

BIMANUAL PREHENSION TO A SOLITARY TARGET

By

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ABSTRACT

Grasping and functionally interacting with a relatively large or awkwardly shaped object requires the independent and cooperative coordination of both limbs. Acknowledging the vital role of visual information in successfully executing any prehensile movements, the present study aimed to clarify how well existing bimanual coordination models (Kelso et al, 1979; Marteniuk & Mackenzie, 1980) can account for bimanual prehension movements targeting a single end-point under varying visual conditions. We therefore, employed two experiments in which vision of the target object and limbs was available or unavailable during a bimanual movement in order to determine the affects of visual or memory-guided control (e.g. feedback vs. feed forward) on limb coordination.

Ten right-handed participants (mean age = 24.5) performed a specific bimanual prehension movement targeting a solitary, static object under both visual closed loop (CL) and open loop 2s delay (OL2) conditions. Target location was varied while target amplitude remained constant. Kinematic data (bimanual coupling variables) indicated that regardless of target location, participants employed one of two highly successful movement execution strategies depending on visual feedback availability. During visual (CL) conditions participants employed a ‘dominant-hand initiation’ strategy characterized by a significantly faster right-hand (RH) reaction time and simultaneous contact of the target with both hands. In contrast, when no visual feedback was available (OL2), participants utilized a ‘search and follow’ strategy characterized by limb coupling at movement onset and a reliance on the dominant RH to contact the target ~62 ms before the left.

In conclusion, the common goal parameters of targeting a single object with both hands are maintained and successfully achieved regardless of visual condition. Furthermore, independent programming of each limb is undeniably evident within the behaviours observed providing support for the neural cross-talk theory of bimanual coordination (Marteniuk & Mackenzie, 1980). Whether movement execution is visually (CL) or memory-guided (OL2) there is a clear preference of RH utilization possibly due to its dynamic and/or hemispheric advantages in controlling complex motor behaviours (Gonzalez et al., 2006). Therefore, we propose that bimanual grasping to a solitary target is possibly governed globally by a higher-level

structure and successful execution is achieved via independent spinal pathway modulation of limbs.

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DEDICATION

I like would to dedicate this project to Canada, a magical place with the most generous and warm people on earth. Thank you all.

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LIST OF ABBREVIATIONS

RT	<i>Reaction Time</i>
MT	<i>Movement Time</i>
PV	<i>Peak Velocity</i>
PA	<i>Peak Acceleration</i>
TPA	<i>Time to Peak Acceleration</i>
TPV	<i>Time to Peak Velocity</i>
BPGA	<i>Bimanual Peak Grip Aperture</i>
TBPGA	<i>Time to Bimanual Peak Grip Aperture</i>
CNS	<i>Central Nervous System</i>
PAM	<i>Perception-Action Model</i>
PCM	<i>Planning-Control Model</i>
IREDs	<i>Infrared Emitting Diodes</i>
OL2	<i>Visual Open Loop 2s Delay</i>
CL	<i>Visual Closed Loop</i>
LH	<i>Left Hand</i>
RH	<i>Right Hand</i>
PG1	<i>Bimanual Precision 1 Grip</i>
PG2	<i>Bimanual Precision 2 Grip</i>
POW	<i>Bimanual Power Grip</i>

Chapter I

Introduction

The ability of humans to co-ordinate two hands during functional activities is a requirement for numerous daily tasks. That is, we frequently necessitate bimanual movements. Borne out of this necessity, a vast expansion in the understanding of relationships between the hands at both behavioral and neural levels has occurred in recent years.

Conflicting theoretical models have been developed for discrete bimanual coordination; one proposed by Kelso, Southard and Goodman (1979) and one by Marteniuk and Mackenzie (1980). Kelso et al.'s (1979) model predicts a close temporal relationship between hands during bimanual tasks, even when each hand is required to move different distances. In opposition, Marteniuk and Mackenzie's model predicts low temporal associations between limbs due to the issuing of separate motor commands to each limb. Despite support for Kelso et al.'s (1979) model during bimanual reach-to-grasp movements to two targets (Jackson, Jackson, & Kritikos, 1999), it is argued that these theoretical models fail to extend to all common goals of bimanual movements as they were developed utilizing manual aiming and rhythmical tapping tasks. To the author's knowledge no research has been conducted to clarify limb coordination during a functional two-handed prehension movement intended to manipulate a solitary static target (e.g. lifting a large vase) or, indeed, the relevance of the existing limb coupling theories to such aiming tasks.

Thus, we proposed the following study, consisting of 3 experiments. The pilot experiment attempted to assess the extent to which present limb synchronization models extend to bimanual reach-to-grasp movements targeting a single object. Additionally, we aimed to clarify whether varying types of bimanual grasps demonstrate similar kinematic characteristics to that of their unimanual counterparts (Jeannerod, 1981). As acknowledged by Casteillo, Bennett and Paulignan (1993), the organization in processing a single-handed precision grip would seem to differ

from that of a power grip. It is plausible to suggest, therefore, that this notion will apply equally in a bimanual setting.

The final two experiments were designed to examine how visual processing affects limb coordination during these specific bimanual prehension tasks. In 1992, Goodale and Milner proposed a division of labor in the visual pathways between a dorsal stream, specialized for the visual control of action, and a ventral stream, dedicated to the perception of the visual world. Although not significantly different from Goodale and Milner's perception-action model, Glover (2004) introduced a new advanced approach of how these two streams process the visual information known as the planning and control model.

Development and support for both these models lie in neurological, neuropsychological, and behavioral studies. Interestingly, virtually all studies have involved right-handed subjects using their dominant hand, which presumably is controlled by the left hemisphere. Recently, it has been suggested that, regardless of handedness, the left hemisphere plays a special role in the visual control of skilled grasping movements (Gonzalez, Ganel, & Goodale, 2006). However, it is not yet clear whether this advantage extends beyond unimanual grasping to other visually guided actions such as bimanual prehension. Indeed, this advantage lead us to speculate that bimanual reach-to-grasp movements processed and executed solely by the dorsal stream (visual control) may demonstrate higher levels of limb synchronization compared to those completed through the ventral pathway. To this end, we aimed to clarify whether available visual feedback (target and limbs) affects limb coordination during a bimanual prehension task. Specifically, we intended to segregate utilization of the ventral and dorsal visual processing streams (perception and action/planning and control) in order to develop further our understanding of co-operative limb movements to a single endpoint.

Literature review

General Context - Bimanual Coordination

For numerous years' movement scientists have been fascinated with the relative influence of one limb on the other. Indeed, Woodworth (1899) was possibly the first to observe effortless execution of simultaneous movements between right and left hands. When each hand simultaneously executes the same task a facilitating effect between the limbs seems to occur. Furthermore, mutual effects are also observed when each hand simultaneously completes a different task (Woodworth, 1899). Following this pioneering work, researchers continued to examine co-mutual effects through syncopated rhythms of fingers, where subjects attempted to tap each hand at the same and different tempos (Davis, 1904; Farnsworth & Poynter, 1931; & Langfield, 1915). Generally, results indicated substantial difficulty in retaining individual hand tempos when both hands tap at the same time, verifying Woodworth's original observations. More recent tapping studies by Klapp, Hill, Tyler, Marten, Jagacinski, and Jones (1985) offer empirical support for earlier polyrhythmic paradigms by indicating that it is the disturbance of relative time, or the non-harmonic nature of tapping rhythms (e.g. 3:2 & 5:4) that lead to mutual interference.

Early literature surrounding this "limb coupling" phenomena offered only instinctual explanations. In 1904, Davis concluded that there must be a "close connection between different parts of the muscular system through neural means". None more informative was Langfield (1914), who stated that limb interference was due to an "innate coordination". Among the first to expand upon earlier explanations, Peters (1981) utilized a tapping paradigm to present evidence for a supraordinate control mechanism accountable for the limb coupling effect. The novel approach by Yamanishi, Kawato, and Suzuki (1980), attributing limb linkage to oscillatory properties of the nervous system was perhaps the least symbolic advance. Nonetheless, this dynamic approach has been supported by more recent oscillatory tapping studies concerning the formation of interlimb patterns (Scholz & Kelso, 1989), and changes in such patterns relative to loss of pattern stability (Scholz & Kelso, 1990).

The efficacy of tapping studies for the exploration of interlimb coupling stems from the ease with which features of movement patterns may be manipulated. It is, however, this strength that also serves as a weakness for such paradigms. First, the simplistic task demands do not reflect motor system complexities, and second, subjects are “instructed” to move their fingers at differing rates, which produces the very effects that researchers oftentimes investigate.

An alternative approach, which has not received the historical popularity of tapping paradigms, is bimanual pointing tasks. Despite this reputation, it was bimanual pointing paradigms that led to the foundations of current contrasting theoretical bimanual coordination models: one proposed by Kelso, Southard, and Goodman (1979) and another by Marteniuk and Mackenzie (1980). These distinct explanations and, hence, the underlying mechanisms responsible for interlimb coordination remain hotly disputed. The essence of the debate concerns whether the brain specifies the states of individual muscles separately in each limb or whether the activity of muscle groups across limbs is coordinated as part of one functional structure.

Models of Bimanual Action

In 1979, Kelso and colleagues utilized a bimanual aiming task over different distances (6cm & 24cm) to assess the strength of upper limb synchronization. In the first of three experiments reported, subjects were required to move their index fingers from a centrally located position so that lateral targets would be touched as quickly and as accurately as possible. No other instructions were provided on how to organize the movements. Two-handed movements were initiated almost simultaneously with the largest interlimb difference in reaction time (RT) being 8 ms. In the two-handed conditions within-subject correlations for RT between left and right hands ranged from 0.95 to 0.97. In addition, movement time (MT) data also revealed that subjects' hands traveled at different speeds to different target endpoints. A main finding of the study was that, despite each limb moving to targets of different distances & traveling at entirely different speeds, time to peak velocity (TPV) and time to peak acceleration (TPA) for each limb showed a synchronous pattern. Calculated over six trials for each subject, mean time difference in peak velocity for each hand was reported at 9ms. Likewise, during the positive peak

acceleration (14 ms) and negative peak acceleration phases (4 ms) of the aiming movement, interlimb variability was remarkably low (Kelso et al., 1979).

In light of these findings Kelso and colleagues (1979) concluded that the brain sends signals to muscle groupings superimposed across the two limbs. Timing was considered the essential variable in bimanual coordination control as it reflects the overall behavioral organization during action. The authors interpreted these data as empirical support for the theoretical notion that actions are controlled via coordinative structures (Turvey, 1977), a concept originally proposed as an answer to the degrees of freedom problem in the human motor system (Bernstein, 1967). Moreover, during bimanual tasks, rather than being controlled independently, the limbs are controlled via across-limb functional groups of muscles. In turn, formation of these muscle action groups reduce the cognitive load placed upon the executive system. Kelso et al. (1979) also suggested that nonessential variables, which change in scale during the action, such as distance and force, provide flexibility for the system to search for optimal values and are free to vary across the limbs.

Marteniuk and Mackenzie (1980) offered an alternative view on bimanual coordination. The authors conducted a series of experiments that required subjects to aim at a 1 mm target, with each hand holding a weighted stylus. Utilizing a similar paradigm to Kelso et al. (1979), subjects executed aiming movements under conditions in which limbs were required to move the same or different distances so that the lateral targets (10 & 30 cm) can be reached. Again, researchers did not give instructions related movement synchronicity; subjects were only instructed to move to the targets as quickly and as accurately as possible.

Strong correlations in temporal sequencing between limbs during the same-distance conditions supported those results of Kelso et al. (1979). No such associations were obtained, however, when the limbs were required to travel different distances to the targets. For example, RT of the left hand was more rapid than the right hand when the left moved the stylus over a greater distance, and MT was quicker for the hand moving to the closer target than that of the hand moving to the farther target. In fact, during different-distance conditions, 25% of total MT differences between each limb exceeded 50 ms. Despite acknowledging significant within-subject correlations for RT (range of $r = 0.96 - 0.98$) and MT (range of $r =$

0.72 – 0.82) of the left and right hands, the authors argued that individual subject means demonstrated only a consistent difference in the relationship between hands. For instance, during same-distance conditions to lateral targets, half the subjects demonstrated quicker MTs with the left hand and half moved faster with the right hand. Finally, similar kinematic profiles for velocity and acceleration patterns were reported during conditions in which each hand had identical displacement requirements with styli of the same weight (average r between hands = 0.91). However, the relationship between acceleration patterns lowered (range of $r = 0.43 – 0.70$) as the mass of stylus or the distance to targets for each hand varied. The authors thus rejected Kelso et al.'s (1979) arguments for a single structure underlying temporal patterning of two limbs during bimanual aiming and forwarded an account depicting the interaction of unique motor commands.

In the arising model of bimanual coordination Marteniuk and Mackenzie (1980) argued that temporal and spatial outcomes of two-handed movements are a function of neural cross talk between motor command centers in the central nervous system (CNS). Such neural cross talk could occur at either or both the cortical and subcortical levels of the CNS via the descending contralateral and ipsilateral neural pathways. Additionally, it was suggested that motor commands sent via one side of the motor cortex to initiate ipsilateral limb movement interfered with movement in the contralateral limb. These authors argued that no interference occurred when limbs were required to move the same distance due to the formation of identical motor commands for each limb. Conversely, separate motor commands issued during conditions in which the arms move different distances are believed to result in bimanual aiming MT and spatial accuracy interference. It was further hypothesized that separate intensity (e.g. impulse) and spatial endpoint commands are required to direct different movement outcomes. Low intensities prescribed for one limb (e.g. the limb traveling the shorter distance) would facilitate contralateral limb activity, whereas higher intensities would have an inhibitory effect. Logically, the issuing of separate commands to each limb increases the cognitive load placed on the CNS, and, consequently, augments the degrees-of-freedom problem (Marteniuk & Mackenzie, 1980).

Discrepancy between these findings sparked the interest of a number of researchers. In explanation, Swinnen et al. (1991) believed that a limitation of previous research using bimanual aiming tasks was that the actions investigated might have differed primarily at the quantitative, metrical level rather than at the qualitative, structural level. In fact, Marteniuk et al. (1984) provided some support for this argument criticizing their own findings of a lack of relationship between hands for TPV and TPA. They suggested that their findings may have been a function of the constraints associated with the specific bimanual task used, in which there was an inherent lack of variability in the early acceleration subcomponents of the movement. Therefore, the degree to which previous research extends to other bimanual coordination tasks is uncertain.

Specific task requirements or constraints are ultimately believed to form the subsequently observed movement (Clark, 1995). Therefore, in the study of interlimb coordination, a major issue concerns the relationship between the specific task and environmental constraints on the performer and the interlimb coordination pattern that emerges in satisfying task goals. For instance, Swinnen et al. (1991) investigated the simultaneous performance of movements that differed both qualitatively and quantitatively. By instructing their subjects to simultaneously perform a flexion-extension-flexion movement with their dominant hand and a flexion movement with their non-dominant hand (both in the horizontal plane) they argued that the movement requirements were inherently different. Their findings, however, were somewhat ambiguous. Some subjects provided support for Kelso and colleagues (1979) proposal, demonstrating synchronous movement patterns through distance and acceleration traces. Other subjects proved successful in dissociating the movement patterns, supporting the position of Marteniuk and co-workers (Marteniuk & Mackenzie, 1980; Marteniuk et al., 1984).

The ability of some individuals to breakdown innate muscles synergies and construct a more diverse movement pattern was offered as explanation for the differences observed by Swinnen et al. (1991). Speculatively, however, in both experiments reported, subjects were instructed to initiate and to terminate both limb movements together. As previously acknowledged, the influence of task instructions must be considered particularly in studies examining the validity of existing

bimanual coordination models. A criticism of the Swinnen et al. experiments would, therefore, be that the observed levels of synchronization between limbs may have been influenced by the experimenter-imposed constraints placed on the subjects prior to movement. In addition, the comparison between Swinnen et al.'s findings and those of Kelso et al. (Kelso et al., 1983; Kelso et al., 1979) and Marteniuk et al. (Marteniuk & Mackenzie, 1980; Marteniuk et al., 1984) becomes difficult, as no instructions pertaining to synchronicity of movement was provided in the earlier studies. In fact, the affect on subjects' task perception through the inclusion or exclusion of such instructions has rarely been discussed. For example, during the experiments mentioned above, the extent of encouragement subjects received to coordinate or dissociate each limb was not clear (see Swinnen et al., 1991). Typically, the exact spatiotemporal movement pattern required to successfully complete a real world activity, such as lifting large objects with two hands, emerges from unique task constraints.

Prehensile Movements

A consequence of early bimanual coordination studies was the importance of addressing real world task constraints within paradigms. Indeed, it was the dominance of bimanual aiming tasks in both Kelso and Marteniuk's experiments that lead to the pioneering work by Casteillo, Bennett and Stelmach (1993), who investigated the coordination of limbs during bimanual prehension movements. In view of the small number of studies reported to date, however, a useful starting point for understanding how bimanual prehension movements are coordinated may be to consider bimanual coordination within the context of theoretical frameworks developed to explain how transport and grasp phases are coordinated during unimanual prehension movements.

Unimanual Prehension

Napier's (1956) seminal examination of the normal human hand suggests that there are two distinct activity-related prehensile patterns. Recognizing that the fundamental requisite of prehension is that the object, whether it is fixed or freely movable should be held securely, Napier acknowledged the importance of grip stability. In the normal hand, stability may be accomplished in one of two ways:

- 1) The object may be pinched between the pads of the digits and the opposing thumb

for delicate grasp and manipulation. This is called a precision grip (Fig. 1.1). 2) The object may be held in a fist-like grasp formed by the partly flexed fingers and the palm, counter pressure being applied by the thumb lying more or less in the plane of the palm. This is referred to as a power grip (Fig. 1.1). Napier is not alone in this functional classification and despite a variety of current taxonomies a general division between accuracy and power remains (e.g., Iberall & Lyons 1984; Cutkosky & Wright 1986; Liu & Bekey 1986).

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Perhaps the most salient feature of Napier's work was his ability to relate natural hand posture to function. Specifically, Napier (1960) established that a continuous and integrated solution to the biomechanical and neurophysiological constraints of any movement is achieved through choreographed hand movements. In addition to demonstrating the physical rationality of these movements, his model showed that the underlying control principles were not only task dependant but also remarkably graceful despite vast aspect variability in force, posture, duration and speed. Since these early studies, expansion of grasping research in both humans and monkeys has occurred with the aim of integrating various domains to ascertain which neural circuits underlie grasping. In 1981, Arbib suggested that prehensile movements directed towards visual stimuli are comprised of three different segmental components; transport, rotation and manipulation. The first component (transport) brings the hand from its initial position to the target; the second component (rotation) orients the hand in a way congruent with the objects orientation; the third component (manipulation) selects and controls the finger grip according to the stimulus size and shape. Demand for clarification of the relationships and coordination between the various components of prehension has lead to the development of numerous theoretical frameworks. Two main classes of frameworks can be distinguished; those suggesting that the coordination of movement components is planned in advance of movement onset and based upon temporal synchronization, and those

proposing the coordination is achieved by on-line control of movement parameters based upon continuous sampling of spatial information.

One of the most influential of these former frameworks was proposed by Jeannerod (1981, 1984). With the original intention of addressing the specific relationship between transport and manipulation components of prehension, Jeannerod conducted a series of studies in which an object's size, shape and distance from the viewer varied. In agreement with other studies (Morasso, 1981; Hogan, 1984), Jeannerod found that the velocity profiles used to analyze the transport component were approximately bell-shaped with an initial phase of acceleration followed by a deceleration phase. Typically, transport time was maintained throughout conditions due to a positive linear relationship between object distance and mean peak velocity. However, the transport component did not change by varying the object size. The manipulation component was found to consist of two phases. The first one (grip formation) was characterized by a finger extension reaching a maximum (maximal grip aperture) proportional to the object size. The second phase (actual grasping) was characterized by finger closure on object. In contrast to the transport segment, stimulus distance did not influence the manipulation component.

On the basis of these data, Jeannerod (1981, 1984) established the 'visuomotor channels hypothesis'. Within this view, prehension consists of two independently computed components: a transport component in which the limb is transferred to the region of the target object, and a grasp component in which the hand is preshaped and oriented so as to facilitate gripping the target (Jeannerod, 1984). Based upon separate visuomotor channel theory, these components are believed to rely on different sources of information concerning the perceptual properties of objects. Dependant upon egocentric representation, the transport component extracts visual world information as to the spatial location of objects relative to the body; whereas, the grasp component is thought to depend upon intrinsic properties such as object size, shape and the orientation of its major axis. Further support for the division of transport and grasp is provided in physiological and anatomical demonstrations of independent neural regions concerned with the programming of distal and proximal movements. (Gallese, Murata, Kaseda, Niki & Sakata, 1994; Gentilucci, Fogassi,

Luppino, Matelli, Camarda & Rizzolatti, 1988; Rizzolatti, Camarda, Fogassi, Gentilucci, Luppino & Matelli, 1988; Sakata & Taira, 1994). Interestingly, Jeannerod's novel approach also proposed frequent synchronization of the independently computed transport and grasp phases. For instance, occurring at approximately 70% of the manipulation time, the time to maximal grip aperture corresponded to the onset of peak deceleration (transport component). Another vital aspect of this model predicted that transport kinematics would not be affected by the experimental manipulations such as object size variation.

In contrast, however, more recent studies have provided evidence that the transport component is influenced by object size (e.g. Gentilucci et al., 1991). The results of these studies showed that changes in object size influenced the movement time after peak deceleration of the transport component (i.e., the smaller the object is, the longer it takes to "home-in" on the object). Thus, later reformulations of this model now acknowledge the role of transport and grasp interaction in determining temporal movement plans. In Hoff and Arbib's update (1993) of Arbib's original (1981) model, they suggested that separate time estimates needed to complete the transport and grasp are relayed to a higher order control system. Being responsible for coordinating lower level movement elements (schemas), this controller then issues both components with a common movement duration. Importantly, the authors emphasize that if time estimates received by the controller differ, whichever estimate is longer will be selected, and the other components will be slowed as a consequence. Two noteworthy features about these models are; firstly, the importance placed on movement planning processes rather than on-line (continuous) control, and, secondly, the notion that movement duration is the coordinating factor.

Rather than focusing on temporal coupling of reaching and grasping, alternative model development suggests that coordination is based upon spatial relations. In particular, these models emphasize the importance of on-line or continuous control of movement variables (e.g. velocity, grip aperture etc.). Moreover, they propose that the later stages of reach-to-grasp movements may operate within object-centered rather than body-centered coordinates. One such model proposed by Bootsma and colleagues (Bootsma & van Wieringen, 1992) suggests that coordination of the transport and grasping components is guaranteed as both components are ultimately

geared to the same information -- specifying time-to-contact between the hand and the object to be grasped. Coordination is not therefore planned, but instead arises as a consequence of each component sharing a common information signal. This framework raises the question of how the sensorimotor system might manage the problem of monitoring two movements simultaneously.

Bimanual Prehension

Execution of bimanual prehensile movements whereby each hand must interact with a different target (e.g. simultaneously grasping a knife with one hand and a fork with the other) is more complex than unimanual prehension and presents numerous problems for the human control system. Such predicaments become increasingly more complex when targets vary in size or differ in distance.

In their pioneering study on this paradigm, Casteillo and co-workers found similar movement times for both hands, both for grasping movements directed at objects of the same size (congruent movements) and of different sizes (incongruent movements) (Casteillo et al., 1993). In contrast, the kinematic temporal landmarks, i.e. the times of maximum wrist velocity and hand aperture, seemed to be implemented independently for both hands. In these studies, analyzing the correlation between temporal landmarks of both limbs assessed functional limb coupling. This correlation was found to depend on the combination of object sizes presented to both hands (congruent vs. non-congruent). It should be acknowledged, however, that subjects' within this study utilized a 'precision' grip to grasp the small target and a 'whole-hand' or 'power' grip to grasp the larger target (Casteillo et al., 1993). More recently, coupling of all major temporal parameters (movement onset, time to peak velocity, time to peak grip aperture, movement end) was found by Jackson and colleagues (1999), who also investigated bimanual prehensile movements to different sized targets. However, in support of the Casteillo et al., (1993) study, independent shaping of each hand relative to the specific target object was observed. This aspect of bimanual movement appears to be particularly robust, being replicated further in a study by Dohle, Ostermann, Hefter and Freund (2000).

Nevertheless, although aspects of bimanual movements are usually coordinated, there are also typically costs to performance. For example, relative to unimanual movements, bimanual reach-to-grasp movements are slower (peak velocity), take

longer (movement duration) and shape larger (peak grip aperture) (Jackson et al., 1999). These changes may represent the level of certainty involved in computing and controlling the movements as the degrees of freedom for the unimanual movements are doubled for bimanual actions. This cost for bimanual movements is typically borne by both hands. Thus the peak grip aperture of both hands increases under bimanual conditions compared to unimanual movements (Jackson et al., 1999)

Present Literature – To what extent can theories predict real world tasks?

