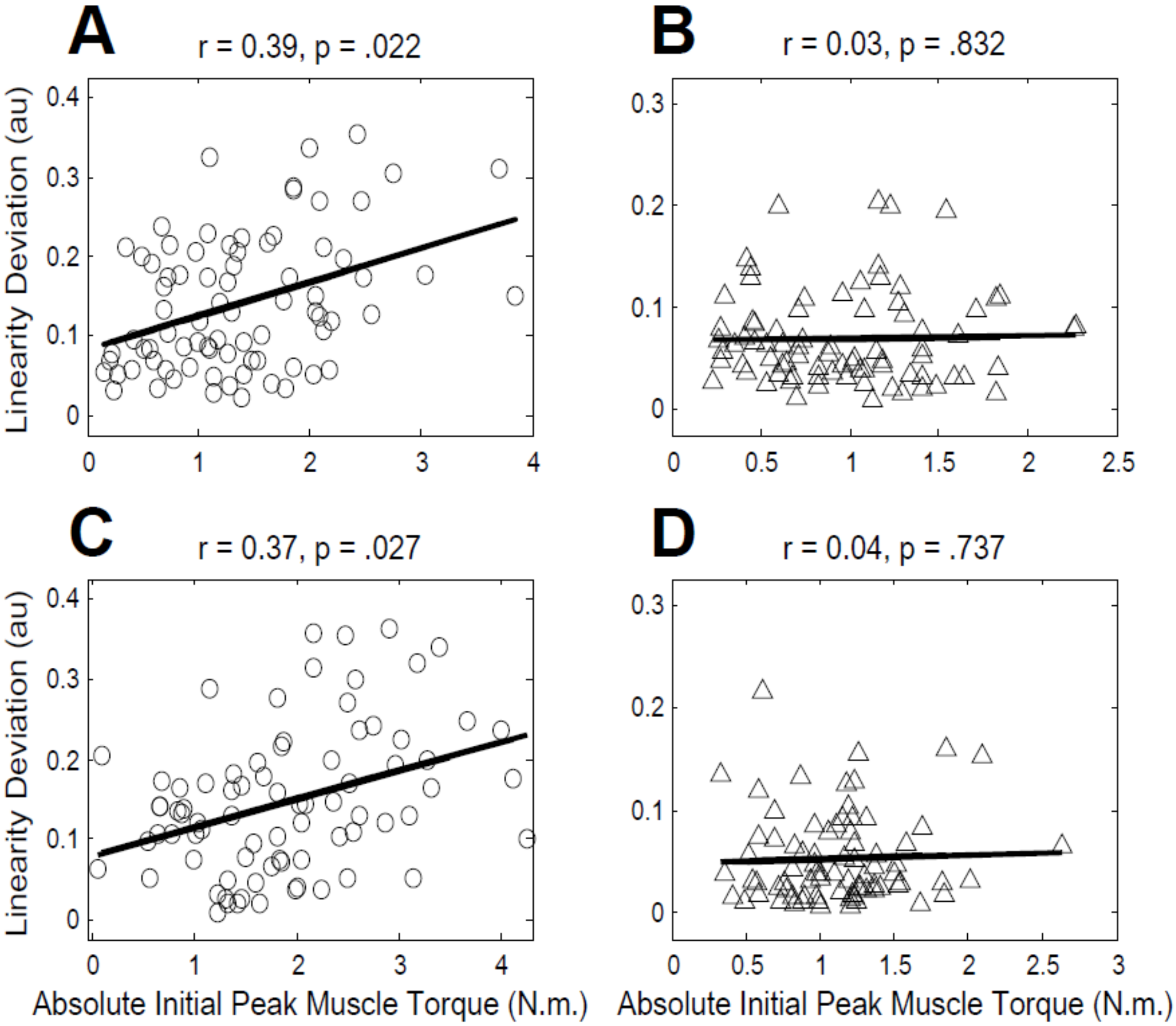


Figure 7. Hand-path deviation from linearity in arbitrary units (minor axis divided by major axis) as a function of absolute initial peak elbow muscle torque on each of 80 non-choice trials. Panels A and B show data from nondominant (circles) and dominant (triangles) reaches to the 90° target. Panels C and D show data from nondominant (circles) and dominant (triangles) reaches to the 270° target.

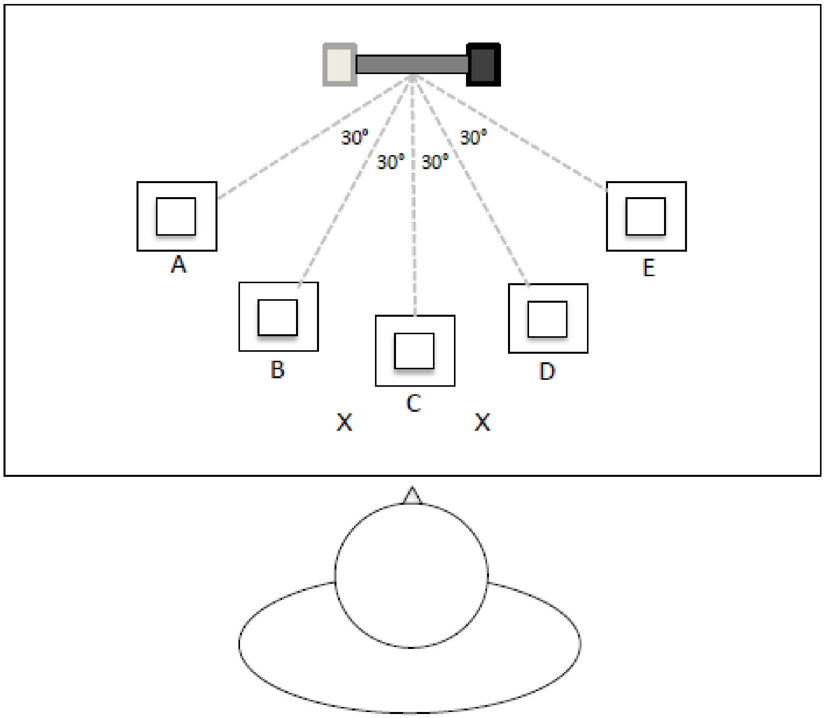


Figure 8. Overhead schematic of experimental setup. The distance between the center of the dowel and each target was 70% of arm length for each participant. The left X and right X were the home locations for the left and right hand, respectively. Not drawn to scale.

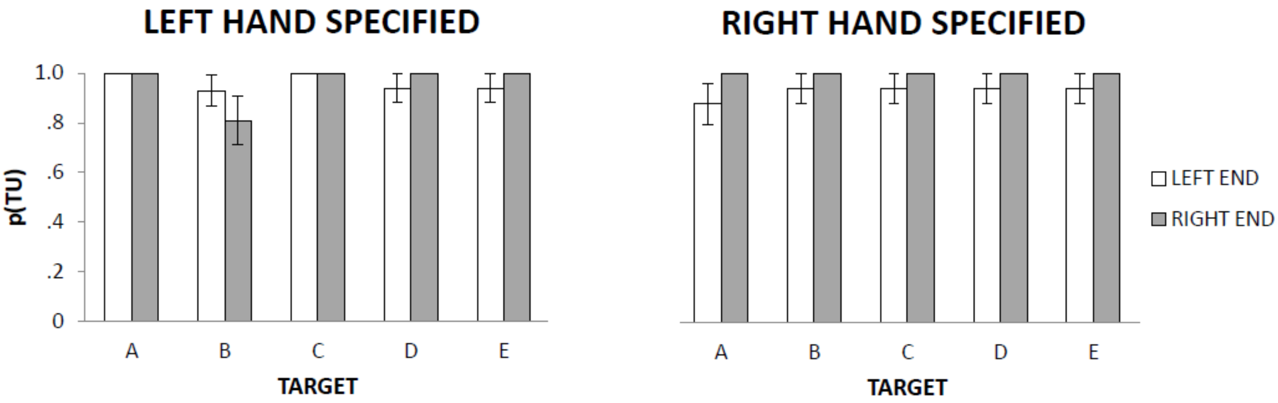


Figure 9. Pooled probability, p(TU), that chosen grasps led to thumb-up final postures. Data are plotted as a function of target (A-E) and of which dowel end (Left / White or Right / Black) was inserted. Left and right panels show data from the Left Hand and Right Hand conditions, respectively. Error bars represent ± 1 standard error of the binomial distribution. N = 16.

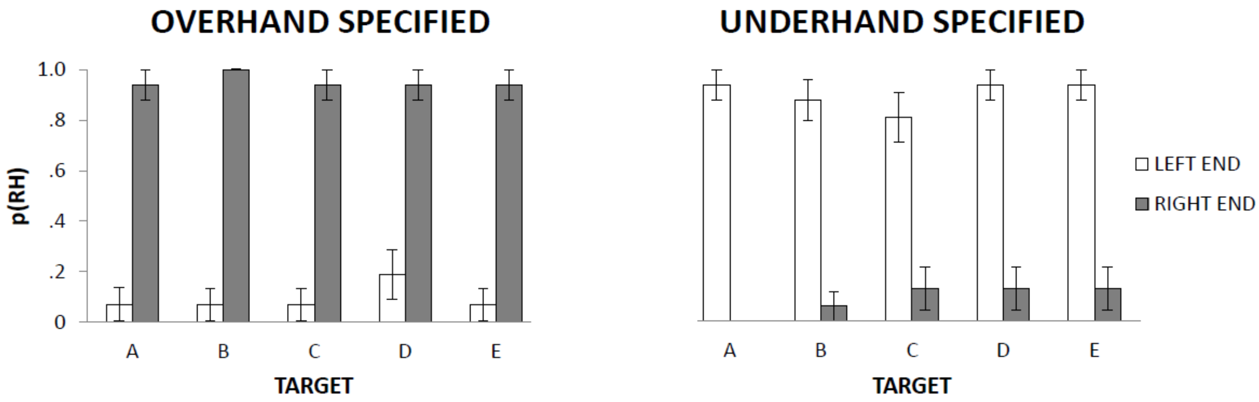


Figure 10. Pooled probability, p(RH), that the right hand was chosen. Data are plotted as a function of target (A-E) and of which dowel end (Left / White or Right / Black) was inserted. Left and right panels show data from the Overhand and Underhand initial grasp conditions, respectively. Error bars represent ± 1 standard error of the binomial distribution. N = 16.

