Neural Mechanisms Underlying Bimanual Grasping

by

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Grasping is fundamentally important for our successful interaction with the environment. Grasping with both hands is phylogenetically older than the hand yet its underlying mechanisms are poorly understood. The objective of this research is to examine bimanual grasping and its underlying mechanisms. Two experiments were conducted to examine whether bimanual grasping involves both hemispheres equally or only one dominant hemisphere, and to examine whether information crosses at an early visual level and/or at later sensorimotor/motor levels.

The first experiment examined participants’ grasping and reaching movements while they fixated either to the left or right of the object. For the second experiment, EEG data was recorded while participants performed a similar task. The results from both experiments suggested that when we grasp an object with both hands, the left and right hemispheres control the action equally, and visual information is shared before it reaches areas that are involved in motor control.
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Chapter 1

1 Introduction

Human hands can grasp objects in multiple ways. Most commonly studied are grasps with one hand, especially the precision grip; that is, when the thumb grasps in opposition to the index finger of the same hand (e.g., Blake, 1992; Castiello, Bennett, & Stelmach, 1993; Castiello & Stelmach, 1994; Churchill, Vogt, & Hopkins, 1999; Danckert, Sharif, Haffenden, Schiff, & Goodale, 2002; Dohle, Ostermann, Hefter, & Freund, 2000; Grafton, 2010; Jackson, Jackson, & Kritikos, 1999; Jeannerod, 1981; Marotta, McKeeff, & Behrmann, 2003; Marotta, Medendrop, & Crawford, 2003; Mason, 2008; Olivier, Davare, Andres, & Fadiga, 2007a; Punt, Riddoch, & Humphreys, 2005; Smeets & Brenner, 1999; Tunik, Frey, & Grafton, 2005; Rice et al., 2006; Tunik, Ortigue, Adamovich, & Grafton, 2008). In contrast, one form of grasping that research has largely neglected is grasping with two hands, such as when you use one hand in opposition to the other to carefully carry a bowl that is filled to the rim with soup.

Bimanual grasping is phylogenetically older than the hand and its underlying mechanisms are poorly understood, yet they are of theoretical interest. That is, how does the brain control the two hands in a coordinated fashion? Do the two hemispheres coordinate their control for bimanual grasping or does one (dominant) hemisphere take over? The objective of this research is to examine bimanual grasping and its underlying mechanisms; specifically, how the brain’s two hemispheres integrate their control processes of grasping for the two hands via the corpus callosum. Here I first review what is known about grasping and bimanual coordination, and then I discuss my experiments to examine bimanual grasping.

1.1 Background on grasping

Grasping involves a large network of brain regions that perform sensorimotor transformations of many kinds (Galletti, Kutz, Gamberini, Breveglieri, & Fattori, 2003). However, embedded within this general network is one fronto-parietal network, also called the dorsolateral circuit, within which brain regions appear to be specifically associated with grasping (Galletti et al., 2003; Grafton, 2010; Tanné, Boussaoud, Boyer-Zeller, & Rouiller, 1995; Sakata & Taira, 1994). One region within the dorsolateral circuit is the superior parietal lobule (SPL), which is responsible for online control of the grip aperture; for example, when targets change in size.
(Tunik et al., 2008; also see Culham & Valyear, 2006). A second region is the ventral premotor cortex (area F5), which contains so called ‘canonical neurons’ that are implicated in the execution of grasping actions as well as during the passive observation of graspable objects (Binkofski & Buccino, 2006; Grafton, 2010; Iacoboni et al., 2005; Ochiai, Mushiake, & Tanji, 2005). This area receives visual input from the anterior intraparietal sulcus (aIPS) to aid in the selection of grasp configurations, and reciprocates back with an efference copy of the motor signal to the aIPS (Olivier et al., 2007a; Tunik, Frey, & Grafton, 2005). Area aIPS is the third area within the dorsolateral circuit. Neurons in this area are functionally similar to those observed in the ventral premotor cortex (Luppino & Rizzolatti, 2000). Indeed, this region is associated with transformations of the sight of an object into grasps of the hand, particularly with the integration of target goal with action plan and the online updating of this action goal (Begliomini, Wall, Smith, & Castiello, 2007; Binkofski et al., 1998; Culham, 2004; Culham et al., 2003; Culham & Valyear, 2006; Frey, Vinton, Norlund, & Grafton, 2005; Grafton, 2010; Jeannerod, Decety, & Michel, 1994; Rice, Tunik, & Grafton, 2006; Tunik et al., 2005; Tunik, Ortigue, Adamovich, & Grafton, 2008; Tunik, Rice, & Grafton, 2007). Thus, the aIPS may be involved in determining the type of grasp that should be used depending on the object size (Begliomini, Wall, Smith, & Castiello, 2007), and in the integration of target goal and emerging action plan for grasping (Tunik, Frey, & Grafton, 2005; Tunik, Rice, & Grafton, 2007).

Moreover, the aIPS has been found to have contralateral specialization (Rice et al., 2006) as well as left hemisphere dominance for precision grasping that is independent of handedness (Davare, Andres, Clerget, Thonnard, & Olivier, 2007; Gonzalez, Ganel, & Goodale, 2006). Indeed, lesion studies in monkeys have found that lesions to this area disrupt grasping behaviour (Brinkman & Kuypers, 1972).

Interestingly, these lesions do not affect reaching (Brinkman & Kuypers, 1972). The control circuits for grasping are distinct from those for reaching (Jeannerod & Biguer, 1982). The latter is controlled by a fronto-parietal network called dorsomedia circuit and consists of the occipito-parietal sulcus, caudal dorsal premotor cortex (Galletti, Kutz, Gamberini, Breveglieri, & Fattori, 2003; Grafton, 2010; Tanné, Boussaoud, Boyer-Zeller, & Rouiller, 1995; Sakata & Taira, 1994) and the parietal reach region (PRR; Batista & Anderson, 2001; Connolly, Andersen, & Goodale, 2003). Contrary to the left hemisphere dominance for grasping, studies have shown that there is
right hemisphere dominance for reaching (Barthélymé & Boulinguez, 2002). This appears to further emphasize that grasping and reaching are controlled by distinct neural circuits.

Consistent with this idea is Jeannerod’s (1981, 1984) influential model of precision grasping. He hypothesized that grasping is governed by two independent channels, one controlling the transport of the hand to the object and the other controlling the size of the grip. The reaching (or transportation) component involves proximal joints and muscle groups and is based on extrinsic properties of the object, such as position and orientation. The grasping (or manipulation) component involves distal joints and muscles and is based on intrinsic object properties, such as size, mass, and shape. These two components are coordinated in time by the synchronization of their onset and a correspondence between the two trajectories.

An alternative model is that by Smeets and Brenner (1999) who abandoned the grip as a variable in their model, and regarded precision grasping as nothing more than the independent reaching movements of the thumb and finger to suitable positions on objects. That is, given that people grasp or reach for the same locations on the object, the trajectories of their fingers would be indistinguishable. Thus the same motor control processes should be involved. Although this approach has its appeal for its parsimony, it neglects central conceptual differences between reaching and grasping. Only the latter requires processing of object features such as weight, surface friction, and fragility. For instance, to grasp an egg without breaking it we would need to take into account the texture, fragility, and shape of the egg, all of which require that we compute how to coordinate our thumb and index finger for the appropriate grip force and shape. If precision grasping was merely the independent reaching movements of the two digits, it would be hard to imagine how two independent reaches, without taking the egg’s particular features into account, would be able to pick up an egg without either dropping or crushing it. Reversely, taking these features into account for reaching would be a waste of neural computations. Furthermore, there is clear neurophysiologic evidence for distinct neural circuits involved in grasping and reaching as mentioned above. A study that directly tested Smeets and Brenner’s hypothesis was conducted by van de Kamp & Zaal (2007) who perturbed the end position of one of the digits while leaving the end position of the opposing digit unchanged. They accomplished this by having participants grasp objects of which the side surfaces were made to slide in and out. They found that perturbing the end position of one digit affected the kinematics of the opposing digit, which was at odds with the hypothesis that grasping is merely the independent reaching
movements of the thumb and finger. Thus although parsimonious, Smeets and Brenner’s model is not without its flaws for describing precision grasping. Nonetheless, it may still successfully apply to other forms of grasping such as bimanual grasping if bimanual grasping is merely the independent reaching movements of the fingers from the two hands. Therefore, it is worthwhile to consider predictions based on the Smeets and Brenner model in the context of the present research.