Despite a number of recent studies, theories based upon both manual aiming (e.g., Marteniuk & Mackenzie, 1980; Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979) and rhythmical tapping tasks (e.g., Heuer, 1985; Kelso, 1984) dominate research examining the coordination of bimanual movements. Consequently, there is a need for research that overcomes the inordinate influence of experimental task constraints by analyzing ongoing movement organization during a real-world activity. Clearly all types of movement goals in bimanual coordination cannot be completely explained by either conflicting coordination models. For instance, in many day-to-day tasks perhaps the most prevalent bimanual coordination requirement is the interaction with relatively large objects that require two limbs to move and lift a solitary target. To date, no convincing comparison has been presented which demonstrates the effectiveness of the existing models predictions in explaining coordination of bimanual movements during real-world tasks such as manipulating a heavy vase. It is clear that the existing data from each of the models cannot describe the underlying coordination dynamics in an activity in which the major task constraint is that the limbs must move over equal or different distances to the same target endpoint.

Based on Jackson et al.'s (1999) findings discussed previously, one might expect that bimanual prehensile movements to a single target would demonstrate limb coupling in line with the single coordinating structure hypothesis (Kelso et al., 1979). Recently, Taylor and Davids (1997) attempted to answer these questions through investigating bimanual coordination during catching with two hands. Findings were consistent with Kelso et al.'s (1979) earlier work, showing coupling of all temporal parameters despite utilizing a single dynamic target (thrown ball) paradigm. However, it can be argued that catching with two hands is more complex than a

functional bimanual prehension movement. Borne out of differing specificity and objectivity, it is plausible to suggest that catching a ball would require different motor organization than that of grasping and lifting an object. For example, a catch executed with two-hands may use an initial blocking strategy to decrease object velocity, followed by a functional grasp. Further, the dynamic and unpredictable nature of a catch incorporates trunk as well as upper limb movement, adding to factors affecting the relevance of extending current bimanual coordination literature to catching with both hands.

Information Processing

Despite differing accounts in the previously discussed models of how temporal synchronization is accomplished for both prehension and limb coupling, proprioceptive signals are likely to be critical for effective synchronization in either case. As demonstrated within the visual attention literature, an individual's ability to attend to more than one object at any one time is limited (Duncan, 1984). Duncan and colleagues (1997) proposed that visual information associated with different objects results in competition between those objects, characterized by a reduction in the efficient processing of each object. Controlling and maintaining synchronicity of two actions unfolding in parallel is an obvious limiting factor during the execution of bimanual movements. In this case, proprioception may play a vital role in allowing bimanual movements to occur without the need to allocate attentional resources.

Visual or proprioceptive information may be utilized to formulate motor commands by the sensorimotor system in controlling upper-limb movements. However, when both are available movement accuracy is maximized (Rossetti et al., 1994). Visual information, serving not only to make on-line corrections to a kinesthetically controlled hand path (Connolly & Goodale, 1999), can also regulate proprioceptive knowledge of initial limb position (Rossetti et al., 1994). Equally, evidence exists suggesting that 'visual' representation of peripersonal space can be updated via proprioceptive signals (Carey & Allan, 1996). It should be noted, however, that the precise role played by visual and proprioceptive signals might vary with task demands such as the requirement for accuracy or the need for manipulation. Specifically, we acknowledge the important role feedback regulation (e.g. online control) plays during coordination of cooperative actions. In light of this,

the present offering examines how visual processing affects limb coordination during specific bimanual prehension tasks where the performer is constrained to interact with a single target. Achievement of such a goal requires understanding of visual processing in order to manipulate subject conditions and interpret findings affectively.

Visual Processing: Dorsal vs. Ventral Streams

The primate visual system is characterized by the separation of visual areas into two broad 'streams'. Each originating from the primary visual cortex (V1), the ventral stream projects towards the infero-temporal cortex whereas the dorsal stream projects dorso-laterally to parietal areas (Ungerleider & Mishkin, 1982). Ungerleider and Mishkin based their anatomical distinction on neurophysiological and behavioral evidence collected from the study of macaque monkeys. Lesions of inferior temporal cortex (ventral) produced deficits in the animal's ability to identify and recognize an objects color, texture and shape but did not affect their performance in tasks of spatial orientation. Conversely, lesions of the posterior parietal cortex (dorsal) produced deficits in performance of locating targets during spatial orientation tasks but their identification capacity was preserved. On this basis, the authors argued that the two streams of visual processing play different but complementary roles in the perception of incoming visual information. According to their original account, the ventral stream plays a critical role in the identification and recognition of objects, while the dorsal stream mediates the localization of those same objects (Ungerleider & Mishkin, 1982). Some have referred to this distinction in visual processing as one between object vision and spatial vision -- 'what' versus 'where.' Although some caution must be exercised in generalizing from monkey to human, it seems likely that the visual projections from primary visual cortex to the temporal and parietal lobes in the human brain may involve a separation into ventral and dorsal streams similar to that seen in the monkey.

Dorsal/Ventral dissociation; Psycho-behavioural models

Since 1982, there has been an explosion of information about the anatomy and electrophysiology of cortical visual areas and, indeed, the connective anatomy among these various areas, which largely confirms the existence of the two broad 'streams', originally proposed by Ungerleider and Mishkin (1982). Almost a decade

after this initial observation, Goodale and Milner (1992) offered a new conceptual account of how visual information is processed within the human brain. According to this theory, a single visual representation is considered to subserve actions, whereas a separate representation subserves perceptions. The core idea of Goodale and Milner's Perception-Action model (PAM) is that the processing of visual information is thought to be carried out through independent streams stemming from the primary visual cortex. Visual processing for goal-directed action is predominantly supported by the occipito-parietal pathway (so-called dorsal stream), while the visual processing for conscious visual perception and identification is performed through the occipito-temporal pathway (so-called ventral stream). Support for this notion lies within the dissociation between the behavior of ataxic patient A.T. and agnosic patient D.F. (Perenin & Vighetto, 1988). Patient D.F., with selective damage to the ventral stream of visual processing (visual form agnosia), exhibits a profound impairment in shape perception coupled with preserved use of vision for the control of action. In contrast, patient A.T., characterized by dorsal stream damage (optic ataxia), manifests a profound inability to reach for targets under visual guidance but no difficulty in observing and recognizing them.

Exploring the evidence for a distinction between planning and on-line control actions of human movement, Glover (2004) introduced the Planning-Control model (PCM). Although in opposition to the PAM, this approach is not significantly different from Milner and Goodale's original theory. However, the PCM introduces a new perspective as to how the two visual streams process information, specifically during action where independent planning and control is thought to occur (Glover, 2004). With the intention of acting, the planning system is responsible for relating the selected visual target with appropriate motor parameters that will bring the hand towards its vicinity (transport kinematics, hand orientation, grasping aperture and force). The control system allows the added benefit of monitoring and adjusting the planning process in flight, but it is restricted to the spatial characteristics of the target. The idea of certain independence between planning and control processes is supported by numerous brain imaging studies and has been already suggested in the past. Indeed, planning in humans is linked with activity in a distributed network including a visual representation in the inferior parietal lobe (IPL), whereas control is

associated with activity in a separate network including a visual representation in the superior parietal lobe (SPL) (Deiber, Ibanez, Sadato, & Hallett, 1996; Desmurget, Grea, Grethe, Prablanc, Alexander, & Grafton, 2001; Grafton, Fagg, & Arbib, 1998; Grafton, Mazziotta, Woods, & Phelps 1992). Prior to a plan being formed, visual input travels to the IPL via the temporal lobe and a 'third' stream (Boussaoud, Ungerleider, & Desimone, 1990). The temporal lobe inputs include the spatial (e.g., orientation, size, and shape) and non-spatial (e.g., function, fragility, weight, and color) characteristics of a target as well as the visual context surrounding the target (e.g., background, other objects). The frontal lobes provide information relating to overarching goals and executive control (e.g., memories and past experiences). The visual and cognitive information used in planning is integrated with proprioceptive information from somatosensory association areas in the selection of an appropriate motor plan (Glover, 2004). The selection and parameterization of simple movements such as reaching and grasping tend to rely on IPL guidance, whereas, complex movements depend more heavily on frontal lobe sequencing and timing mechanisms. Once a motor act is planned, a copy of the motor schema for the upcoming action is forwarded to the SPL and cerebellum. Upon movement initiation, this efference copy is integrated with visual and proprioceptive feedback and utilized by the control regions to execute any necessary online adjustments. Monitoring of the body likely involves the SPL more heavily than the cerebellum. Comparing the movement with the motor plan likely involves the cerebellum more heavily than the SPL (Glover, 2004).

In summary then, the notion that visual perception is independent of visually guided action has found empirical support in numerous neurological, neuropsychological, and behavioral studies. However, the majority of these studies are based entirely on evidence from right-handed subjects utilizing only their dominant hand (unimanual). This popularity is largely due to the considerably higher proportion of right-handers in the population and consequently, this lack of subject availability has led to a bias within the literature to right-handers. Control of the right hand has a vast history and association with the left hemisphere. Indeed, such an association was initially conceived from primate studies in which, arm, hand and finger movements were found to be controlled predominantly by motor areas

located in the contralateral hemisphere, with some ipsilateral control being present only for governing axial and proximal forelimb musculature (Brinkman & Kuypers, 1972, 1973). Moreover, almost 85% of the proprioceptive afferent information from the limbs reaches the contralateral hemisphere (Gardner, 1963; Ruch, 1965).

Therefore, bimanual coordination and cooperation is likely to involve a good deal of interhemispheric coupling (Semmes, 1968; Luria, 1973). Despite the nature of this coupling being relatively unknown in humans, an understanding of the functional differences between the cortical hemispheres is vital when investigating an action in which both hands are controlled simultaneously primarily with visual information.

Hemispheric Advantages

Owing to advances in neuroimaging techniques coupled with clinical work, considerable progress has been made in understanding the functional rules of brain organization. Within the neurosciences, as a consequence of evidence in favor of anatomical segregation, the majority of attention is focused on the premise of functional specialization, which refers to the idea that particular neural regions perform specialized computations. Building on the seminal ideas of Franz Gall (1758–1828), identification of functional specializations associated with the two cerebral hemispheres soon followed. These ideas laid the foundation for a dominant theme in the laterality literature that arose in the twentieth century and continues to the present day: namely, that the left hemisphere has a dominant role in linguistic abilities whereas the right hemisphere is responsible for visuospatial functions.

While there is no longer any serious challenge to the claim that the left hemisphere plays a special role in the control of speech, there is increasing evidence that speech may be only one of a large number of motor behaviors in which the left hemisphere mechanism are uniquely involved. Indeed, studies of cerebral dominance have emphasized the greater role of the left than the right hemisphere in the control of specific components of a variety of motor tasks performed by the arm and hand. The left hemisphere is thought to play a dominant role in the sensorimotor integration and timing of movement sequences as shown by behavioral (Kimura 1982; Tzeng & Wang, 1984) and imaging studies (Kim et al., 1993; Chen et al., 1997) in healthy subjects, as well as in studies of subjects with stroke (Wyke 1967; Haaland & Harrington, 1989; Winstein & Pohl, 1995) and corpus callosotomy

(Geffen et al., 1994). For example, during a simple aiming task, the ballistic component of the rapid arm movement is thought to preferentially be processed within the left hemisphere (Wyke, 1967; Haaland & Harrington, 1989, 1994). In addition, patients with cerebrovascular accident (CVA) in the left hemisphere are more impaired than those with right-hemispheric lesions in the scheduling or timing of a series of actions within a sequence when moving with the ipsilateral, non-paretic arm (Kimura, 1982; Tzeng & Wang 1984; Winstein & Pohl, 1995). The greater importance of the left hemisphere in the control of sequential movements involving the distal musculature, and specifically the left (dominant) primary motor cortex (M1), is supported by functional magnetic resonance imaging (fMRI) studies showing substantially more ipsilateral M1 activation with the left hand movements than right during sequential movements involving finger-to-thumb opposition (Kim et al., 1993). Taken together, these results have led to the suggestion that the left hemisphere is important for processing temporal information.

Tentative evidence from earlier neurological studies suggests that the encapsulated visuomotor networks that mediate rapid target-directed movements may have evolved preferentially in the left hemisphere alongside the well-established specialization of the left hemisphere for the selection of hand posture and other complex movements. To test this idea Gonzalez, Ganel and Goodale (2006) designed two experiments. The first involved pictorial illusions, which are known to have robust effects on perceptual judgments but little influence on grasping. Right and left-handed subjects reached out and grasped objects embedded in two different visual illusions with either their dominant or their non-dominant hand. For both right- and left-handed subjects, precision grasping with the left hand, but not with the right, was affected by the illusions. In a follow-up experiment, they examined precision grasping in a more natural setting and showed that left-handed subjects use their non-dominant hand (right) significantly more as compared with right-handed subjects. On this basis, the authors concluded that a definite left hemisphere advantage for visual control of complex motor behaviors exists and that this hemispheric specialization evolved independently of handedness.

Objectives and Hypothesis

The extent to which current bimanual coordination models can account for the performance of all possible real-world prehensile objectives remains an issue within the academic community. Specifically, the present study addressed the usefulness of existing models for predicting execution of a bimanual prehension task whereby each hand is required to work cooperatively to interact with single stationary target. Moreover, we aimed to investigate the influence of visual feedback on the performance of such a task by experimentally segregating dorsal (visual) and ventral (memory-guided) processing streams.

Our first task however, was to account for the possibility that varying prehension styles may be associated with different organization and processing. As indicated within the unimanual literature Casteillo et al. (1993) suggested that the programming of the transport component may be inherently different in activities where the hand and fingers are required to utilize a whole-hand grip compared to a more precise grip. Indeed, support for this notion came from Rizzolatti et al. (1988) who found that in monkeys, the choice of grasping type was strictly determined by object size. Additionally, each type of grasp is subserved by different neural structures. Therefore, three bimanual prehension styles, one power and two precision grips, were investigated within the initial pilot study. Utilizing a relatively simple bimanual task in which both hands were required to move the same distance, cooperate and successful interact with a single target object, we aimed to identify one bimanual grasp for further analysis based on the following criterion; 1) The *most consistent* with existing bimanual and unimanual prehension literature, 2) comprise of the *most predictable* or *stable* components, and 3) being the *most realistic/common* movement. We hypothesized that due to the congruent nature of the task all grasps would support existing bimanual coordination models by demonstrating both temporal and spatial synchronization (Kelso et al., 1979 and Marteniuk & Mackenzie, 1980). Selection of a single grasp would consequently lie within the consistency to unimanual prehension literature (Jeannerod 1981, 1984).

The objectives of the final two experiments were to examine the predictive usefulness of current bimanual coordination models. Further, acknowledging the importance of visual information programming we intended to investigate

any coordination differences when utilizing the two separate visual streams. The existence of the two visual streams is largely accepted and therefore, so is the idea of both visually (dorsal) and memory (ventral) –guided control of movement. We hypothesized that when targeting a solitary object, bimanual prehension under visual control would demonstrate a higher level of limb coupling compared to those executed via memory-guided control. Foundations for the suggestion lie not only within the presence of visual feedback allowing for online limb control but also in the special role that the left hemisphere plays when the right-hand executes a prehensile task with vision (Gonzalez et al., 2006).

Figure Caption

Figure 1.1. A) Precision grip between index finger and thumb. B) Power grip between thumb and all fingers.

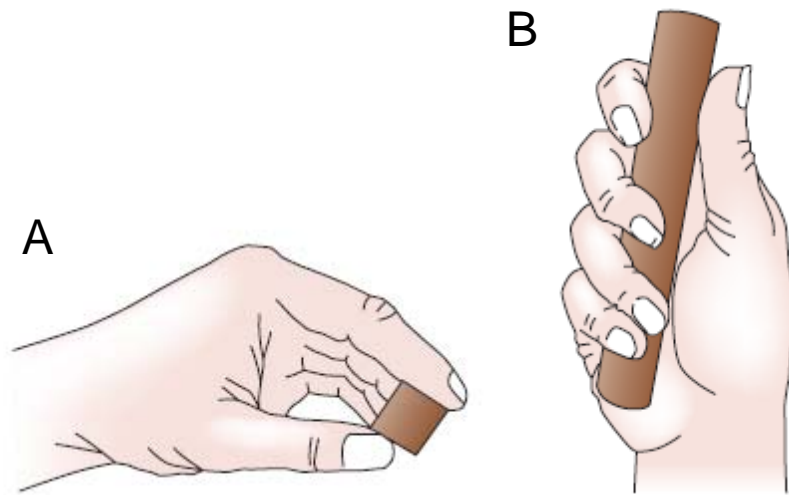


Figure 1.1

Chapter II: Pilot Study

Introduction

Countless human actions involve the synchronized coordination of more than one limb. While it is frequently advantageous to be able to use limbs independently, many actions demand employment of limbs co-operatively. Indeed, a variety of skills (e.g. using a can-opener, driving a car or juggling balls) demonstrate both the independence of two limbs and also the cooperation between them. Recent focus has led to a vast expansion in the understanding of relationships between the hands at both behavioral and neural levels. For instance, Kelso, Southard and Goodman (1979) showed that, regardless of speed, when hands move to targets of variable direction and distance, limbs demonstrate a definite coupling with almost synchronous movement onsets, times to peak velocity and movement end.

The developed ability of humans to efficiently coordinate movements of two hands during functional reach-to-grasp (prehensile) activities has sparked a great deal of attention. Execution of bimanual prehensile movements, whereby each hand must interact with a different target (e.g. simultaneously grasping a knife with one hand and a fork with the other) present numerous heuristic and computational challenges to the human control system. Such quandaries become increasingly more complex in dynamic environments -- when targets vary in size or differ in distance. For instance, can subjects maintain limb movement onset and end synchrony while independently scaling velocity to two targets of differing distance, or independently shaping each hand to targets of differing size? Casteillo and colleagues (1993) seminal work on bimanual prehensile movements would indicate that subjects can. Typically, subjects demonstrated a tendency to synchronize movement onset and movement endpoints when moving to targets of differing sizes, while maintaining independent shaping of each hand based on the relative size of the target (Casteillo et al., 1993). However, coupling of all temporal parameters was not found. Indeed, it was shown that the hand moving towards the smaller target reached point of peak

velocity earlier than the hand moving towards the larger target and demonstrated a longer deceleration period.

Synchronization of onset and endpoints also occurs when the two hands move to two targets differing in distance (Kelso et al., 1983). Achieving such synchronization requires appropriate velocity profile scaling of each hand by the subject (slower to the near target, faster to the far target). However, it is this tendency to synchronize the hands when performing mixed tasks that violate Fitt's law, which predicts that movement duration is affected by the distance moved and the precision required by the size of the target (Fitts, 1954). As the target becomes smaller or moves further away, the index of difficulty increases; as the target gets closer or becomes larger, so the index of difficulty decreases. Interestingly, when moving to targets of mixed difficulty, one might predict the movements synchronize to the movement with the higher index of difficulty. However, this does not appear to be the case. Kelso et al. (1979) showed that the hand with the higher index of difficulty moved faster and the hand with the lower index of difficulty moved slower in order to achieve the synchronization. On the basis of this evidence, Kelso et al. (1979) have proposed that during bimanual movements, the two limbs are coupled together with a single coordinating structure (an organized functional group of muscles) and are therefore constrained to act simultaneously.

The degree of synchronization attained during bimanual movements has been questioned by other authors. Marteniuk and Mackenzie (1980; see also Marteniuk, Mackenzie & Baba, 1984) showed that the limbs are significantly less synchronized when reaching to mixed- compared to same-difficulty targets. They argue that the similarity between the movements of the two hands under mixed-difficulty conditions arises as a result of neural cross-talk between the hands; concluding that hands are not coupled to a single timing structure but are controlled separately. It should be noted, however, that while there are significant departures from synchrony when limbs are moving to mixed-difficulty targets, the absolute differences in movement onset times and movement duration between the limbs are relatively small (~20 ms; Marteniuk et al., 1984).

In the studies cited above, bimanual coordination was examined during simple aiming movements. To date, however, it is only Kelso et al.'s (1979) single

coordinating structure theory that holds true for bimanual prehensile movements (Jackson et al., 1999). Therefore, in summary, utilization of both manual aiming (e.g., Marteniuk & Mackenzie, 1980; Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979) and rhythmical tapping tasks (e.g., Heuer, 1985; Kelso et al., 1979; Kelso, Putnam & Goodman, 1983) has dominated research into the coordination of bimanual movements. Experimental protocols are restricted to the use of tasks in which subjects moved the same and different distances to different, static targets. Consequently, it is argued that both conflicting theoretical frameworks cannot satisfactorily account for all movement goals of bimanual coordination. For instance, in many day-to-day tasks perhaps the most prevalent bimanual coordination requirement is the interaction with relatively large objects that require two limbs to move and lift a solitary target. To date, no convincing comparison has been presented which demonstrates the effectiveness of the existing models predictions in explaining coordination of bimanual movements during real-world tasks such as manipulating a heavy vase. It is clear that the existing data from each of the models cannot describe the underlying coordination dynamics in an activity in which the major task constraint is that the limbs must move over equal or different distances to the same target endpoint. Based on Jackson et al.'s (1999) findings previously discussed, one might expect that bimanual prehensile movements to a single target would demonstrate limb coupling in line with the single coordinating structure hypothesis (Kelso et al., 1979).

Therefore, we had two overriding aims of the present investigation as a whole. The first was to develop our understanding of human interlimb coordination by examining how well the existing predictions of the models could extend to the specific task constraints in which the hands move to the same target endpoint. Our further aim, under varying visual conditions, was to assess the predictive usefulness of the theories with regard to a common bimanual aiming task whose endpoint is a single large target. However, prior to these primary objectives being satisfied it was important to address the idea that organization in processing a single-handed precision grip would seem to differ from that of a power grip (Casteillo et al., 1993, see Chap. I). Despite Casteillo utilizing a unimanual paradigm, it is plausible to suggest that this notion will apply equally in a bimanual setting. Therefore, our pilot

study investigated the extent to which three bimanual prehension styles, two precision and one power, differed when performing a relatively simplistic bimanual task where both limbs are required to move the same distance in order to interact with a single target. With the aim of identifying a single prehensile style for further investigation and thus, completion of the primary objectives, the pilot study assessed each grasp on the following criteria; 1) The *most consistent* with existing bimanual and unimanual prehension literature, 2) comprise of the *most predictable* or *stable* components, and 3) being the *most realistic/common* movement. As limbs were required to travel the same distance to grasp the target it was hypothesized that a successful bimanual grasp would demonstrate not only a synchronous pattern with regard to velocity and acceleration data but also simultaneous movement initiation and termination of both hands (Kelso et al., 1979; Marteniuk et al., 1984). The congruent nature of the task lends itself to support both bimanual coordination theories and therefore selection of a bimanual grasp style for further analysis was predicted to lie within consistency to unimanual literature (Jeannerod 1981; 1984; 1988, see Chap. I).

Pilot study: Methods

Participants

Ten right-handed participants were recruited and provided their informed consent to participate in the experiment (Range = 19-30 years old, mean = 24.5, SD = 3.5, five females and five males). Handedness was assessed with a modified version of the Edinburgh Handedness Inventory (Oldfield, 1971), where the criterion for inclusion was scores > 70. All participants were naive as to the purpose of the experiment and reported no visual, neurological or skeletomotor abnormalities. The elements of the protocol have been previously forwarded and approved by the University of Saskatchewan Behavioral Science Research Ethics Board for ethical consideration in Human Experimentation in accordance with Declaration of Helsinki (1964).

Stimuli

Stimuli consisted of three solid black plastic cylindrical objects. A small cylinder (diameter 15.24 cm, height 10.16 cm, weight 1.05 kg), a medium cylinder (diameter 20.32 cm, height 10.16 cm, weight 2.05 kg), and a large cylinder (diameter 24.50 cm, height 10.16 cm, weight 2.6 kg). The target object was presented on a white cardboard background and located at a distance of either 35 cm (near) or 45 cm (far) from the initial hand position in the sagittal plane (Fig. 2.1). The background was divided into two sections, one (65 cm x 91 cm) positioned horizontally on a table, and the other (80 cm x 91 cm) placed vertically flush on the table surface in order to ensure a homogenous environment. The distance between the floor and the near edge of the horizontal plane surface was 80 cm (Fig. 2.1).

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 Insert Figure 2. 1 about here
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Apparatus

Hand movements were recorded with an Visualeyex 3000 three-dimensional system (Phoenix Technologies Inc., Burnaby, BC, Canada) equipped with a row of three cameras placed 1.5 m above the working surface. The camera monitored displacements of eight active markers (infrared-emitting diodes, IREDs) which were

attached to the skin overlying the following areas: (1) distal phalanx of the each thumb (thumb IREDs); (2) distal phalanx of the each index finger (finger IREDs); (3) metacarpophalangeal joint of each index finger (knuckle IREDs); and (4) the region of the trapezium-metacarpal joint of both thumbs (wrist IREDs) (Fig. 2.2). The transport component was studied by analyzing the kinematics of the participant's wrist IREDs. Depending on adopted grip, a combination of either the finger, thumb and knuckle IREDs were utilized to analyze the manipulation component of the movement. Position of the IREDs was sampled at 200 Hz for 3 s following an auditory initiation cue at the start of each trial. In addition, Liquid Crystal Goggles (Translucent Technologies Inc. Plato Model: P1) were used to achieve participant visual occlusion whilst the researcher manipulated target objects between trials.

Motion tracking data was collected using a personal computer (BOXX Technologies Inc.) running Visualeyze Soft 2.70. Randomized trials and liquid crystal goggles were triggered by a second computer (IBM ThinkCentre) running E-Prime Studio soft Version 1.1.