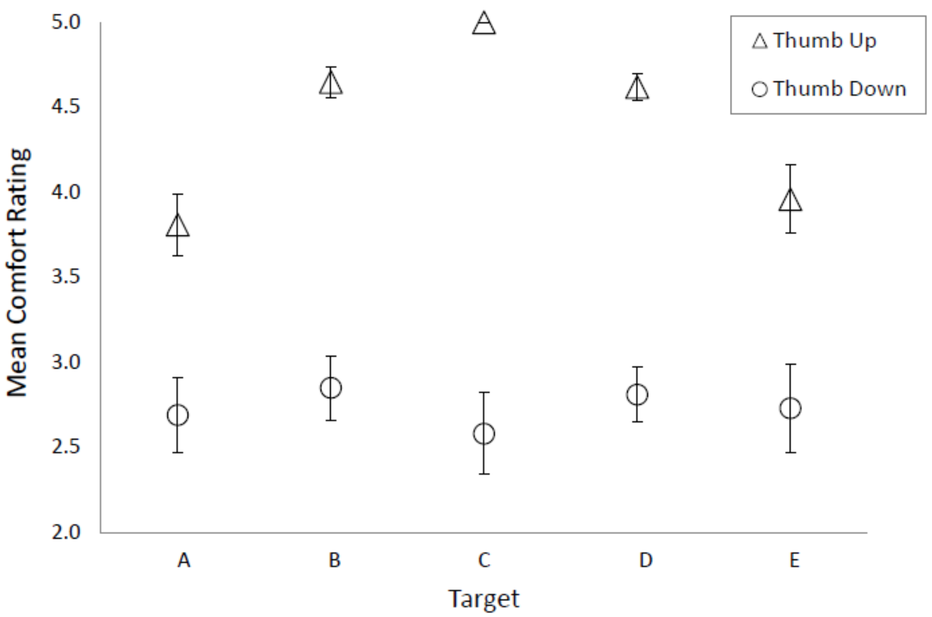


Figure 11. Mean comfort ratings (± 1 SE), pooled across the hands, showing a two-way interaction between grasp orientation and target. While ratings of thumb-up postures peaked at midline and decreased for targets farther from midline, thumb-down ratings were equally low, statistically speaking, for all targets. Error bars represent ± 1 standard error of the binomial distribution. N = 12.

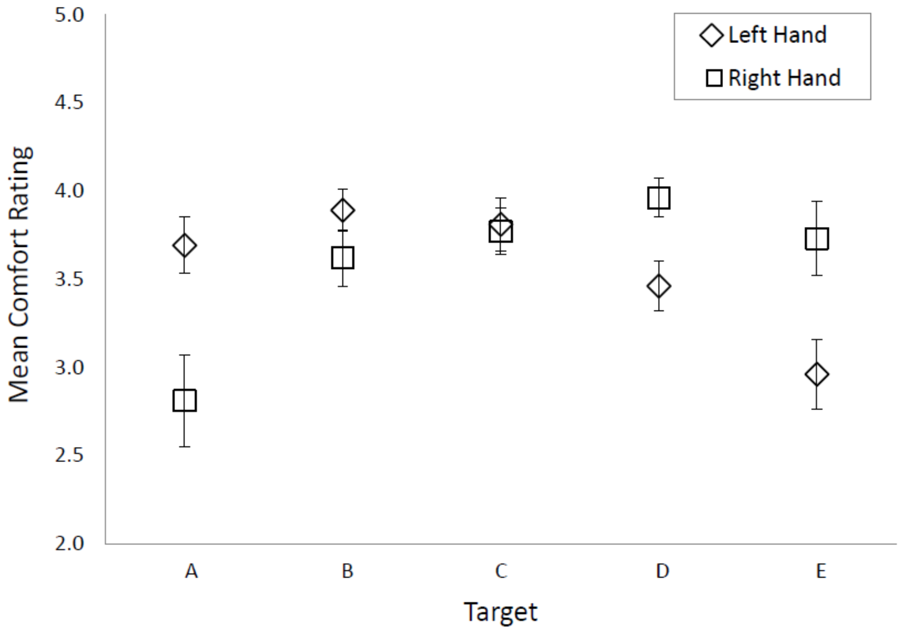


Figure 12. Mean comfort ratings (± 1 SE), pooled across grasp orientation, showing a two-way interaction between hand and target. Ratings for each hand were higher at targets in the ipsilateral workspace than for targets in the contralateral workspace. Error bars represent ± 1 standard error of the binomial distribution. N = 12.

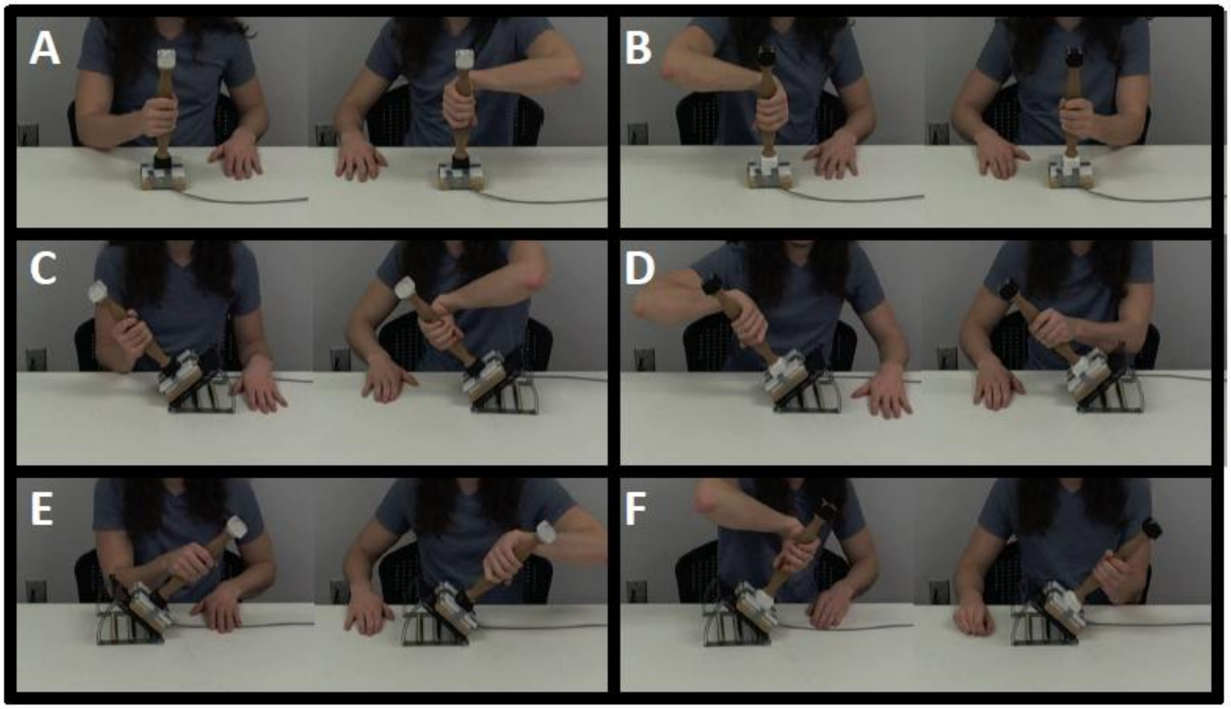


Figure 13. Examples of some possible final postures. Each panel (A-F) displays a binary choice set in the overhand-specified condition. Top row shows the up-facing target. Middle row shows the right-facing target. Bottom row shows the left-facing target.

