NEUROBEHAVIOURAL REPRESENTATIONS OF OBSERVED ACTION VIEWPOINT

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A thesis submitted to

The University of Birmingham

for the degree of

DOCTOR OF PHILOSOPHY

School of Sport and Exercise Sciences

College of Life and Environmental Sciences

The University of Birmingham

April 2010

ABSTRACT

This thesis aimed to examine whether the viewpoint from which an action is observed could modulate the behavioural performance and neural activity of the observer. Four chapters of empirical data are presented. Chapter 2 presents motion capture data from a manual prehension task which examined the effects of manipulating observed reach height. Actions were observed from two allocentrically framed viewpoints. The data revealed no differences between the viewpoints, but did reveal effects of relative spatial direction congruency. Chapter 3 further examined this effect of direction congruency. Recording simple arm movements using motion capture, observed task and direction congruency were split by presenting movements of the experimenter from different viewpoints relative to the participant. The data revealed effects of direction congruency dependent on observed action viewpoint. Chapter 4 presents three experiments using response time measurements to further examine the effects of observed action viewpoint. The data was consistent with the notion that participants considered observed actions in terms of agency; if participants could potentially perform an observed action themselves (i.e. the action was egocentrically framed), they were faster to respond to it than if the observed action could only naturally be performed by another person (i.e. the action was allocentrically framed). Chapter 5 used functional Magnetic Resonance Imaging to further examine this agency effect. The data suggest that stronger representations of observed actions are present for egocentrically framed actions compared to allocentrically framed actions. Collectively, this thesis demonstrates that relative spatial direction kinematics are a key factor in action observation, and that the viewpoint from which an action is observed can indeed modulate participant behavioural responses and brain activity, as participants distinguish between egocentrically and allocentrically framed actions.

ACKNOWLEDGEMENTS

The completion of this thesis would not have been possible without the help of a number of people, and I would like to take this opportunity to express my thanks to them.

First, I would first like to thank my supervisor Martin. I will always be grateful to you for providing the opportunity to study for this PhD, and also for your support, encouragement and friendship throughout its completion. I hope that the future provides many opportunities for us to build upon the work we have started here. Special thanks must also go to my second supervisor Jennifer and ‘third supervisor’ Craig, for their efforts in shaping my development.

Secondly, I would like to thank the postgraduate students, project students, old housemates and friends who have assisted me during this PhD, whether they have helped with my work or provided respite from it. Particular thanks must go to Dan and Rich for setting such high standards to follow, and Ed for his fMRI tutorials. The efforts of the technical staff (especially Dave and Steve) have also been essential, and I thank them for their valued assistance.

Louise, thank you for the years of humour we have shared; may it continue for many more.

Finally, and most importantly, I would like to thank my parents Elaine and George, without whom none of this would have been possible. Thank you for the sacrifices you have made to allow me to further my education. Above all, thank you for your continued belief in my ability to succeed. I dedicate this thesis to you.

TABLE OF CONTENTS

Chapter 2: Observed Reach Trajectory Influences Executed Reach Kinematics in Prehension

Chapter 3: Facilitation and Interference Effects of Viewpoint on Concurrent Action and Observation

Chapter 4: Effects of Observed Viewpoint on Movement Priming

Chapter 5: Does Observing Actions from Different Viewpoints Lead to a Gradual or Categorical Shift in Brain Activity?

Chapter 6: General Discussion

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1:

GENERAL INTRODUCTION

1.1 Introduction

The aim of this thesis is to examine how the observation of actions performed by others can influence the execution of motor tasks, and furthermore, how the viewpoint from which an action is observed can lead to further modulation of the motor system. This introductory chapter will review current experimental and theoretical evidence relating to action observation, and explain why investigating the effect of the observer’s viewpoint is both a practical and logical extension of the existing literature. The introduction will first present direct evidence of neuronal co-activation for action observation and execution in studies taking single cell recordings from the brains of primates. This will be followed by evidence suggesting the presence of a homologous system for action representation in the human brain, reviewing data from studies using the methods of Transcranial Magnetic Stimulation (TMS) and functional Magnetic Resonance Imaging (fMRI). The importance of examining the effects of viewing actions from different viewpoints will then be addressed. Finally, an overview of the experiments which comprise the thesis will be provided, and the relative strengths and limitations of these different methodologies will be discussed.