1.2 Background on bimanual coordination

It is clear that in order for bimanual grasping to occur, some sort of coordination between the two hands (and therefore coordination between the two hemispheres) must occur. This is one way in which the mechanisms underlying bimanual grasping may be similar to the mechanisms underlying bimanual coordination (e.g., Andres, Mima, Schulman, Dichgans, Hallett, & Gerloff, 1999; Gerloff & Andres, 2002; Kelso, Southard, & Goodman, 1979; Marteniuk, & Mackenise, 1980; Swinnin, 2002). However, to date most research on bimanual coordination has used tasks that are quite different from bimanual grasping. These tasks include bimanual finger tapping (e.g., Andres et al., 1999; Duque et al., 2009; Gerloff & Andres, 2002; Hughes & Franz, 2008; Hummel & Gerloff, 2006; Rilk, Andres, Hummel, Hansmann, Hallett, & Gerloff, 2002), bimanual movements to two separate targets (e.g., Castiello, Bennett, & Stelmach, 1993; Castiello & Stelmach, 1994; Churchill, Vogt, & Hopkins, 1999; Dohle, Ostermann, Hefter, & Freund, 2000; Hughes & Franz, 2008; Jackson, Jackson, & Kritikos, 1999; Kelso et al., 1997; Marteniuk & Mackenise, 1980; Mason, 2008; Punt, Riddoch, & Humphreys, 2005; Swinnin, 2002), and intermanual prehension (i.e., the passing of an object from one hand to another; e.g., Churchill, Vogt, & Hopkins, 1999; Domkin, Laczko, Djupsjobacka, Jaric, & Latash, 2005; Olivier, Hay, Bard, & Fleury, 2007b). What is important is that these previous studies examined the two hands having independent or alternating movement goals, which is unlike a bimanual grasping task where both hands move towards the same goal.

The latter is the case in a recent study by Duque and colleagues (2009). These authors compared a task in which bimanual movements had to be coordinated towards a single target goal with a task in which bimanual movements were performed towards two different goals. In the coordination task, participants controlled two joysticks with their two hands so that the two joysticks were always circling in a predefined, simple speed ratio, such as 2:1 (i.e., the right hand
had to turn twice as fast as the left hand). In this task, the movements of both hands needed to adapt to each other in order to reach a common goal. In the control “independent” task, the joysticks needed to circle at more complicated, non-integer speed ratios (e.g., 11:10). This made it virtually impossible for participants to represent the circling speed of the two joysticks by one ratio. Instead, they needed an independent representation of speed for each joystick. In other words, each hand had a separate goal. Using functional magnetic resonance imaging (fMRI), Duque and colleagues pinpointed three areas in the right hemisphere that were activated during the coordination condition: the superior temporal gyrus (STG), the supplementary motor area (SMA), and the primary motor cortex (M1). They then used transcranial magnetic stimulation (TMS) to disrupt these three regions in order to distinguish between a causal role and a merely correlational role in bimanual coordination. Duque et al. found that bimanual coordination was impaired only when they stimulated the right STG. Thus, if bimanual grasping has similar mechanisms to bimanual coordination, a right hemisphere dominance may be observed for bimanual grasping.

1.3 Objectives and hypotheses

Based on previous findings on grasping and on bimanual coordination, I ask the following questions: Given that there is coordination between the two hemispheres, at which level is the information coordinated for bimanual grasping? That is, grasping involves “earlier” processes of visual perception and “later” processes of sensorimotor transformations and motor control (see Culham, 2004). It is clear that the coordination between hemispheres at the later stage of motor control must exist, otherwise no online control of ongoing movements of the two hands would be possible (e.g., Hummel & Gerloff, 2006; Liuzzi et al., 2009). Moreover, even unimanual actions involve both hemispheres (Petreska, Adriani, Blanke, & Billard, 2007; Pulvermüller, Lutzenberger, Preißl, Birbaumer, 1995). However, it is unclear whether there is coordination between earlier sensory areas for bimanual grasping. That is, does information coordination occur at earlier sensory areas as well as later motor areas? (I will refer to the neural coordination between hemispheres as “cross-talk” to prevent confusion with “coordination” in the sense of overt grasping behaviour.) This cross-talk will depend on whether bimanual grasping involves left hemisphere dominance similar to unimanual precision grasping, whether it involves right hemisphere dominance similar to bimanual coordination, or whether it involves both hemispheres equally. Hence, bimanual grasping could be the result of neural processes
predominantly based on one hemisphere (either the left or the right) or processes equally shared by the two hemispheres. Also, there could be either late sensorimotor/motor cross-talk with no early cross-talk or there could be both late as well as early cross-talk.

To test these 2 x 2 possible scenarios, I use behavioural measurements (Experiment 1) and electroencephalography (EEG, Experiment 2). In Experiment 1, I ask participants to grasp objects with both hands while fixating either to the left or to the right of the objects. I also ask participants to reach for the lateral edges of the objects to control for the possibility that grasping and reaching are governed by the same neural mechanisms (Smeets & Brenner, 1999), as well as the possibility that all effects are simply caused by attention (e.g., Umiltà, 1994). In Experiment 2, I use the same grasping task but record EEG data at the same time. This allows us to observe the time course of bimanual coordination at a neural level.
Chapter 2

2 Experiment 1

In this experiment, I ask participants to either grasp or reach for objects with both hands while fixating either to the left or to the right of the objects. This kind of paradigm has been successfully utilized to examine interhemispheric transfer for visuo-motor information (e.g., Aglioti, Berlucchi, Pallini, Rossi, & Tassinari, 1993; Bisiacchi, Marzi, Nicoletti, Carena, Mucignat, & Tomaiuolo, 1994; Braun, 1992; Di Stefano, Morelli, Marzi, & Berlucchi, 1980; Marzi, Bisiacchi, & Nicoletti, 1991; van der Staak, 1975; Velay & Benoit-Dubrocard, 1999; Velay, Daffaure, Raphael, & Benoit-Dubrocard, 2001). We expect that this paradigm will have sufficient signal-to-noise ratio to measure any differences in timing between the two hands.

2.1 Hypotheses and Predictions

I expect different results depending on whether there is left/right hemisphere dominance for bimanual grasping and whether there is early cross-talk between hemispheres. Here I illustrate my predictions while assuming that the right hemisphere is dominant. Corresponding predictions apply for left hemisphere dominance, except that the respective effects would be reversed (e.g., instead of reacting faster if the object appears in the left visual field, the participant would react faster if the object appears in the right visual field).