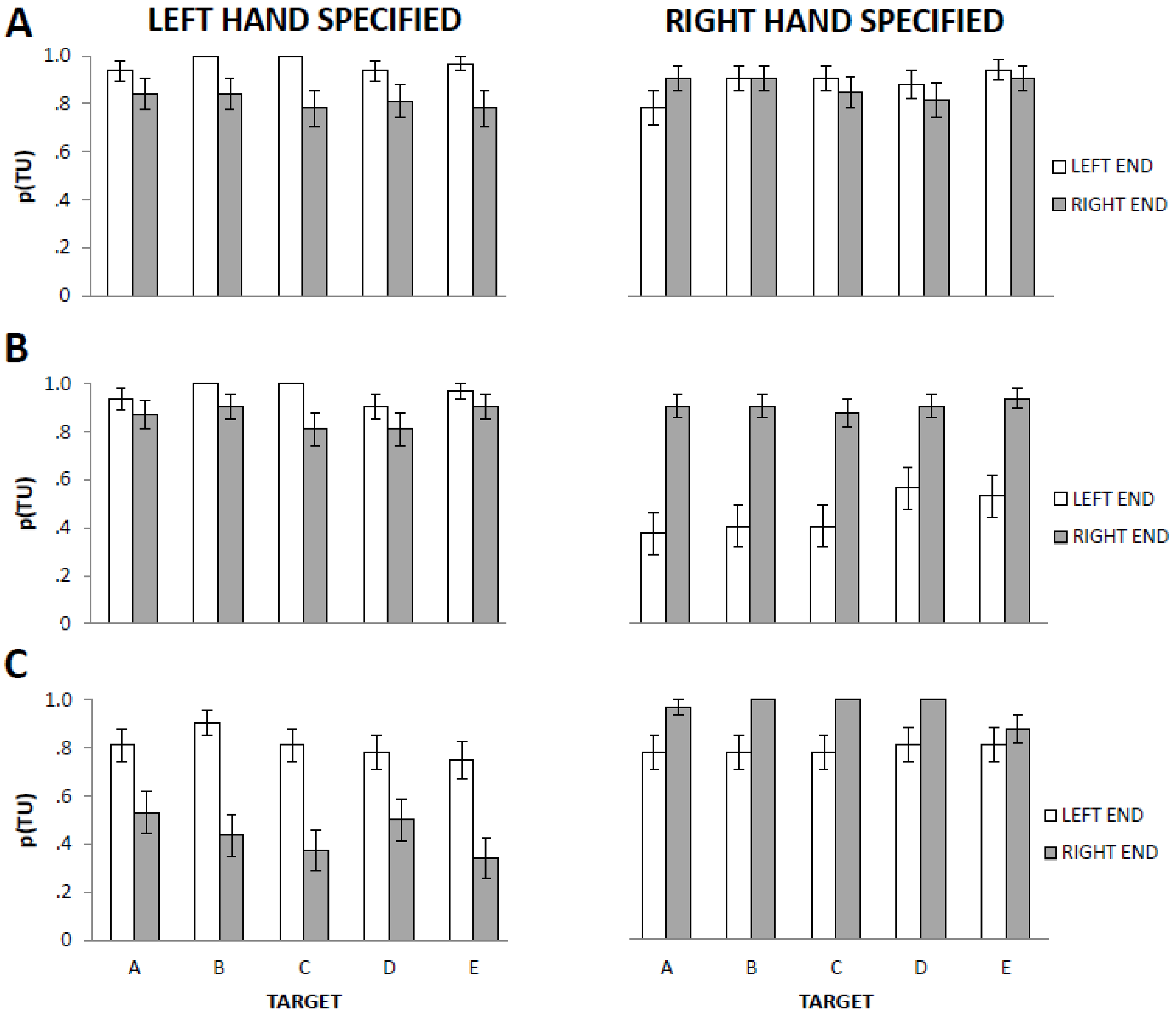


Figure 14. Pooled probability, p(TU), that participants chose initial grasps that led to thumb-up final postures. Data are collapsed across self-paced and speeded groups and plotted as a function of target (A-E) and of which dowel end (Left / White or Right / Black) was inserted. Rows, A, B, and C, show results from up-facing, right-facing, and left-facing target conditions, respectively. Left panels show results from Left-hand conditions. Right panels show results from Right-hand conditions. Error bars represent ± 1 standard error of the binomial distribution. N = 32.

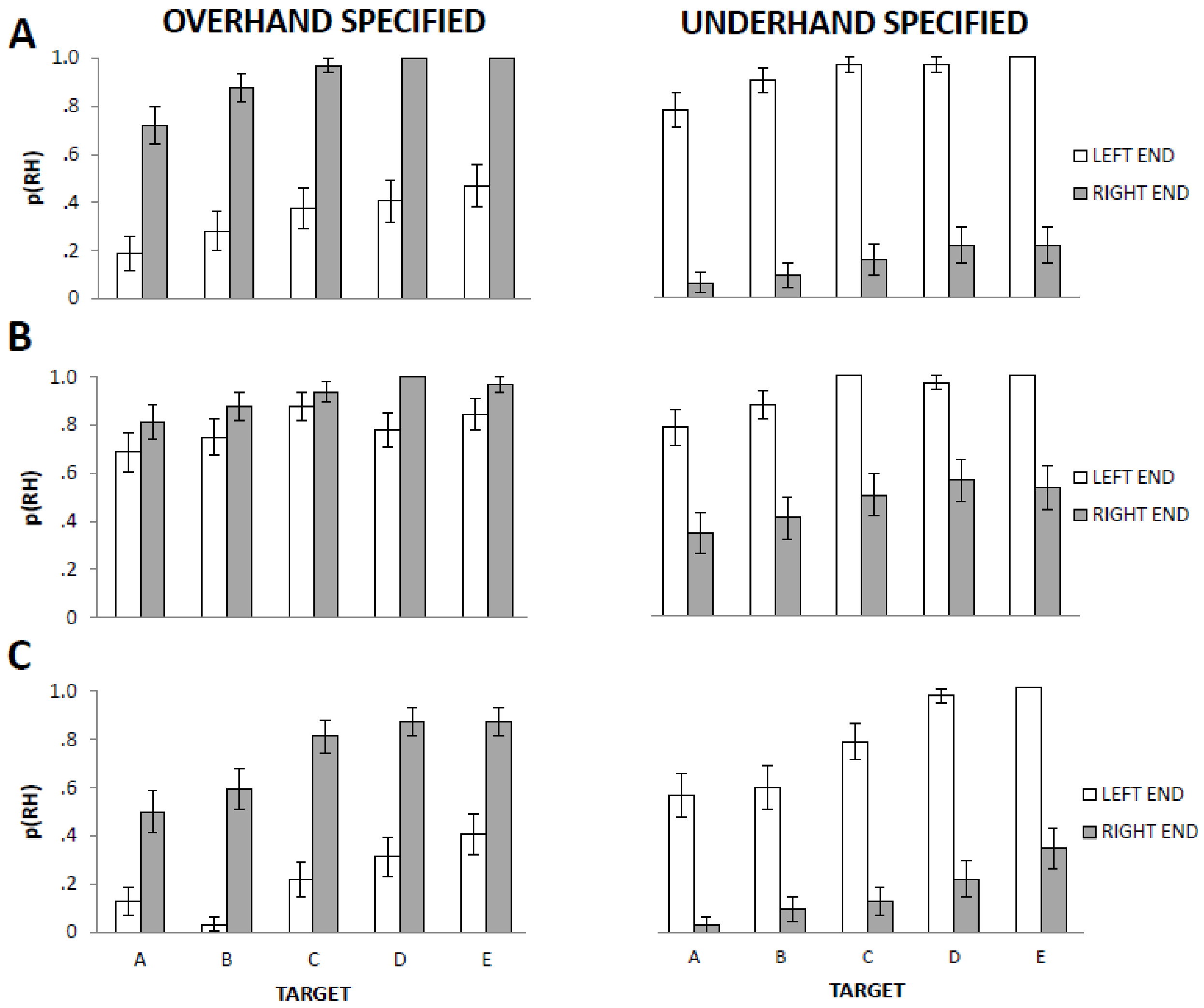


Figure 15. Pooled probability, p(RH), that participants chose the right hand. Data are collapsed across self-paced and speeded grasp-specified groups and plotted as a function of target (A-E) and of which dowel end (Left / White or Right / Black) was inserted. Rows, A, B, and C, show results from up-facing, right-facing, and left-facing target conditions, respectively. Left panels show results from Overhand-specified conditions. Right panels show results from Underhand-specified trials. Error bars represent ± 1 standard error of the binomial distribution. N = 32.

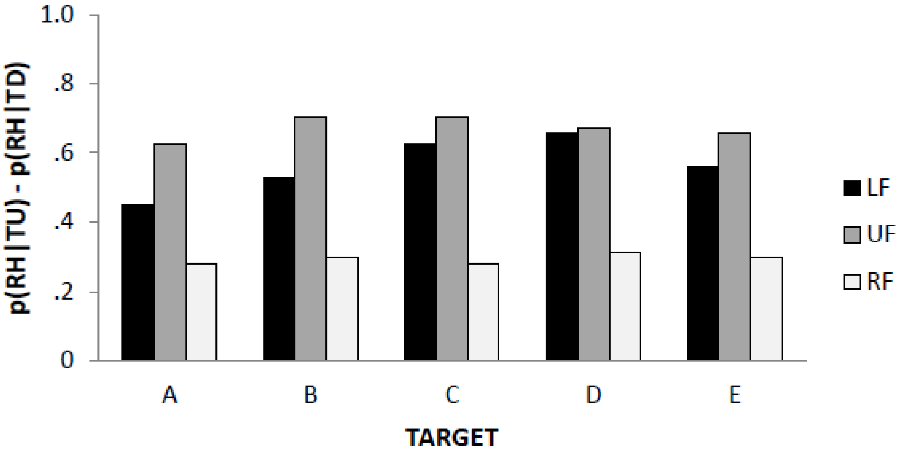


Figure 16. Conditional probability, p(RH|TU), that the right hand was chosen given that the right- hand option led to a thumb-up (TU) posture minus the conditional probability, p(RH|TD), that the right hand was chosen given that the right-hand option led to a thumb-down (TD) posture. Data are plotted as a function of target and target angle (LF = left-facing, UF = up-facing, RF = right-facing). Data show a three-way interaction between target, target angle, and right-hand options on overall p(RH).

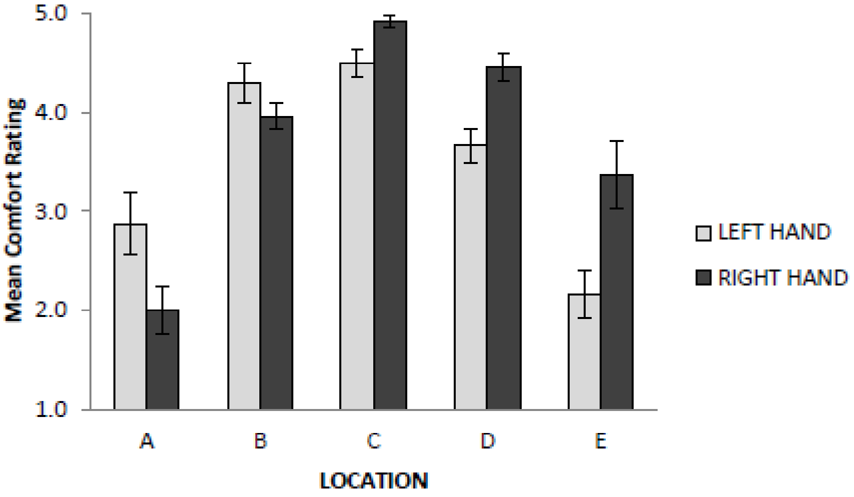


Figure 17. Mean comfort rating of initial grasps as a function of location (A-E) and of hand (Left and Right). Data show a two-way interaction between location and hand.