1.1.1 Mirror Neurons in the Primate Brain

The field of action observation research has gained much momentum following the discovery and subsequent investigation of ‘mirror neurons’ in the primate brain (di Pellegrino, Fadiga, Fogassi, Gallese and Rizzolatti, 1992; Gallese, Fadiga, Fogassi and Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese and Fogassi, 1996; for a review see Rizzolatti et al., 2001). These neurons were first discovered as a by-product of a neurophysiological study examining the Premotor cortex of the macaque monkey (di Pellegrino et al, 1992). The original aim of the study was to examine the activity occurring in the Premotor cortex (area F5 of the primate brain), while a trained monkey performed grasping actions directed towards different geometric shapes. Previous studies had demonstrated that area F5 contained two specific types of neurons; motor neurons which discharged during the execution of specific goal-directed actions (such as prehension), and canonical neurons which discharged in response to visual stimuli requiring a particular type of grasp (such as a precision grip, or whole hand prehension; for a review see Fadiga et al., 2000). However, following initial testing, the experimenters discovered a number of area F5 neurons that had firing patterns which were modulated both when the monkey observed the experimenter perform a goal directed action (such as grasping a piece of food) and also when the monkey performed the same motor task themselves. Further investigation of these neurons revealed that approximately 10% of the 184 neurons tested displayed ‘mirror like’ function, firing both for the observation and execution of goal directed actions. These neurons were clearly distinguishable from canonical neurons as they did not fire in response to the observation of an object alone, but instead required an *interaction* between the object and an agent (i.e. human or monkey) acting to it. Following this initial discovery, Gallese et al. (1996) conducted a further investigation to provide a more detailed description of the properties of these neurons. Recordings from area

F5 of two monkeys (the first was studied bilaterally, while recordings were taken from only the left hemisphere of the second) revealed that approximately 17% (92/532) of the neurons examined had firing patterns that were modulated by both action observation and execution. The majority of these neurons responded to grasping actions; many showing selective modulations of their firing patterns for particular types of grasping actions such as precision grip, finger prehension or whole hand prehension. However, there were also several mirror neurons that responded to the observation of more than one type of action, such as neurons which responded to both the grasping and placing of objects. The mirror neurons only exhibited weak responses to observed actions performed using tools, or to the observation of intransitive movements such as pantomime actions (movements performed with the same kinematics as normal goal directed actions, but in the absence of an object). Further testing involving a small sub-section of mirror neurons revealed similar responses when the monkey performed an action both with and without illumination. These data revealed that this firing activity was truly due to a motor response caused by the primate *performing* an action, rather than being a consequence of the monkey *observing* the performance of their own actions.

Rizzolatti et al. (1996) described a similar detailed study of mirror neuron function, again reporting activity recorded from area F5 of the brains of two monkeys. In addition to procedural testing as described by Gallesse et al. (1996), a number of ‘highly congruent’ mirror neurons were also examined. For example, they describe a neuron which discharged during the observation of an experimenter rotating their hands in opposite directions (as though twisting an object in order to break it apart). The neuron fired during the observation or performance of twisting performed only in a certain direction (e.g. for anti-clockwise twisting movements, but not for clockwise twisting movements). This provided further evidence that the responses exhibited by mirror neurons are highly specific in nature.

Since these initial studies examining area F5 neurons in the primate Premotor cortex, subsequent investigations of the Inferior Parietal Lobule have also demonstrated the presence of mirror neurons (Gallese, Fadiga, Fogassi and Rizzolatti, 2002; Fogassi, Ferarri, Gesierich, Rozzi, Chersi and Rizzolatti, 2005). For example, Fogassi et al., (2005) demonstrated that mirror neurons in area PF discharged in response to the observation and execution of grasping actions, with some showing greater firing activity when the action was followed by bringing the object to the mouth, while others revealed greater activity for grasped objects to be placed in other locations (such as a container placed on the shoulder of the monkey). They suggested that the neurons were connected by intention, with one motor act leading to the facilitation of another.