2.1.1 Scenario 1: Right-hemisphere dominance and no early cross-talk

In the first scenario, bimanual grasping is assumed to be predominantly controlled by one hemisphere and there is no early, visual cross-talk (Figure 1a). Here I expect a visual field effect on reaction times. That is, assuming that there is right hemisphere dominance, participants should react faster for right fixation than for left fixation. This is because in the latter case visual object information needs to cross the corpus callosum before reaching the dominant motor circuits in the left hemisphere. Also, the right hand should be slower than the left hand. This is because in the former case visual object information needs to cross the corpus callosum one more time compared to the left hand in order to reach the left motor areas that are needed for the control of the right hand. For example, for the right hand while fixating left, information needs to cross the corpus callosum once to get to the dominant motor circuits in the right hemisphere, and
a second time to get to the left motor areas. For the left hand while fixating left, information only needs to cross once to the right hemisphere. Indeed, additional interhemispheric transfer of information might rely on smaller-sized fibre tracts and/or take more time than merely intrahemispheric transfer (van der Staak, 1975; also see Bisiacchi, Marzi, Nicoletti, Carena, Mucignat, & Tomaiuolo, 1994; Marzi, Bisiacchi, & Nicoletti, 1991; van der Staak, 1975; Velay & Benoit-Dubrocard, 1999; Velay, Daffaure, Raphael, & Benoit-Dubrocard, 2001).

In addition, interhemispheric transfer should also cause bimanual grasps to be somewhat less coordinated if an object appears in the right visual field (i.e., left fixation) as opposed to the left visual field (i.e., right fixation). This is because object information from the right visual field might be more likely to trigger the unwanted, less proficient motor areas in the left hemisphere than object information from the left visual field. As a consequence, maximum grip aperture between the two hands (an important grasp phase before the hands touch an object) might be more variable, and grasped objects might lift off along less steady, more curved trajectories.

2.1.2 Scenario 2: No hemisphere dominance and no early cross-talk

According to the second scenario, bimanual grasping involves both hemispheres equally with no early visual cross-talk between them (Figure 1b). In this case, reaction times for each arm should be faster for objects appearing in the ipsilateral visual field (i.e., for the left hand when the object is in the left visual field as opposed to the right visual field, and vice versa for the right hand).

For instance, if the object is in the left visual field, visual information should arrive in the right hemisphere before arriving in the left hemisphere and should trigger right-hemisphere motor programs before triggering left-hemisphere motor programs. Importantly, the resulting differences in reaction time for the ipsilateral versus contralateral visual field should be symmetrical for both hands. This difference should be independent of potential time differences due to increased training for the dominant arm and hand. In addition, no early cross-talk might mean that objects appearing in only one visual field activate contralateral motor areas too early to properly coordinate the two hands. However, this would difficult to observe because it happens for the right as well as the left visual field.
2.1.3 Scenario 3: Right-hemisphere dominance and early cross-talk

The third scenario assumes that bimanual grasping is subserved by the dominant right hemisphere and that there is early, visual cross-talk (in addition to later cross-talk for motor control; Figure 1c). In this case, information from objects in the right visual field (but not information from the left visual field) would need to transfer from visual areas in the left hemisphere to visual areas in the right hemisphere before activating motor control in the right hemisphere. Therefore, similar to the first scenario, participants should react faster for right fixation than for left fixation. Also similar to the first scenario is that the right hand should be slower than the left hand because in the former case visual object information needs to cross the corpus callosum one more time compared to the latter in order to reach the left motor areas. I expect no visual field effects on the coordination of the two hands because visual information, regardless of coming from the left or right visual field, would have been gathered by the right visual areas before being sent to the right motor areas.

2.1.4 Scenario 4: No hemisphere dominance and early cross-talk

The fourth scenario assumes that bimanual grasping involves both hemispheres equally with early visual cross-talk (Figure 1d). Here I expect no visual field effects on reaction times or bimanual coordination. Visual information from both visual fields would be shared by both hemispheres before being transferred to their ipsilateral motor areas, which would then control the respective contralateral hand. Thus, motor performance should be the same regardless of the visual field in which the object is presented.
Figure 1. The four possible scenarios based on our predictions of either right/left or dominance, and of either early plus late cross-talk or only late cross-talk. This figure illustrates right hemisphere dominance, but that left hemisphere dominance could occur as well. a) Right hemisphere dominance with no early cross-talk. Within the big light gray circle, which represents the brain, the bottom two dark gray circles represent visual areas, and the top two circles represent sensorimotor/motor areas. The dotted rectangle represents a dominant hemisphere. Note that this may be a simplified view of the brain regions involved in grasping. However, we will only use these four general regions to help illustrate the predictions in a concise manner. b) No hemisphere dominance with no early cross talk. c) Right hemisphere dominance with early cross-talk. d) No hemisphere dominance with early cross-talk.

2.1.5 Implications

It is important to note that all four scenarios could be observed regardless of whether grasping and reaching are subserved by the same or different neural circuits. If different circuits are involved, then visual field effects on reaching will be different from those on grasping. The precise effects will depend on the degree to which bimanual reaching requires coordination
between the two hands. However, it is also possible that visual field effects will be the same for reaching and grasping. This could indicate that reaching involves the same circuits as grasping (see Smeets & Brenner, 1999). Alternatively, this could indicate that the visual field effects are confounded with attentional effects. As one important example, people fixating on one side might not only pay more attention to the opposite side where the object will appear but also to the contralateral arm. This could alter manual response times in a way that mimics the results as expected for scenario two (i.e., no hemisphere dominance, no early cross-talk). However, the opposite is possible as well, that is, shifting one’s eyes to the fixation point on the left side might direct attention to the left arm, and thus speeding up the left arm, and shifting attention and eyes to the right side might speed up the right arm, similar to a Simon effect (Umiltà, 1994).

2.2 Methods

2.2.1 Participants

Thirty-two undergraduate students at the University of Toronto Scarborough participated in the experiment. However, due to technical problems with the experimental apparatus, data from 22 participants (11 females, mean age of 20.4 years) were included for the data analysis. Exclusion criteria were a history of neurological as well as vision problems. Furthermore, only right-handed participants, as confirmed with Oldfield’s (1971) laterality inventory, were tested. All procedures were approved by an ethics committee and all participants gave informed consent. Each participant was tested for approximately 1.5 hours, with 30 minutes for equipment set up.

2.2.2 Apparatus

Participants wore a set of Plato goggles (Translucent Technology, Toronto) and sat in front of a table with their head stabilized in a chin rest while facing a CRT monitor positioned approximately 60 cm away at eye level. The height of the chin rest was adjusted to keep the eyes level with the centre of the computer monitor. A wooden block (8.7 cm by 5.0 cm by 2.4 cm, weight: 43 g) on a pedestal was placed 40 cm away from the eyes and 3 cm below the line of sight (see Figure 2). I measured the movement trajectories of both hands using three infrared Qualisys motion tracking cameras (Qualisys, 240 Hz) and four spherical, infrared light reflecting markers fixed on the tips of the two index fingers and on the two wrists of both hands. I also used an EyeLink II eye tracker (SR Research, Ottawa; sampling rate 250 Hz) to record eye
movements of the left eye to ensure proper fixation behaviour. The eye recordings and visual stimuli were controlled by Matlab (MathWorks) using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and Eyelink Toolbox extensions (Cornelissen, Peters, & Palmer, 2002). The shutters of the Plato goggles were controlled by a custom-made program.

Figure 2. Experimental set up for Experiment 1.

2.2.3 Procedure

Before the start of a trial, the Plato goggles were set to opaque and the participants rested both of their index fingers on a tactile marker placed on the table that was 24 cm in front of their trunk. During this period, I used a random protocol to place the object in one of two possible orientations on the pedestal and then started the Qualisys (QTM) recordings. This triggered the Plato shutters to turn on (i.e., become transparent), allowing participants to see the computer monitor in front of them. At the same time, the eye tracking system detected that the eyes were visible, and on the monitor, a red fixation dot appeared on a black background either 15 degrees to the left or to the right of the centre. Participants were asked to fixate on the dot and to continue fixating on it throughout the remainder of the trial. Seven hundred milliseconds later, the black background became white (the red fixation dot remaining in its location), thus illuminating the object in front of the monitor. Participants then grasped, lifted the object off the pedestal with index finger and middle finger of both hands, placed the object back onto the pedestal, and
moved their hands back to the origin. Alternatively, for the reach trials, participants pushed the block at the lateral edges of its face with their index fingers, and then moved their hands back to the origin. After 2500 ms, QTM recordings stopped, the monitor turned black with no fixation point, and the goggles become opaque once again.