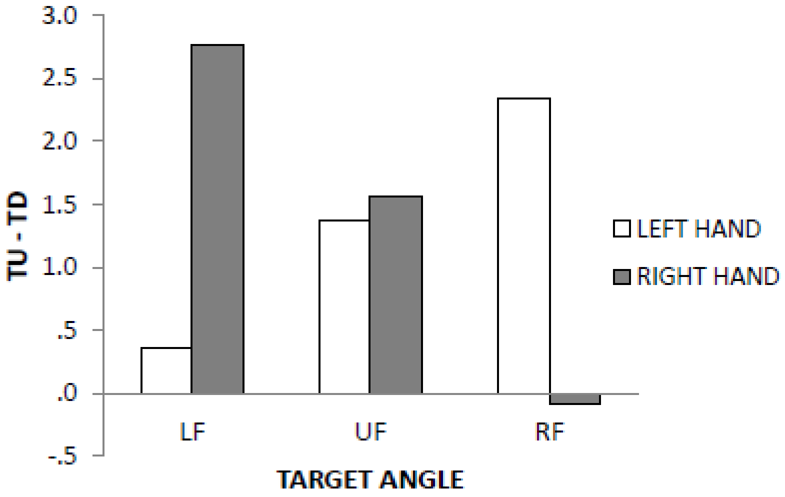


Figure 18. Difference between mean comfort ratings of thumb-up (TU) and thumb-down (TD) postures as a function of target angle (LF = left-facing, UF = up-facing, RF = right-facing) and hand (Left or Right). Data are collapsed across target to show a three-way interaction between final grasp orientation, target angle, and hand.

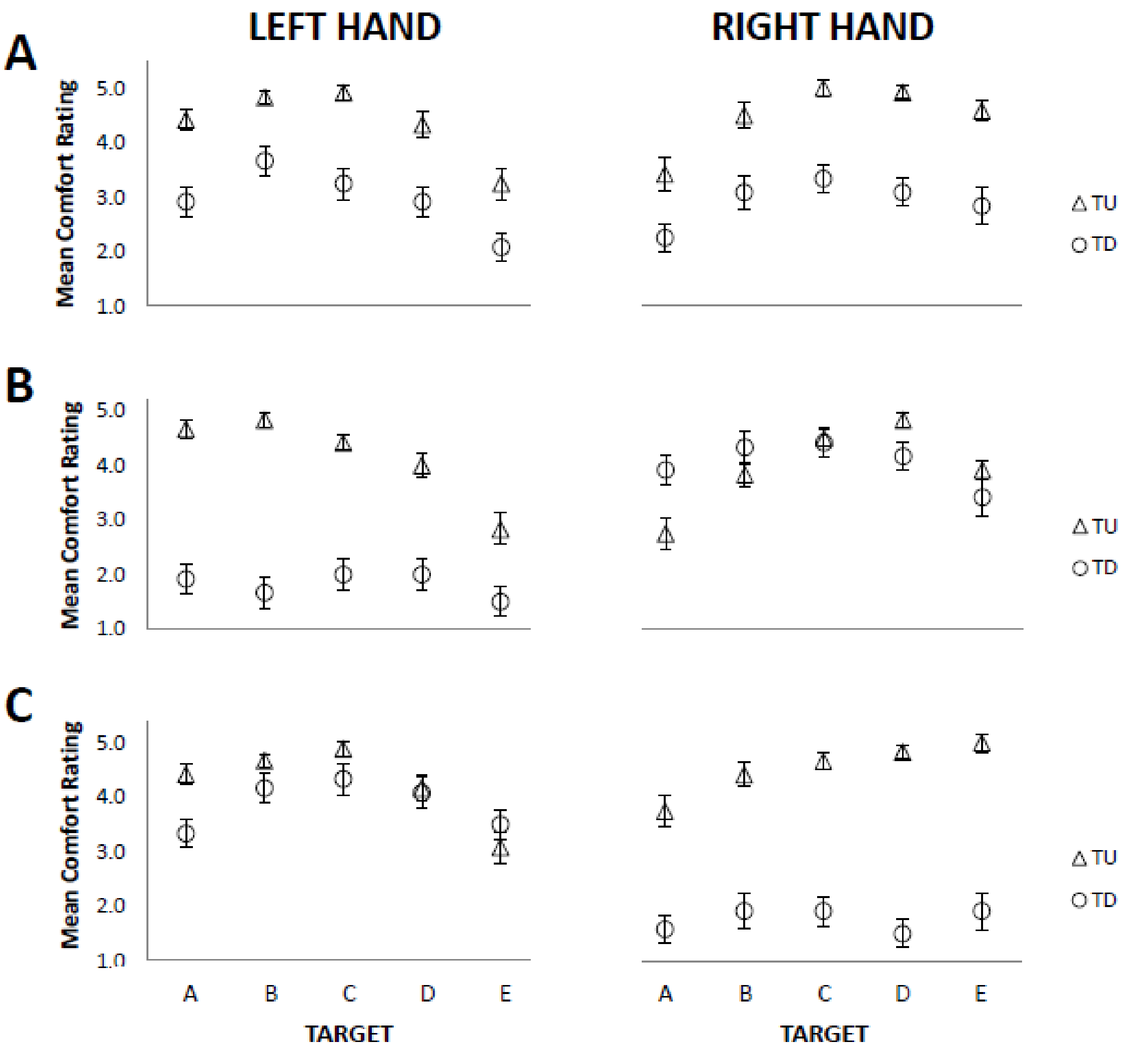


Figure 19. Mean comfort ratings as a function of target (A-E) and final grasp orientation (Thumb-up {TU} or Thumb-down {TD}). Left and right panels show data for the left and right hands, respectively. The data reflect a four-way interaction between hand, target, target angle, and final grasp orientation.

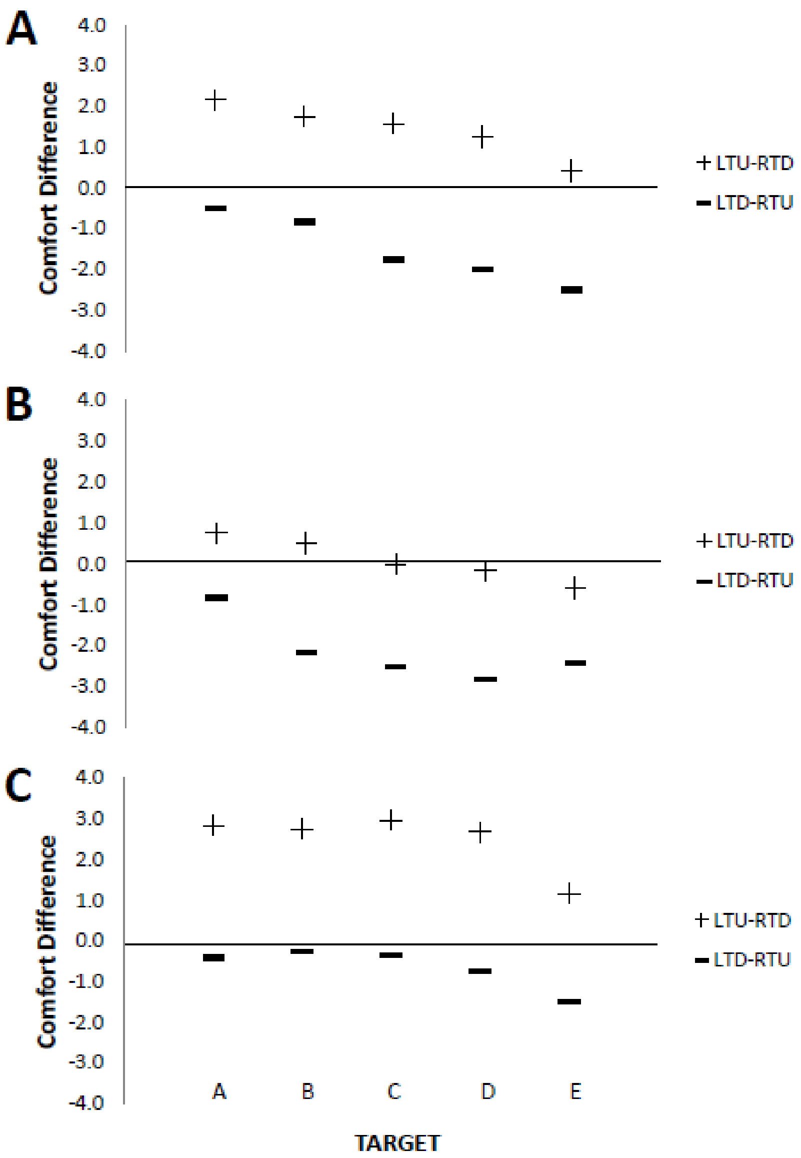


Figure 20. Differences of mean comfort ratings as a function of target (A-E) and target angle (Up-facing, panel A; Right-facing, panel B; and Left-facing, panel C). Data show that the comfort of left-hand thumb-up (LTU) postures became more similar to the corresponding right-hand thumb-down (RTD) postures in the right-facing group (panel B) and less similar in the left-facing group (panel C). The opposite pattern is seen for the left-hand thumb-down (LTD) postures relative to the corresponding right-hand thumb-up (RTU) postures.