As well as the mirror neurons revealed in areas F5 and PF, the primate Superior Temporal Sulcus also contains neurons with similar action encoding properties (Perrett et al., 1989). While these neurons do not share the motor responses of mirror neurons, they do have firing patterns which are modulated in response to the observation of biological goal-orientated actions, including hand-object interactions such as object manipulation, holding and tearing. Unlike mirror neurons, these cells are not selective in their responses to grasping actions, activating to the observation of the grasping of large and small objects alike; furthermore, their responses are described as purely visual, unlike mirror neurons which also fire for unseen actions (Umilta et al., 2001). Therefore, while these cells are not mirror neurons themselves, they are often considered to contribute to the primate mirror system (Miall, 2003), as both the Superior Temporal Sulcus and Premotor Cortex are connected to the Inferior Parietal Lobule (Rizzolatti, Fogassi and Gallese, 2001), and it is likely that they encode the visual information that the mirror neurons later receive.

In summary, these data demonstrate the existence of mirror neurons in the brains of primates. Mirror neurons have firing patterns which are modulated both when the monkey performs an action themself and when the monkey observes another agent perform a similar action. Mirror neurons are found in areas F5 and PF of the primate brain, and form part of a larger system of brain areas collectively termed the ‘mirror system’, which is likely to receive input from the Superior Temporal Sulcus (an area which contains cells with similar visual properties to those of mirror neurons).

1.1.2 The Human Mirror System

In their detailed study of the properties of mirror neurons in primates, Rizzolatti et al., (1996) suggested that a similar mirror system for action observation may exist in the brains of humans, and identified Broca’s area as a potential human homologue of primate area F5 (this area is often referred to as the Inferior Frontal Gyrus or Premotor areas 6 and 44 when presenting the human brain Premotor area: see Kilner, Neal, Weiskopf, Friston and Frith, 2009; Buccino et al., 2001). To date, numerous studies have provided evidence of the existence of a human mirror *system*, though the issue of whether mirror *neurons* are present within this system still remains contentious.

The first evidence of an analogous mirror system in the human brain was provided using Transcranial Magnetic Stimulation (TMS), when Fadiga et al. (1995) reported a modulation of corticospinal excitability associated with the observation of action. In two experimental action observation conditions, participants observed an experimenter grasping different 3D objects (including geometric shapes such as spheres and boxes, as well as commonly used objects), or tracing shapes in the air (letters of the Greek alphabet) with a prone hand. Baseline conditions consisted of the observation of the objects alone, or (in order to control for potential effects due to greater requirements of attention) the participant attempting to detect the dimming of a computerized LED. Motor Evoked Potentials (MEPs) were elicited via stimulation of the hand area of the Primary Motor cortex and recorded from muscles of the contralateral hand and forearm. Analysis revealed that MEPs collected during the action observation conditions were greater in magnitude than those collected during the baseline condition. Furthermore, this modulation of activity was specific only to muscles involved in the performance of the observed action; the observation of grasping led to an increase in excitability of the opponens pollicus (a muscle used to oppose the thumb and fingers) and first dorsal interosseus (a muscle used primarily to abduct the index finger), while the observation of shape tracing resulted only in modulation of MEPs recorded from the first dorsal interosseous. This pattern of modulation reflected the activity in the muscles when they were used to perform the observed actions (i.e. the opponens pollicus was used only in the performance of grasping actions, while the first dorsal interosseous was active during both grasping and shape tracing), demonstrating that the modulation revealed was specific to the muscles involved in the observed task, rather than showing a general increase in overall excitability. The authors proposed that this effect reflected changes in activity occurring in the Premotor cortex, and was measurable via stimulation of the Motor cortex due to the robust anatomical connectivity between these two areas.

Neuroimaging studies have also demonstrated evidence of Premotor and Parietal lobe activity during the observation of action, similar to the activity found in primates. For example, Buccino et al. (2001) had participants observe movements performed by different effectors: mouth actions (e.g. biting and chewing), hand actions (e.g. reaching and grasping), and foot actions (e.g. pushing down the brake pedal of a car). When participants observed these stimuli performed as *actions* (i.e. the participants saw goal directed acts performed to target objects), somatotopic activity was revealed in Premotor and Parietal areas of the brain in accordance to the classical motor homunculus (i.e. the observation of mouth actions activated areas located inferior to the observation of hand actions, which were in turn inferior to the areas activated by the observation of foot actions). Interestingly, when these stimuli were observed as *movements* (i.e. the participants saw pantomimed kinematics performed in the absence of an object), somatotopically organised activity was still present in the Premotor cortex. These data provided further evidence of the existence of a mirror system in the brains of humans, similar to the mirror system found in the brains of primates (i.e. that observation of action activates the same areas of the brain as those used for execution).