The lateralization of the fixation point and the orientation of the object were randomized across trials. Grasp and reach trials were sorted into 4 separate blocks of 30 trials each (15 trials with a left fixation point), and these blocks were arranged in an ABBA fashion where A represented grasping and B represented reaching, or vice versa. The dependent measures included reaction time, movement trajectories, location of the maximum grip aperture (MGA), size and variability of the MGA, and the correlation between MGA and object size.

2.2.4 Data analysis

Motion data were first analyzed trial-by-trial with the native QTM software, identifying each marker (left index, left wrist, right index, right wrist) using a relative-position model and excluding artifacts. The data was then exported to TSV format for analysis in MATLAB. Eye tracking data were compiled with the TSV motion data and integrated for analysis in MATLAB. The peak velocity of the fingers was calculated, and the initiation and termination of hand movement was defined as 5% of this velocity. The maximum grip aperture (MGA) was defined as the largest distance between the index fingers during our participants’ reach-to-grasp movements (more specifically, MGA was identified as maximum distance after the fingers reached peak velocity and before they touched the object). Reaction time was recorded as the time from the computer screen turning white to the initiation of movement criterion. Once all the data for each trial were combined, they were then analyzed trial-by-trial to determine which trials were to be included for further analysis. Exclusion criteria were: looking away from fixation point after the onset of the white screen; trials with reaction times smaller than 50 ms; and incomplete grasp/reach actions. The data for individual trials were then compiled for each individual participant, and then group statistics were performed on all participants.
2.3 Results

Figure 3 shows the velocity profile for the index fingers of both hands (dark gray = left hand; light gray = right hand) for one participant while they were grasping and fixating to the left (dotted magenta line) or to the right (solid red line) of the object. We can see here that there was no difference in the profile between fixating left and right for the right and left hand. This observation is consistent with aggregate data for the reaction time results (Figure 4) where there was no main effect of condition (grasping vs. reaching; $F(1,21) = 2.328, p = .142$), visual field ($F(1,21) = 0.949, p = .341$), and hand ($F(1,21) = 0.172, p = 0.683$); and no interaction effects either ($p > .05$). So far, the lack of reaction time differences is consistent with the scenarios of no hemispheric dominance for the bimanual grasp. Specifically, the reaction time results are consistent with the fourth scenario (i.e., no hemisphere dominance, early cross-talk), which predicts that there should be no visual field effects for reaction time. The results here are not consistent with the second scenario (i.e., no hemisphere dominance, no early cross-talk) because this scenario predicts that the reaction time for each arm should be faster for objects appearing in the ipsilateral visual field than the contralateral visual field, and we did not observe this in our data (i.e., the hand x visual field interaction was not significant).
Figure 3. Velocity profile for a typical participant while grasping. Dark gray curve plots the left hand, light gray curve plots the right hand. Magenta curve plots fixation to the left, red curve plots fixation to the right.

Figure 4. a) Average reaction time for grasping. b) Average reaction time for reaching.
Figure 5 shows the trajectories for the index fingers of both hands while the participants were grasping and fixating to the left (magenta) and right (red) of the object. Figure 6 shows the same trajectory but for reaching (left = cyan, right = blue). Here we observed no visual field effects on the trajectories for both grasping and reaching. Indeed, there were no visual field effects on the size of the maximum grip aperture (MGA) that was proportional to object size (for grasping, $t(21) = 1.275, p = .216$) or the standard deviation of the size of MGA that was proportional to object size (for grasping, $t(21) = 0.045, p = .964$). Moreover, there were no differences in the location of the MGA for grasping, in x, y, and z coordinates ($p > .05$). I did, however, find visual field effects on the time at which MGA occurred ($t(21) = 3.426, p = 0.002$) with MGA occurring much later for left fixation ($M = 1314 \text{ ms}, SD = 27.06$) than for right fixation ($M = 1299 \text{ ms}, SD = 27.85$). We report the MGA statistics for only grasping because MGA is specific to grasping, and is not typically seen in reaching movements (Jeannerod, 1981, 1984).
Figure 6. Trajectories of the two hands for grasping. Fixation to the left is in cyan, whereas fixation to the right is in blue. Left hand is the top curve, right hand is the bottom curve.

I also found that the size of the MGA was positively correlated with object size for grasping (Figure 7; for left fixation, $r = 0.526$, $p < .001$; for right fixation, $r = 0.550$, $p < .001$), which is consistent with current literature on unimanual grasping (e.g., Jakobson & Goodale, 1991). Together, the evidence here suggests that the trajectories and the MGA, which are both measures of bimanual coordination, are mostly unaffected by visual field (with the exception of the time of MGA), indicating that there is early cross-talk (i.e., fourth scenario).
For control analyses, I wanted to rule out any differences between the four conditions in the start position of the index fingers that may have confounded our results. Start position was calculated as an average x and y coordinate between the two hands. (The y coordinate is on the plane that is to the left and right of the body midline, whereas the x coordinate is on the plane that is to the front and back of the body midline. The origin is the body midline.) In general, there was no evidence of differences in start position for left and right fixation while grasping or reaching (Figure 8, \( p > .05 \)), with the exception that for reaching when fixating to the left, the right index was slightly further away from the origin in the y coordinates compared to fixating to the right (right index was 37.10 mm from the origin, \( p < .05 \)). This one difference in start position for the right index when reaching, however, does not confound with our reaction time or trajectory results given that we did not find visual field effects in those measures. Moreover, our significant MGA-time result is only for grasping, so this start position difference in reaching does not confound that result either.

I also wanted to rule out any speed-accuracy trade-offs to ensure that any effects in our results were not simply due to differences in movement strategy adopted by our participants between the different conditions. To examine speed-accuracy trade-offs, reaction time was correlated with accuracy. For grasping, accuracy was measured by the standard deviation (SD) of the MGA location. Similarly, for reaching, accuracy was measured by the SD of the location of the maximum distance between the two index fingers during the reaching trajectory. A negative
correlation indicates speed-accuracy trade off (i.e., the faster the reaction time, the more variable the maximum aperture), whereas a positive correlation indicates no speed-accuracy trade off. Most of the correlations were positive (for grasping, fixating right, $r = 0.209, p = .174$; for reaching, fixating left, $r = 0.219, p = .153$; and reaching, fixating right, $r = 0.320, p = .033$). The correlation for grasping, fixating left was negative, but was not significant ($r = -0.006, p = .968$). Therefore, there was no evidence of speed-accuracy trade-off (Figure 9). Moreover, although the positive correlation for reaching, fixating right was significant, this correlation was relatively weak ($r = 0.320$) and does not confound with our results given that there were no significant visual field effects on reaction time or trajectory between the four conditions and that our significant visual field effect on MGA-time was for grasping only.