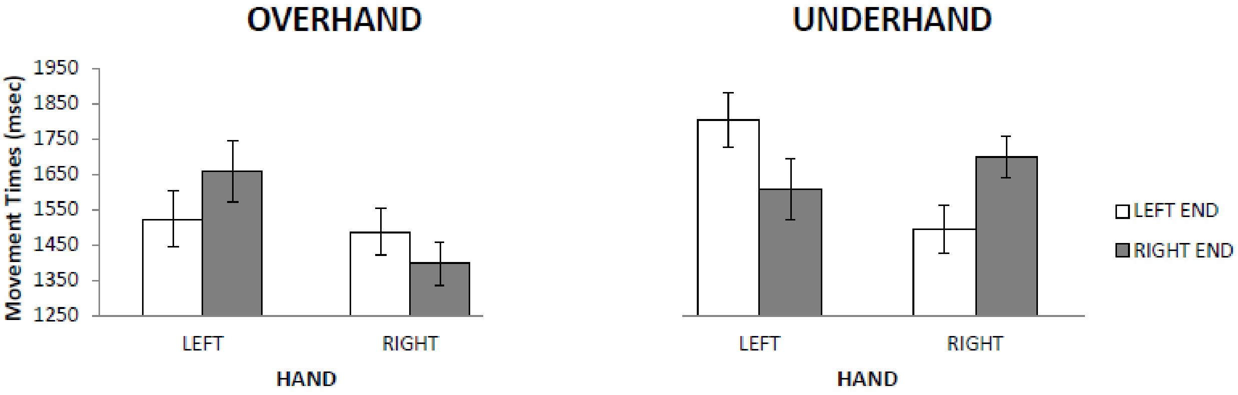


Figure 21. Mean movement times for dowel transports from the platform to the target in the Overhand and Underhand initial-grasp groups. Data show a three-way interaction between hand (Left or Right), which dowel end (Left / White or Right / Black) was inserted, and initial grasp (Overhand or Underhand). Error bars are represent ± 1 standard error of the mean.

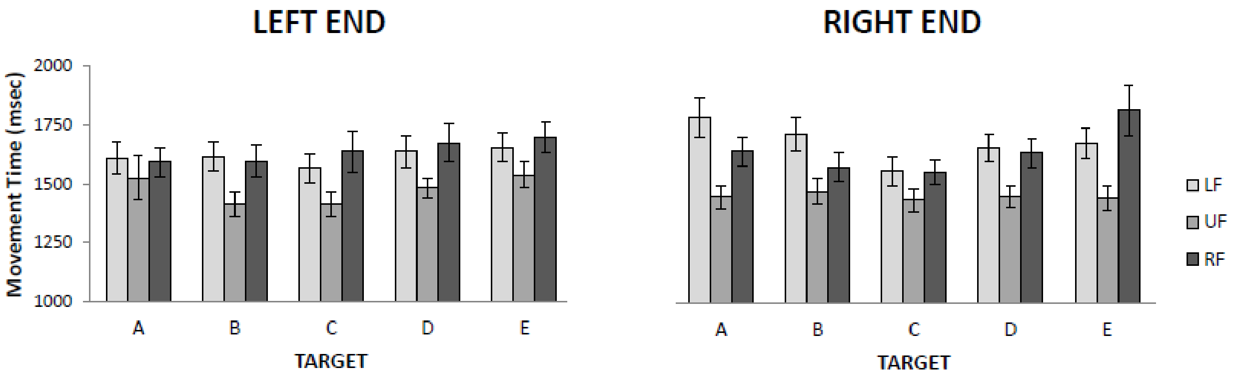


Figure 22. Mean movement times for dowel transports from the platform to the target when the Left / White end (left panel) and Right / Black end (right panel) of the dowel was inserted. Data show a three-way interaction between which dowel end was inserted, target (A-E), and target angle (LF = left-facing, UF = up-facing, and RF = right-facing). Error bars represent ± 1 standard error of the mean.

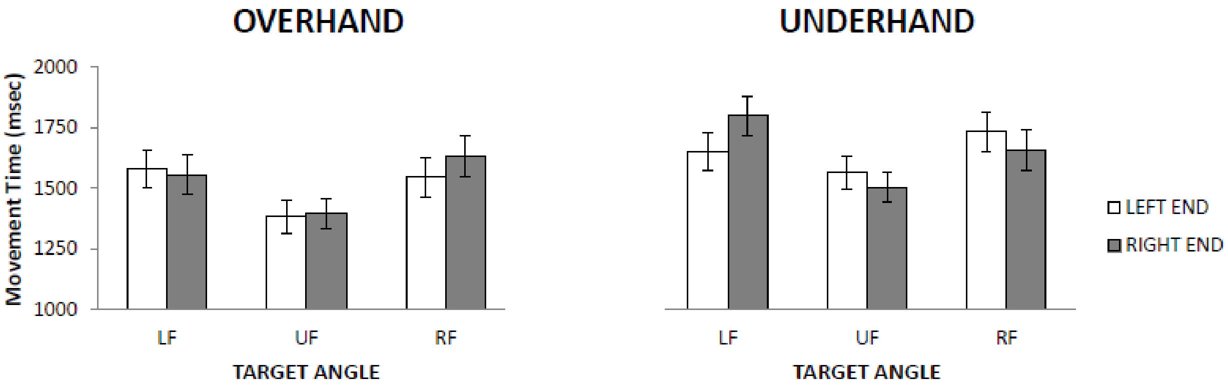


Figure 23. Mean movement times for dowel transports from the platform to the target in Overhand (left panel) and Underhand (right panel) initial-grasp groups. Data show a three-way interaction between target angle (LF = left-facing, UF = up-facing, RF = right-facing), which dowel end (Left / White or Right / Black) was inserted, and initial grasp groups (Overhand or Underhand). Error bars represent ± 1 standard error of the mean.

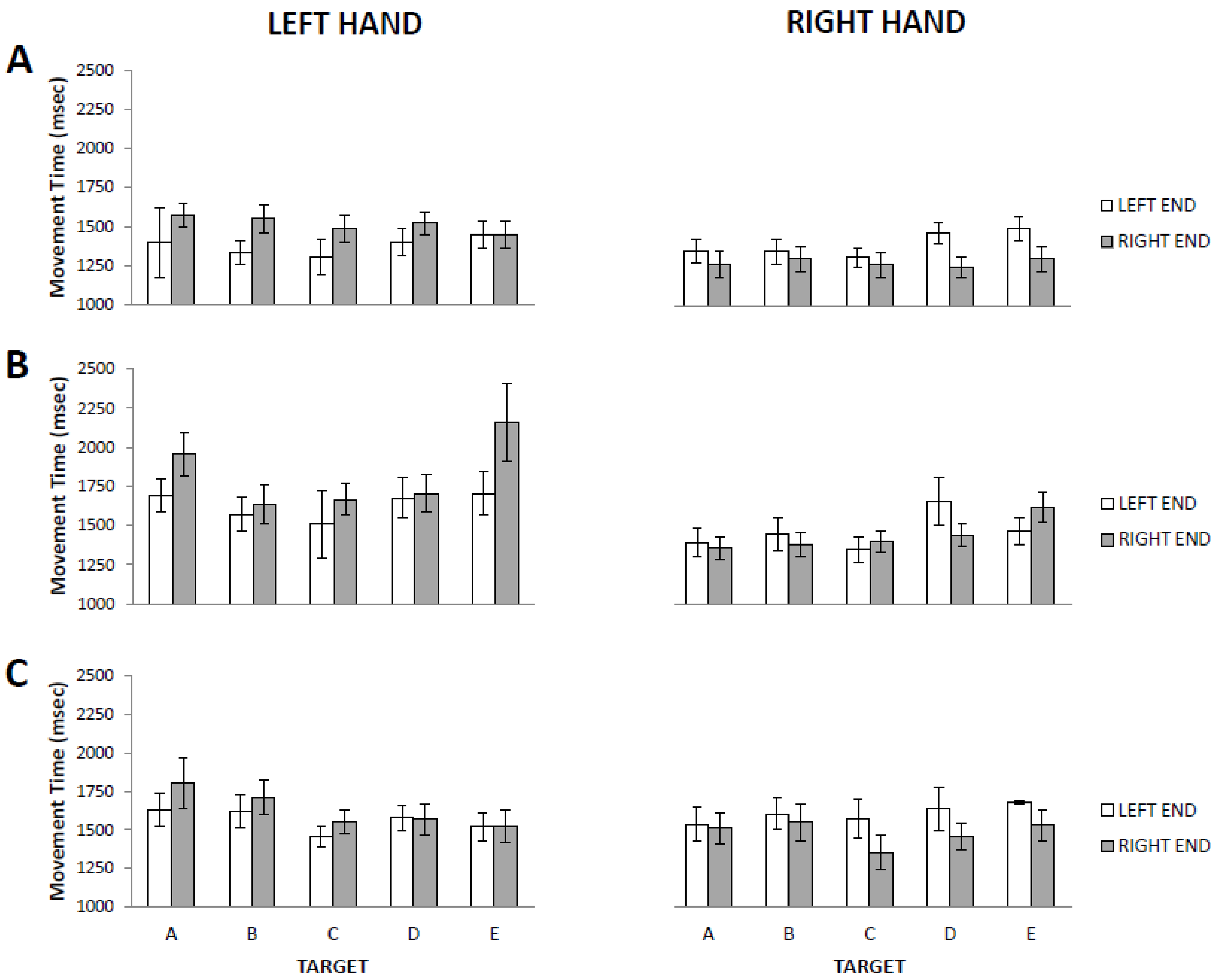


Figure 24. Mean movement times for dowel transports from the platform to the target in the Overhand initial-grasp group. Data are plotted as a function of target (A-E), which dowel end (Left / White or Right / Black) was inserted, and hand (Left or Right). Rows A, B, and C show times from the up-facing, right-facing, and left-facing target conditions, respectively. Error bars represent ± 1 standard error of the mean.