One key distinction between the mirror system demonstrated in the primate brain and the mirror system demonstrated in the human brain is that they differ in their responses to intransitive, non-goal directed movements. Classically, mirror neurons in primates have been demonstrated to activate only in response to specific, goal directed actions performed to objects (di Pellegrino et al., 1992; Gallesse et al., 1996; Rizzolatti et al., 1996), but not to the observation of intransitive or pantomimed movements. However, evidence from both TMS and fMRI studies in humans suggests that the human mirror system responds not only to goal directed, object orientated actions, but also to intransitive movements such the observation of shapes being traced in the air (Fadiga et al., 1995) or pantomimed actions (Buccino et al., 2001). Furthermore, there is comparable evidence that imagining of the execution of both goal directed and intransitive movements will lead to activity in the human mirror system, as demonstrated using TMS (Fadiga, Buccino, Craighero, Fogassi, Gallese and Parvesi, 1999). These additional properties suggest that the mirror system as demonstrated in humans may be different, if not more complex than the mirror system found in primates, allowing for a wider range of mirroring activities. Alternatively, it might be that future studies which examine the primate mirror neuron system in greater detail will reveal similar effects to those found in humans, especially when it is considered that a typical primate study will measure less than 100 neurons.

In support of the notion that the human mirror system may be more complex than the equivalent system found in primates, Blakemore and Frith (2005) proposed a human mirror system with at least three levels; a low level which would mirror movement kinematics, a higher level which would mirror goal directed actions (where mirror neurons themselves would be found), and a further theoretical level at which the intentions of others would be represented. This presents a further point for discussion; Blakemore and Frith (2005) suggest that in the human mirror system, mirror neurons themselves may only be present at the level of action mirroring. Furthermore, while the evidence discussed above suggests that mirror neurons exist within the brains of humans, it is important to note that it is only recently that direct evidence of this claim has been provided from single cell recordings (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). While single cell recordings in primates have directly demonstrated the existence of mirror neurons by detailing the properties of individual cells (di Pellegrino et al., 1992; Gallesse et al., 1996; Rizzolatti et al., 1996), the data from

TMS and fMRI in humans do not provide direct evidence that the same neurons are active during both action observation and execution; TMS studies take measurements from the Motor cortex (which is not classically considered to be part of the mirror system), presumably via a mechanism involving input from the Premotor cortex (see Fadiga et al., 2005), while fMRI studies measure changes in the haemodynamic response of the brain (which effectively provides a correlate of the activity of neurons within the area examined). The interpretation of data from traditional fMRI studies has been a contentious issue, as a recent review highlighted the proposition that mirror system activation revealed by traditional fMRI studies could actually be due to the activity of unrelated populations of neurons responding separately to either visual or motor stimuli, but not to both (Dinstein, 2008; Dinstein, Thomas, Behrmann and Heeger, 2008). The authors proposed that repetition suppression and adaptation paradigms would provide stronger evidence of the existence of mirror neurons in the human brain via cross modal adaptation (the attenuation of neural activity occurring for action execution trials immediately followed by action observation trials, and vice versa). They suggested that an attenuation of the activity recorded would suggest the same neurons were responding to both observed and executed action modalities (signalling the presence of mirror neurons), while a rebound in the response would suggest that the activity was due to separate populations responding to the different modalities.

Such cross-modal repetition suppression has since been demonstrated for goal directed actions (Kilner, Neal, Weiskopf, Friston and Frith, 2009). In this study, participants performed grasping actions made to a specially designed manipulandum, or observed the same type of actions being performed to the same apparatus. Analysis revealed cross-modal repetition suppression effects in the Inferior Frontal Gyrus, and also suggested a similar attenuation in the Anterior Intraparietal Sulcus (an area of the Parietal Lobe considered to be part of the mirror system which responds to the observation and execution of grasping actions). It is interesting to note that similar studies which have used intransitive, non-goal directed movements such as pantomimed actions have failed to demonstrate cross-modal repetition suppression (Dinstein, Hasson, Rubin and Heeger., 2007; Chong, Cunnington, Williams, Kanwisher and Mattingley., 2008; Lingnau, Gesierich and Caramazza., 2009). This data is consistent with the theory that while the human mirror *system* is activated by the observation and execution of intransitive movements, this may occur at a lower level of the system in which mirror *neurons* are not directly involved (Blakemore and Frith, 2005).