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Insert Figure 2. 2 about here

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Procedure

Participants were seated in a height-adjustable chair so that the thorax pressed gently against the front edge of the table. A visible home position was located 10cm anterior to the participant's midline. With opposition between the pads of the each index finger and thumb the participant were asked to place each digit coupling together and on the home position (Fig. 2.3). This resulted in a starting position where the ulnar side of the hand is in contact with the table surface, with slight shoulder flexion, 90° of elbow flexion, semipronation of the forearm, and 5-10° of wrist extension.

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Insert Figure 2.3 about here
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Within a fully illuminated room, participants were required to grasp and slightly lift a target object with full vision as quickly and as accurately as possible in response to a start tone (880 Hz; duration 250 ms). Each trial began with the participant in the correct start posture as described previously. Vision was then occluded whilst the researcher positioned the target object in accordance with the randomized order presented by EPrime software. Once target position was correctly ascertained, the researcher initiated each trial with a keyboard press. A full vision preview ensued, allowing the participant to become aware of location and size of the object prior to the start tone. To reduce expectancy and rhythmical effects, the duration between vision of the target and this start tone was randomly set at 500, 1000, 1500, or 2000ms. Following each trial the participant returned to the start posture. Data acquisition began at the start tone and continued until after the cylinder has been lifted. Participants performed trials under each of the following blocked conditions: (1) Precision Grip 1 (PG1), (2) Precision Grip 2 (PG2), and (3) whole-hand or Power Grip (POW). Within each condition there was six secondary conditions obtained through all possible combinations of: (1) the target object size (small, medium, large); and (2) target object location (near, far). The experiment consisted of 144 trials, each blocked condition accounting for 48 trials. All conditions and secondary conditions were randomized across all participants. At the start of each block, participants were given homogenous visual and verbal instructions pertaining to the type of prehension movement to be adopted. No practice trials were permitted.

Prehension Conditions

During PG1 trials participants were instructed to grasp the target with the thumb and all fingertips of one hand in opposition with thumb and all fingertips of the other. Movements utilizing PG2 required participants to employ a grasp where all fingertips of each hand were in opposition only. Lastly, POW trials were

characterized by flexion of all fingers around an object, with the palms of both hands in contact (Fig. 2.4).

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 Insert Figure 2.4 about here
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Data Reduction and Analysis

Kinematic parameters were initially calculated for each hand separately. Movement onset was defined as the first frame in which the wrist marker attained and maintained a velocity (in direction of the movement) of 50 mm/s for ten consecutive frames (i.e., 50 ms; Binsted & Elliott, 2001; Elliott, Heath, Binsted, Ricker, Roy, & Chua, 1999); reaction time (RT) was the time that elapsed from collection start to movement onset. Movement endpoint was defined as the frame at which finger velocities fell below and remained below 50 mm/s for ten consecutive frames (i.e., 50 ms). Position data for all IREDs were filtered off-line using a second-order dual-pass Butterworth filter (low-pass, 15 Hz). Instantaneous velocities were calculated by differentiating displacement data using a five-point central finite difference algorithm.

Inferring Feedback-based Control

A type of regression analysis originally adapted from Elliott, Binsted and Heath (1999) and more recently by Heath, Westwood and Binsted (2004) was used to infer the nature of limb control. Utilizing 3D coordinates of the wrist markers, this procedure quantifies the proportion of variability (R^2) in endpoint position that can be predicted from the position of the limb at 20%, 50% and 70% of total movement time. The underlying logic of this technique is that movements executed without feedback-based control should unfold according to a programmed spatiotemporal pattern. Thus, the final position of the limb should be highly correlated with the position of the limb at any other point in time during the response; that is, overshooting or undershooting errors early in the movement would not be corrected by compensatory adjustments to the later trajectory. In contrast, if feedback-based

control is available, early undershooting or overshooting errors should be detected and eliminated by adjusting the later trajectory of the movement. In this case, the position of the limb in the early or latter stages of the trajectory need not predict the ultimate endpoint (Heath et al., 2004).

Dependant Measures

A series of dependent measures computed from the 3D coordinates for the wrist marker, was used to analyze the kinematics of the transport phase: (1) peak velocity in the direction of the movement (PV); (2) absolute time between movement onset and the point where peak velocity is achieved (msecs) (TPV); (3) peak acceleration (PA); and similar to TPV (4), absolute time to peak acceleration (TPA).

Due to the nature of the varying prehension strategies investigated the dependent variables computed from the 3D coordinates for the markers placed on the thumb, index finger, knuckle and wrist differed in terms of grip aperture definitions. For PG1 and POW conditions (5) bimanual peak grip aperture (BPGA) was defined between left and right knuckle markers (measure in mm); and for PG2 (6) BPGA was defined between left and right finger markers (measure in mm). The following variable defined as (7) time taken to reach BPGA as a percentage of the total movement duration (TBPGA percentage) was subsequently computed for each condition.

In addition to the above measures, we also computed a series of relative measures in which the kinematics of the left hand are indexed to those of the right (dominant) hand. The remaining measures were organized around a set of key questions as follows: (a) Do the hands begin to move at the same point in time? (8) *Movement onset lag* (RH-LH): A positive difference would indicate that the right hand began to move after the left hand while a negative difference would indicate that the right hand moved first; (b) Do the hands reach peak velocity at the same point? (9) *Peak velocity lag* (RH-LH); (c) Do the hands reach peak acceleration at the same point? (10) *Peak acceleration lag* (RH-LH); and finally, (d) Do the hands make contact with the target objects at the same time? (11) *Movement end-point lag* (RH-LH).

Statistical Analysis

All hand dependent measures were analyzed using a 3 prehension conditions (PG1, PG2, POW) x 3 target sizes (small, medium, large) x 2 locations (near, far) repeated measures ANOVA, with each score based on the median values. Where appropriate, *F* statistics were corrected for violations of the sphericity assumption using the Huynh-Feldt correction. Simple effect analysis and Bonferroni correction for multiple analyses was used when necessary to specify the nature of any significant effect. Alpha was set at $p = .05$ for all statistical analyses.

Pilot study: Results

With the exception of 16 trials (< 1.5 % of total), which were removed from the analysis due to poor marker readings, the participants exhibited consistent patterns of movement and performed well across all conditions. Overall, participants produced their response with a latency of 281.5 ± 61.9 ms and subsequent movement duration of 422.4 ± 69.9 ms. No missed trials occurred (i.e. unsuccessful grasping of target object) as all participants were able to complete the task proficiently.

Limb Transport

Temporal Latency Measures

Examination of reaction time revealed a significant main effect of amplitude for PG1 ($F(1, 9) = 7.12, p = 0.02$) and POW ($F(1, 9) = 28.81, p = 0.00$) bimanual grasps. In both cases reaction time to the closer target was significantly slower. No main effect of hand was found for all three adopted grasps indicating no significant difference in reaction time between hands regardless of target size or amplitude (see Table 2.1). Analysis of movement time exposed a significant main effect of hand for PG1 ($F(1, 9) = 7.34, p = 0.02$) and PG2 ($F(1, 9) = 180.6, p = 0.00$). For both PG1 and PG2 movement times of the RH were significantly smaller than that of the LH. In contrast, no main effect of hand was found for POW grasp indicating no movement time differences between hands ($F(1, 9) = 2.8, p = 0.14$) (see Table 2.1). Similar to movement time, the response time exhibited a significant main effect of hand for PG1 ($F(1, 9) = 7.34, p = 0.02$) and PG2 ($F(1, 9) = 180.6, p = 0.00$). For both PG1 and PG2 response times of the RH were significantly smaller than that of the LH. The main effect of hand was not statistically significant for POW ($F(1, 9) = 0.14, p = 0.7$) indicating that both hands contacted the target simultaneously (see Table 2.1).

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Insert Table 2.1 about here

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Kinematic Measures

An examination of limb path length demonstrated a significant main effect of amplitude for all three adopted grasps [PG1 ($F(1, 9) = 30.8, p = 0.00$), PG2 ($F(1, 9) = 388.9, p = 0.00$) and POW ($F(1, 9) = 458.7, p = 0.00$)]. As expected, hand path lengths of bimanual grasps to closer targets were significantly smaller than those of greater target amplitude.

Inspection of limb peak acceleration revealed a number of effects. The magnitude of acceleration (as an index of initial propelling force) revealed a significant main effect of target amplitude for PG1 ($F(1, 9) = 34.7, p = 0.00$), PG2 ($F(1, 9) = 22.2, p = 0.01$) and POW ($F(1, 9) = 38.2, p = 0.00$). For all three grasps peak acceleration was significantly smaller for both hands when grasping for the closer targets. Hand main effects did not reach statistical significance. The time to reach peak acceleration however, yielded a significant main effect of hand for PG2 ($F(1, 9) = 11.2, p = 0.00$). Peak acceleration was reached significantly quicker during PG2 grasps by the LH compared to the RH. The time elapsed between movement onset and peak wrist acceleration did not differ between the hands during PG1 ($F(1, 9) = 2.7, p = 0.21$) and POW ($F(1, 9) = 1.8, p = 0.18$) as the main effect of hand did not reach statistical significance (see Table 1). A main effect of amplitude was also revealed for PG2 ($F(1, 9) = 47.2, p = 0.01$) and POW ($F(1, 9) = 35.8, p = 0.00$). Time to reach peak acceleration was significantly slower when grasping with either a PG2 or POW grasp to the closer targets regardless of size.

Identical to peak acceleration, the analysis peak velocity revealed a significant main effect of target amplitude for PG1 ($F(1, 9) = 36.9, p = 0.00$), PG2 ($F(1, 9) = 24.2, p = 0.00$) and POW ($F(1, 9) = 37.6, p = 0.00$). For all three grasps peak velocity was significantly smaller for both hands when grasping for the closer targets. No main effect of hand was found for all grasps. Subsequent examination of the latency of peak velocity exposed a significant main effect of hand for PG2 ($F(1, 9) = 6.7, p = 0.03$). During PG2 grasps the LH reached peak velocity significantly quicker than the RH. No significant main effect of hand was found for both PG1 ($F(1, 9) = 2.7, p = 0.13$) and POW ($F(1, 9) = 1.93, p = 0.20$) thus, the time elapsed between movement onset and peak wrist velocity did not differ between the hands (see Table 1). A main effect of amplitude was also revealed for PG2 ($F(1, 9) = 51.6,$

$p = 0.00$) and POW ($F(1, 9) = 33.4, p = 0.00$). Time to reach peak velocity was significantly slower when grasping with either a PG2 or POW grasp to the closer targets regardless of size.

Proportion of Endpoint variance

Examination of the proportion of endpoint variability revealed no significant main effects or interactions. These analyses examined the proportion of variance (R^2) in movement endpoints explained by the position of the limb position at 20%, 50% and 70% of total movement time. Figures 2.5, 2.6 and 2.7 depict representative subject trials for both LH and RH utilizing all three grasps. As demonstrated in figure 2.5 and 2.6, the R^2 values for both hands when utilizing the PG1 and PG2 are relatively small at each time point, indicating that the position of limb at 20%, 50% and 70% of the movement was not strongly predictive of the final movement endpoint. Conversely, participants adopting the POW show relatively high R^2 values across both hands in the latter time percentages (Figure 2.7).

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Insert Figure 2.5 about here

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Insert Figure 2.6 about here

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Insert Figure 2.7 about here

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Grasp

Bimanual Grip Aperture

The examination of peak grip aperture (BPGA) revealed significant main effects of size for all three grasps [PG1 ($F(1, 9) = 144.1, p = 0.00$); PG2 ($F(1, 9) = 49.5, p = 0.00$); POW ($F(1, 9) = 423.2, p = 0.00$)]. Importantly, the main effect of size

demonstrates scaling of bimanual grip aperture to target size across all grasps investigated (Fig 2.8). Series comparisons indicate significantly larger BPGA for large compared to the medium and small targets regardless of adopted grasp (Fig. 2.9). Further, the analysis of the latency of BPGA demonstrated main effects of size for all three grasps [PG1 ($F(1, 9) = 7.9, p = 0.02$); PG2 ($F(1, 9) = 32.3, p = 0.00$) ; POW ($F(1, 9) = 101.2, p = 0.00$)]. Post-hoc comparisons indicate that the time elapsed between movement onset and bimanual peak grip aperture is significantly smaller when grasps are executed to closer oppose to further targets. No effect of size was found.

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Insert Figure 2.8 about here

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Insert Figure 2.9 about here

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Bimanual Coupling

As noted above, we also computed a set of relative measures in which the kinematics of the left hand were indexed to those of the right (dominant) hand. These measures were organized to test the extent to which the hands reached important kinematic markers at the same point in time.

Examination of movement onset revealed that, at initiation, all grasps were performed in synchrony (i.e., lags were not significantly different from zero [PG1 ($F(1, 9) = 7.9, p = 0.07$); PG2 ($F(1, 9) = 1.5, p = 0.25$) ; POW ($F(1, 9) = 1.43, p = 0.26$)]). The relative lags at TPA similarly revealed no significant difference from zero across all grasps [PG1 ($F(1, 9) = 0.79, p = 0.39$); PG2 ($F(1, 9) = 1.9, p = 0.19$); POW ($F(1, 9) = 0.24, p = 0.63$)]. A similar null effect was evident at PV where means were not significantly different from zero ($F(1, 9) = 1.7, p = 0.18$). Both time to peak acceleration and velocity were therefore reached at the same time by both hands regardless of grasp adopted, target size or direction. Conversely, temporal

coupling was not observed movement completion for PG1 ($F(1, 9) = 7.35, p = 0.02$) and PG2 ($F(1, 9) = 12.8, p = 0.00$). However, hands were synchronized (i.e. no difference from zero was evident) for POW ($F(1, 9) = 0.14, p = 0.72$) demonstrating that simultaneous contacting of the target by both hands occurred only when subjects utilized the POW grip.

Pilot study: Discussion

Accounting for the possibility that the processing or organization of a bimanual precision grip may differ from that of a bimanual power grip as seen within unimanual prehension (Casteillo et al., 1993), the primary aim of the pilot study was to examine three different bimanual grasps (PG1, PG2 and POW) and select one for further investigation. Grasp selection was based on best satisfying the following criterion; 1) The *most consistent* with existing bimanual and unimanual prehension literature, 2) comprise of the *most predictable* or *stable* components, and 3) being the *most realistic/common* movement.

Limb Synchronization

A strong coupling of temporal parameters (TPV and TPA) between the limbs for the all task conditions regardless of adopted grasp is seen throughout the experimental findings and summarized in Table 2.1. As expected, synchronization of velocity and acceleration was evident across all three bimanual grasps and would seem to lend support for both bimanual coordination theories when the distance traveled by each limb to a target is identical (Kelso et al., 1979; Marteniuk & Mackenzie, 1980). However, despite this initial support for limb coupling, movement onset and endpoint lag data revealed that when implementing PG1 and PG2 grips subjects initiated hand movement together but due to the greater movement time of left hand (LH), contact of the target was not synchronized (see Table 2.1). In contrast, when subjects adopted the POW grip, both hands initiated and terminated tasks simultaneously. From a theoretical viewpoint, both Kelso and Marteniuk's positions would agree that the congruent nature of the task lends itself to synchronization of temporal and spatial parameters and thus, our PG1 and PG2 findings are contrary to existing bimanual coordination literature (Kelso et al., 1979; Marteniuk & Mackenzie, 1980). Nonetheless, support for both theoretical frameworks came through demonstration of complete spatiotemporal coupling during bimanual POW grip execution. Certainly, further investigation is needed, particularly during incongruent tasks (e.g. limbs traveling different distances) to elucidate the extension of these frameworks to bimanual task -- presented in later chapters.

Linear Scaling and Peak Grip Aperture

For all three prehension styles, bimanual peak grip aperture data revealed that before the target is touched, the aperture reaches a maximum, which is larger than the size of the target. This maximum grip aperture is linearly related to target size (Fig. 2.8) empirically supporting Jeannerod's pioneering work on unimanual prehension (Jeannerod, 1981, 1984). Further, Jeannerod suggests that at the point in time whereby the thumb-finger opening is the largest (maximum grip aperture) there is a clearly identifiable landmark, which occurs within 60-70% of the duration of the reach. Despite all grasps demonstrating linear scaling, only the POW grip demonstrated a bimanual grip aperture landmark or peak that occurred at approximately 90% of total movement duration (Fig. 2.9). The discrepancy between POW grip and Jeannerod's landmark occurrence may be explained through the increased performance costs associate with the control of two limbs oppose to one limb (Jackson et al., 1999).

Proportion of Endpoint variance

The proportion of variability (R^2) in endpoint position predicted from the position of the limb between at 20%, 50% and 70% of total movement revealed that the POW is the most predictable bimanual prehension style (Fig. 2.7). As the execution of a POW grasp unfolded the R^2 values became increasingly higher for both the LH and right hand (RH) indicating that the planned trajectory and grasp, created prior to movement initiation, is the major determinant of successfully grasping and lifting the target. Smaller R^2 values, reported during PG1 and PG2 execution, are indicative of fine adjustments occurring near the end of the movement. The use of online control during a relatively simplistic bimanual task in full vision suggests that within the constraints of the current experiment, both PG1 and PG2 are less predictable and effective.

Realistic prehension

Subjective analysis of all experimental trials as well as verbal feedback from subjects lead to the conclusion that both PG1 and PG2 are not appropriate grasps for this specific bimanual task. Due the nature of the PG2 grasp (opposition of all fingers of one hand with all fingers of the other) and the weight of targets, successful grasp formation varied in terms of upper limb and body positioning (e.g. elbows in

contact with table or excessive forward trunk lean). In particular, complaints of fatigue and undue stress on the back, shoulders, wrists and fingers were verbalized more prominently when subjects adopted PG2 but also while implementing PG1. No such observations or complaints were forthcoming when subjects performed the task with a POW grip suggesting that this type of grip formation is more realistic and efficient for completing a bimanual task to a single target.

To summarize, in spite of the tendency for all three grasps to linearly scale bimanual grip aperture to target size, only the POW grip demonstrated complete consistency with both unimanual and bimanual literature. Support for POW grip reliability was found within the temporal and spatial limb coupling as well as a definite landmark of bimanual peak grip aperture. Additionally, progressively stronger endpoint correlations across both hands within the POW proportion of variability data are indicative of a grasp, which is highly predictable and stable. This stability was further confirmed through subjective analysis and therefore the POW grip was the only grasp to successfully satisfy all areas of the selection criteria. Based on this evidence, further analysis of the POW grip, characterized by full flexion of the fingers around the object with the palms in opposition with each other, were used in experiment 1 and 2.

Table 2.1. Bimanual grasp transport kinematics; Mean (SD in brackets).

Full Vision	Bimanual Grasp					
	Precision 1		Precision 2		Power	
	LH	RH	LH	RH	LH	RH
Transport kinematics						
Reaction Time (ms)	284 (24)	285 (21)	281 (17)	284 (30)	276 (15)	278 (13)
Movement Time (ms)	449* (31)	440 (34)	445* (38)	284 (30)	459 (27)	456 (30)
Response Time (ms)	733* (33)	725 (39)	726* (41)	568 (60)	735 (25)	734 (31)
Time to Peak Acceleration (ms)	85 (14)	89 (27)	93* (25)	108 (16)	90 (18)	94 (23)
Time to Peak Velocity (ms)	179 (45)	184 (44)	184* (42)	190 (43)	168 (39)	184 (50)

* Significant differences between LH and RH results (post-hoc t-test; $p < .05$).

Figure Captions

Figure 2.1. Experimental setup. (A) Background consists of two sections, one (80 cm x 91 cm), and the other one (65 cm x 91 cm). The distance between ground and near edge of the horizontal plane surface will be 80 cm. (B) The target object could be located at a distance of either 35 cm or 45 cm from the initial hand position in the sagittal plane.

Figure 2.2. IRED placement. (1) distal phalanx of the each thumb (thumb IREDs); (2) distal phalanx of the each index finger (finger IREDs); (3) metacarpophalangeal joint of each index finger (knuckle IREDs); and (4) the region of the trapezium-metacarpal joint of both thumbs (wrist IREDs).

Figure 2.3. Start position, digit coupling. Opposition between the pads of the each index finger and thumb the participant will be asked to place each digit coupling together and on the home position with the first metacarpals in contact.

Figure 2.4. Prehension conditions. (PG1) Grasp the target with the thumb and all finger tips of one hand in opposition with thumb and all finger tips of the other. (PG2) Grasp with all finger tips of each hand in opposition only. (POW) Characterized by flexion of all fingers around an object, with the palms of both hands in contact.

Figure 2.5. Precision 1- The proportion of variance (R^2) in movement endpoints explained by limb position at three movement time percentages (20%, 50% and 70%) is presented for both hands when a representative subject utilizes a Precision 1 grip.

Figure 2.6. Precision 2 - The proportion of variance (R^2) in movement endpoints explained by limb position at three movement time percentages (20%, 50% and 70%) is presented for both hands when a representative subject utilizes a Precision 2 grip.

Figure 2.7. Power - The proportion of variance (R^2) in movement endpoints explained by limb position at three movement time percentages (20%, 50% and 70%) is presented for both hands when a representative subject utilizes a Power grip.

Figure 2.8. A representative subject trial of linear scaling of bimanual peak grip aperture (mm) to target size seen in all three bimanual grasps.

Figure 2.9. Bimanual grip aperture (mm) in the resultant axis as a function of movement time (%) for all bimanual (PG1 = Precision 1; PG2 = Precision 2; POW = Power).