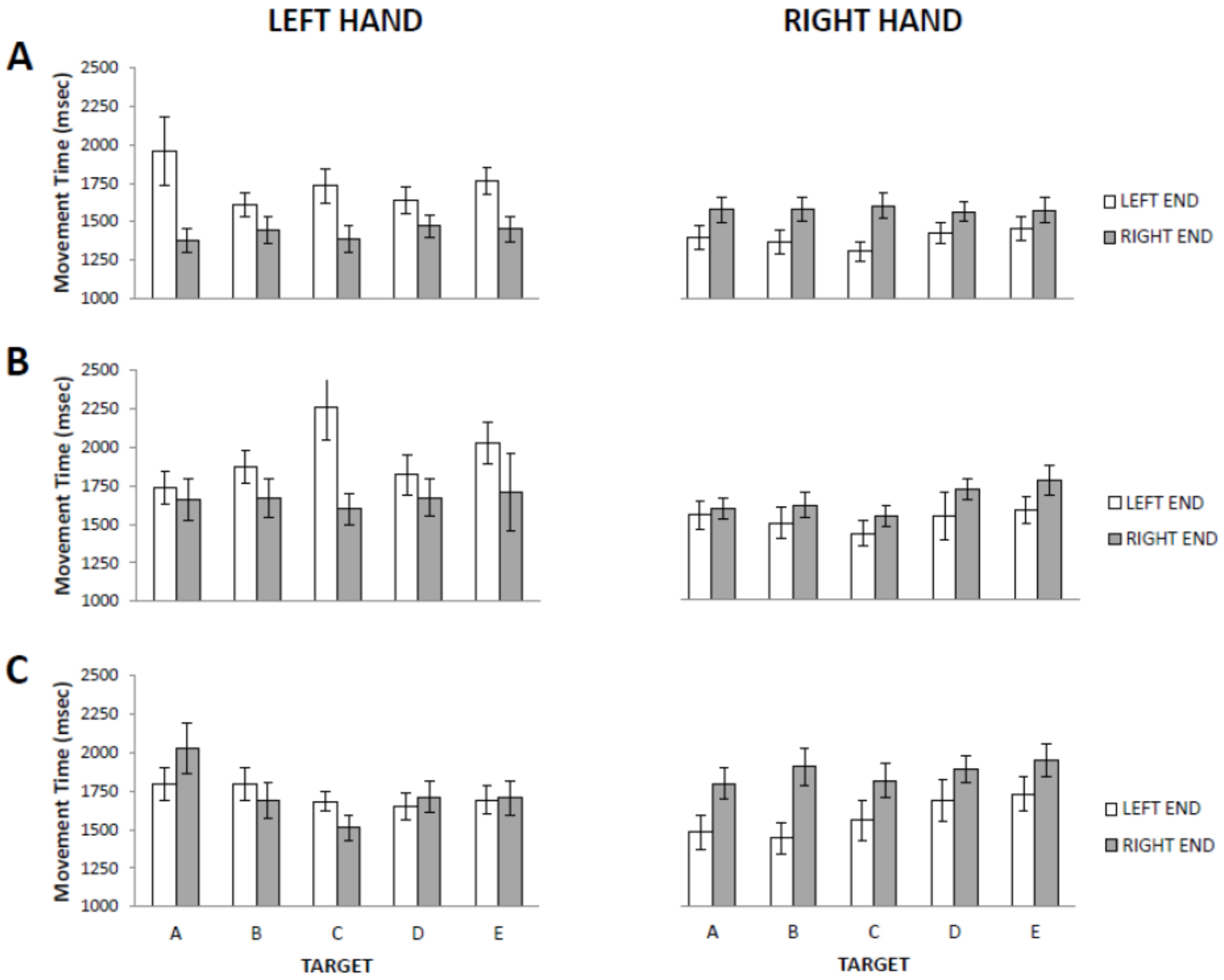


Figure 25. Mean movement times for dowel transports from the platform to the target in the Underhand initial-grasp group. Data are plotted as a function of target (A-E), which dowel end (Left / White or Right / Black) was inserted, and hand (Left or Right). Rows A, B, and C show times from the up-facing, right-facing, and left-facing target conditions, respectively. Error bars represent ± 1 standard error of the mean.

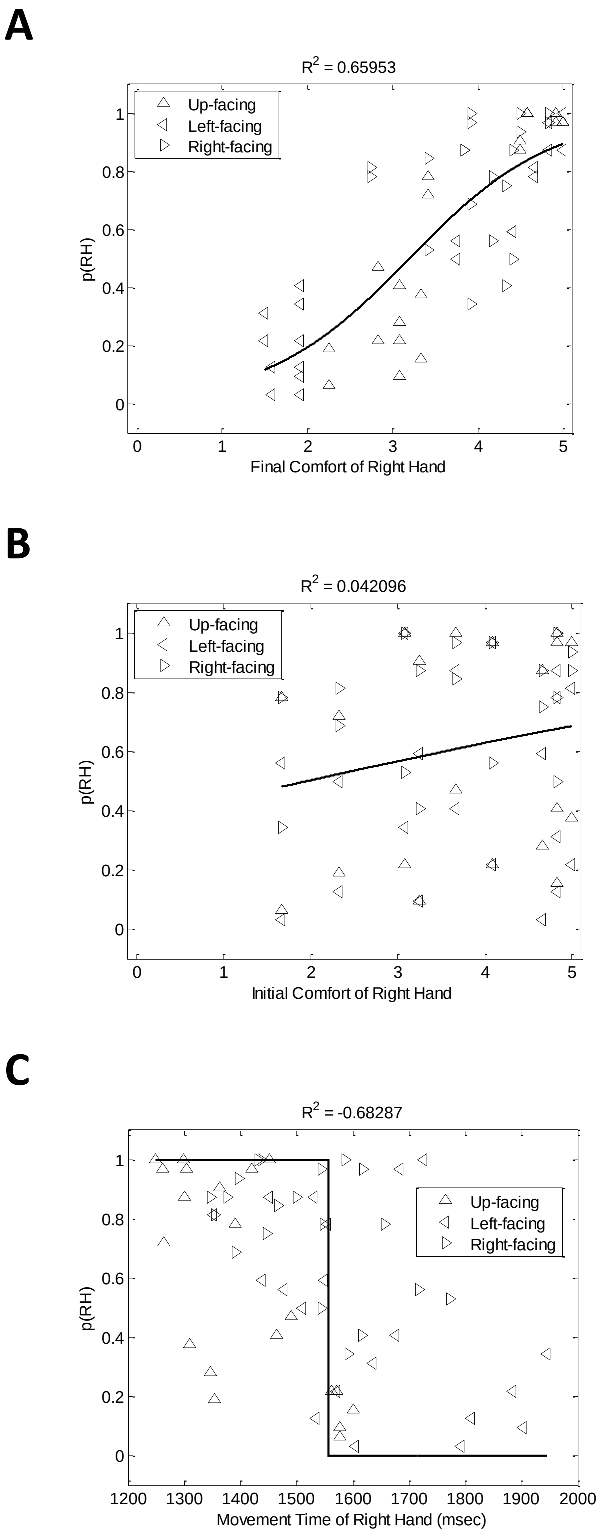


Figure 26. Probability, p(RH), that the right hand was chosen in Experiment 3A as a function of mean final comfort (panel A), mean initial comfort (panel B), and mean movement time (panel C) for the right hand options. Up-, left-, and right-facing triangles represent up-, left-, and right-facing targets, respectively. Regression line shows the best least-squares fit of the logistic function.

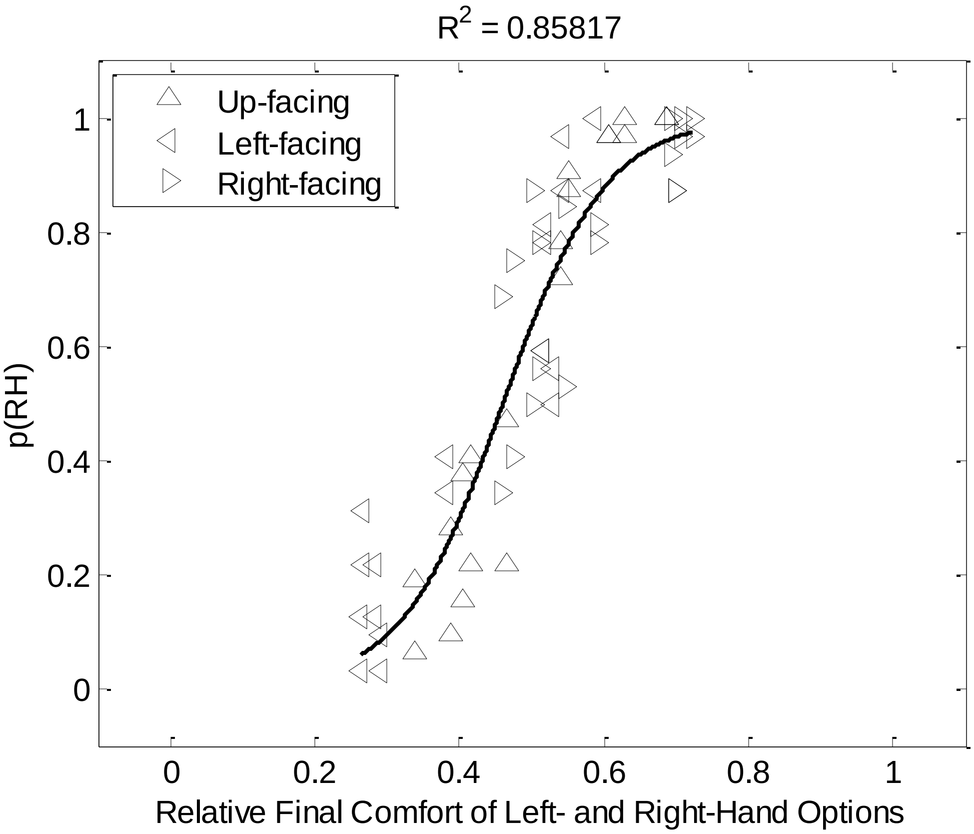


Figure 27. Probability, p(RH), that the right hand was chosen as a function of the relative comfort of left- and right-hand options; x-values represent the predictions of the Luce Choice Axiom. Up-, left-, and right-facing triangles represent up-, left-, and right-facing targets, respectively. Regression line shows the best least-squares fit of the logistic function.