Figure 8. Start position (in x and y coordinates) for left and right index fingers, calculated as the average location of the two hands. Locations are calculated as distance from the origin (0, 0). a) Start position for left index, x coordinates. b) Start position for left index, y coordinates. c) Start position for right index, x coordinates. d) Start position for right index, y coordinate.
2.4 Discussion

Little is known about the specific mechanisms that contribute to bimanual grasping. Based on current literature, it is possible that bimanual grasping is similar to unimanual grasping (and thus has left hemisphere specialization) or is similar to bimanual coordination (and thus has right hemisphere specialization). In the present experiment, the reaction time results together with the trajectory and MGA results suggest that there may be no hemisphere dominance with early cross talk (i.e., fourth scenario) for bimanual grasping. That is, our results suggest that when you are required to bimanually grasp an object, it may be the case that both hemispheres equally control the action and visual information is shared before they reach the motor areas.
One interesting result that may challenge this speculation that both hemispheres equally control bimanual grasps is that there was a visual field effect on the time at which MGA occurred. Specifically, MGA occurred later when participants were fixating to the left than when they were fixating to the right. This finding is consistent with Tunik et al. (2005), who also found a delay in the MGA-time when they stimulated the aIPS with TMS as participants were unimanually grasping, which suggested that whichever brain area is more directly linked to grasping should normally be faster with processing grasp-related information than areas that are not directly linked to bimanual grasping. Indeed, one possible explanation for our finding is that if the right hemisphere is specialized for bimanual grasping, any visual information that goes into the left hemisphere (i.e., when fixating to the left) will need to be transferred to the right hemisphere for motor control. This interhemispheric transfer does not happen when visual information goes directly into the right hemisphere (i.e., when fixating to the right). Thus, MGA is delayed when fixation is to the left because information needs to be transferred from the left to the right hemisphere. Supporting this view is the nonsignificant trend in our reaction time results (see Figure 4) which showed that reaction times for grasping were slower when participants were fixating to the left ($M = 320.35$ ms) than to the right ($M = 307.25$ ms). These results also suggest that bimanual grasping may be controlled by a dominant right hemisphere. However, this is not for certain because the trend in the reaction times was not significant, and all other MGA measures did not have a visual field effect.

Thus the present results may or may not be in contrast to the existing literature on bimanual coordination where a right hemisphere dominance has been observed (e.g., Duque et al., 2009). This uncertainty is based on the fact that in this experiment, I base my speculations on behavioural data only. Duque et al., for example, did not report reaction times and did not measure visual field effects, and their conclusion of a right hemisphere dominance for bimanual coordination was based on functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS). Thus, it is unclear whether my results are fully contradicting those of Duque et al.'s, or whether they are partially consistent. To resolve this problem, I plan to conduct further experiments (see below) to more directly examine the neural mechanisms underlying bimanual grasping.

The present results are, however, in contrast to existing literature on unimanual precision grasping where a left hemisphere dominance has been observed (e.g., Davare, Andres, Clerget,
Thonnard, & Olivier, 2007; Gonzalez, Ganel, & Goodale, 2006). Davare et al. (2007) stimulated participants’ aIPS using TMS while the participants were asked to grip and lift an object with their thumb and index finger. They found that stimulation to the left aIPS 170 – 200 ms before object contact affected participants’ grip force. Gonzalez et al. (2006) found similar results but used a different paradigm that looked at the effects of visual illusions on grasping. These visual illusions are known to have robust effects on perceptual judgments but have little influence on grasping, meaning that if the left hemisphere is specialized for grasping, the right hand should not be affected by the illusions. Gonzalez and colleagues found that, for both right- and left-handed subjects, precision grasping with the left hand, but not with the right, was affected by the illusions. Just like Davare et al., Gonzalez et al.’s results suggest that the left hemisphere plays a crucial role in grasping and that this hemispheric specialization is unaffected by handedness. One possible explanation for the difference between their results and my results is that in my study I examined bimanual grasping, and perhaps more interaction between the two hemispheres is needed in this case than for unimanual grasping. Thus, having just one hemisphere controlling both hands for bimanual grasping may not be sufficient, and that the interaction between two hemispheres may be necessary for this type of action.

Aside from the aforementioned results, another interesting finding is that for both grasping and reaching, the two hands had the same reaction time (RT) regardless of visual field. This is intriguing given that simple manual RT studies looking at interhemispheric transfer have found that responses of the hand can be up to 15.1 ms slower when visual information appears in the contralateral visual field compared to when visual information appears in the ipsilateral visual field. I did not observe this contralateral effect for either of the two hands, and furthermore, the two hands did not significantly differ from each other in their reaction time. This indicates that when bimanually grasping and reaching the two hands wait for each other before responding, providing evidence that there is bimanual coordination and that the two hands are typically well synchronized for bimanual movements to a single target.

One last interesting finding is that grasping and reaching had very similar results (i.e., there were no visual field effects on reaction times or trajectories for both tasks). This suggests that bimanual grasping and reaching may be subserved by the same neural circuits, as previously suggested by Smeets and Brenner (1999). However, this is in contrast to existing literature on unimanual grasping and reaching which has shown that these two types of movement have their
own neural circuits (e.g., Brinkman & Kuypers, 1972; Galletti et al., 2003; Jeannerod & Biguer, 1982; Tanné, Boussaoud, Boyer-Zeller, & Rouiller, 1995; Sakata & Taira, 1994). If it is the case that bimanual grasping and reaching are not subserved by the same neural circuits, perhaps it is the case that bimanual grasping and reaching have the same visual field effects because of an attentional confound. However, given that there was a lack of visual field effect and even hand effect for both grasping and reaching, an attentional confound is unlikely. More likely is that although behaviourally the two tasks seem similar, they may still be different on a neural level. Our next experiment (Experiment 2) will help confirm whether bimanual grasping and reaching are different on a neural level.

Therefore, merely having behavioural data may not give us the full picture. As I suggested above, using methods that more directly examine the neural mechanisms of bimanual grasping will allow us to draw stronger conclusions about whether this type of grasping is similar in its neural structure to unimanual grasping or to bimanual coordination. These methods will also help us better discern whether there is a right hemisphere dominance for bimanual grasping or not. Furthermore, by using electroencephalography (EEG), we will be able to better determine which brain areas are crucial for bimanual grasping, and the time course of the brain activity and interactions. Thus, in Experiment 2, I use EEG, which will allow us to further examine and confirm the results from Experiment 1.
Chapter 3

3 Experiment 2

The objectives of Experiment 2 are (a) to examine the time-course of the neural mechanisms of bimanual grasps, and (b) to confirm whether there is a right hemisphere dominance for bimanual grasping. The reasoning behind the second objective is that I found weak evidence of right hemisphere dominance in Experiment 1. However, this finding would be better confirmed through electroencephalograph (EEG) data where we can observe specifically the differences in amount of activity between the two hemispheres in visual and/or motor areas. Thus, continuous EEG will be recorded while participants fixate to the left or to the right of the screen and then perform the grasping task as described in Experiment 1. A control condition where participants touch the object with their knuckles will be included as well. It is predicted that when aligning the data according to stimulus onset, we should see grasp-related event-related potential (ERP) components in the difference waves between the ERPs for the grasping condition and the control condition.

3.1 Hypothesis and Predictions

Grasp-related ERP components should show up in the difference waves between grasping trials and control trials matched for fixation side. The latencies of these components should be within the time range of the P100 or earlier and should be strongest for electrodes over dorsal parietal cortex that are contralateral to the visual field in which the object appears. (Tunik et al., 2008 reported two components at 50-100 ms and 100-150 ms after movement onset that are associated with aIPS and SPL, respectively, but their paradigm was different from mine.)

Regardless of its visual field dependency, the grasp-related component should be consistently stronger over the right hemisphere than the left hemisphere – that is, if bimanual grasping is predominantly controlled by the right hemisphere. If both hemispheres share control equally, the grasp-related component should be the same for both sides. Also, grasp-related components on both sides may or may not show the same latencies depending on whether bimanual grasping involves early interhemispheric cross-talk or only late cross-talk.
3.2 Methods

3.2.1 Participants

Twenty-two undergraduate students at the University of Toronto Scarborough participated in the experiment. However, due to technical problems with the experimental apparatus, data from 16 participants (6 females, mean age of 21.75 years) were included for the data analysis. Exclusion criteria were a history of neurological as well as vision problems. Furthermore, only right-handed participants, as confirmed with Oldfield’s (1971) laterality inventory, were tested. All procedures were approved by an ethics committee and all participants gave informed consent. Each participant was tested for approximately 2 hours.