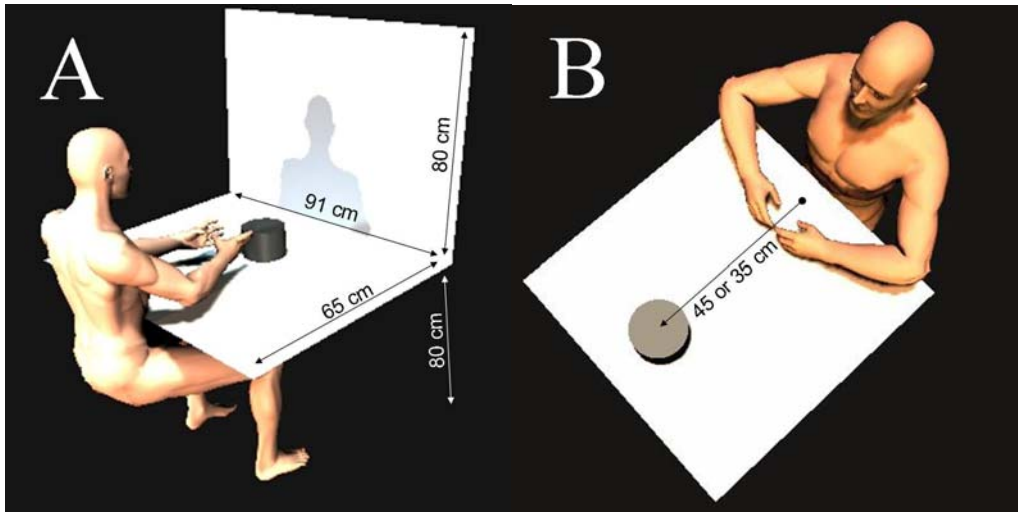


Figure 2.1

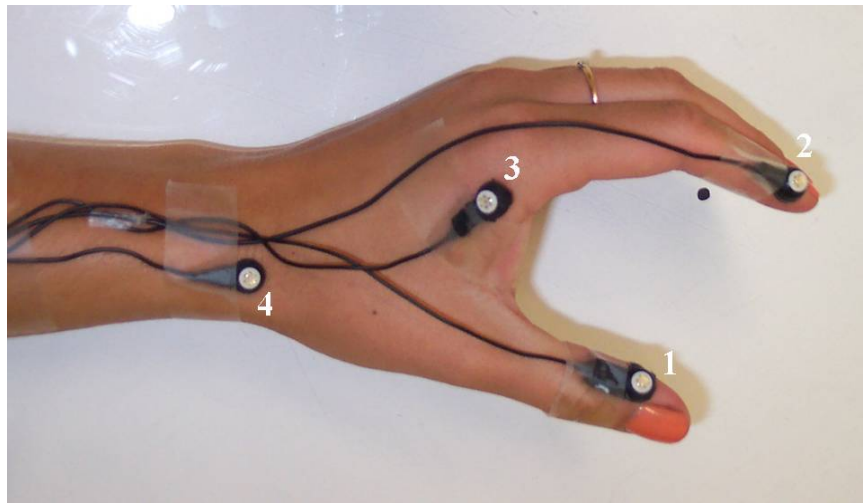


Figure 2.2



Figure 2.3

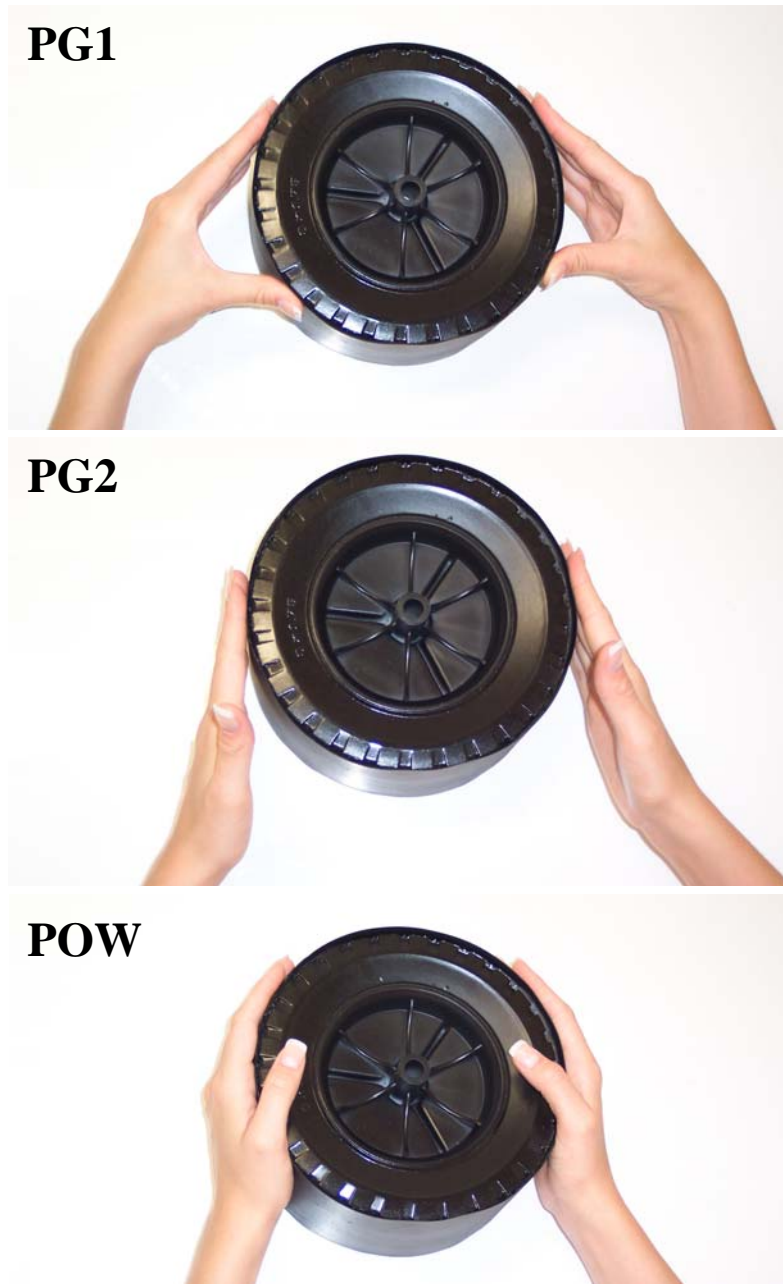


Figure 2.4

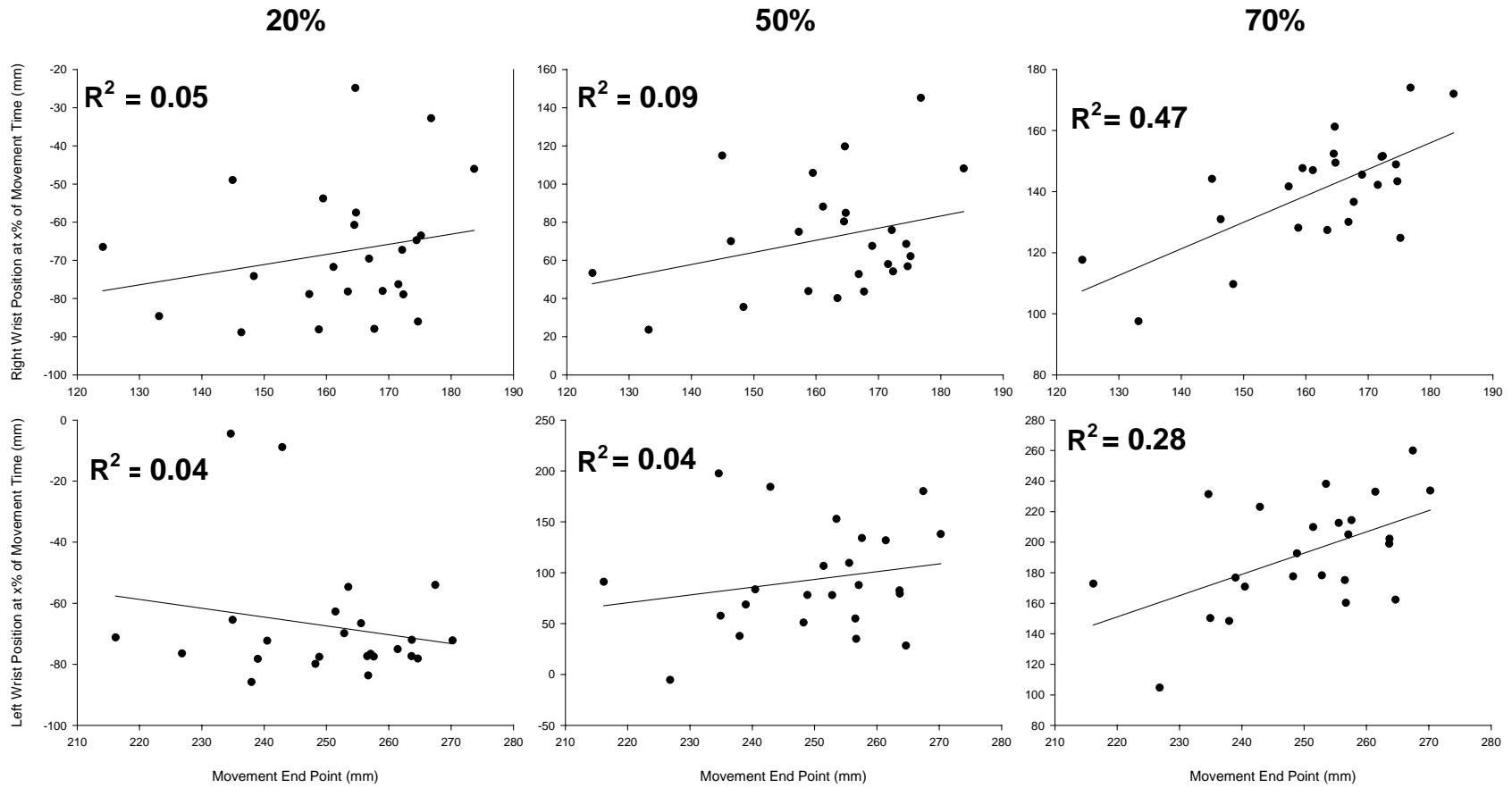


Figure 2.5

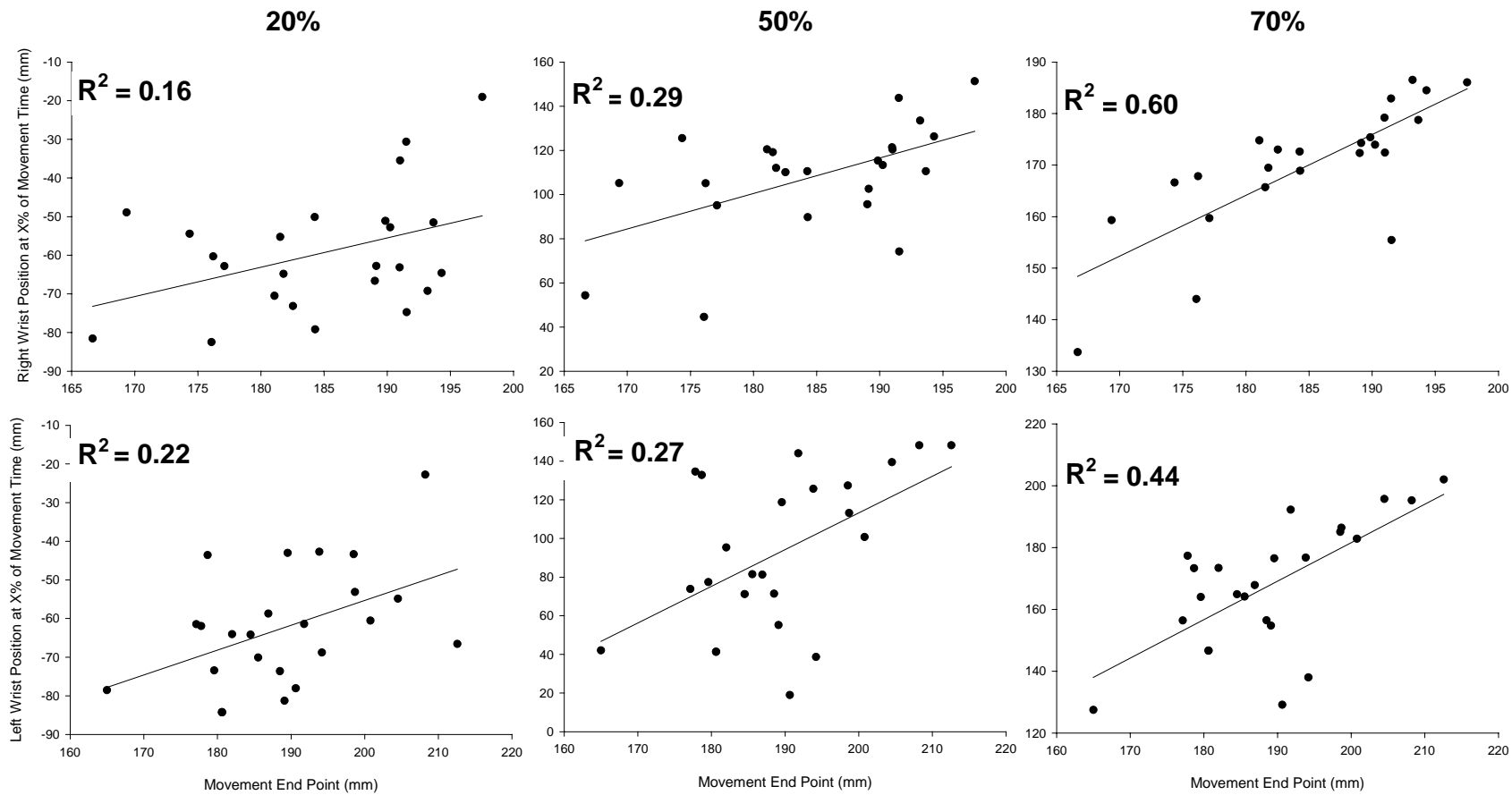


Figure 2.6

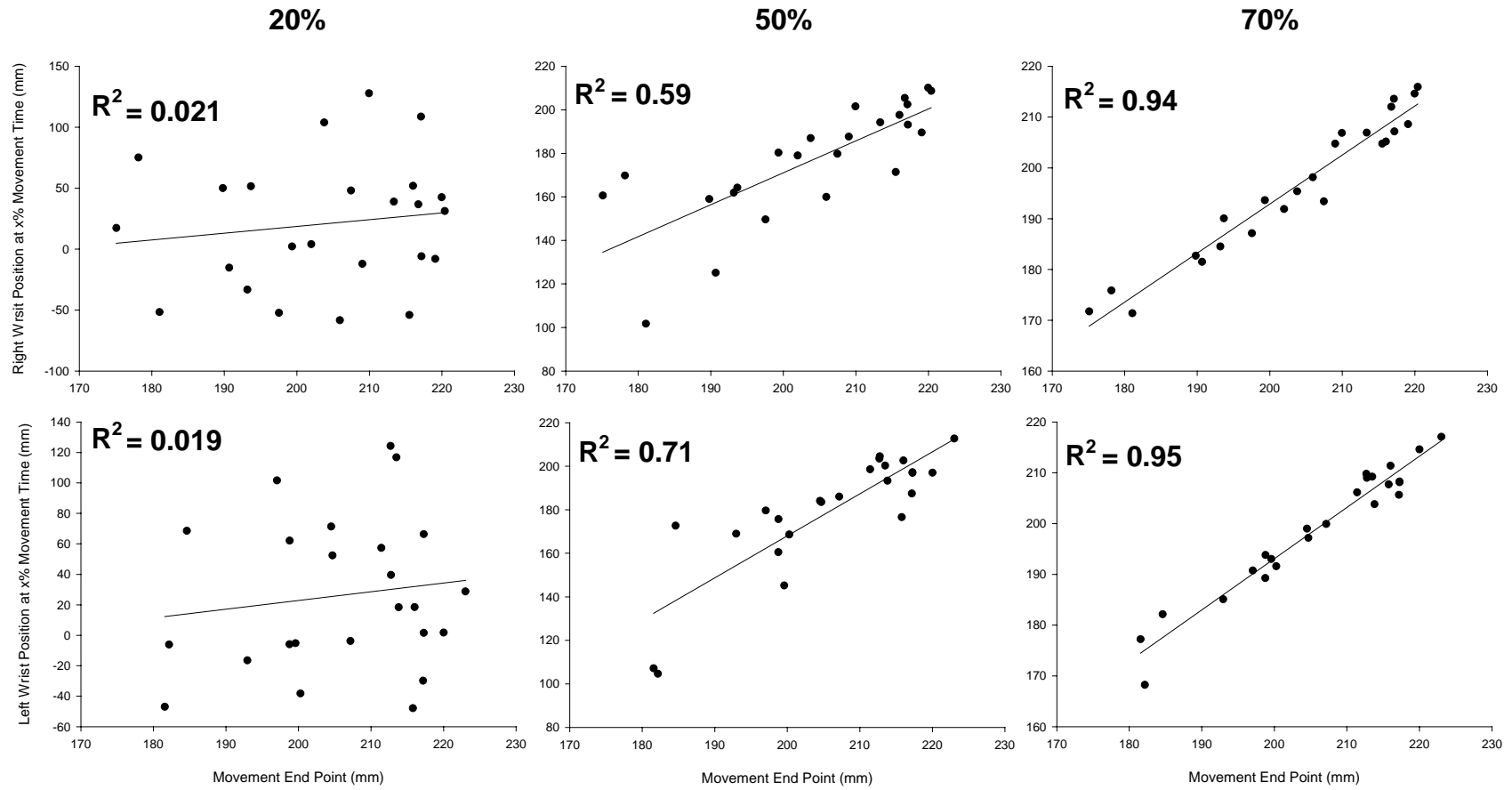


Figure 2.7

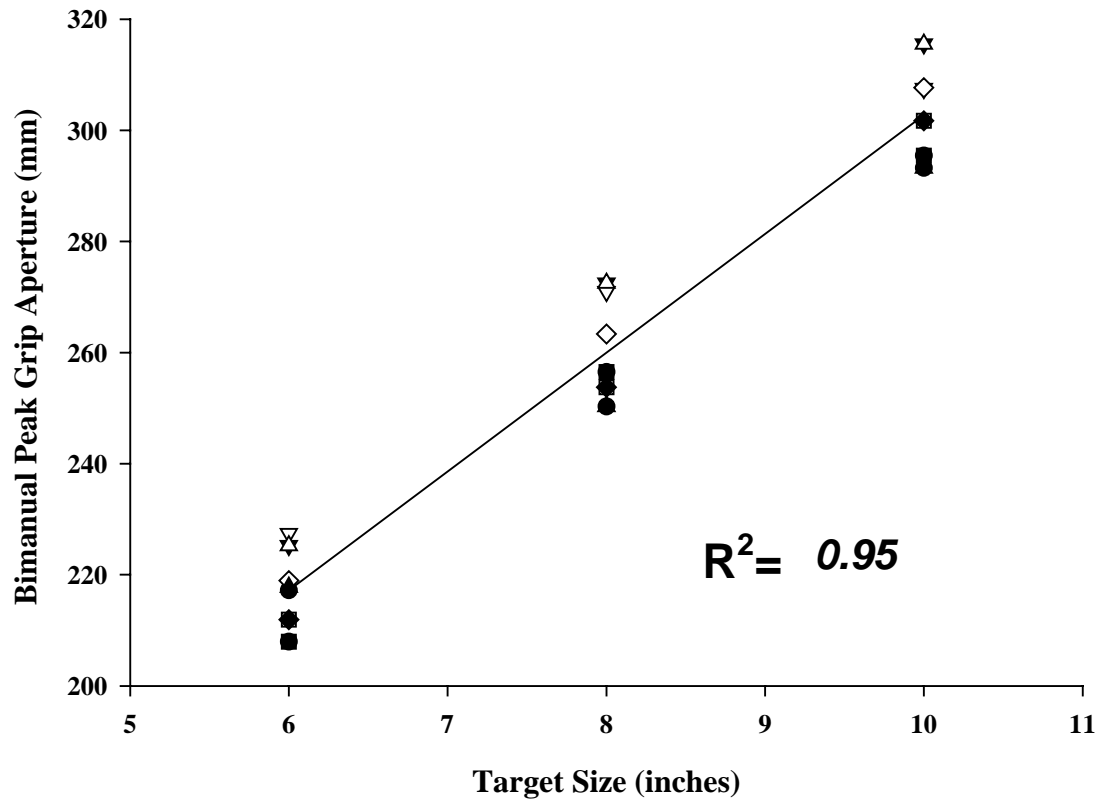


Figure 2.8

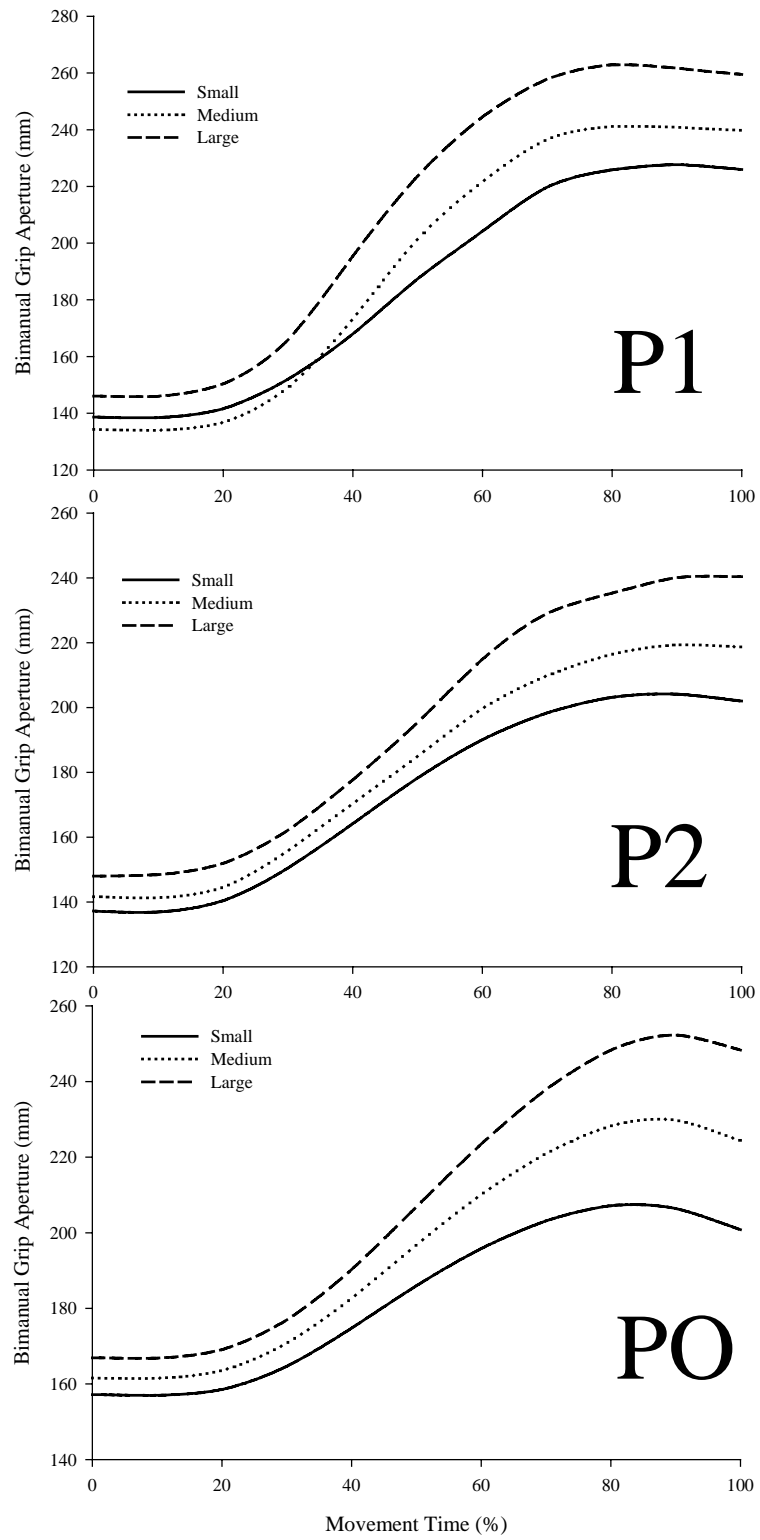


Figure 2.9

Chapter III: Experiment 1 and 2

Introduction

Humans are capable of reaching and grasping objects with great dexterity, and vision plays a vital role in the control of this fundamental skill. A key feature of the primate visual system is the separation of visual areas into two major cortico-cortical processing pathways. Based on neurophysiological and behavioral studies of macaque monkeys, Ungerleider and Mishkin (1982) first proposed an anatomical distinction between these pathways suggesting that objects are represented differently during action than they are for a purely perceptual task. Through identifying the “where” and “what” pathways, the authors argued that the brain’s visual pathways split into two distinct streams. Running dorsally from the primary visual cortex into posterior parietal cortex, the “where” pathway processes information required for spatial location of objects. Conversely, the “what” pathway integrates information concerned with object identification and runs ventrally from primary visual cortex into inferotemporal cortex.

Over a decade after Ungerleider and Mishkin’s initial observation, Milner and Goodale (1992) offered a reinterpretation of the psychological and functional significance for anatomical segregation of the ‘what’ and ‘where’ pathways. According to Perception-Action model (PAM) the processing of visual information is thought to be carried out through independent streams stemming from the primary visual cortex. Visual processing for goal-directed action is predominantly supported by the occipito-parietal pathway (so-called dorsal stream), while the visual processing for conscious visual perception and identification is performed through the occipito-temporal pathway (so-called ventral stream). Alternatively, by exploring the evidence for a distinction between planning and on-line control actions of human movement, Glover (2004) introduced the Planning-Control model (PCM). Although in opposition to the PAM, this approach is not significantly different from Milner and Goodale’s original theory. However, the PCM introduces a new perspective as to

how the two visual streams process information, specifically during action were independent planning and control is thought to occur (Glover, 2004; for review see Chap. I)

Since its conception, the notion that visual perception is independent of visually guided action has found empirical support in numerous neurological, neuropsychological, and behavioral studies. Remarkably, the majority of these studies are based entirely on evidence from right-handed subjects utilizing their dominant hand, which presumably is controlled by the left hemisphere (see Chap. I). To clarify, a vast amount of research and clinical observations has associated production and comprehension of language with the left hemisphere. Whilst no serious challenge exists in opposition to this claim, there is increasing evidence suggesting that speech may be only one of a large number of behaviors in which left hemisphere mechanisms are involved. In fact, there is tentative evidence from earlier neurological studies suggesting that the encapsulated visuomotor networks that mediate rapid target-directed movements may have evolved preferentially in the left hemisphere alongside well established specialization of the left hemisphere for the selection of hand postures and other complex movements (Goodale, 1988; Gazzaniga 2000). More specifically, a recent study utilizing a unimanual illusion paradigm concluded that, regardless of handedness, the left hemisphere plays a special role in the visual control of skilled grasping movements (Gonzalez et al., 2006). Nonetheless, it is not yet clear whether this advantage extends beyond unimanual grasping to other visually guided actions such as bimanual prehension. Indeed, this advantage leads us to speculate that bimanual prehensile movements processed and executed solely by the dorsal (visual control) stream may demonstrate higher levels of limb synchronization when compared to those completed through the ventral pathway.

Although hemispheric specialization provides an interesting prospective from which limb synchronization can be examined, it should be acknowledged that both hemispheres, regardless of visual pathway accessed, contribute to activation within the premotor areas (e.g. F5) prior to any movement execution. Furthermore, single neuron recording studies have showed that different neurons from the premotor area

F5 are involved in grasping compared to that of reaching (Rizzolatti et al., 1988; Gallase et al., 1996). Specifically, a more recent study reported that the anterior intraparietal (AIP) region of the human brain produces a greater response for visual grasping tasks than for reaching tasks (Culham, Danckert, & Goodale, 2002). Based on this evidence, if similar synchronization affects were demonstrated through ventral or dorsal processing of a bimanual prehension movement this may be due to the regulation of every grasping movement, regardless of hemisphere activation, through the premotor areas. To this end, we aimed to clarify whether available visual information (target and limbs) affects limb coordination during a bimanual prehension task. Specifically, we intended to segregate utilization of the ventral and dorsal visual processing streams (perception and action/planning and control) in order to develop further our understanding of co-operative limb movements to a single endpoint.

Experiment 1: Methods

Experiment Rationale – Visual Closed Loop Conditions

When executing a prehensile movement to a visible target, highly accurate performance is thought to be subserved by dedicated visuomotor mechanisms that reside in the posterior parietal cortex of the dorsal visual stream (Milner & Goodale, 1992). Accuracy of such movement is heightened through constant visual feedback, which allows for the detection and elimination of movement errors at any stage of limb trajectory (online control) (Connolly & Goodale, 1999). Consequently, the aim of the experiment 1 (E1) was to investigate the influence of visual feedback or online control on the performance, in line with current bimanual coordination models (Kelso et al., 1979; Marteniuk et al., 1980 see review, Chap. I), of a bimanual task targeting a solitary object.