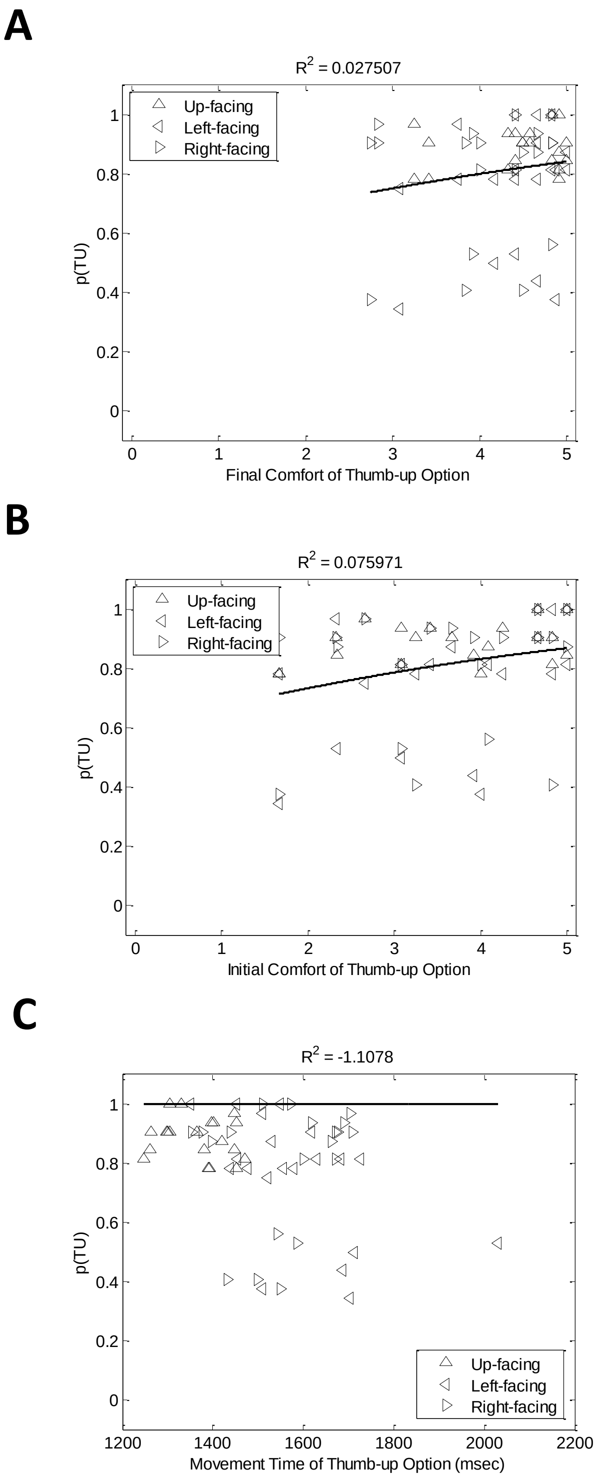


Figure 28. Probability, p(TU), that a grasp that led to a thumb-up final posture was chosen in Experiment 3A as a function of mean final comfort (panel A), mean initial comfort (panel B), and mean movement time (panel C) for the thumb-up option. Up-, left-, and right-facing triangles represent up-, left-, and right-facing targets, respectively. Regression line shows the best least-squares fit of the logistic function.

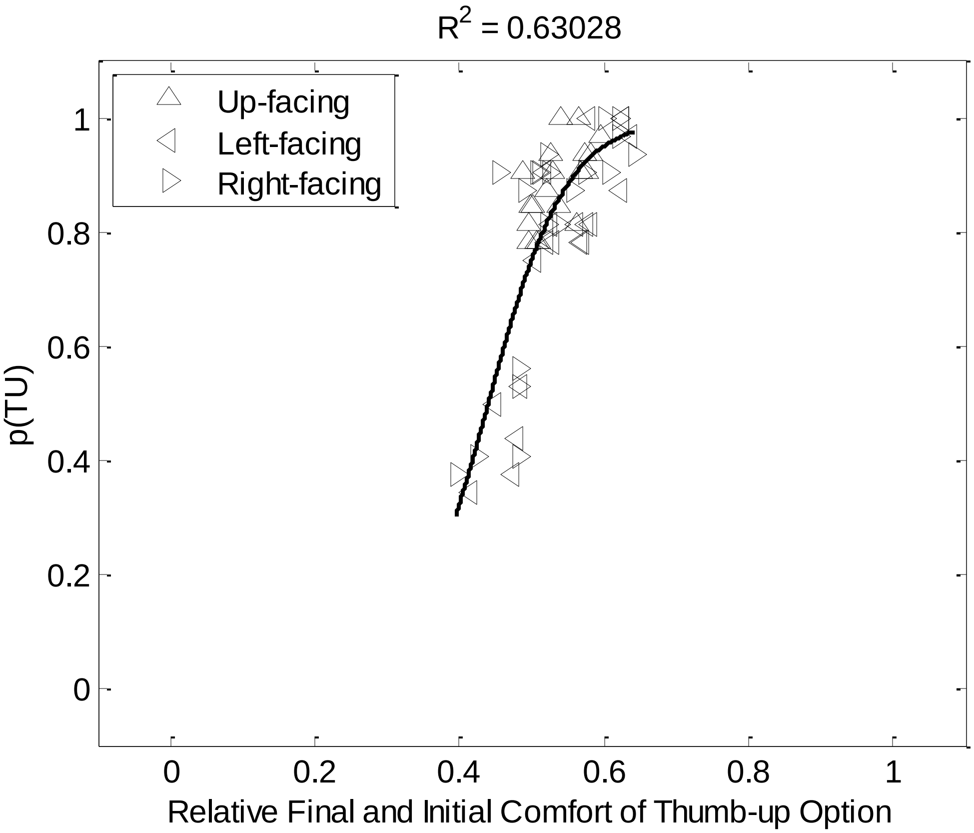


Figure 29. Probability, p(TU), that an initial grasp was chosen that led to a thumb-up final posture as a function of the relative final plus initial comfort of the thumb-up option; x-values represent the predictions of the Luce Choice Axiom. Up-, left-, and right-facing triangles represent up-, left-, and right-facing targets, respectively. Regression line shows the best least-squares fit of the logistic function.

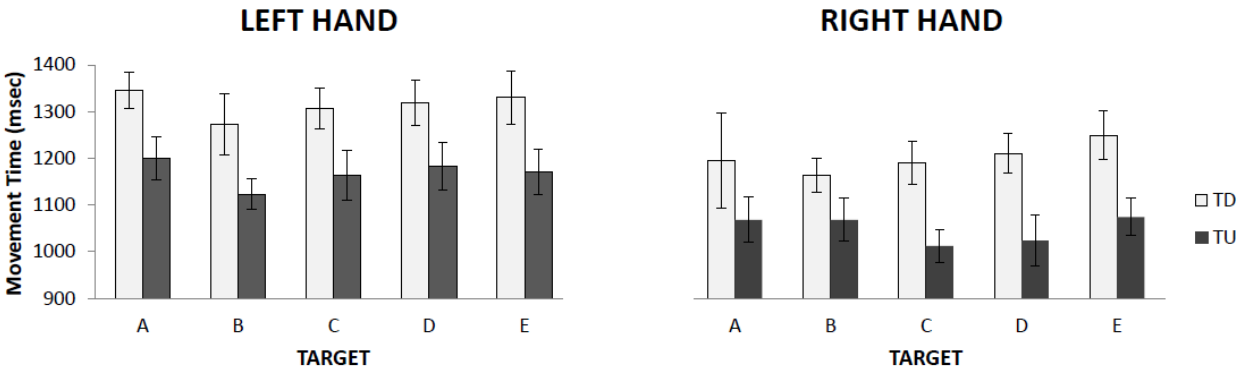


Figure 30. Mean inter-target movement times (± 1 SE) as a function of hand (Left or Right), grasp orientation (Thumb-up {TU} or Thumb-down {TD}), and target (A-E). Data are pooled across both blocks because the block variable did not interact with hand or orientation.