3.2.2 Apparatus and data analysis

Apparatus was similar to Experiment 1, except to simplify matters (and to avoid electromagnetic interference), I only recorded hand movement onsets through a custom-made response box that had two buttons which participants pressed with their index fingers between trials and released when grasping the object. Electrooculography replaced the EyeLink tracker, and Plato goggles were not used. The monitor was covered with black cardboard to keep the room as dark as possible, so that the participants could not see the object in-between trials. Three holes were cut into the black cardboard. Two lateral ones allowed the participants to view parts of the monitor where fixation dots might have occurred. The third, central hole was used to illuminate the object during trial (see Figure 10a). Therefore, light was funneled from the centre hole upwards and then downwards with aluminum foil clad pieces of cardboard (see Figure 10b). Arm rests (23 cm high) were used during the experiment to reduce arm movements to a minimum in order to avoid movement artifacts in the EEG data. Correspondingly, the button box and the pedestal were elevated 13.5 cm and 14 cm away from the table surface, respectively, so that participants only had to move their wrists and hands to grasp or reach for the objects. The wooden block was placed 45 cm away from the eyes and 11 cm below eye level. The fixation points were placed in the lower part of the monitor, where the line of sight matched that of the object. The height of the participants’ chair (approximately 80 cm away from the CRT monitor) was adjusted to keep the eyes level with the top of the monitor. All cables, wires, and the monitor were shielded and grounded to reduce the effects of electrical (60Hz) noise in the EEG data.
Figure 10. a) Front view of the monitor set-up. Three holes were cut into the black cardboard that was covering the screen. b) The centre hole was covered by two pieces of cardboard that were covered in aluminum foil on the insides. This was to allow for the light coming from the hole to be reflected.

EEG was acquired using an EGI system (Electrical Geodesics, Oregon, US) with 128 scalp electrodes (impedances < 10kΩ), which were referenced to the average of all electrodes as calculated offline. Data were band-pass filtered from 3 Hz (to reduce the effects of lateral eye positions) to 100 Hz, epoched from -100 ms prestimulus to 600 ms poststimulus, and baseline-corrected based on the time period -100 to 0 ms. Trials with blinks and improper eye fixation behaviour were rejected on the basis of vertical and horizontal electrooculogram or of recordings from electrodes Fp1 and Fp2 (i.e., electrodes directly above the eyes). An artifact rejection criterion of ±60 µV was used at all other scalp sites to reject trials with excessive noise. Channels with corrupted signals or with substantial noise throughout the recording were replaced by interpolation of signals from neighbouring electrodes. Data from the surviving trials and channels were then averaged for each condition (i.e., grasping left fixation, grasping right fixation, knuckling left fixation, knuckling right fixation) within each participant. The resulting averages were then grand averaged across the 16 participants, producing one grand average for each condition.
3.2.3 Procedure

This experiment contained blocks of grasping trials much like that described for Experiment 1. That is, before a trial began, the experimenter placed the object on the pedestal in one of two randomly chosen orientations. Then the experimenter pressed the space bar on the keyboard and a beep was emitted from the speakers to signal the start of the trial. The participant then pressed the buttons on the button box, which triggered the fixation point to appear on the monitor, either on the left or the right side. The participant was asked to fixate on the point. During this time the object remained virtually invisible. Seven hundred milliseconds after fixation point onset, the portion of the screen behind the central aperture turned white thus illuminating the grasp object in front of the monitor. The participant was then required to release the buttons and to grasp the object. In separate blocks of control trials, the participants were asked to touch the front surface of the object with their index knuckles. I used this modified version of the control task because our previous reaching control task may have been too similar to grasping. By having a control task that is more different from grasping, I can control for the possibility that participants are able to use the same movement strategy for the experimental and control tasks. Indeed, comparing grasping and “knuckling” has been routinely used to identify neural mechanisms specifically involved in unimanual grasping where the knuckling task allows the researchers to avoid any shape processing that might be necessary to compute the centroid of the object and any preshaping of the hand (Culham et al., 2003).

3.3 Results

After aligning the data according to stimulus onset, inspection of group-averaged evoked potentials at occipital electrodes revealed typical patterns of visual activity where components P1 and N1 occurred at 175 and 225 ms, respectively (see Luck, 2005). Both components appeared comparatively late perhaps due to the low visual contrast settings of this experiment (e.g., Foxe, McCourt, & Javitt, 2003; Figure 11).
Parietal electrodes, specifically ones that were over motor areas (i.e., electrodes #47, 50, 51, 52, 98, 101, 97, 92), had a negative component at 210 ms, but generally showed no differences in the ERP waveform for all four conditions (i.e., grasping fixation left, grasping fixation right, knuckling fixation left, knuckling fixation right; see Figure 12). Successive t-test plots were conducted for each time point at each electrode where p-values for amplitude differences are considered significant if they fell below 5% for 12 or more consecutive time points. In general, I did not find significant extended sets of electrodes in the successive t-test for grasping vs. knuckling (averaged across visual fields; Figure 13). In fact, I did not find extended sets of significant parietal electrodes either when I parsed the analysis into fixation to the left (Figure 14; $p > .05$) and fixation to the right (Figure 15; $p > .05$).
Figure 12. Typical parietal electrodes. a) Electrodes #52 (left parietal), c) and 92 (right parietal). b) Difference waves (grasping left fixation minus knuckling left fixation) for electrodes 52 and 98. d) Difference waves (grasping right fixation minus knuckling right fixation) for electrodes 52 and 98. Blue = knuckling left fixation, red = grasping left fixation, magenta = grasping right fixation, cyan = knuckling right fixation.

Figure 13. For grasping vs. knuckling (averaged across visual field), successive t-test plot for each time point, for all electrodes listed from most posterior (occipital electrodes) to most anterior (frontal electrodes). For each area (e.g., occipital), electrodes were listed from left to right, and top to bottom. On the right, p-values are colour-coded, with red being as most significant.
Figure 14. For fixation left (grasping vs. knuckling), successive t-test plot for each time point, for all electrodes listed from most posterior (occipital electrodes) to most anterior (frontal electrodes). For each area (e.g., occipital), electrodes were listed from left to right, and top to bottom. On the right, p-values are colour-coded, with red being as most significant.

Figure 15. For fixation right (grasping vs. knuckling), successive t-test plot for each time point, for all electrodes listed from most posterior (occipital electrodes) to most anterior (frontal electrodes). For each area (e.g., occipital), electrodes were listed from left to right, and top to bottom. On the right, p-values are colour-coded, with red being as most significant.
For a direct comparison of left versus right electrodes over the left and right hemispheres, I calculated global field power (GFP) values for the two regions for each time point across participants. GFP is a single, reference-independent measure of response strength (Lehman & Skrandies, 1980; Murray, Brunet, & Michel, 2008). Mathematically, GFP is equal to the standard deviation of all electrodes at a given time, and indicates how strong a potential is being recorded on average across the electrode montage (see Murray et al., 2008). Because there were no differences in ERP for grasping and knuckling, I only compared the GFP values for grasping left/right fixation. I conducted t-tests using these GFP values to compare electrodes in the left versus right hemisphere. Similar to the successive t-test plots, differences were considered significant if they fell below 5% for 12 or more consecutive time points. For both left (Figure 16a) and right fixation (Figure 16b), GFP values for right and left hemispheres had the same trend across time. In fact, there were no extended sets of significant p-values for both left (Figure 16c) and right fixation (Figure 16d). Therefore, the left and right hemispheres did not differ in their GFP values, which suggest that the two hemispheres had the same amount of response strength.