To summarise, there is data to suggest that a similar mirror system for action representation as found in the brains of primates is present in the brains of humans. Experimental evidence from studies using TMS and fMRI suggests that the human mirror system differs from the primate mirror system, as it displays mirrored activation not only for goal directed actions, but also for intransitive movements. Whether mirror neurons are actually present in the brains of humans is still a contentious issue. While the cross-modal repetition suppression revealed by Kilner et al. (2009) demonstrates strong evidence that mirror neurons are present in the brains of humans, there is still no direct evidence from single cell recording which demonstrates that the same neurons in the human brain have firing patterns which are modulated by both the execution and observation of action. However, this technicality does not negate the wealth of evidence which demonstrates that the neural representations of both executed and observed actions in the human brain are closely matched. These data show that even in the unlikely case that mirror *neurons* are not present in the human brain, there is an equivalent mirror *system* which acts in a similar (if not more advanced) manner, mirroring the movements, actions, and perhaps even the intentions of others.

1.2 Role of Viewpoint

Previous studies of the primate and human mirror system have demonstrated that the observation of action can modulate activity recorded from the observer. However, few studies have examined the effect of changing the viewpoint of the observer, or to much the same end, observing the same movement being performed in different orientations.

Some evidence from primate studies provides examples of situations where the viewpoint from which an action was observed modulated mirror neuron activity, though this issue was not specifically examined in a systematic manner. For instance, Gallese et al. (1996) detail the firing properties of a small sub-population of 32 mirror neurons, noting that 12 of these neurons had firing patterns which were modulated by the hand observed to perform an action, and the viewpoint from which actions were observed. When considered anatomically, five neurons showed greater activity for the right hand, and seven showed greater activity for the left hand. However, they also noted that in some cases these neurons displayed preferences for the ‘ipsilateral’ and ‘contralateral’ hand (nine preferring the ipsilateral hand, and three the contralateral hand), but do not explain exactly what they mean when using this terminology. It is assumed that the experimenter performed their actions when positioned directly opposite the primate so that, when considered in relation to the *right* hand of the monkey, the ‘ipsilateral’ hand would refer to the experimenter’s *left* hand. No mention of whether these actions were examined with the experimenter in different positions is provided, even though the relative position of the experimenter to the monkey would lead to a change in which hand should be considered to be ipsilateral or contralateral. It was also noted that of 47 neurons examined, 30 showed directional preference, with 83% of these neurons showing greater activity when the direction of observed movement occurred towards the hemisphere being recorded from, regardless of the position of the action in the monkey’s hemispace. This data suggests that the relative direction of the movement in relation to the observer may modulate action observation effects.

The data from Rizzolatti et al. (1996) also suggest that possible modulations dependent on observed action viewpoint could occur in the activity of mirror neurons, again presenting data which may be influenced by the issue of the relative spatial direction of the movement. As stated earlier, this study described that some neurons were responsive to the observation and performance of twisting actions performed in a certain direction (e.g. anticlockwise twisting movements), but it is important to note that the relative direction of this movement is open to interpretation, and depends on the viewpoint from which it is observed. For example, if the primate’s hand pointed away from their body (e.g. using the hand to twist a piece of food held by an experimenter positioned directly opposite), then supination of their forearm would lead to an *anticlockwise* movement. However, when considered in a situation where the primate’s hand pointed towards their own body (e.g. using the hand to twist a piece of food held between the teeth), the same supination action of the forearm would produce a *clockwise* movement. Unfortunately, as the latter situation was not examined in the experiment, it was not possible to determine whether the response of the neuron was primarily influenced by the motor properties of the neuron (i.e. the performance of forearm supination regardless of the relative direction in which this act occurred), or the visual properties of the neuron (i.e. the observation of anticlockwise movement, regardless of whether this was achieved via supination or pronation).

The notion that the viewpoint from which an action is observed can modulate brain activity has been examined in greater detail in human participants. Evidence from a study using TMS has demonstrated that manipulating the viewpoint from which an action is observed can lead to modulatory effects on mirror system activity (Maeda, Kleiner-Fisman and Pascual-Leone., 2002). Participants observed pre-recorded video clips of hands performing different movements (thumb abduction, index finger abduction, index finger moving vertically). These hands were presented in a viewpoint either congruent or incongruent with that of the observer. When participants observed movements performed by hands in a congruent viewpoint, MEP responses were greater than when they observed movements performed by a hand in an incongruent viewpoint. These data suggest that the observation of actions from a viewpoint similar to one's own leads to greater mirror system activity than observing actions from dissimilar vantage points.