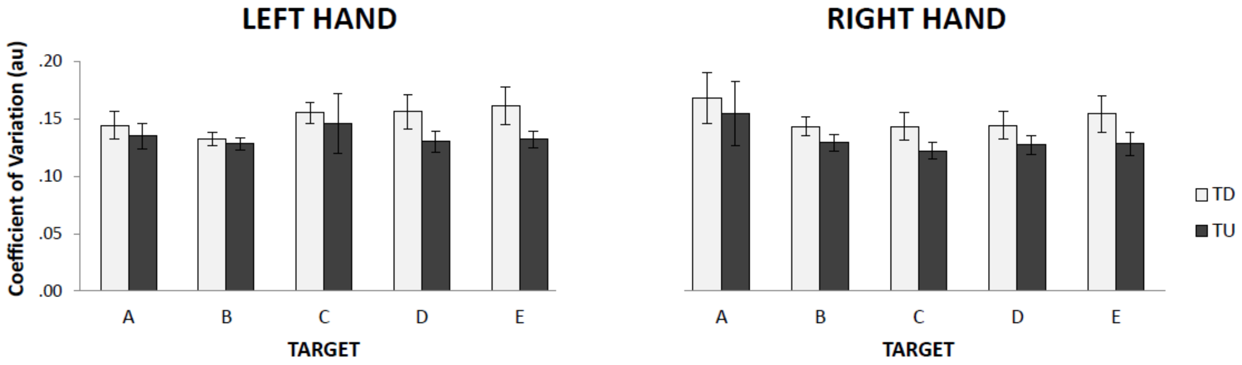
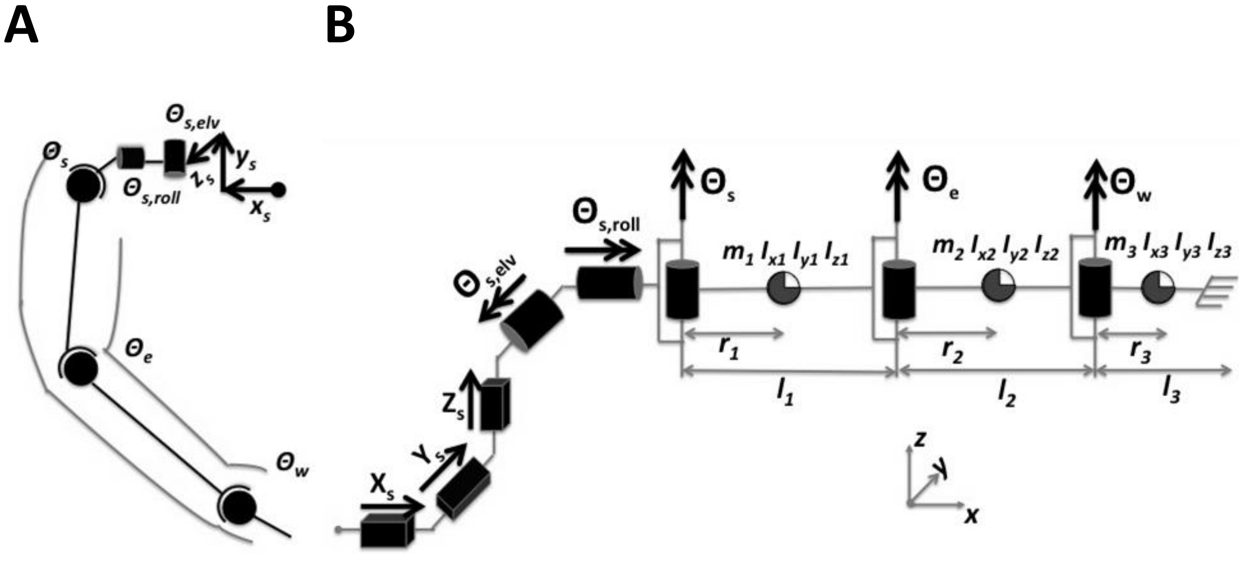


Figure 31. Mean inter-target movement coefficients of variation (± 1 SE) as a function of hand (Left or Right), grasp orientation (Thumb-up {TU} or Thumb-down {TD}), and target (A-E). Data are pooled across both blocks because the block variable did not interact with hand or orientation.

Appendix Figure



Appendix Figure. The human arm modeled as a 3-link system with three translational DOFs and five rotational DOFs (panel A). The mechanical equivalent of the human arm model in zero configuration (panel B).

Tables

Table 1

Order of experimental conditions.

Order	Condition/Block	Trials	Limb
1	Practice Choice	32	Both
2	Choice	80	Both
3	Non-choice	32	Nondominant
4	Non-choice	32	Dominant
5	Non-choice	32	Nondominant
6	Non-choice	32	Dominant

Note. The experimental design was fully within-subjects. N=10.

Table 2

Number of final comfort violations as a function of the given instructions for all participants who had any violation

Given	Left Hand		Right Hand		Overhand		Underhand		
Participant	W	B	W	B	W	B	W	B	Total
2	0	0	0	0	3	1	1	0	5
3	0	0	0	0	0	0	0	1	1
6	2	0	1	0	1	0	1	1	6
7	0	0	1	0	0	0	0	0	1
9	0	0	1	0	2	1	0	3	7
10	1	0	3	0	0	0	3	2	9
12	0	0	0	0	0	1	0	0	1
13	0	0	0	0	0	0	2	0	2
15	0	0	0	0	0	1	1	0	2
Total	3	0	6	0	6	4	8	7	34

Note. Data are collapsed across targets. W = white end down; B = black end down. There were 16 participants altogether. The number of trials per participant was 40. The number of trials per given condition was 5. The total number of trials across all participants was 635; 5 trials were skipped due to clerical error.

Table 3

Demographic information for choice groups in Experiment 3A

Group	Height (cm)	Weight (kg)	Handedness
Hand-Specified (HS)			
Mean	172.09	65.20	10.75
SD	7.39	6.62	0.58
Grasp-Specified (GS)			
Mean	167.48	66.45	10.94
SD	11.18	11.50	0.25
Hand-Specified Speeded (HSS)			
Mean	165.02	62.71	10.25
SD	8.61	10.01	1.73
Grasp-Specified Speeded (GSS)			
Mean	170.89	68.55	10.31
SD	12.23	15.19	0.95
Overall Mean	168.87	65.73	10.56
Overall SD	10.20	11.19	1.05

Note. Handedness measure is the mean number of Edinburgh Handedness Inventory items participants endorsed as right-limb tasks. Groups HS, GS, HSS, and GSS contained 11, 8, 12, and 15 females, respectively. N=16.

Table 4

Demographic information for comfort rating groups in Experiment 3B.

Group	Height (cm)	Weight (kg)	Handedness
Up-facing Target (UFT)			
Mean	169.12	63.31	10.50
SD	8.96	9.07	0.67
Right-facing Target (RFT)			
Mean	173.78	67.47	10.58
SD	10.13	15.36	1.00
Left-facing Target (LFT)			
Mean	169.33	69.89	10.42
SD	13.67	14.17	0.67
Initial Grasp (IG)			
Mean	175.15	64.52	9.17
SD	11.89	14.55	2.66
Overall Mean	171.85	66.82	10.17
Overall SD	11.29	13.30	1.56

Note. Handedness measure is the mean number of Edinburgh Handedness Inventory items participants endorsed as right-limb tasks. Groups UFT, RFT, LFT, and IG had 7, 6, 8, and 8 females, respectively. N=12.

Table 5

Performance of models for grasp-specified / hand-choice groups

Model	DV	Factors in Model	R^2	*a*	*b*	Inflection Point Coordinates	Slope
1	p(RH)	FC *	.86	.46	.07	(.46, .50)	3.55
2	p(RH)	FC, MT *	.77	.49	.03	(.49, .50)	8.33
3	p(RH)	FC, IC *	.71	.48	.05	(.48, .50)	5.05
4	p(RH)	FC	.66	3.97	.84	(3.20, .50)	0.30
5	p(RH)	MT *	.52	.50	.50	(.50, .50)	9.04
6	p(RH)	FC, IC, MT *	.27	.67	.07	(.67, .50)	3.52
7	p(RH)	IC *	.07	.42	.20	(.42, .50)	1.26
8	p(RH)	IC	.04	1.95	3.88	(1.95, .50)	0.06
9	p(RH)	FC, IC *	.01	.62	.22	(.62, .50)	1.13
10	p(RH)	MT	-.68	1555.60	.00	(1555.60, .50)	172.22

Note. Models formed according to LCA are denoted with an asterisk (*). Models are ranked from best to worst performers by the amount of variance they explained. DV = Dependent variable; FC = Final comfort; MT = Movement time; IC = Initial comfort. When movement times were normalized, the R^2 for the MT factor alone was .24. Normalizing did not affect the variance explained by FC or IC alone.

Table 6

Performance of models for hand-specified / grasp-choice groups

Model	DV	Factors in Model	R^2	*a*	*b*	Inflection Point Coordinates	Slope
1	p(TU)	EC, IC *	.63	.44	.05	(.44, .50)	4.62
2	p(TU)	MT *	.56	.52	.03	(.52, .50)	9.03
3	p(TU)	EC, IC, MT *	.48	.46	.03	(.46, .50)	7.43
4	p(TU)	EC *	.31	.40	.13	(.40, .50)	1.97
5	p(TU)	IC *	.29	.33	.11	(.33, .50)	2.26
6	p(TU)	EC, MT *	.09	.37	.10	(.37, .50)	2.27
7	p(TU)	IC	.07	-1.44	3.40	(-1.44, .50)	0.07
8	p(TU)	IC, MT *	.06	.36	.10	(.10, .50)	2.52
9	p(TU)	EC	.03	-.91	3.53	(-.91, .50)	0.07
10	p(TU)	MT	-1.10	1204.00	.00	(1204.00, .50)	177.73

Note. Models formed according to LCA are denoted with an asterisk (*). Models are ranked from best to worst performers by the amount of variance they explained. DV = Dependent variable: FC = Final comfort; MT = Movement time; IC = Initial comfort. When movement times were normalized, the R^2 for the MT factor alone was .10. Normalizing did not affect the variance explained by FC or IC alone.

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CURRICULUM VITAE, AUGUST 2013

Education

Pennsylvania State University, University Park, PA	Ph.D.	expected August 2013
Pennsylvania State University, University Park, PA	M.S.	awarded May 2011
University of California at Los Angeles, Los Angeles, CA	B.S.	awarded June 2007

Awards

Penn State Graduate Exhibition Second Runner-Up in Social and Behavioral Sciences	2013
National Science Foundation Graduate Research Fellowship Program: Honorable mention	2010
Pennsylvania State University Social Science Research Institute Grant: Collaborating Investigator	2009
National Scholars Honor Society	2009
Nominated Collegiate Scholar International Golden Key International Honor Society (declined)	2007
President of Psi Chi National Honor Society in Psychology at UCLA	2006 - 2007
Golden Key International Honor Society	2007
UCLA Departmental Highest Honors in Psychology	2007
UCLA Dean’s Honors List	2006 - 2007
UCLA University Merit Grant Recipient	2005
Saddleback Dean’s List	2003 - 2005
Saddleback Honors Program	2005
Saddleback Community College Scholarship Foundation Award	2005
California Governor’s Scholarship Award	2003

Publications

Coelho, C.J., Studenka, B.E. & Rosenbaum, D.A. (in revision). Comfort trumps handedness in object manipulation.

Rosenbaum, D.A., Chapman, K.C., Coelho, C.J., Gong, L. & Studenka, B.E. (in press). Choosing actions. Frontiers in Cognition.

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