Participants

Ten participants were recruited for this experiment (Range = 19-30 years old, mean = 24.5, SD = 3.5, five females and five males). All participants were right-handed, reported no visual, neurological or skeletomotor abnormalities and were naive to the purpose of the experiment. Handedness was assessed with modified versions of the Edinburgh Handedness Inventory (Oldfield, 1971) and a simple Finger Tapping task (Brown et al., 2004; see Table 3.1). The elements of the protocol have been previously forwarded and approved by the University of Saskatchewan Behavioral Science Research Ethics Board for ethical consideration in Human Experimentation in accordance with Declaration of Helsinki (1964).

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Insert Table 3.1 about here

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Stimuli

Three solid black stimuli were used; a small cylinder (diameter 15.24 cm, height 10.16 cm, weight 1.05 kg), a medium cylinder (diameter 20.32 cm, height 10.16 cm, weight 2.05 kg) and a large cylinder (diameter 24.50 cm, height 10.16 cm, weight 2.6 kg). Presented on a white cardboard background and 45cm from starting position of

the hands, the target object was positioned at one of three locations; either 45° to the left, 45° to the right, or on the sagittal axis passing through the participants midline (Fig. 3.1). The background was divided into two sections, one (65 cm x 91 cm) positioned horizontally on a table, and the other (80 cm x 91 cm) was placed vertically flush to the table surface, ensuring a homogenous environment. The distance between the floor and the near edge of the horizontal plane surface was 80 cm (Fig. 3.1).

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Insert Figure 3.1 about here
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Prehension style

A whole-hand or power grip (POW) was selected based on the results of our pilot experiment (see Chap. II). Therefore, every trial was completed with a POW grip characterized by flexion of all fingers around an object, with the palms of both hands in contact (Fig. 3.2).

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Insert Figure 3.2 about here
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Apparatus

Three-dimensional kinematic data was collected using an Visualeyze 3000 system (Phoenix Technologies Inc., Burnaby, BC, Canada) sampling at 200 Hz for 3 s and placed 1.5 m above the working surface. Four infrared-emitting diodes (IREDs) were placed on the skin overlying the following areas: (1) metacarpophalangeal joint of each index finger (knuckle IREDs); and (2) the region of the trapezium-metacarpal joint of both thumbs (wrist IREDs) (Fig. 3.3). The transport component was studied by analyzing the kinematics of the participant's wrist IREDs. Knuckle IREDs were utilized to analyze the manipulation component of the movement.

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Insert Figure 3.3 about here

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Liquid Crystal Goggles (Translucent Technologies Inc. Plato Model: P1) were used to achieve participant visual occlusion whilst the researcher manipulated target objects between trials. Motion tracking data was collected using a personal computer (BOXX Technologies Inc.) running Visualey Soft 2.70. Randomized trials and the liquid crystal goggles were triggered by a second computer (IBM ThinkCentre) running E-Prime Studio soft Version 1.1.

Procedure

Participants were seated in a height-adjustable chair so that the thorax pressed gently against the front edge of the table. A visible home position trigger was located 10cm anterior to the participant's midline. With opposition between the pads of the each index finger and thumb the participant was asked to place each digit coupling together and on the home position, depressing the trigger, with the first metacarpals in contact (Fig. 3.4). This resulted in a starting position where the ulnar side of the hand is in contact with the table surface, with slight shoulder flexion, 90° of elbow flexion, semipronation of the forearm, and 5-10° of wrist extension. It should be acknowledged that the home position trigger was deactivated during E1 conditions. Activation of this trigger was vital, however, in experiment 2 (E2) and therefore, in the interest of consistency, participants were instructed to depress the trigger regardless of experiment.

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Insert Figure 3.4 about here

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On a given trial and in response to an auditory start tone (880 Hz; duration 250 ms) participants were instructed to grasp a target object as quickly and as accurately

as possible utilizing a POW bimanual grip. Within a fully illuminated room, execution of each trial began with the participant in the previously described start position.

Visual Condition

Each trial was performed under a closed-loop (CL) visual condition, whereby the availability of visual information was controlled using a set of liquid-crystal goggles (Milgram, 1987), the lenses of which could be triggered to adopt a transparent or opaque state. A 2 s preview phase preceded each trial, during which time the goggles were made transparent and participants viewed the target. Immediately following this phase, the goggles became opaque occluding vision for a further 2 s. An ensuing auditory tone then cued participant movement (Fig. 3.5). To allow each participant sufficient time to complete the task in full vision the goggles remained transparent for 4 s following the auditory cue.

Utilizing all possible combinations of: (1) target object size (small, medium, large); and (2) target object location (middle, left, right) nine conditions were obtained. Each experiment consisted of 72 trials. All conditions were randomized.

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 Insert Figure 3.5 about here
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Data Reduction and Analysis

Kinematic parameters were initially calculated for each hand separately. Movement onset was defined as the first frame in which the wrist marker attained and maintained a velocity (in direction of the movement) of 50 mm/s for ten consecutive frames (i.e., 50 ms; Binsted & Elliott, 2001; Elliott, Heath, Binsted, Ricker, Roy, & Chua, 1999); reaction time (RT) is the time elapsed from collection start to movement start. Movement endpoint was defined as the frame at which finger velocities fell below and remained below 50 mm/s for ten consecutive frames (i.e., 50 ms). Position data for all IREDs were filtered off-line using a second-order dual-pass Butterworth filter (low-pass, 15 Hz). Instantaneous velocities were calculated by

differentiating displacement data using a five-point central finite difference algorithm.

Inferring Feedback based Control

The nature of limb control in both CL (visually guided) and OL2 (memory-guided) was examined using a regression analysis. Originally adapted from Elliott, Binsted and Heath (1999) and more recently by Heath, Westwood and Binsted (2004), this procedure utilizes the 3D coordinates of the wrist markers to quantify the proportion of variability (R^2) in endpoint position which can be predicted from the position of the limb at 20%, 50% and 70% of total movement duration. Further clarification and rationale for the inclusion of this variable is provided within the method section for the pilot study in chapter II.

Dependant Measures

A series of dependent measures were computed from the 3D coordinates for the wrist marker, and were used to analyze the kinematics of the transport phase: (1) peak velocity in the direction of the movement (PV); (2) absolute time between movement onset and the point where peak velocity is achieved (msecs) (TPV); (3) peak acceleration (PA); and (4) time to peak acceleration (TPA).

The following dependent variables were computed from the 3D coordinates of thumb, index finger, knuckle and wrist IREDs. (5) Bimanual grip peak aperture (BPGA) was defined between left and right knuckle markers (measure in mm). The following variable defined as (6) time taken to reach BPGA as a percentage of the total movement duration (TBPGA percentage) was subsequently computed for each condition.

In addition to the above measures, we also computed a series of relative measures in which the kinematics of the left hand are indexed to those of the right (dominant) hand. The remaining measures were organized around a set of key questions as follows: (a) Do the hands begin to move at the same point in time? (7) *Movement onset lag* (RH-LH): A positive difference would indicate that the right hand began to move after the left hand while a negative difference would indicate that the right hand moved first; (b) Do the hands reach peak velocity at the same point? (8) *Peak velocity lag* (RH-LH); (c) Do the hands reach peak acceleration at the same point?

(9) *Peak acceleration lag* (RH-LH); (d) Do the hands make contact with the target objects at the same time? (10) *Movement end-point lag* (RH-LH).

Statistical Analysis

All hand dependent measures were analyzed using a 2 hand (right, left) x 3 target sizes (small, medium, large) x 3 locations (left, middle, right) repeated measures ANOVA, with each score based on the median values. Where appropriate, *F* statistics were corrected for violations of the sphericity assumption using the Huynh-Feldt correction. Simple effect analysis and Bonferroni correction for multiple analyses were used when necessary to specify the nature of any significant effect. Alpha was set at $p = .05$ for all statistical analyses.

Experiment 1: Results

Visual Closed Loop Conditions

Overall, removal of only 12 trials (< 1.4%) due to poor marker detection occurred and consistent patterns of movements were demonstrated across all conditions. Participants produced their response with a latency of 214.2 ± 46.5 ms and subsequent movement duration of 836.8 ± 169.7 ms. No missed trials occurred (i.e.; unsuccessful grasping of target object) as all participants were able to complete the task proficiently.

Transport Kinematics

Temporal Latency Measures

Examination of reaction time revealed a significant main effect of hand ($F(1, 9) = 63.3, p = 0.02$). Across all conditions the RH responded with a significantly faster reaction time (RT) than the LH (Table 3.1). Analysis of movement time exposed significant main effects of hand ($F(1, 9) = 7.6, p = 0.02$) and target size ($F(2, 18) = 5.7, p = 0.01$). Movement times of the LH were significantly smaller than that of the RH (Table 3.1). The main effect of target size revealed that movement times were significantly longer for bimanual reaches to the small target compared to the medium ($F(1, 9) = 11.9, p = 0.00$) and large ($F(1, 9) = 7.6, p = 0.02$). In contrast, no movement time differences were found between medium and large targets ($F(1, 9) = 1.9, p = 0.25$). The ANOVA utilized to examine response time exhibited a significant main effect of size ($F(2, 18) = 6.6, p < 0.01$). The main effect of hand was not statistically significant ($F(1, 9) = 5.0, p = 0.07$) indicating that both hands contacted the target simultaneously (Table 3.1). The main effect of size was again examined in pairwise comparisons. Similar to movement times, these analyses revealed that response times were significantly longer for bimanual reaches to the small target compared to the medium ($F(1, 9) = 11.2, p = 0.01$) and large ($F(1, 9) = 8.1, p = 0.02$). In contrast, no response time differences were found between medium and large targets ($F(1, 9) = 2.9, p = 0.1$).

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Insert Table 3.2 about here

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Kinematic Measures

An examination of limb path length demonstrated significant main effects of hand ($F(1, 9) = 6.1, p = 0.04$), size ($F(2, 18) = 6.7, p = 0.01$) and direction ($F(2, 18) = 14.5, p < 0.01$). Overall, path lengths of the LH were significantly greater than the RH (Table 3.1). The main effect of direction was examined using pairwise comparison collapsing across hand and size. These analyses revealed that path length was significantly different for every target location. Inspection of similar comparisons for the main effect of size showed for grasps to small targets that path lengths were significantly larger compared to medium ($F(1, 9) = 8.3, p = 0.02$) and large ($F(1, 9) = 10.9, p < 0.01$) targets. No such difference was found when comparing path lengths for grasps to medium and large targets ($F(1, 9) = 0.01, p = 0.92$).

Importantly, the ANOVA revealed a significant hand x direction interaction effect ($F(2, 18) = 11.7, p < 0.01$). Further analyses were carried out using pairwise comparisons to examine the interaction effect. The path length of the LH was significantly greater than the RH when subjects grasped both the left ($F(1, 9) = 7.1, p = 0.04$) and right ($F(1, 9) = 12.1, p < 0.01$) target (Fig. 3.6). In contrast, path lengths of the LH and RH did not differ significantly when the subject grasped for the middle target ($F(1, 9) = 0.02, p = 0.88$).

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Insert Figure 3.6 about here

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Inspection of peak acceleration revealed a number of effects. The magnitude of acceleration revealed a significant main effect of direction ($F(2, 18) = 4.1, p = 0.03$). Both hand and size main effects did not reach statistical significance ($F(1, 9) = 1.9, p = 0.2$; $F(2, 18) = 0.47, p = 0.6$). Planned comparison were carried out and analyses revealed that peak accelerations were significantly greater when reaching to targets located to right compared to those located on the left ($F(1, 9) = 16.1, p < 0.01$). Peak accelerations for both hands during bimanual reaches to the middle target did not differ from those located on the right ($F(1, 9) = 0.49, p = 0.4$) or the left ($F(1, 9)$

= 2.1, $p = 0.1$). The ANOVA also revealed a significant hand x direction interaction effect ($F(2, 18) = 11.7, p < 0.01$) of peak acceleration. Pairwise comparisons revealed that LH and RH peak acceleration differed only when executing a bimanual reach to targets located on the right ($F(1, 9) = 15.3, p < 0.01$). In contrast, peak acceleration of the LH and RH did not show significant differences when reach and grasping for targets located to the left ($F(1, 9) = 0.25, p = 0.62$) or directly in front ($F(1, 9) = 0.3, p = 0.59$) of the subject.

The time to reach peak acceleration yielded significant main effects of hand ($F(1, 9) = 139.0, p < 0.01$) and direction ($F(2, 18) = 7.7, p < 0.01$). Overall, time to peak acceleration was reached significantly quicker by the RH compared to the LH (Table 3.2). Main effect of direction analyses show that the time to peak acceleration for both hands was significantly longer when grasping a target on the right hand side compared to targets on the left ($F(1, 9) = 21.4, p < 0.01$) and in the middle ($F(1, 9) = 10.3, p = 0.01$). No significant time differences were demonstrated for both hands when performing grasps to the left or directly in front of the subject ($F(1, 9) = 0.8, p = 0.39$).

Analysis of peak velocity revealed no significant main effects. However, a significant hand x direction interaction effect was found ($F(2, 18) = 13.2, p < 0.01$). Pairwise comparisons were again utilized to examine the effects of hand for each direction. Identical to the peak acceleration data, analyses revealed that LH and RH peak velocity differed only when executing a grasp to targets located on the right ($F(1, 9) = 10.8, p = 0.03$). In contrast, peak velocity of the LH and RH did not show significant differences when reach and grasping for targets located to the left ($F(1, 9) = 6.5, p = 0.83$) or directly in front ($F(1, 9) = 0.01, p = 0.91$) of the subject. Subsequent examination of the latency of peak velocity exposed a significant main effect of direction ($F(2, 18) = 4.5, p = 0.03$). No significant main effect of hand was found ($F(1, 9) = 2.07, p = 0.69$) thus, the time elapsed between movement onset and peak wrist velocity did not differ between the hands (Table 3.2). However, further planned comparison analyses reveal that times to reach peak velocity were significantly longer for grasps to targets on the subject's right side compared to targets located on the left ($F(1, 9) = 6.6, p = 0.03$) or in the middle ($F(1, 9) = 5.95, p$

= 0.04). Times to peak velocity were not significantly different when performing grasps to the left or directly in front of the subject ($F(1, 9) = 0.11, p = 0.75$).

Proportion of Endpoint variance

These analyses examined the proportion of variance (R^2) in movement endpoints explained by the position of the limb position at 20%, 50% and 70% of total movement time. No main effects or interactions were revealed through statistical analysis. As expected, further examination yielded that the R^2 values for both hands when performing within closed conditions were relatively small at each time point, indicating that the position of limb at 20%, 50% and 70% of the movement was not strongly predictive of the final movement endpoint. Figure 3.7 illustrates a representative subject closed loop condition trial for both LH and RH.

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 Insert Figure 3.7 about here
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Grasp

Bimanual Grip Aperture

The examination of bimanual peak grip aperture (BPGA) revealed significant main effects of size ($F(2, 18) = 37.5, p < 0.01$) and direction ($F(2, 18) = 4.7, p = 0.03$). Importantly, the main effect of size demonstrates scaling of bimanual grip aperture to target size. Pairwise comparisons indicate significantly larger BPGA for the large target compared to the medium ($F(1, 9) = 45.9, p < 0.01$) and small ($F(1, 9) = 38.4, p = 0.00$) target. Strong positive linear correlations between target size and bimanual grip aperture are shown in Figure 3.8. Directional comparisons revealed that when grasping to targets located on the right the BPGA is significantly larger than that created when grasping to the left ($F(1, 9) = 5.3, p = 0.04$) and middle ($F(1, 9) = 8.4, p = 0.01$) targets. Bimanual peak grip apertures created to interact with targets on the left and directly in front of subjects did not differ ($F(1, 9) = 0.54, p = 0.48$). Further, the analysis of the latency of BPGA demonstrated no significant main or interaction effects. Thus, the time that elapsed between movement onset and

bimanual peak grip aperture did not differ between the hands, or vary across movements of different direction, or between target sizes (Figure 3.9).

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Insert Figure 3.8 about here

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Insert Figure 3.9 about here

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Bimanual Coupling

As noted above, we also computed a set of relative measures in which the kinematics of the left hand were indexed to those of the right (dominant) hand. These measures were organized to test the extent to which the hands reached important kinematic markers at the same point in time.

Examination of movement onset revealed no coupling of limbs at movement initiation (e.g. lags were significantly different from zero [$F(1, 9) = 11.3, p < 0.01$]). Similarly, no coupling was demonstrated within the relative lags at TPA (e.g. significant difference from zero [$F(1, 9) = 14.1, p < 0.01$]). In contrast, TPV lags did not reach statistical significance when compared to zero ($F(1, 9) = 2.05, p = 0.18$) indicating that each hand reached peak velocity at the same time regardless of direction or target size. Finally, temporal limb coupling was observed at movement completion across all conditions as relative lags revealed no significant difference from zero ($F(1, 9) = 0.14, p = 0.68$) was found.

Experiment 1: Discussion

Earlier the author outlined two theoretical frameworks which have been proposed to explain how the bimanual coordination might be brought about during the execution upper limb movements (see Chap. I). The first of these frameworks, which we refer to as the single coordinating structure theory, proposes that control is exerted across limbs via a functional group of muscles (coordinative structure), resulting in spatiotemporal synchronization (Kelso et al., 1979). This can be contrasted with a second framework, referred to as the neural cross-talk theory, which instead argues for the independent programming of each limb and the CNS individually controlling muscles (Marteniuk & Mackenzie, 1980). Consequently, the aim of the E1 was to examine how well each framework can account for the novel bimanual prehension movement data obtained under CL conditions where visual feedback is available.

Indeed, with regard to our specific bimanual movements executed within a CL (vision) condition, this experiment revealed several interesting findings. First, and in contrast to our pilot study findings, the velocity and acceleration data in the present study, lend some support to the neural cross-talk theory of bimanual coordination proposed by Marteniuk and Mackenzie (1980). In their investigations no temporal limb coupling was found when limbs were required to move different distances. As confirmed within our path length data, each hand traveled significantly different distances when targets were located either to the left or to the right of the subject (Fig. 3.6). This path length differential is the most plausible explanation for the discrepancy between the current experimental findings compared to that of the pilot study, which reported both temporal and spatial limb coupling. As previously alluded to, within E1 no temporal coupling was reported for grasps executed to the targets located on the left or right. Despite both hands reaching TPV at the same time, the TPA was not synchronized regardless of target size (Table 3.2) supporting the neural cross-talk theory.

A somewhat unexpected finding, however, is a lack of temporal coupling seen within the velocity and acceleration data of the centrally located target. Again, both hands reached TPV simultaneously with no coupling of TPA despite the distance travelled by each hand being identical (Table 3.2). This is in contrast, to Marteniuk

and Mackenzie (1980) who explained the coordination of bimanual tasks in terms of intensity and endpoint specification for each individual limb: When limbs are required to move different distances, the limb moving the greater distance receives a higher intensity specification than the contralateral limb does. Subsequently, there is interference with the movement topology of that limb resulting in no apparent interlimb coupling. However, the authors argue that no interference occurs when limbs are required to move similar distances and that interlimb coupling is due to the formation of identical motor commands for each limb. The lack of coupling found during same-distance conditions within our study could plausibly be attributed to the relationship between dorsal stream processing (visual control) and cerebral hemisphere specialization; a notion that will be discussed later.

A second finding of interest concerns the kinematic parameters, which describe movement onset and endpoint of the bimanual movements. In contrast to all previous bimanual prehension studies, movement onset of both hands to a solitary target does not occur simultaneously under CL conditions. All movements in the present study were characterized by a RH movement initiation, confirmed by reaction time data where the RH is significantly faster than the LH in all trials. Despite no apparent movement onset coupling, inspection of movement endpoint lag data clearly indicates that, even when they are not given explicit instructions to do so, participants readily couple bimanual prehension movements so that they make contact with their target objects at approximately the same point in time. How is this achieved in circumstances where each hand does not start together and is required to carry out a co-operative action? One possible answer, in support of the coordinative structure theory proposed by Kelso et al. (1979), appears to be that while other movement parameters of each hand are free to vary, a movement duration (response time) is chosen which is common across the two hands. This is arguably evident in Table 3.2, which illustrates that a quicker RH reaction time is counterbalanced by the LH's shorter movement time resulting in the same movement duration, bringing the hands together and simultaneously contacting the target. These findings suggest that a key aspect of bimanual coupling within CL conditions is the selection of a common movement duration within which the actions to be performed by each hand must be scaled accordingly (see Hoff & Arbib, 1993 for a similar account of how the

transport and grasp phases of unimanual prehension movements may be temporally coordinated).

However, in opposition to this explanation, it can be argued that the lack of movement onset and temporal coupling observed indicates that the limbs are programmed separately. Again, this standpoint supports Marteniuk and Mackenzie's (1980) theory that the CNS individually controls muscles and that any synchronization occurs due to neural interference. Indeed, it is may be more plausible to suggest that any synchronization present at the end of this specific bimanual movement is due to the overriding constraint for the two limbs to meet the target simultaneously in order to execute a successful interaction (e.g. grasp and lift). The notion that specific task constraints play a vital role within the kinematic planning of limb movement can also be argued within the context of hemispheric specialization. Gonzalez and co-workers (2006) proposed that the left hemisphere has an advantage in terms of visually controlling complex motor behaviors. The direct access of the RH to this hemispheric advantage could arguably be characterized by the significantly quicker RH reaction times reported during all trials. In fact, the advantage would be more prominent within this E1 visual condition where movement programming and execution is based solely on dorsal stream information (visual control).

In summary, although somewhat ambiguous, our E1 results provide support for the neural cross-talk theory of bimanual coordination within CL conditions. Under these visual conditions there is evidence that the model of Marteniuk and Mackenzie (1980) can be generalized to the study of bimanual prehension movements, in which the hands are required to arrive simultaneously at the same target endpoint position so that rather precise task constraints can be satisfied.

Experiment 2: Methods

Experiment Rationale – Visual Open Loop 2s Delay Conditions

Visually occluding a target prior to movement initiation disrupts the normal online operation of the visuomotor system and forces the reliance on a stored, memory-dependent representation of target information thought to be retained in the inferotemporal cortex of the ventral visual stream (Milner & Goodale, 1992).

Although typically less accurate and more variable than visually guided movements (e.g. Flanders, Helms, Tillery, & Soechting, 1992; Westwood, Heath, & Roy, 2001, 2003; Woodworth, 1899), memory-dependent actions can remain remarkably accurate even with considerable delays (Elliott, 1988). Therefore, E2 utilizes a visual open-loop 2 s delay (OL2) condition to investigate the performance of bimanual prehension to a single target under memory-guided (ventral) control.

Identical Protocol

As described previously, this study consisted of two experiments, each experiment utilizing a different visual condition (Visual Closed loop vs. Visual Open loop 2 s Delay). Both E1 and E2 followed exactly the same procedure, data analysis, data reduction and statistical analysis, the difference lying only in the visual condition utilized. All ten participants recruited completed both E1 and E2 in a random order. Due to the length of each experiment and to avoid fatigue affects, each experiment was completed on a different day.

Visual Condition

The OL2 condition began with a 2 s target preview phase followed by visual occlusion, whereby the goggles changed and remained in an opaque state for the duration of the response and execution phases. Two seconds after visual occlusion an auditory tone cued participant movement (Fig. 3.10).

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Insert Figure 3.10 about here

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The participant could see neither the target nor their hand throughout the entire movement, thereby, requiring a representation to be retained in memory for 2 s (e.g.

two-second delay). Participants were instructed to move as quickly and as accurately as possible, however, in the event that the target was missed, participants were instructed to search for the object until a stable grasp was affected.

Experiment 2: Results

Visual Open Loop 2sec Delay

Removal of only 28 trials (< 2 %) due to poor marker detection occurred and consistent patterns of movements were demonstrated across all conditions. Participant's reaction time was reported at 70.2 ± 20.3 ms with subsequent movement duration of 863.9 ± 163.7 ms. It should be noted that reaction times were lower than normally expected across all subjects due to the nature of the visual condition. The standardized 2 sec delay prior to movement initiation lead to regular participant anticipation of the start tone and resulted in relatively low mean reaction times for both hands.

Transport Kinematics

Temporal Latency Measures

Inspection of reaction time yielded no significant main or interaction effects. Thus, the produced response latency produced did not differ between the hands, or vary across movements of different direction, or between target sizes (Table 3.3). Movement time analysis revealed significant main effects of hand ($F(1, 9) = 12.3, p < 0.01$) and target size ($F(2, 18) = 9.0, p < 0.01$). Left hand movement times were significantly slower than that of the RH (Table 3.3). The main effect of size was further examined with pairwise comparison. These analyses revealed that movement times were significantly longer for bimanual reaches to the small target compared to the medium ($F(1, 9) = 11.9, p < 0.01$) and large ($F(1, 9) = 7.6, p = 0.02$). In contrast, no movement time differences were found between medium and large targets ($F(1, 9) = 1.5, p = 0.25$). Response time exhibited a significant main effect of hand ($F(1, 9) = 13.2, p < 0.01$) and target size ($F(2, 18) = 32.3, p = 0.01$). The main effect of hand revealed that the LH had a significantly longer response time than the RH (Table 3.3). The main effect of size was again examined in a series of pairwise comparisons and similar to movement times, these analyses revealed that response times were significantly longer for bimanual reaches to the small target compared to the medium ($F(1, 9) = 8.8, p < 0.01$) and large ($F(1, 9) = 8.9, p = 0.01$) target. In contrast, no response time differences were found between medium and large targets ($F(1, 9) = 3.3, p = 0.11$).