Figure 16. a) Global field power plotted over time for grasping fixation to the left. Red = left hemisphere; magenta = right hemisphere. Note that because the left and right hemispheres are so similar in their GFP values, the magenta curve is occluded by the red curve. b) Global field power for grasping fixation to the right. c) p-values plotted over time for grasping fixation to the left. A grey rectangle was programmed to mark sections that had more than 12 consecutive time points that were below 5%. The grey rectangle is not present in this plot because there were no sections that had 12 or more consecutive significant time points. D) p-values plotted over time for grasping fixation to the right.
3.4 Discussion

The objectives of this experiment were to examine the time-course of the neural mechanisms of bimanual grasps, and to follow up on the rather weak evidence from Experiment 1 for a right hemisphere dominance for bimanual grasping using a functional method instead of a behavioural method. The results in the present experiment showed no evidence for hemisphere dominance but suggested that both hemispheres share equal control for bimanual grasping. Indeed, a t-test comparison between right and left hemisphere electrodes showed no difference in response strength over the two hemispheres, and the successive t-test comparisons (for fixation to the left and right) between the ERP amplitudes for grasping versus knuckling showed no differences for electrodes at both left and right hemispheres. The results also suggested that there may be early interhemispheric cross-talk in visual areas, given that the ERP components for grasping had the same latency for both fixation to the left and right. These results are consistent with our findings in Experiment 1 where we concluded that bimanual grasping may be controlled by both hemispheres equally with early visual cross-talk. Consistent with what Experiment 1 suggested, it seems that bimanual grasping is indeed a special form of action that is different from unimanual grasping (where left hemisphere dominance is expected; e.g., Tunik et al., 2008) and from mere bimanual coordination (where right hemisphere dominance is expected; e.g., Duque et al., 2009).

This bimanual grasp, albeit being a special form of action, may be similar to bimanual reaching/knuckling in that they may be subserved by the same neural circuits. That is, the successive t-tests showed that there were no differences in ERP amplitudes between grasping and knuckling for both fixation to the left and right. This is consistent with the findings in Experiment 1 where there were no differences in reaction time or trajectory between bimanual grasping and reaching. One counter-argument for this conclusion, however, may be that perhaps the grasping and knuckling/reaching tasks were too similar. However, this is unlikely given that Culham et al. (2003) compared unimanual grasping with a very similar knuckling task and found significant activations of the aIPS for grasping but not for knuckling. Therefore, the knuckling control task does in principle provide enough contrast from a grasping task to drive different neural mechanisms. Then again, Culham et al. used functional magnetic resonance imaging (fMRI) rather than EEG, where the former has much better spatial resolution. This suggests that perhaps the reason why we did not find any differences between grasping and knuckling is
because the present EEG data did not have enough spatial resolution to detect differences in neural activity. To resolve this issue, further investigation with fMRI will be needed.

Nevertheless, although EEG data tend to have poor spatial resolution, one advantage of this type of data is that it has good temporal resolution (Luck, 2005). In fact, Tunik et al. (2008) found temporal differences in EEG patterns associated with two grasping tasks that were much more similar than what was used in the present study. Specifically, Tunik et al. used electroencephalography during unimanual grasping to test whether the temporal contribution of the aIPS and SPL would change when the task goal was perturbed. To perturb the task goal, Tunik et al. used a rectangular object that did (perturbation trials) or did not change its orientation (non-perturbation trials). In the perturbation trials, the object changed its width once participants started moving their hand towards it. Tunik et al. found that during perturbed object grasping, there were two distinct evoked responses at 50 –100 and 100 –200 ms after movement onset. Based on source estimation of these scalp potentials, they localized the sources to the left parietal lobe, specifically the aIPS and then the SPL. The authors concluded that their results support a two-stage process whereby there is first an integration of target goal and an emerging action plan within aIPS and then subsequent on-line adjustments within the SPL.

The paradigm and results from my experiment are quite different from those of Tunik et al.’s. First of all, Tunik et al. used a unimanual grasping task with only the right hand. Not surprisingly, they found evoked responses in the left hemisphere. In contrast, I used a bimanual grasping task that did not involve mid-trial perturbations, and perhaps by using a bimanual task, we recruited both hemispheres equally and not just the left hemisphere. Second, Tunik found grasping-related ERPs at 50 – 100 and 100 – 200 ms after movement onset whereas I found a bimanual-related component at 210 ms after stimulus onset and no bimanual- or grasp-related component after movement onset. (I calculated that the participants’ average reaction time was 376.81 ms (SD = 0.068) for grasping-left fixation, 374.53 ms (SD = 0.060) for grasping-right fixation, 393.03 ms (SD = 0.085) for knuckling-left fixation, and 394.53 ms (SD = 0.075) for knuckling-right fixation. Therefore, movement onset occurred at those times after stimulus onset. As we can observe in Figures 12 – 15, there were no significant bimanual- or grasp-related components after movement onset for both fixation to the left and right.) This difference in finding may be due to the fact that I did not use a perturbation paradigm like Tunik et al., and therefore was not able to capture any activity that is associated with online updating of target
goals. Third, Tunik et al. only used grasping as their tasks, and did not use reaching/knuckling as a control. Therefore, it is unclear whether the ERP components they found were truly grasp-related or whether the components could have been present for a reaching task as well. Despite these differences between my study and Tunik et al.’s study, their study nevertheless shows that EEG can allow us to identify differences, if any, between different grasping tasks and more importantly between grasping and reaching.

Similarities between bimanual tasks go beyond just grasping and reaching. Indeed, there is evidence to suggest that other types of bimanual tasks may also be similar to our bimanual grasping and reaching tasks. For example, there exists an array of ERP studies on bimanual coordination (e.g., Andres et al., 1999; Gerloff & Andres, 2002; Hummel & Gerloff, 2005; Serrien, 2008) where most of them use bimanual tasks such that each hand has a separate goal. Gerloff and Andres (2002), for instance, used a bimanual tapping task that required participants to recite certain sequences of finger tapping for both hands. Using task-related coherence analyses, which enable researchers to directly measure the amount of interaction or correlation in brain activity between different regions (see Shaw, 1981, 1984), these studies have generally found coherence between left and right parietal regions of the brain (e.g., Andres, 1999). Although the paradigm and analysis in these studies are different from my present experiment, the results from these studies are consistent with mine in that they found both hemispheres interacting and equally contributing to the bimanual movement.

Despite the evidence from Experiments 1 and 2 that support the idea that bimanual grasps are equally controlled by both hemispheres with early cross-talk, one issue that may undermine our conclusions is that both experiments used a paradigm where participants were required to fixate to the right and left of the object. That is, one can argue that our results are simply due to the fact that the object was viewed in peripheral vision where visual information was less precise than foveal vision. Alternatively, one can argue that motor processes using peripheral vision are different from those using foveal vision (see Pisella, Tilikete, Vighetto, Desmurget, Rode, Boisson, & Rossetti, 2000). For instance, when motor programming is based on peripheral visual information, online visuomotor control plays a much larger role in adjusting the end of a grasp or reach action.
With respect to the first concern, although the object was presented in peripheral vision, it was not presented in the far periphery. In fact, the object was only approximately 8 and 11 visual degrees away from the centre of vision in Experiment 1 and 2, respectively. Therefore, the object was only slightly away from the fovea, and thus visual resolution should not have been extremely poor. With respect to the second concern, it may be the case that by presenting the object in the periphery, I was actually using a much more sensitive paradigm to measure the mechanisms of bimanual grasps. This is because the brain regions that are involved in grasping (such as the aIPS and SPL) are more active when there is a need for online adjustments of the grasps. Therefore, instead of being a potential problem, my paradigm may actually have been better for capturing any activity related to bimanual grasps. Further support for the sensitivity of my paradigm comes from a review and meta-analysis by Braun (1992) who outlined the experimental conditions that are most apt to yield salient, reliable, and statistically significant interhemispheric-transfer effects. Braun suggested that (a) the index fingers should be used for responding, (b) low luminance for the stimulus should be used, (c) stimulus should be presented in the periphery, and (d) stimulus presentation times should be relatively short. The paradigms for both experiments are consistent with the first three suggestions. (I did not keep the presentation times short, however. In fact, the presentation time was 2500 ms because brain regions involved in grasping such as the aIPS require objects that are constantly visible; Culham, 2004). Therefore, Braun’s suggestions indicate that my paradigm was indeed sensitive enough for measuring any interhemispheric-transfer effects.
Chapter 4

4 Conclusion

The aim of this research project was to examine bimanual grasping and its underlying mechanisms. I asked if bimanual grasping involves both hemispheres equally or if one hemisphere predominantly seizes control. I also asked if the information crosses at an early visual level and/or at a later sensorimotor/motor level. I conducted two experiments to address these issues.