Data from behavioural studies provide similar evidence, demonstrating that observing actions from a viewpoint congruent to one's own vantage point is preferable to observing actions seen to be performed by another. Vogt, Taylor and Hopkins (2003) had participants perform grasping action to an unseen bar, notifying the participants to its orientation prior to each trial. Participants were presented with a hand shown in a posture either congruent or incongruent to the grasping action to be performed, shown from a viewpoint either consistent with observing their own hand performing the action, or consistent with observing the hand of a person located directly opposite performing the action. The data revealed a preference in the congruently orientated stimuli for hand postures observed from the viewpoint consistent with the vantage point of the participant. These data suggest that observing actions from a viewpoint consistent with one's own vantage point can be advantageous to performance.

There is also data from fMRI which suggests that actions are represented by the mirror system in different ways depending on the location of the observer. Shmuelof and Zohary (2008) had participants observe grasping actions performed from either an egocentric viewpoint (the observed hand was congruent with the view the participant would see if performing the action themselves) or an allocentric viewpoint (congruent with the participant observing somebody directly opposite perform the action). The observed actions were performed with both left and right hands, and could be presented in either hemifield of the participant's view (to control for simple lateralisation effects).

When participants observed egocentric actions, the data revealed a preference for contralateral Parietal lobe activity (when observing the left hand, there was greater activity in the participant's right hemisphere), consistent with when participants perform actions themselves. However, when participants observed allocentric actions, there was a preference for ipsilateral Parietal lobe activity (when observing the left hand, there was greater activity in the participant's left hemisphere). The authors explained this effect in terms of imitation. When imitating an action performed by an actor positioned directly opposite, it would be most natural to match movements performed by their left hand with one's own right, which would in turn activate the participant's left hemisphere, leading to the preference for ipsilateral Parietal lobe activity.

Further data suggesting the viewpoint of an observer can modulate mirror system activity has been provided using Magnetoencephalography (Kilner, Marchant and Frith, 2006). Participants observed video sequences depicting an actor moving their hand up towards their ear (always performed so that the right hand would move towards the right ear and the left hand moved towards the left ear). Importantly, for each video the actor observed could be facing either towards or away from the participant. When the actor was facing the participant, Parietal lobe activity was modulated both according to the hemisphere of the participant being recorded from and the hand being observed to move, with activity increasing in the hemisphere contralateral to the observed hand and decreasing in the hemisphere ipsilateral to the observed hand. However, when the participant observed video clips depicting the actor facing away from them, no modulation of Parietal lobe activity was present; the authors attributed this to the decrease in the social relevance of the actor when their back was turned compared to when they faced the participant. These data provide further evidence that the viewpoint from which an action is observed can modulate mirror system activity, and suggest that higher level processes account for such effects.

Taken together, these data demonstrate that observing the same movements from different viewpoints can lead to modulations in the activity of the mirror system. However, the majority of these studies have examined the simple relationship between actions performed from a viewpoint congruent with the natural vantage point of the observer to actions performed from a viewpoint congruent with observing another person. To date, no studies have examined the effects of observing actions from different viewpoints consistent with observing other people, such as comparing the effects of observing an actor positioned directly opposite the observer with an actor positioned side on to the observer. This manipulation is important as it may reveal more complex relationships between the observer and the actor. For example, the data of Shmuelof and Zohary (2008) suggest that actions observed from an egocentric viewpoint are represented in an anatomically matched manner, while actions observed from an allocentric viewpoint (in which the actor appeared to be positioned opposite the observer) were represented in a mirror like fashion. From these data, it is not clear whether actions observed from a side on position would be represented in an anatomical or mirror like fashion, and it is therefore of interest to examine how these representations would change with the viewpoint from which an action is observed. If the main function of the mirror system is to encode the intentions of others (see Blakemore and Frith, 2005), then examining the viewpoint from which actions are observed would theoretically reveal large differences between actions observed from egocentric and allocentric viewpoints (i.e. differences between ‘self’ and ‘other’), and only small differences for actions observed from different egocentric viewpoints (i.e. all self) and different allocentric viewpoints (i.e. all other). Alternatively, if the mirror system is involved in lower level processes, the opposite effect may be revealed.