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 Insert Table 3.3 about here
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Kinematic Measures

Limb path length analysis demonstrated significant main effects of hand ($F(1, 9) = 73.3, p = 0.00$), target size ($F(2, 18) = 33.6, p < 0.01$) and direction ($F(2, 18) = 34.7, p < 0.01$). Overall, path lengths of the RH were significantly greater than the LH (Table 3.3). The main effect of direction was examined using a series of pairwise comparisons collapsing across hand and size. These analyses revealed that path length was significantly different for every target location. Inspection of similar comparisons for the main effect of size showed that path lengths were significantly different for grasps executed to all sized targets. Additionally, analysis also yielded a significant hand x direction interaction effect ($F(2, 18) = 88.3, p < 0.01$; Fig. 3.11). Left hand path lengths were significantly greater than those of the RH when subjects grasped both to the left ($F(1, 9) = 63.5, p < 0.01$) and right ($F(1, 9) = 9.6, p = 0.01$) target. Conversely, path lengths of the LH and RH did not differ significantly when the subject grasped for the middle target ($F(1, 9) < 0.01, p = 0.94$).

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 Insert Figure 3.11 about here
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The magnitude of limb peak acceleration exhibited significant main effects of hand ($F(1, 9) = 11.2, p < 0.01$) and direction ($F(2, 18) = 5.4, p = 0.01$). The main effect of hand indicates that the RH has significantly greater peak acceleration than the LH (Table 3.2). Pairwise comparisons were carried out to examine the main effect of direction. Direction analyses revealed that peak accelerations were significantly greater for grasps to targets located on the right compared to those located on the left ($F(1, 9) = 14.5, p < 0.01$) and directly in front ($F(1, 9) = 8.3, p = 0.02$) of the subject. Peak accelerations for both hands during bimanual grasps to the middle target did not differ from those located on the left ($F(1, 9) = 4.9, p = 0.055$).

The ANOVA also revealed a significant hand x direction interaction effect ($F(2, 18) = 7.4, p < 0.01$). Subsequent analyses revealed that LH and RH peak acceleration differed only when executing a bimanual reach to targets located on the right ($F(1, 9) = 16.2, p = 0.03$). In contrast, peak acceleration of the LH and RH did not show significant differences when reach and grasping for targets located to the left ($F(1, 9) = 0.78, p = 0.40$) or directly in front ($F(1, 9) = 4.4, p = 0.66$) of the subject. Significant main effects of hand ($F(1, 9) = 135.7, p < 0.01$) and direction ($F(2, 18) = 39.2, p = 0.01$) were also revealed through the analysis of time to peak acceleration. Overall, time to peak acceleration was reached significantly quicker by the LH compared to the RH (Table 3.2). Pairwise comparison analyses of direction effects showed that time to reach peak acceleration for both hands is significantly longer when grasping a target on the right hand side compared to targets on the left ($F(1, 9) = 8.9, p = 0.01$) and in the middle ($F(1, 9) = 8.8, p = 0.01$). No significant time differences were demonstrated for both hands when performing grasps to the left or directly in front of the subject ($F(1, 9) = 0.93, p = 0.39$).

Peak velocity examination revealed significant main effects of hand ($F(1, 9) = 8.1, p < 0.01$) and target direction ($F(2, 18) = 9.5, p < 0.01$). The main effect of hand indicates that overall the RH has a significantly greater peak velocity than the LH (Table 3.2). Direction effect analyses revealed that peak velocities were significantly greater for grasps to targets located on the right compared to those located on the left ($F(1, 9) = 3.2, p = 0.01$) and directly in front ($F(1, 9) = 7.1, p = 0.04$) of the subject. Peak velocities for both hands during bimanual grasps to the middle target did not differ from those located on the left ($F(1, 9) = 11.8, p = 0.054$). Further peak velocity analysis also revealed a significant hand x direction interaction effect ($F(2, 18) = 12.7, p < 0.01$). Pairwise comparisons were again utilized to examine the effects of hand for each direction. Unlike the peak acceleration data, analyses revealed that LH and RH peak velocity differed when executing a grasp to targets located on the right ($F(1, 9) = 8.7, p = 0.01$) and to the left ($F(1, 9) = 9.3, p = 0.00$). In contrast, peak velocity of the LH and RH did not show significant differences when reach and grasping for targets located centrally ($F(1,9) = 2.1, p = 0.08$). Subsequent examination of the latency of peak velocity exposed a significant main effect of direction ($F(1, 9) = 33.8, p = 0.03$). Further pairwise comparison

analyses reveal that times to reach peak velocity were significantly longer for grasps to targets on the subjects right side compared to that of targets located centrally ($F(1, 9) = 7.4, p = 0.02$). Times to peak velocity were not significantly different when performing grasps to the left ($F(1, 9) = 2.3, p = 0.12$) or directly in front of the subject ($F(1, 9) = 0.35, p = 0.48$). No significant main effect of hand was found ($F(1, 9) = 1.2, p = 0.21$) thus, the time elapsed between movement onset and peak wrist velocity did not differ between the hands.

Proportion of Endpoint variance

The proportion of variance (R^2) in movement endpoints explained by the position of the limb position at 20%, 50% and 70% of total movement time was examined across both hands. No main effects or interactions were revealed through statistical analysis. Subsequent inspection revealed that the R^2 values for the RH when performing within OL2 conditions were relatively small at each time point, indicating that the position of limb at 20%, 50% and 70% of the movement was not strongly predictive of the final movement endpoint. Conversely, R^2 values for the LH were relatively high as expected within OL2 condition, indicating a strong predictive relationship between the kinematics markers and endpoint. Figure 3.12 illustrates a representative subject OL2 condition trial.

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 Insert Figure 3.12 about here
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Grasp

Bimanual Peak Grip Aperture

Inspection of bimanual peak grip aperture (BPGA) yielded significant main effects of target size ($F(2, 18) = 118.6, p < 0.01$) and direction ($F(2, 18) = 78.2, p = 0.03$). Importantly, the main effect of size demonstrates scaling of bimanual grip aperture to target size (Figure 3.13). Series comparisons indicate significantly larger BPGA for the large target compared to the medium ($F(1, 9) = 8.8, p < 0.01$) and small ($F(1, 9) = 9.2, p = 0.00$) target. Directional comparisons revealed that when grasping to targets located on the left BPGA is significantly larger than that created when

grasping to the right ($F(1, 9) = 11.4, p < 0.01$) and middle ($F(1, 9) = 14.3, p = 0.03$) targets. Bimanual peak grip apertures created to grasp targets on the right and directly in front of subjects did not differ ($F(1, 9) = 1.3, p = 0.72$). Further, analysis of the latency of BPGA demonstrated no significant main or interaction effects. Thus, the time that elapsed between movement onset and bimanual peak grip aperture did not differ between the hands, or vary across movements of different direction, or between target sizes (Figure 3.14).

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Bimanual Coupling

A set of relative measures in which the kinematics of the LH were indexed to those of the RH (dominant). These measures were organized to test the extent to which the hands reached important kinematic markers at the same point in time.

Examination of movement onset lags revealed no significant main effects or interactions of direction or size. Further analyses indicate that, regardless of target size and direction both hands simultaneously initiate movement (e.g. lag values revealed no significant difference from zero ($F(1, 9) = 13.2, p = 0.08$)). Similar inspection of relative lags at TPA exhibited a significant main effect of direction ($F(2, 18) = 3.8, p = 0.01$). Statistical analyses of collapsed values across size revealed no significant lag difference from zero for grasps executed to targets on the right ($F(1, 9) = 10.6, p = 0.10$) and in front of the subjects ($F(1, 9) = 2.8, p = 0.12$). In contrast, when grasping targets located on the left, subjects TPA lag was significantly different from zero ($F(1, 9) = 5.2, p = 0.02$). These analyses indicate that, regardless of target size, both hands simultaneously reached peak acceleration when targets are located on the right and middle only. Analysis of TPV lags

demonstrated no significant main effects or interactions of direction. Subsequent statistical analyses indicated that the hands reached peak velocity simultaneously regardless of direction or size (e.g. lag values revealed no significant difference from zero ($F(1, 9) = 3.1, p = 0.11$). Finally, no limb coupling at movement completion was evident through similar analyses which revealed no significant main effects or interactions (e.g lag values yielded a significant difference from zero ($F(1, 9) = 4.7, p = 0.02$). These analyses indicate that, regardless of target size and direction, the RH contacted the target on average 62ms prior to LH contact.

Experiment 2: Discussion

Two opposing theoretical frameworks have been proposed to explain bimanual coordination between limbs; the single coordinating structure (Kelso et al., 1979) and the neural cross-talk theory (Marteniuk & Mackenzie, 1980; see review, Chap. I). Therefore, the aim of the E2 was to investigate the predictive ability of each framework for the performance of our specific bimanual prehension movement under memory-guided control (OL2 conditions).

Similar to E1, the results of this experiment revealed several interesting findings with regard to performing a bimanual prehensile movement targeting a single object under OL2 conditions. Again, path length data confirmed that each hand travelled significantly different distances when targeting objects located to the left and to the right of the subject, whereas hand path lengths to the central target were identical (Fig. 3.11). Unlike E1, however, the velocity and acceleration data are contradictory in their support of either theories of bimanual coordination theory. Despite TPV coupling across all target sizes and conditions, TPA synchronisation only occurred when movements were performed to the right and central targets regardless of size. Temporal coupling of TPA and TPV supports Kelso's coordinative structure theory, initially suggesting that control is exerted across limbs when grasping for targets located centrally or to the right. Conversely, support for Marteniuk and Mackenzie's (1980) neural cross-talk theory, hence limbs being programmed separately, is present when grasps are executed to the left target as no coupling of TPA occurs.

Inspection of bimanual coupling parameters reveals that movement onset of both hands occurs simultaneously across all conditions. This expected coupling of movement initiation is supported by previous bimanual prehension studies (Casteillo, 1993; Jackson et al. 1999; Taylor & David's, 1997). Interestingly, however, our findings demonstrate that the RH contacts the targets on average 62 ms before the LH regardless of target condition. From a theoretical point of view, this unexpected finding is equivocal in providing support for either existing bimanual coordination model. Both the neural cross-talk and single structure theories report simultaneous contact of hands with target objects despite arguing the source of motor control for each limb.

Even though coupling across all temporal and spatial variables is inconsistent it is important to note within all our trials target objects were successfully grasped and lifted. The question arises; how is task success consistently achieved with no synchronization of the end-point effectors and utilization of only ventral stream (perceptual) information? One plausible explanation may lie in participants employing a specific search strategy, whereby the RH purposefully contacts the target before the LH. Indeed, interpretation of our endpoint variability data would provide speculative evidence for such a strategy (Fig. 3.12). Once movement is initiated the RH demonstrates a faster movement time and more endpoint variability than the LH, as if searching for an end location. The LH, however, is slower in executing the task but very precise in terms of endpoint variance, indicating the use of a planned trajectory. Once in contact, it is may be possible for the LH to adjust accordingly and successfully interact with the target using sensory feedback from the RH. However, due to the small time difference between RH and LH target contact (~62 ms) it is speculative as to whether such feedback could be used competently. Alternatively, and as a consequence of neural cross talk, it is more likely that during transport, programming of the left limb is aided through right limb motor command interference. Such a proposal not only assumes independent control of limbs but also acknowledges neural cross talk, again lending support for the theoretical framework of Marteniuk and Mackenzie (1980). As seen in E1, any synchronization or employment of search strategies is arguably due to the specific task constraints for the two limbs to meet the target simultaneously in order to execute a successful interaction (e.g. grasp and lift). The possible role that hemispheric specialization might play during bimanual grasp is again brought into question and will be discussed further in the general discussion.

In summary, our E2 results again provide some support for Marteniuk and Mackenzie (1980) neural crosstalk theory of bimanual coordination within OL2 conditions. Evident from consistent task success and no end-effector coupling, it would seem that the independent programming of each limb during bimanual prehension to a single target is essential during memory guided control.

Table 3.1. Handedness Tests

Subject	Respective Laterality Quotient	
	Edinburgh Handedness Test (EHT)	Finger Tapping Test (FTT)
1	77.8	6.48
2	90	7.92
3	73.3	3.27
4	85.7	1.41
5	100	5.40
6	85.7	8.33
7	71.4	4.18
8	81.5	8.02
9	85.7	2.09
10	90	3.43
<i>Mean ± SD</i>	<i>82.6 ± 8.4</i>	<i>5.05 ± 2.55</i>

* For EHT right hand dominance is indicated with a score >70.

** For FTT right hand dominance is indicated with a score > 0.

Table 3.2. Closed loop condition; Mean (SD in brackets) transport kinematics.

Closed loop condition (Vision)		
Left / Right Hand	LH	RH
Transport kinematics		
Reaction Time [#] (ms)	222* (45)	205 (49)
Movement Time [#] (ms)	796* (167)	869 (163)
Response Time (ms)	1016 (191)	1074 (190)
Path Length [#] (mm)	544* (61)	502 (31)
Peak Acceleration (mm/s ²)	26528 (12326)	18191 (11662)
Peak Velocity (mm/s)	1993 (475)	1703 (322)
Time to Peak Acceleration [#] (ms)	374 *(58)	337 (56)
Time to Peak Velocity (ms)	494 (78)	481 (68)

[#] Significant main effect of hand (ANOVA; $p < .05$).

* Significant differences between LH and RH results (post-hoc t-test; $p < .05$).

Table 3.3. Open loop 2s delay condition; Mean (SD in brackets) transport

Open loop 2s delay condition (No vision)		
Left / Right Hand	LH	RH
Transport kinematics		
Reaction Time (ms)	70 (62)	69 (56)
Movement Time [#] (ms)	895* (162)	832 (178)
Response Time [#] (ms)	963* (141)	901 (164)
Path Length [#] (mm)	449* (44)	492 (66)
Peak Acceleration [#] (mm/s ²)	18607* (7669)	30865 (12074)
Peak Velocity [#] (mm/s)	1449* (288)	1785 (524)
Time to Peak Acceleration [#] (ms)	193* (22)	158 (85)
Time to Peak Velocity (ms)	309 (83)	297 (89)

[#] Significant main effect of hand (ANOVA; $p < .05$).

* Significant differences between LH and RH results (post-hoc t-test; $p < .05$).

Figures Caption

- Figure 3.1.* Experimental setup. (A) Background consists of two sections, one (80 cm x 91 cm), and the other one (65 cm x 91 cm). (B) 45cm from starting position of the hands, the target object could be positioned at one of three locations; either 45° to the left, 45° to the right, or on the sagittal axis passing through the participants midline.
- Figure 3.2.* Power Grip (POW) Characterized by flexion of all fingers around an object, with the palms of both hands in contact.
- Figure 3.3.* IRED placement. (1) metacarpophalangeal joint of each index finger (knuckle IREDs) and (2) the region of the trapezium-metacarpal joint of both thumbs (wrist IREDs).
- Figure 3.4.* Start position, digit coupling. With opposition between the pads of the each index finger and thumb the participant will be asked to place each digit coupling together and on the home position with the first metacarpals in contact.
- Figure 3.5.* (CL) Closed-loop visual condition. The downward arrow indicates the auditory initiation cue.
- Figure 3.6.* Hand X Direction Interaction - Path length (mm) in the resultant axis as a function of hand and target direction.
- Figure 3.7.* Closed Loop- The proportion of variance (R^2) in movement endpoints explained by limb position at three movement time percentages (20%, 50% and 70%) is presented for both hands when a representative subject executes a bimanual prehensile movement in closed loop conditions.
- Figure 3.8.* Linear scaling of bimanual peak grip aperture (mm) to target size
- Figure 3.9.* Bimanual grip aperture (mm) in the resultant axis as a function of movement time (%) and target size.
- Figure 3.10.* (OL2) Open-loop two-second delay visual condition. The downward arrow indicates the auditory initiation cue.
- Figure 3.11.* Hand X Direction Interaction - Path length (mm) in the resultant axis as a function of hand and target direction.
- Figure 3.12.* Open loop 2s delay- The proportion of variance (R^2) in movement endpoints explained by limb position at three movement time percentages (20%, 50% and 70%) is presented for both hands when a representative subject executes a bimanual prehensile movement in open loop 2s delay conditions.
- Figure 3.13.* Linear scaling of bimanual peak grip aperture (mm) to target size.
- Figure 3.14.* Bimanual grip aperture (mm) in the resultant axis as a function of movement time (%) and target size.

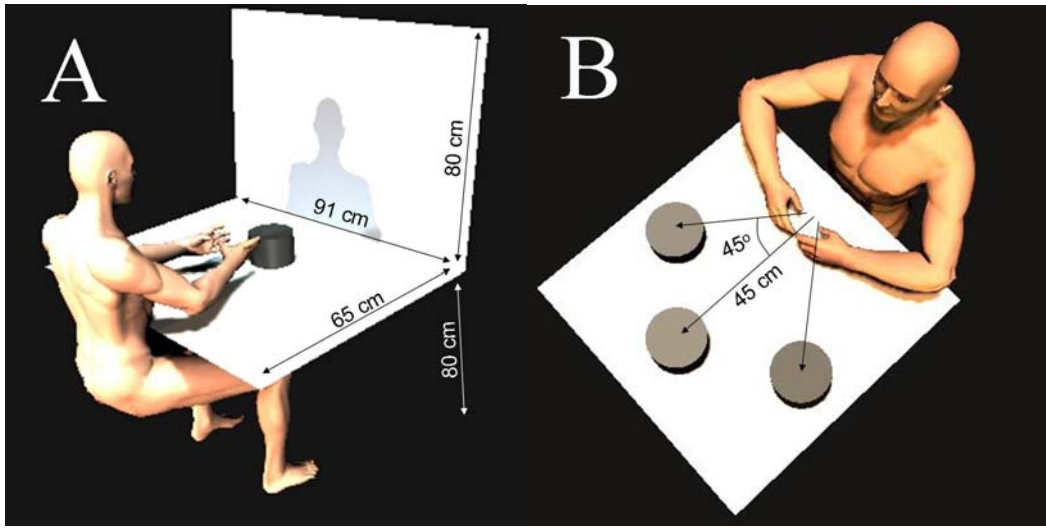


Figure 3.1



Figure 3.2

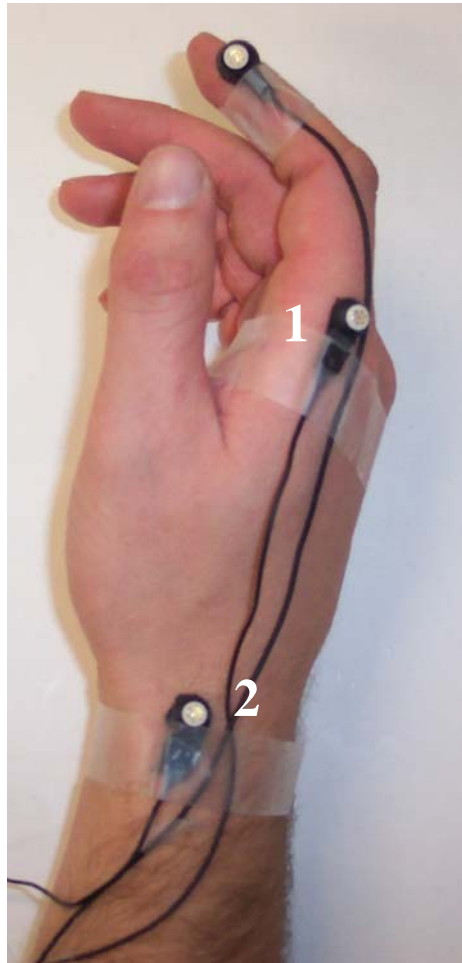
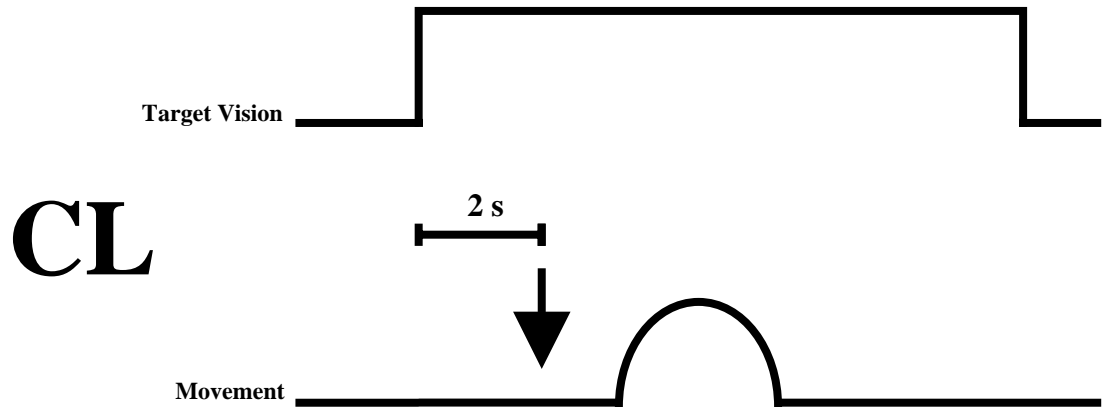