In the first experiment, participants grasped or reached for a centrally-located object while fixating either to the left or right of this object. I recorded the participants’ hand movements and found no visual field effects on the reaction times, the grasp trajectories, or on the maximum grip aperture. This suggests that when we are required to bimanually grasp an object, both hemispheres equally control the bimanual grasp and visual information is shared before they reach the motor areas. Moreover, the results suggest that bimanual grasping is a special form of action, and is different from mere bimanual coordination and from unimanual grasping.

In the second experiment, participants performed tasks similar to those of the first experiment. I recorded EEG data, and did not find any major differences in ERPs between grasping and knuckling, which suggested that grasping and knuckling/reaching are subserved by the same neural circuits. Moreover, t-test comparisons on the ERP amplitude for grasping versus knuckling were insignificant for both left and right hemispheres, and t-test comparisons between left and right hemisphere electrodes revealed that the two areas were not significantly different in their response strength, which suggested that both hemispheres share equal control of bimanual movements. Also, ERP components had the same latency for both fixating left and right, which suggested that there is early interhemispheric cross-talk in visual areas. Therefore, the results in the second experiment were consistent with those in the first experiment.

One intriguing question that arises from the results of both experiments is that if bimanual grasping and bimanual reaching involve the same mechanisms but are different from the respective unimanual actions, does that mean that there is a different group of brain regions for bimanual actions? This is unlikely because having separate groups of brain regions for
unimanual and bimanual actions would cause redundancy in the brain and would probably be inefficient in terms of neural resources. Therefore, what seems more likely is that the same group of brain regions subserves both unimanual and bimanual actions, but effective connectivity between these brain regions is different for the two types of actions. Indeed, this view is consistent with theories about other functions in the brain such as the modeling of semantic knowledge (see Le, Rondina, & Cree, 2008) and the influence of modality input on the prefrontal cortex (PFC; e.g., Protzner & McIntosh, 2009). For instance, it has been proposed by the conceptual structure account (Taylor, Moss & Tyler, 2007; Tyler & Moss, 2001) that semantic knowledge (e.g., functional and sensory properties of objects) is thought to be stored in a single region of the brain. That is, all properties of objects are stored within this region, but specific objects activate specific networks of properties. Moreover, different objects may have a similar group of properties, but the connectivity between these properties may be different. Similarly, Protzner and McIntosh (2009) found that the PFC would show contextually dependent changes in functional connectivity in relation to the modality of input (visual or auditory) despite similar cognitive demands.

To investigate the possibility that unimanual and bimanual actions are supported by the same group of brain regions with different network connections, I plan to conduct an extensive analysis of the spectral aspects of the current EEG data. Specifically, I plan to conduct an event-related coherence analysis (Gerloff & Andres, 2002; Hummel & Gerloff, 2005; Pfurtscheller & Lopes da Silva, 1999; Rilk, Andres, Hummel, Hansmann, Hallett, & Gerloff, 2006; Shaw, 1981, 1984). This method explores the frequency domain of the EEG signal to estimate the extent to which neurons in different brain areas fire in synchrony, thus establishing functional connectivity between the areas. Specifically, I will focus on dorso-parietal and occipital electrodes in the alpha (8 – 12.9 Hz; related to sensorimotor activities) and the beta bands (13 – 30 Hz; related to motor activities) of the EEG signal (Gerloff & Andres, 2002; Serrien, 2008). I predict that the coherence analysis will reveal that although the areas involved in unimanual and bimanual grasping/reaching are the same, the connectivity between these areas will be different.

It is important to note however, that there are limitations with EEG studies. Indeed, one limitation of EEG studies is that typically the data can only establish correlative relationships and not causal ones (Luck, 2005). Moreover, given its poor spatial resolution, it is hard to pinpoint where exactly the activity is coming from (Luck, 2005). One way to overcome this limitation is
to use TMS, which will give us a much better idea of the anatomy underlying bimanual grasping. As such, I plan to use transcranial magnetic stimulation of reach and grasp related areas in parietal cortex such as aIPS and SPL to examine the contribution of these areas to bimanual grasping. Based on behavioural evidence suggesting that bimanual grasping is in some ways similar to unimanual precision grasping in its grip and load force (Freitas, Krishnan, & Jaric, 2007) and in its aperture and transport components (Tresilian & Stelmach, 1997), I predict that bimanual grasping involve the same neural structures as unimanual grasping with aIPS being one key area.

For the prospective TMS experiment, I will use a perturbation paradigm with transcranial magnetic stimulation of aIPS (guided by anatomical brain scans) to examine this area’s contribution to bimanual grasping. For this experiment, objects will change their orientation upon hand movement onset, requiring participants to make online adaptive adjustments of the hand movement (Rice et al., 2006, 2007; Tunik et al., 2005, 2008). I will use this perturbation paradigm because grasping has been found to be most sensitive to virtual lesions of the aIPS during this task (Rice et al., 2006, 2007; Tunik et al., 2005, 2008). I will use a factorial design with the independent variables of grasp condition (unimanual left, unimanual right, bimanual) and stimulation condition (left aIPS, right aIPS, control area cIPS left and right, and no stimulation). If bimanual grasping is similar to unimanual grasping in its network of brain regions, stimulating the aIPS should disrupt bimanual grasping. Specifically, stimulating the aIPS in one hemisphere may disrupt the trajectories of both hands or the trajectories of just the contralateral hand.

Given the similarities between unimanual grasping and bimanual grasping on variables such as grip force and transport (e.g., Freitas, Krishnan, & Jaric, 2007; Tresilian & Stelmach, 1997), I expect that stimulation of aIPS will disrupt both unimanual and bimanual grasping behaviour. Furthermore, the way in which grasping is disrupted will help us further confirm and understand the contributions of aIPS to bimanual grasping. If bimanual grasps are predominantly controlled by aIPS in the right hemisphere, then only stimulations of this area (but not stimulations of the left aIPS) should affect trajectories of both hands during bimanual grasps. In contrast, if stimulations of the left and the right aIPS have the same effect, this will argue against a right hemisphere dominance at the level of aIPS. Disrupted trajectories for both hands after both forms of stimulation will suggest that interhemispheric cross-talk occurs at the level of aIPS or earlier.
More pronounced disruption of the contralateral hand will suggest that cross-talk occurs after the aIPS.

To conclude, this research is significant to the field of perception and action because it will add breadth to our current knowledge about hand-object interactions. In addition, a better understanding of the interplay of the two hemispheres for bimanual actions will have medical significance for developing rehabilitation programs for patients who have brain damage that resulted in unimanual motor control deficits. Indeed, our findings will add to our comprehension of the various types of grasping in humans, specifically that of bimanual grasping to a single target. That is, we will be better able to understand how the two hemispheres interact for bimanual grasping tasks, and how this interaction may be affected by any hemispheric dominance for grasping.
References


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