1.3 Empirical Data

This thesis aims to further investigate the role of the viewpoint from which an action is observed, using behavioural and brain imaging measurements. Effectively, the thesis will examine the processes that allow for modulation of performance in response to observed actions. In order to achieve this aim, behavioural experimental paradigms adapted from previous studies in the literature were implemented to examine the effects of manipulating the viewpoint of the observer in manual prehension (Chapter 2), simple arm movement tasks (Chapter 3) and simple finger movement tasks (Chapter 4). In the final empirical chapter, fMRI was used to measure brain activity during the observation of actions from different viewpoints (Chapter 5). By utilising a variety of complementary methods, it was hoped that a more comprehensive range of evidence would be provided to probe the effects of the observer's viewpoint during action observation.

1.3.1 Methods Used

While it was hoped that employing a multi-methodological approach would help to provide a more complete understanding of the role of viewpoint in action observation, it is important to consider that each technique used had a number of different advantages and limitations. Here the different techniques employed during the empirical chapters of the thesis are examined, and their relative merits and flaws discussed.

1.3.1.1 Motion Capture

Motion capture is a technique in which markers are attached to points of interest on the body, and their movements tracked in 3D space. This allows for the non-intrusive examination of complex movements with high levels of spatial and temporal accuracy; the 8 camera infrared motion capture and reflective marker system used to collect the data presented in this thesis allowed for movements to be recorded with millimetre accuracy at a frequency of 120 samples per second. For example, in Chapter 2 participant reach height was recorded using motion tracking. This was achieved by first calibrating the motion tracking system to record movements relative to the height of a table surface. The calibration procedure involved a static phase, in which a calibration frame was placed on the table-top, and a dynamic phase, in which a wand was moved in the volume of space where measurements were to be made. The calibration procedure allowed the software to determine the position of the cameras used. Following this calibration, the software was able to calculate the 3D position of any markers that were simultaneously viewed by at least two of the cameras. In order to record the movements of the participant, a reflective marker was placed on their wrist, and infrared light projected from the camera system fell onto the marker and was reflected back to the cameras. From this, the motion capture system was able to triangulate the marker position in 3D space (X, Y and Z coordinates). For each trial, the marker position was recorded over time (i.e. 120 frames a second) and stored for offline analysis. In this manner, participant reach height was calculated by taking the value of the Z coordinate at different points of the reaching action.

Problems specific to the system used in this thesis include the possible loss of data through marker occlusion, an issue occurring when reflective markers are blocked from the view of the cameras (i.e. less than two cameras are able to see the marker simultaneously). Similar problems occur if the reflective markers move outside the field of view of the cameras. This can be compounded by the system's inability to present marker movements in real time during data collection, making it difficult to detect when occlusion has occurred on a trial-by-trial basis. However, these minor issues can easily be avoided by using careful camera positioning, and as the movements recorded during data collection for this thesis were generally small in nature very few trials were lost from analyses.

1.3.1.2 Computer Based Reaction Time Measurements

This technique allows measurement of response time (effectively a measure of the efficiency with which responses are encoded) and response accuracy, with increasing response times and errors indicating that a task places greater demands on a participant. The DMDX software used to collect the data presented in this thesis allowed for the recording of responses with high temporal accuracy (See Forster and Forster, 2003). This technique also provided the opportunity to present movements recorded from viewpoints highly congruent with the participant’s own vantage point, an advantage of particular relevance to studies of action observation.

A limitation of this approach is that the performance measurements available are limited to response time and accuracy, with no kinematic measures of participant performance being available. This makes the technique most suited to simple tasks requiring straightforward responses, and experimental paradigms should be adapted to take note of this issue.

1.3.1.3 Functional Magnetic Resonance Imaging

The primary limitation of the techniques described previously is that any effects thought to be occurring at a neural level can only be inferred. In contrast, fMRI measures the haemodynamic response of the brain, providing an effective correlate of neural activity. The technique allows the recording of brain activity in 3D space and has excellent spatial resolution; in the case of this thesis activation was measured using voxels with dimensions of 3 x 3 x 3mm. This allows the mapping of entire brain networks involved in the task being investigated. Similar to the computer based reaction time measurement methodology described above, an additional advantage of this technique is that the stimuli used in fMRI studies can also be presented from a viewpoint congruent with the natural vantage point of the observer.