Figure 3.3



Figure 3.4



CL

Figure 3.5

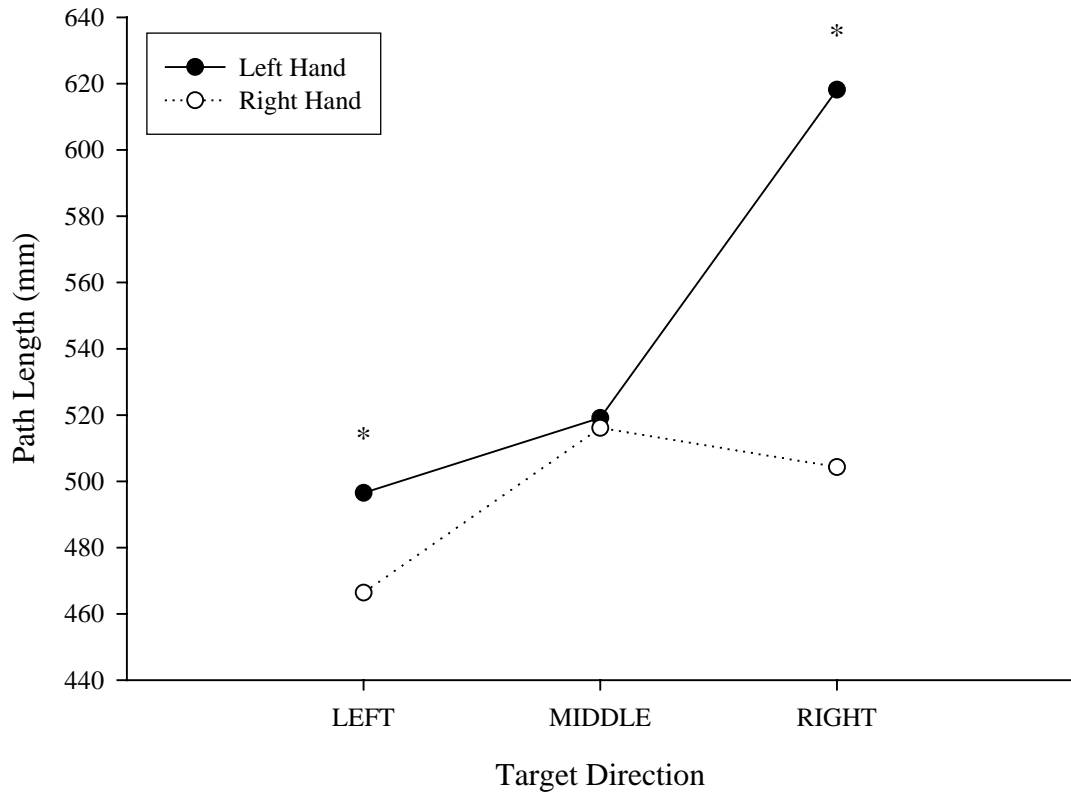


Figure 3.6

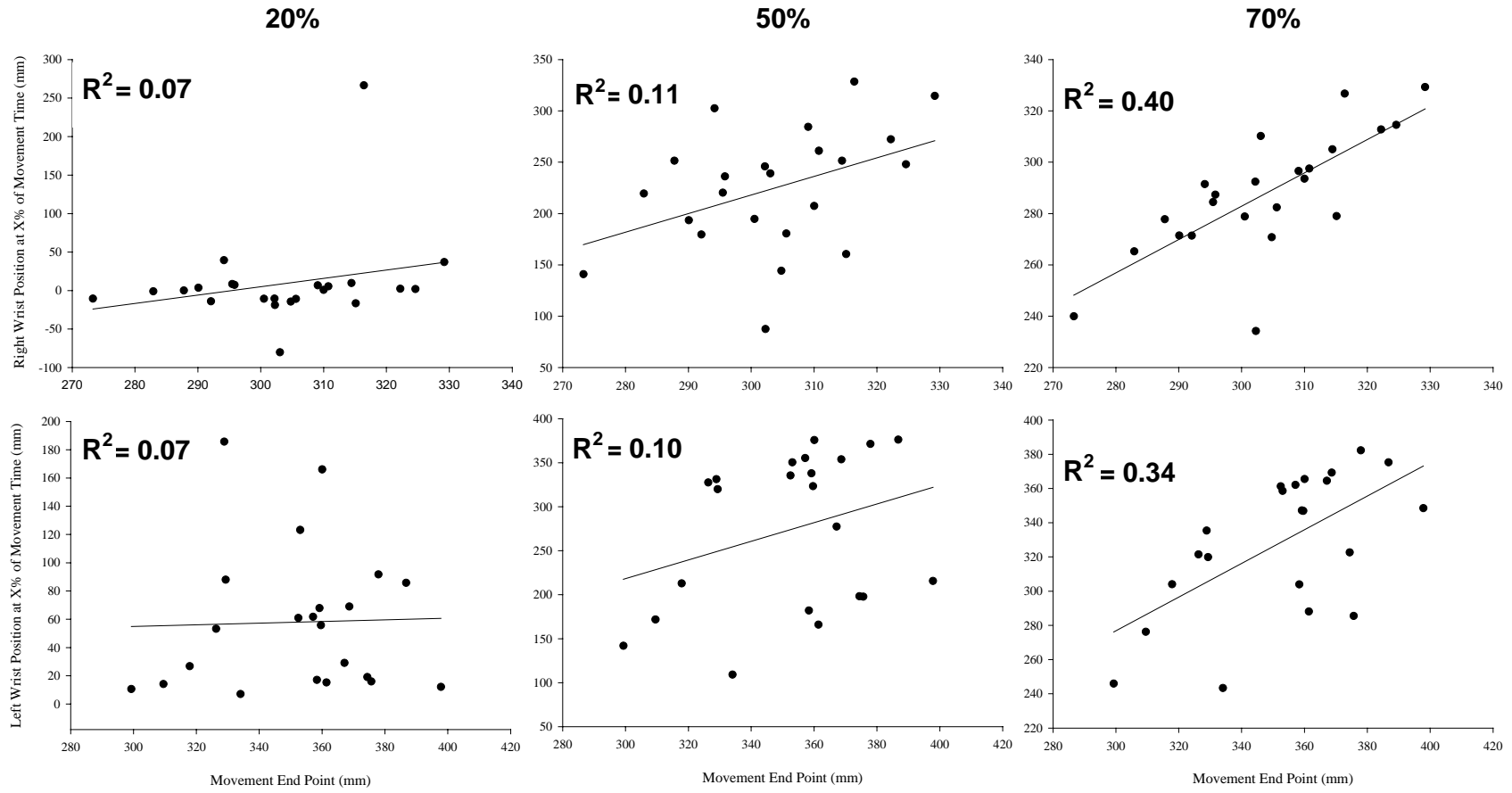


Figure 3.7

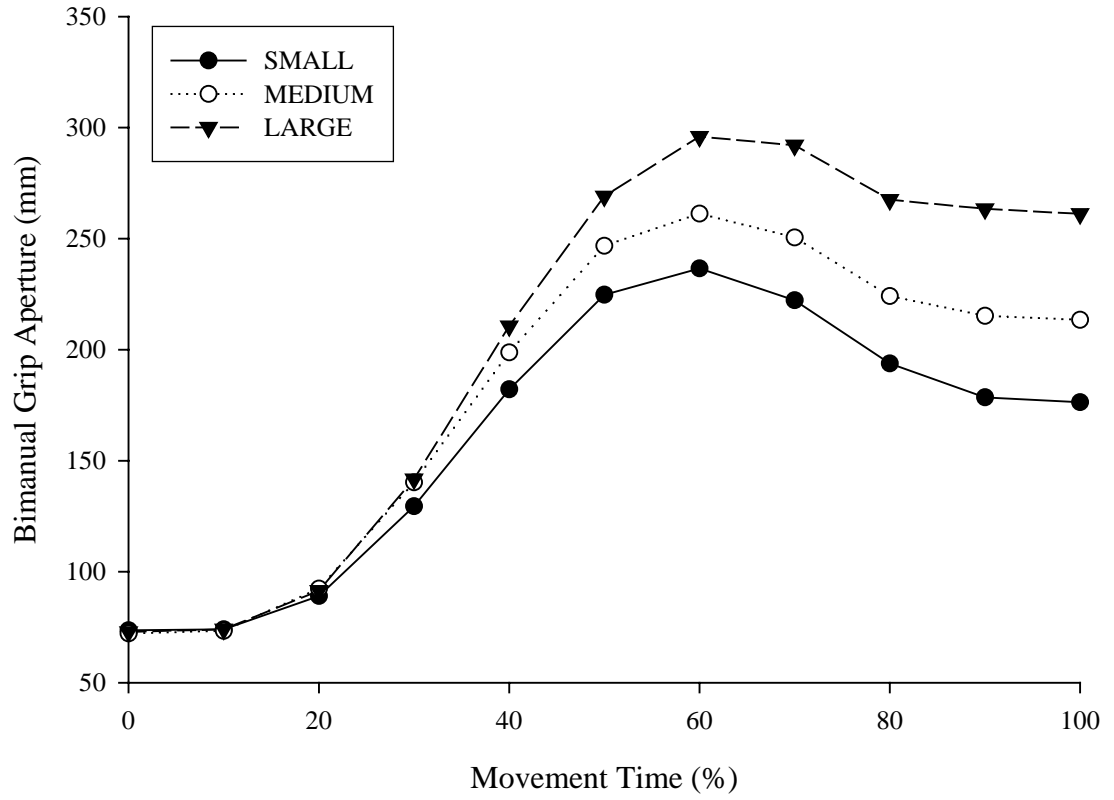


Figure 3.8

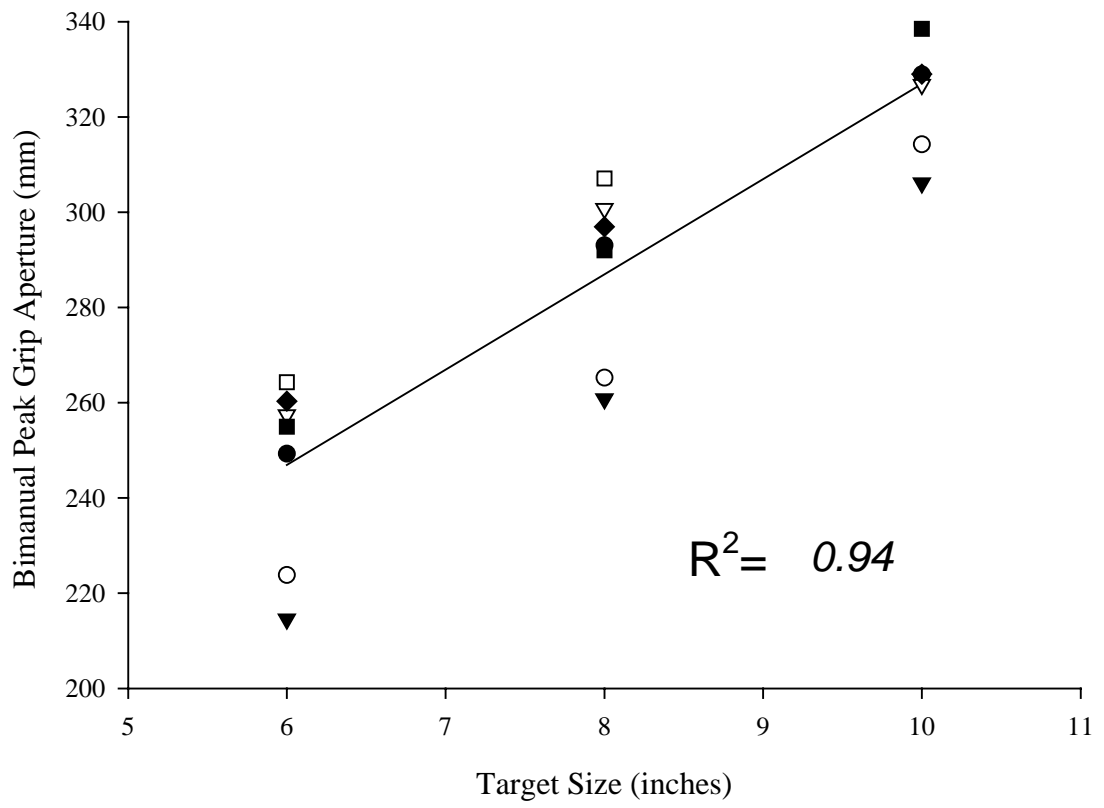


Figure 3.9

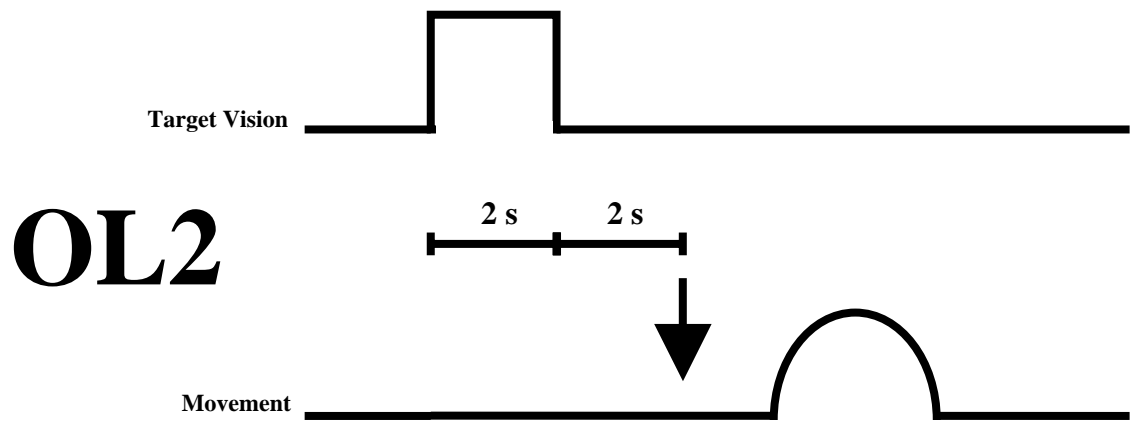


Figure 3.10

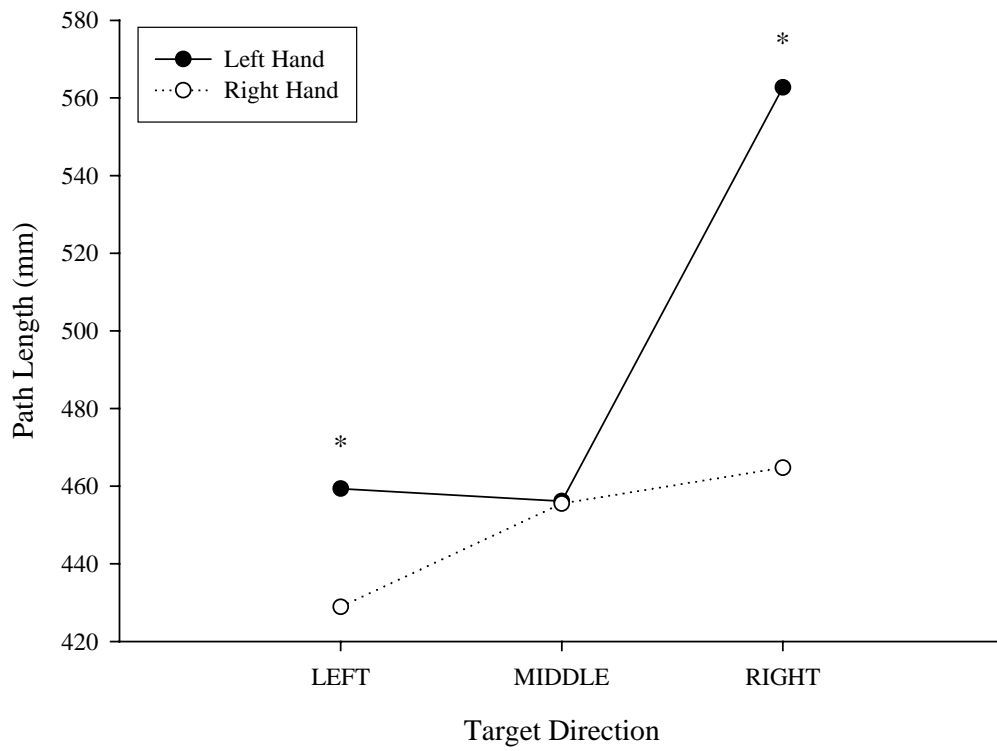


Figure 3.11

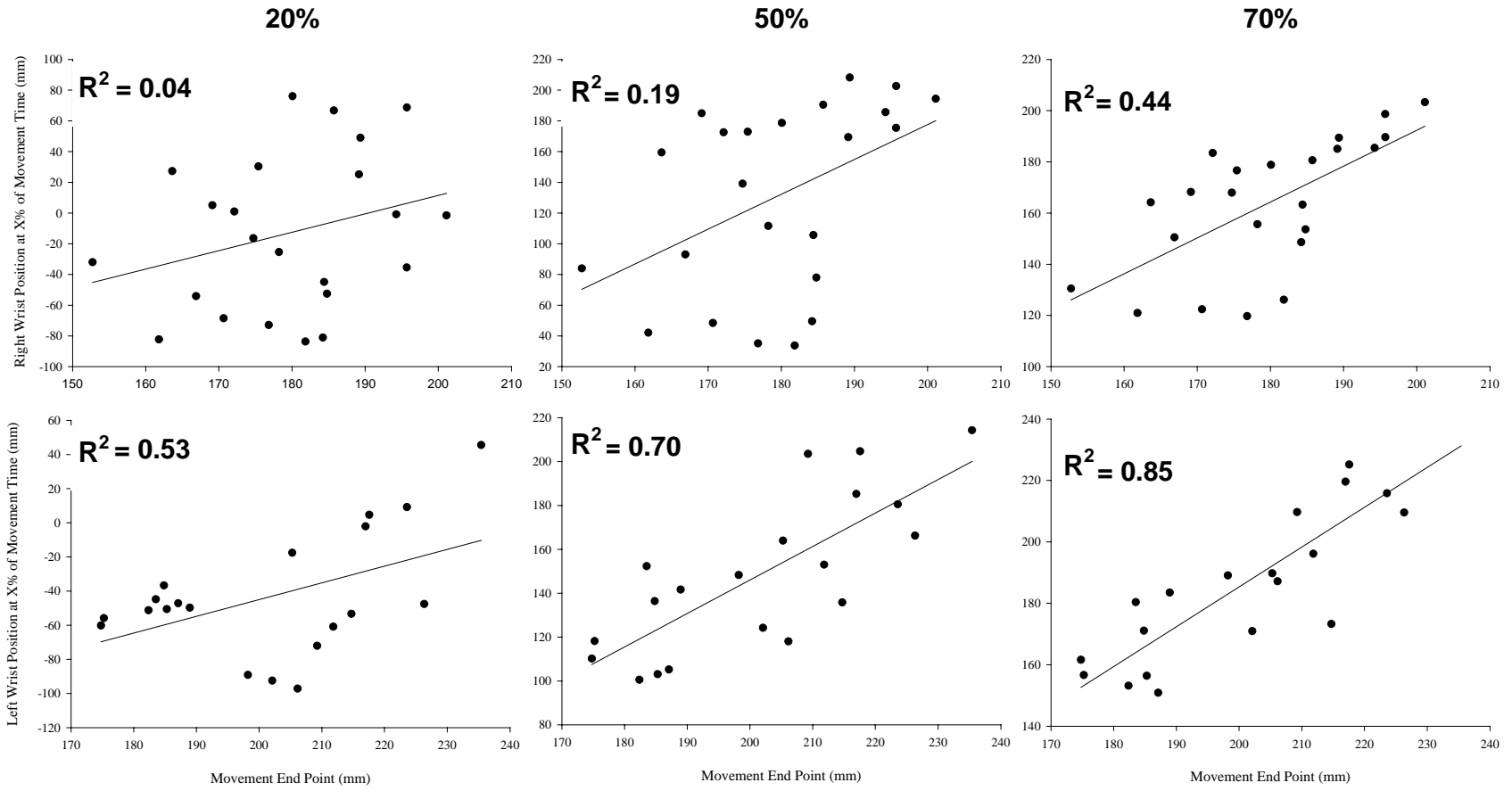


Figure 3.10

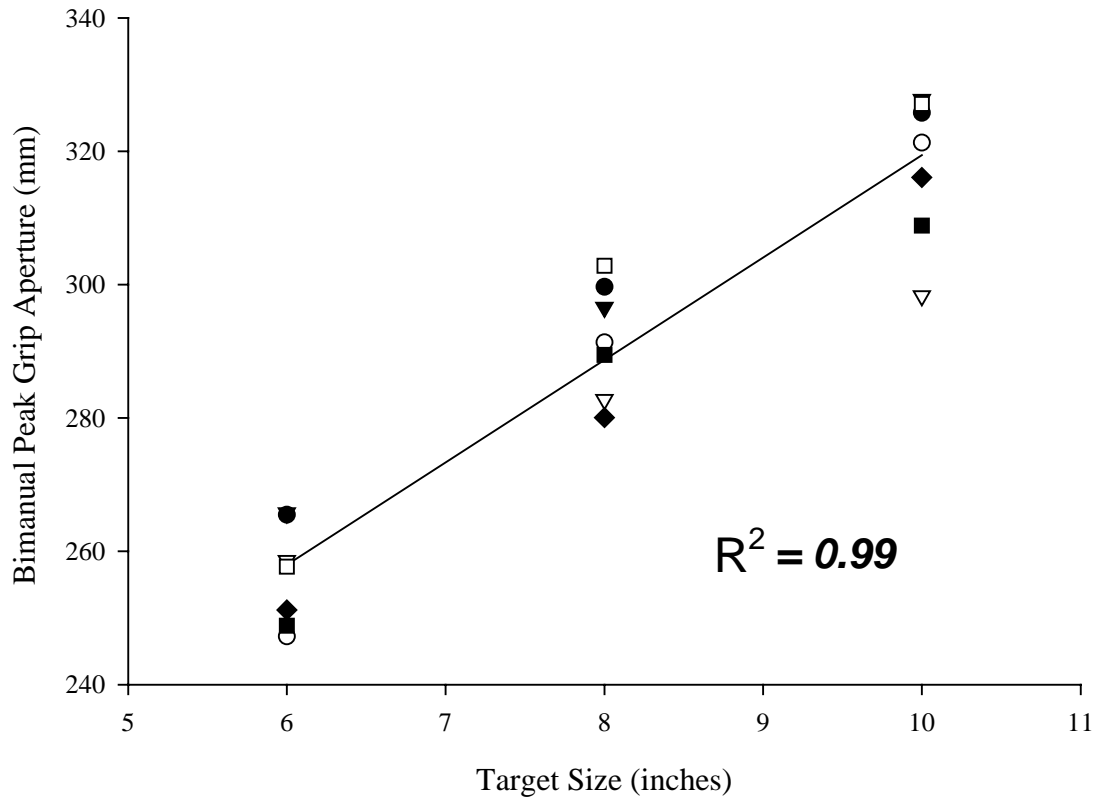


Figure 3.13

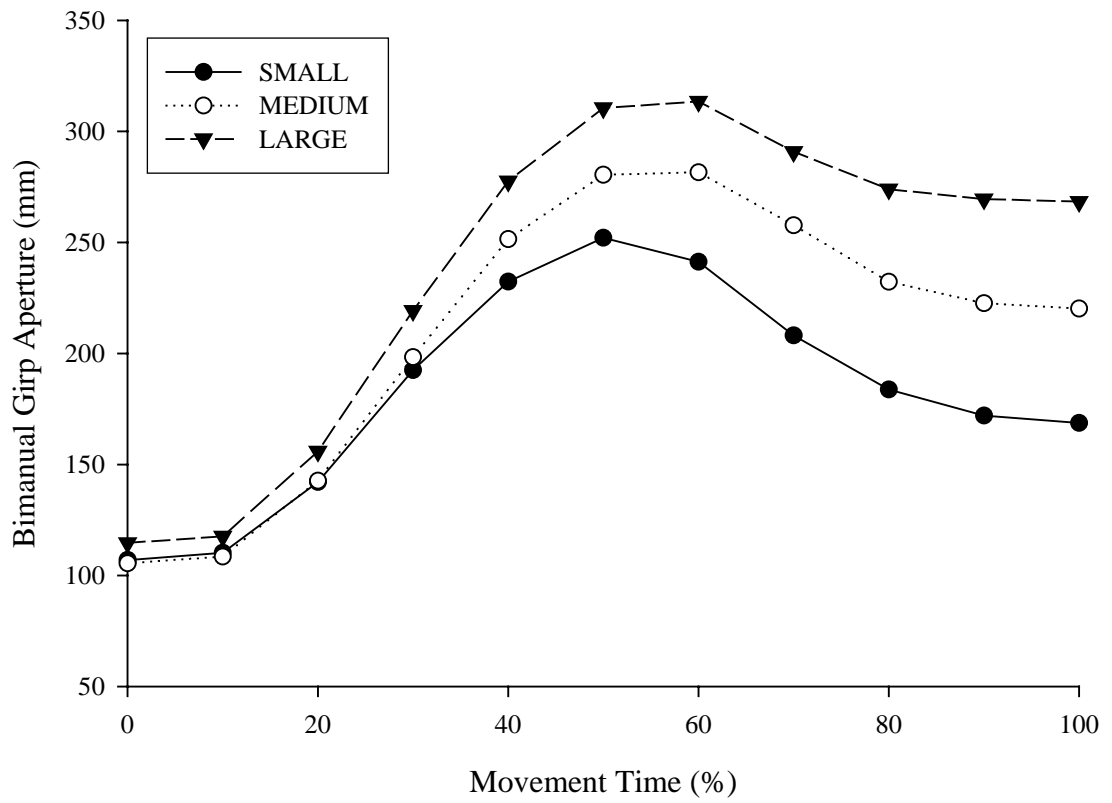


Figure 3.14

Chapter IV: General Discussion

This study investigated the extent to which the current bimanual coordination models can account for coordinated bimanual movements. More specifically, we aimed to elucidate on how online usage of visual feedback compared with memory-guided control influences the performance of these specific bimanual movements in line with theoretical framework[§]. At the onset of this study, we hypothesised that bimanual prehensile movements processed and executed solely by the dorsal (visual) stream may demonstrate higher levels of limb coupling and success compared to those completed through the ventral (perception) pathway. This hypothesis was based not only the availability of vision to aid online control during CL conditions, but also on the notion that participants would be able to utilise the RH-left hemisphere advantage for visual control of target-directed movements (Gonzalez, et al. 2006). In general, our findings indicate that visual feedback not only influenced movement coupling characteristics between each arm, but also affected the apparent strategy selected when performing a bimanual prehensile movement to a solitary target.

Influences of Planning vs. Control: Coupling

The nature of the OL2 visual condition meant that comparing many temporal variables such as reaction time etc. was extremely difficult. However, the influence of visual feedback on the level of temporal synchronisation of hands provides evidence for independent programming of each limb and possible lateralisation of the dorsal and ventral streams. Indeed, a common trend within both the CL and OL trials was the independent movement of each limb demonstrated by the variability of overall synchronisation between movement onset and times to both peak velocity and acceleration. Rarely, was complete temporal synchronisation achieved in any condition and is possibly indicative of visual stream lateralisation.

Like temporal coupling, evidence for the independent representation of visual stream within each hemisphere is present within spatial coupling observations. In the presence of visual feedback a tendency to lead movement onset with the RH was

evident across all target directions and size. Conversely, absence of vision during trial execution in the OL2 condition was characterised by a definite limb coupling. The occurrence of coupling in the presence of visual feedback provides support for the dominant hand lead of rhythmical bimanual coordination (e.g. Stucchi & Viviani, 1993, see *Right-Hand Reliance* section) but challenge the relevance of both bimanual coordination models (Kelso et al. 1979; Marteniuk & Mackenzie, 1980). With no evidence of asymmetry at movement onset, a reversal of theoretical support was found in the absence of vision as both bimanual coordination models predict synchronised movement initiation (Kelso et al. 1979; Marteniuk & Mackenzie, 1980).

A similar disparity between visual conditions was seen in the synchronisation of movement endpoint. Under the influence of visual feedback and despite the RH lead, a smaller LH movement time allowed both hands to contact the end target simultaneously. Again, a reversal of coupling was exhibited in the OL2 condition, where, driven by a faster dominant hand transport phase, the RH contacts the target before the LH. Taking a holistic view of the levels of spatial coupling evident both in the absence and presence of visual feedback, support for a dominant hand reliance and more importantly independent control of each limb is evident. Such independence reflects the need for equal visual processing stream representation in both hemispheres.

Proportion of Endpoint Variance

Support for Milner and Goodale's (1992) independent visual processing streams proposal and hence confirmation of successful experimental ventral and dorsal stream segregation was found within our proportion of endpoint variability data (see Table 4.1). Used to infer the nature of limb control, a high degree of within-trial correspondence suggests that the final position of the limb was largely specified prior to movement onset and not adjusted during the action (e.g. memory-guided/ventral control). Conversely, a low degree of within-trial correspondence would suggest that movements were modified during reaching trajectory (e.g. visual/dorsal control). As expected, with visual feedback (CL) the variability differences of both hands reflect the importance of direct visual input in nullifying endpoint error through fine limb adjustments near the end of the movement. The OL2 condition provided slightly less

predictable variability data. As evident in table 4.1, the LH exhibits the typically high degree of within-trial correspondence associated with memory-guided or pre-planned control. However, the RH exhibits lower than anticipated correlations suggesting that a form of feedback-based control may be present. Possible explanation of such a result may lie in a specific ‘search and follow’ strategy employed by all participants during OL2 conditions that will be discussed later.

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Insert Table 4.1 about here

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In brief, within CL conditions a tendency for participants to initiate all trials with the RH was balanced by a greater LH movement time during transport, resulting in simultaneous grasping of the target across both hands (Fig. 4.1). Further, within all OL2 trials, movement initiation was synchronised across limbs but a greater RH velocity and movement time resulted in the target being contacted by the RH on average 62 ms before the LH (Fig. 4.2). Borne out of task specific constraints, a unifying characteristic between the two conditions is the ability of both limbs to form an opposition axis through the targets centre of mass. That is, the axis along which the two hands can transmit opposite forces for effectively grasping and lifting an object (Napier, 1956) was always formed regardless of trial or visual condition. Due to the variability of spatiotemporal coupling evident in bimanual prehension execution (both dorsally and ventrally mediated) general support was provided for the neural cross-talk theory of bimanual coordination (Marteniuk & Mackenzie, 1980; also see discussions in Chap. III). Furthermore, the assumption of visual stream lateralization made from levels of spatiotemporal coupling is enhanced through our endpoint variability data. In the next sections we offer possible explanations for the specific strategies exhibited to successfully interact with the endpoint target under CL and OL2 conditions and discuss how each provides support for independent limb programming.

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Insert Figure 4.1 about here

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Insert Figure 4.2 about here

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Is Competitive Processing between Limbs a Limiting Factor?

It should, of course, be acknowledged that neither of the above frameworks of both Kelso et al. (1979) and Marteniuk & Mackenzie (1980) were developed to specifically account for bimanual prehension movements. However, in our view it has proven informative to test these models against the data observed in the bimanual case. One question raised by this comparison, however, is why these theories should offer such a relatively poor account of bimanual prehension movements under visual control given its success in describing the kinematics of unimanual prehension? One possible answer to this question may revolve around the processing demands required in the CL condition case during bimanual movements. Duncan, Humphreys and Ward (1997) posited an integrated competition hypothesis: visual information produces activity within multiple brain systems, and an important aspect of this processing is that within such systems activations related to different objects compete with one another; in behavioural terms, such competition is characterized as interference in which the efficient processing of each object is impaired. The author's argue that for the sensorimotor network to work as a whole, mechanisms must therefore exist to reduce competition so that the tendency is to settle into a state whereby different brain systems converge to work on the same dominant object, analysing its multiple visual properties and implications for action. Further, at the neural level, there should be widespread maintenance of the selected object's representation, accompanied by widespread suppression of response to ignored objects (Duncan et al., 1997). Within this view then, one obvious limiting factor during our specific bimanual prehension movements would be the visuomotor demands involved in attempting to continuously sample two independent ` remaining

time-to-contact' signals (i.e. the hand-target separations for each hand) when the task constraint requires cooperative limb action to a single endpoint target. In this particular case, one solution to this problem might be for the sensorimotor system to adopt an intermittent sampling strategy during bimanual movements, in which the remaining time-to-contact signal is independently sampled for each hand by intermittently switching attention between the hands and solitary target. One prediction which can be generated from such a discrete sampling solution, and which is arguably confirmed the BPGA data of the current study, is that there is a tangible cost to performing bimanual prehension movements compared to unimanual movements (Jackson et al., 1999). An alternative solution, which both avoids the problem of having to concurrently monitor two remaining time-to-contact signals is for the sensorimotor system to reconfigure the task description so that only one time-to-contact signal need be monitored. This could be achieved by coupling the two limbs together so that they are constrained to act as a single functional unit as suggested by Kelso (e.g. Kelso et al., 1979). As previously acknowledged, within this view, each limb would commence moving at the same time, but would move at different velocities, so as to arrive at their respective targets simultaneously. Under visual control, the lack of coupling demonstrated at the start of all bimanual movements within our study, however, would challenge such a proposal. Although we do not dispute the possible use of a common time frame within these movements, we would speculate that due to the competition for attention the sensorimotor system adapts by concentrating its effort on the preferential limb, in the case the RH. The contralateral limb (LH) is then programmed after the initial ipsilateral limb initiation on the basis of this selective attention and receives motor programming aid via neural pathways.

Although it is speculative to infer such a strategy, the results from the OL2 may in fact provide more evidence for not only the preference of the right limb in guiding control of bimanual movements but also neural modulation or interference between limbs. Within all OL2 trials, movement initiation was synchronised across limbs but a greater RH velocity and movement time resulted in the target being contacted by the RH on average 62 ms before the LH (Fig. 4.2). Therefore, as in the CL condition, it could be argued that sensory feedback from the right limb aids the

control of the left. Indeed, although originally it was thought that 62 ms was not enough time for any feedback to be utilised affectively by the contralateral limb, if such feedback was incorporated directly by the spinal cord then this becomes a definite possibility. As a consequence of the search for an understanding more in terms of structural properties of the movement system, a point of departure may be found in the neurophysiological mechanisms involved in stability of rhythmic interlimb coordination.

Neurophysiological Bases of Interlimb Interaction

Several studies suggest that afferent feedback arising from movement assumes an important role in determining the stability of rhythmic interlimb coordination in humans. It has been demonstrated that the passive movement of one limb entrains the phase and frequency of the contralateral limb (deGuzman & Kelso, 1991). On the basis of adaptations to elastic and inertial loads, Baldissera et al. (1991) argued that peripheral signals have an entraining influence, supporting the interlimb coordination between the limbs.

The influence of peripheral signals, arising from movement, upon the stability of interlimb coordination may be a consequence of the modulations of the excitability of spinal pathways, which have been demonstrated in a variety of rhythmic movement tasks. Inhibition of the H-reflex, for example, is minimal during the phases of movement in which the target muscle is active, and maximal during the phases in which it is inactive (e.g. Brooke et al. 1992; Brooke et al. 1995). Yet, the degree of modulation is not simply dependent upon the level of muscle activation required to drive the limb (e.g. Brown & Kukulka 1993; Capaday & Stein 1986; Capaday & Stein 1987; Crenna & Frigo 1987). Rather, it appears to be attributable to “movement-elicited afference” (McIlroy et al. 1992) that is mediated primarily by muscle spindles rather than by cutaneous, joint, or pressure receptors (Burke et al. 1984; Cheng et al. 1995). Such an association is highly relevant considering the nature of our bimanual task where only slight differences in muscle sequencing and recruitment occurs between each limb.

Recent findings emphasise that in addition to being contingent on the joint angle of the target limb (Brooke et al. 1992), the magnitude of the H-reflex is also dependent on the position and frequency of movement of the contralateral limb

(Carson et al. 1999; McIlroy et al. 1992). Although significant modulation of reflex gain appears to require relatively large ranges of motion and angular velocities of the joints (Brooke et al. 1995), the receptor discharge that arises from even passive rotation of a limb exerts a strong influence upon the reflex pathways on the opposite side. The extent of this contralateral modulation is in turn increased with the velocity of passive rotation (Collins et al. 1993), and appears to be related directly to the rate of change of length of the muscles of the moving limb (Cheng et al. 1995). However, whereas this crossed inhibition is dependent on the movement phase of the other limb when it is actively moving, no such phase dependency is observed when the inhibition is induced by passive motion of the contralateral limb (Cheng et al. 1998). The evidence available at present suggests that the modulation is accounted for largely by presynaptic inhibitory mechanisms (see Brooke et al. 1997). These findings suggest a possible means by which afferent feedback, arising from specific elements of the somatosensory receptor array during movement, may promote the entrainment of the limbs during bimanual movements (Hasan et al. 1985).

Movement-induced modulation of reflex gain has been shown to be highly adaptive. In particular, the regulation of reflex pathways innervating soleus (during locomotion) may serve to ensure that the gain is high during stance, and reduced when the amplitude of leg movement is increased following the initiation of the step cycle. The contralateral component to such modulation has been attributed to the redundancy that is characteristic of the mammalian nervous system (Brooke et al. 1997). In spite of the phylogenetic separation of function of the upper and lower limbs, a similar phase-dependent modulation of spinal reflex responses can be observed in the wrist flexor (flexor carpi radialis) during rhythmic flexion-extension movements of the ipsilateral foot (Baldissera et al. 1998) and during movement of the contralateral wrist (Carson et al. 1999). The presence of pathways in the upper limb that mediate crossed inhibition suggests the specific means by which afferent feedback, arising from movement-elicited discharge of somatosensory receptors may mediate interactions between the limbs during bimanual coordination.

To summarise, there are a number of neurophysiological mechanisms that may mediate interactions between the limbs during rhythmic coordination. The question remains, however, as to whether or not these mechanisms are essential in generating

the observed response seen during bimanual prehension tasks in the current study. Undeniably, it is now clear that the movement of a single limb may lead to modification of the excitability of the contralateral Ia spinal reflex pathway (McIlroy et al., 1992) and the extent of this contralateral influence increases with the velocity of movement (Collins et al., 1993). Further, Carson and Reik (1998) proposed that entrainment tendencies may provide a means by which limbs that are initially moving out of phase become synchronised (Carson & Riek, 1998; Hasan et al. 1985). Although referring to rhythmical coordination it would seem that such a proposal provides clarity or at least feasible sense when considering the lack of synchronization observed at various stages of bimanual prehension to a solitary target. Certainly, during CL conditions when movement onset was not synchronised, such limb entrainment tendencies could have provided essential means by which endpoint synchronisation was achieved. Conversely, the disparity of 62ms between hand contact with the target within OL2 conditions, is sufficient time for the modulation of spinal pathway excitability in the contralateral limb.

Right-Hand Reliance: Dynamic control

Another important observation during the present study was the utilization of the RH (dominant hand) to drive or direct each cooperative action in both visually and memory-guided conditions. This preference for the use of the RH to drive or direct the execution of bimanual prehension may be borne out of the limbs greater proficiency during goal-directed movements. In a series of studies, Sainburg and coworkers examined such interlimb differences of reaching in right-handed subjects. The participant's arm was supported over a horizontal surface by an air-jet system, so that the effects of gravity and friction were minimized, and the reaching movements were carried out in a horizontal plane (Sainburg & Kalakanis, 2000). The hand was moved to different targets while vision of the arm and hand was blocked. Only shoulder and elbow joint angles changed, whereas all joints distal to the elbow were immobilized and the trunk was restrained. The joint coordination patterns differed systematically between the dominant and non-dominant arm. Inverse dynamic analyses indicated that dominant arm movements were characterized by a more skilful coordination of muscle action with intersegmental dynamics. Despite the dominant arm advantage in dynamic control, however, the targets were reached

with similar accuracy by both hands (Sainburg & Kalakanis 2000; Sainburg 2002). Arguably, this finding is in accordance with our data, although the paradigm and experimental setup of Sainburg and coworkers are different. However, with a similar final position accuracy of both hands and participants reliance on the RH to initiate or terminate movement a dynamic advantage in the dominant hand would seem a more than adequate explanation for our findings.

Hemisphere-dominance model

Alternatively, support for our finding of dominant hand lead can also be found within bimanual coordination and hemispheric specialisation literature. Franz, Rowse, and Ballantine (2002) examined the performances of left- and right-handers on a task of bimanual circle drawing to determine whether the dominant hand always leads the non-dominant hand. Consistent with the findings of previous studies, the dominant hand tended to lead the non-dominant hand when the bimanual task was performed in a mirror-symmetrical manner (Amazeen, Amazeen, Treffner, & Turvey, 1997; Franz, 2004; Treffner & Turvey, 1996). Given that circle drawing involves spatial representations, among other planning properties that might be lateralized (Franz, 2004), as well as feedback processes, the extent to which such findings can related to the current study is debatable. However, in combination with similar dominant hand lead findings in a number of simple bimanual reaction pattern studies, one would argue a strong relevance (Shen & Franz, 2005).

A number of theoretical models have been proposed to account for dominant hand lead effects. One theoretical view that has received some support is that the left hemisphere is dominant for bimanual responses, as suggested by symmetrical circle drawing tasks in which the right hand generally leads (Stucchi & Viviani, 1993). In the hemisphere-dominance model, it would be predicted that the RH receives motor commands before the LH, given that the LH's motor command would take longer to arrive from the left cerebral hemisphere than would the RH's motor command. Within the confines of this model we argue that the existence of a left hemisphere advantage for target-directed movements provides a promising perspective from which our RH reliance findings during bimanual prehension can be rationalized. Until recently, only tentative neurological evidence existed which linked the RH with a left hemisphere visual control advantage during prehensile movements (Perein &

Vighetto, 1988). However, more recently Gonzalez and co-workers (2006) provided more solidifying evidence proposing that the resistance of the RH to the size-contrast illusions during target-directed movement may reflect the specialization of the left hemisphere for visuomotor control of complex behaviours (Gonzalez et al., 2006).

Therefore, alternative explanation for our dominant hand lead findings invokes left-hemisphere specialization rather than RH dynamic control advantages. In other words, the use of the RH might have preferentially engaged the left hemisphere and thus the drive seen at movement initiation (CL) or direction at movement termination (OL2) would reflect any control bias that was present within the dominant hand. Further, any preferential spatiotemporal planning of the right limb could potentially aid the left through transfer of motor commands across numerous neural cross-talk pathways outlined by Marteniuk & Mackenzie (1980) as well as in the neurophysiological mechanisms section.

Table 4.1. Proportion of variability (R^2).

Visual Condition	Proportion of Variability (R^2)			
	Closed Loop		Open Loop 2s Delay	
	LH	RH	LH	RH
Endpoint position				
20%	0.07	0.07	0.53	0.04
50%	0.10	0.11	0.70	0.19
70%	0.34	0.40	0.85	0.44

Footnotes

§ It is acknowledged that learning affects during both E1 and E2 may have contributed to the current studies results. In order to test this a hypothesis we arranged our bimanual coupling data in trial order, regardless of condition (e.g. Start = trial 1 to 24, Middle = trial 25 to 48, End = trial 49 to 72). Results from a 2 hand (right, left) x 3 (Start, Middle, End) repeated measures ANOVA revealed no differences in bimanual coupling from those reported in our study. Therefore, we can conclude that practice or learning affects were not responsible for the observed strategies employed by participants during bimanual prehension to a solitary target under CL or OL2 conditions.

Figures Caption

Figure 4.1. Closed Loop Condition: Spatial coupling summary

Figure 4.2. Open Loop 2s Delay Condition: Spatial coupling summary

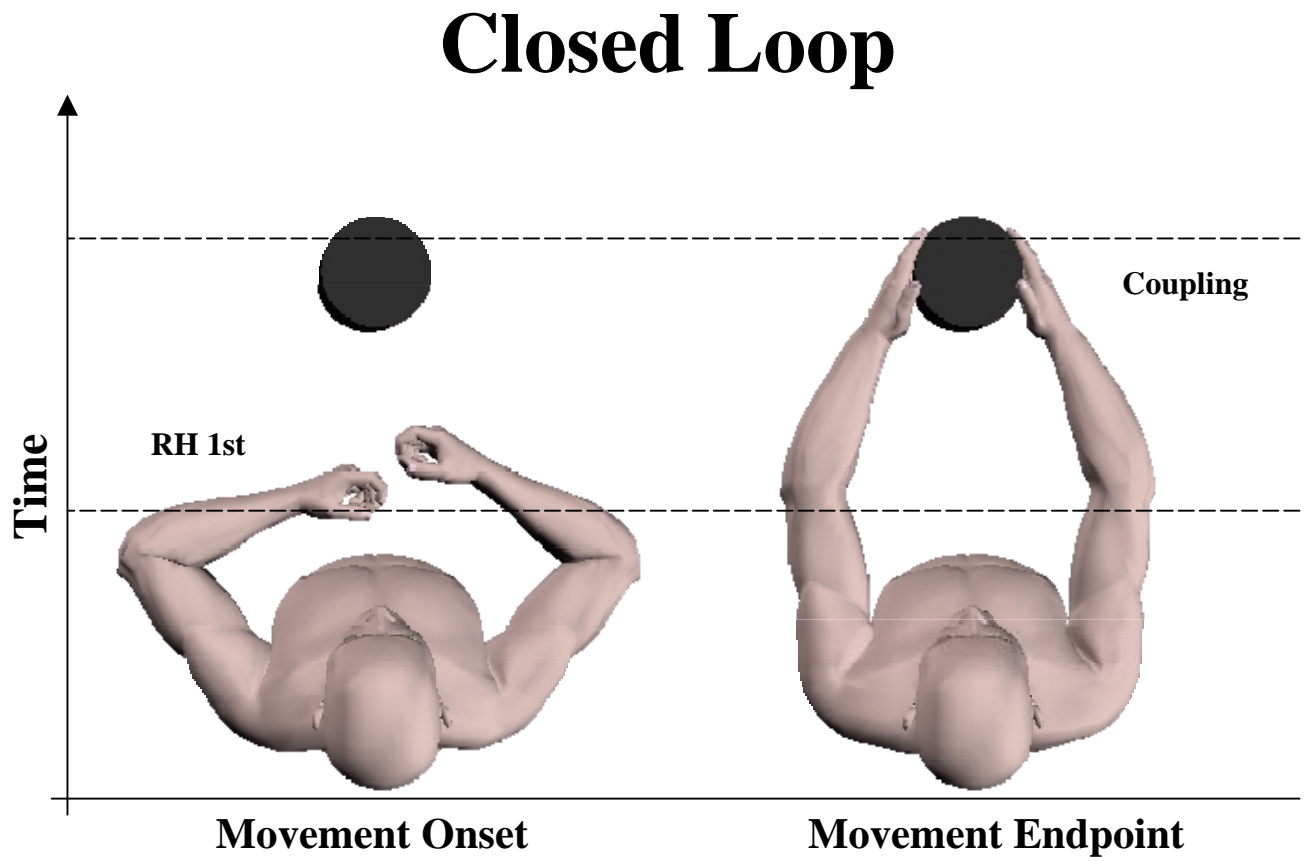


Figure 4.1

Open Loop 2s Delay

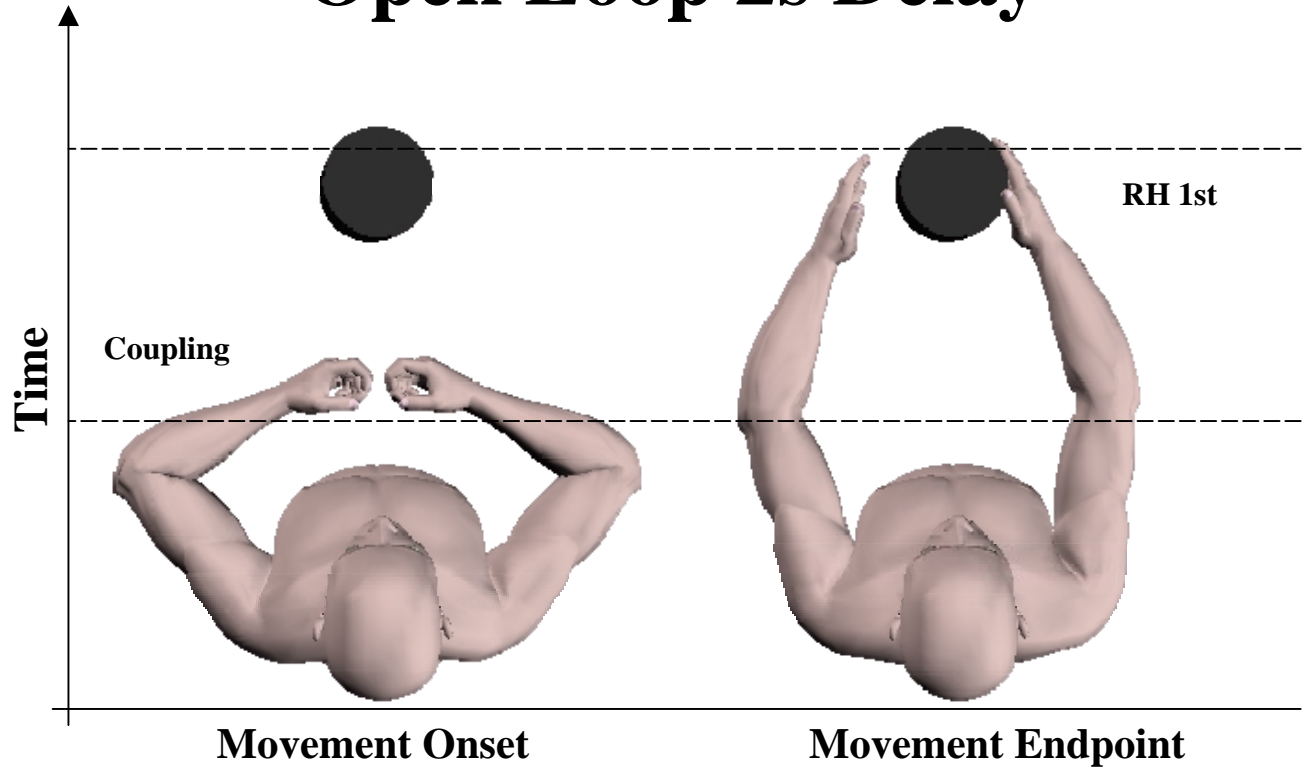


Figure 4.2

Chapter V: Thesis Summary

Conclusions

During the pilot study each limb executed the same distal grasping action. When participants utilised a POW grip the kinematic parameters did not demonstrate differences between the two hands: the acceleration and velocity data showed similar patterns and the limbs were coupled in time. For these congruent tasks, the proximal and distal components require the activation of similar sets of muscles for each limb. Similarly, and as found by Kelso et al. (1979), for the bilateral pointing studies the kinematic profiles of each limb are very similar. Kelso et al. (1979) proposed that this "fixed and reproducible" interlimb coordination reflects the concept of coordinative structure control signals that act to group the muscles of both limbs as a single functional unit for the purpose of attaining the bilateral goal. The high degree of interlimb kinematic coordination was not thought to favour the concept of a separate programming for each limb. Consider, however, the rarity of performing the same task simultaneously with both hands. Even within the context of our specific bimanual task, where both hands target the same endpoint, the distances differ consistently between hands. Therefore, what purpose is served by synergic groupings which largely ignore differences between the limbs? The results from the current bimanual experiment whereby cooperation between limbs is required to interact with a single target do not entirely support the idea of both limbs acting as a single unit. Despite the activation of corresponding muscle groups for the transport component and consequently the bilateral recruitment of the same neural pathways kinematic organization differs according to visual condition. The patterning of the transport component for one limb does not resemble that of the other when the participants utilise visual or memory-guided control. However, due to the proficient consistency with which all trials were completed we speculated (see general discussion, Chap. IV) that one limb may influence the kinematic organization of the other through spinal mediated cross-talk. Given the multiple requirements of operating both hands for manipulation of and interaction with objects in the environment, a control mechanism which groups muscles as a single unit does not

seem feasible for most functional tasks. This does not imply that a "coordinative structure" does not operate. It is clear from the results of the pilot study that the limbs adopt the same parameterization for congruent tasks (see Chap. II). Thus, with a low criterion for individual programming of each limb in a rare congruent bimanual prehension task, the number of globally controlled parameters thus appears to increase. Movement duration and temporal settings for kinematic landmarks of the transport and manipulation components are processed as if for a single unit. Control is thus simplified by minimizing the number of output process requirements. With a high criterion for individual programming of each limb (incongruent tasks), the number of globally controlled parameters decreases. Movement duration remains the common parameter however temporal settings for kinematic landmarks such as peak velocity or peak acceleration are processed separately for each limb. The system thus determines what can be independently specified for each limb but, where possible, retains output requirements that are common to both limbs.

Indeed, there is at least some evidence from brain imaging studies in humans supporting that movements of either hand share some cortical representations. In right-handed subjects, the cortex lining the left intraparietal sulcus was active during the execution of simple and complex finger movements by the LH and RH (Kuhtz-Buschbeck et al. 2003). Bilateral activity of dorsal premotor areas was demonstrated during complex movements of either hand by Kawashima et al. (1998). A recent fMRI study found nearly symmetrical bilateral activation of the anterior intraparietal cortex during grasping movements performed with the dominant RH (Culham et al., 2003). Since these left and right parietal areas were more strongly activated by grasping than reaching, they seemed to be specifically involved in the control of pre-shaping of the right fingers. Also other imaging studies demonstrated bilateral activation of the anterior intraparietal and premotor cortex during RH grasping (Binkofski et al. 1998). The parietal-premotor circuit is known to be involved in the transformation of an object's intrinsic properties into specific grips (Sakata & Tiara 1994; Rizzolatti & Luppino, 2001).

In summary, independent programming of each limb is undeniably evident within the behaviours observed. Whether movement execution is visually or memory-guided there is a clear preference of RH utilization due to its dynamic and/or

hemispheric advantages in controlling motor behaviours. Although it is highly speculative to infer higher-level control over each limb during a bimanual task within our study, it would seem that despite this independent limb control, the common goal parameters of targeting a single object are maintained regardless of visual condition. Therefore, we propose that bimanual grasping to a solitary target is possibly governed globally by a higher-level structure (perhaps parietal-premotor circuit) and successful execution is achieved via independent spinal pathway modulation of limbs.

Further Directions

The data from the present study suggest that the role of task and environmental constraints should not be ignored in future research into bimanual coordination. Further elucidation of the specific strategies observed within in each visual condition is required specifically in terms of dominant hand lead regardless of handedness. Another important area of future study concerns the development of coordinative structures underlying two-handed prehension in children.

Chapter VI: References

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