It should be noted that the technique also has a number of shortcomings, perhaps the greatest of which is its susceptibility to artefacts caused by large movements. This leads to limitations on the tasks which can be performed in the scanner, meaning that only relatively small movements can be undertaken. fMRI also has relatively poor temporal resolution, primarily due to the signal that it measures; fMRI does not measure neuronal spiking itself, but rather the Blood-Oxygen-Level-Dependent (BOLD) signal associated with changes in levels of oxyhaemoglobin and deoxyhaemoglobin. Furthermore, while this signal correlates well with neuronal firing (Logothetis, Pauls, Augath, Tornsten and Oeltermann, 2001), a change in the BOLD signal represents a change in the input to a neural area, without giving any indication as to whether the underlying neuronal activity causing this change is excitatory or inhibitory in nature. The majority of these limitations can be overcome with careful experimental planning; ensuring that any required movements are small in nature, that the time allowed for each experimental condition is long enough to overcome the temporal delay in data collection, and providing enough rest time between conditions to allow the BOLD signal to return to its resting state are all factors which can help to optimise experimental conditions for fMRI data collection.

1.3.2 Empirical Chapters

The first experimental chapter (Chapter 2) used motion capture to examine whether having an experimenter positioned directly opposite the participant would lead to differential action observation effects than when the same experimenter was observed performing the same action positioned side on to the participant. A number of further issues were examined, such as whether the timing of the action observation intervention would lead to different modulations of participant performance. Chapter 3 also used motion capture to examine whether effects of spatial congruency would modulate action observation. By manipulating the position of the experimenter, both the (relative spatial) direction congruency and task congruency of observed movements were manipulated (relevant to the movement performed by the experimenter), in order to determine their respective effects on participant performance.

Chapter 4 aimed to further examine spatial congruency effects between the motor system of the participant and the observed action. This time, response time and accuracy measurements to a simple finger movement task were taken to determine whether increasing or decreasing the congruency between the participant’s own viewpoint and the spatial congruency of movements would have significant modulatory effects on participant performance.

The final empirical chapter (Chapter 5) used fMRI to examine whether there is an underlying difference in the representation of actions observed from different viewpoints. Using an approach similar to the experiments seen in Chapter 4, observed movement viewpoint was manipulated in order to examine its potential effects on brain activity.

These experimental paradigms were used to examine the main hypothesis of this thesis; that the viewpoint from which an action is observed should reveal modulations in both behavioural performance and brain function.

CHAPTER 2:

OBSERVED REACH TRAJECTORY INFLUENCES EXECUTED REACH KINEMATICS IN PREHENSION

2.1 Abstract

Previous literature has demonstrated that the observation of action can modulate motor performance. In the present study, observed reaching actions were manipulated in order to examine whether observed movement kinematics can drive differences in performance. Motion capture was used to record the prehension movements of eight participants. Participants observed an experimenter grasp a target object using either a normal or exaggeratedly high reaching action (as though reaching over an obstacle). When participants observed the experimenter perform actions with a high reach trajectory, their own movements took on aspects of the observed action, showing greater wrist height throughout their reaching trajectory. This occurred regardless of whether the participant's actions were performed sequentially or concurrently with those of the experimenter. The data are discussed in terms of previous findings, which suggest that kinematic aspects of movements or the intentions of the actor are imitated by the observer.

2.2 Introduction

While there is a large volume of research demonstrating that the neural processes of perception and action are distinct (Milner & Goodale, 1992;1995), there is also evidence suggesting these processes are coupled. This is demonstrated by a reciprocal priming relationship whereby the presentation of a visual or motor stimulus[1] can prime subsequent action (Craighero, Fadiga, Umilta, & Rizzolatti, 1996; Edwards, Humphreys, & Castiello, 2003) and furthermore, the preparation of an action can also prime perception (Symes, Tucker, Ellis, Vainio, & Ottoboni, 2008).

Data from neuroscience can explain these priming effects. Several single cell recording studies conducted with nonhuman primates provide evidence of ‘mirror neurons’, the firing activity of which are modulated both when a monkey performs an action, and also when they observe another agent perform a similar action (di Pellegrino et al, 1992; Gallese et al, 1996; Rizzolatti et al., 1996; Gallese et al, 2002; Fogassi et al., 2005; for a review see Rizzolatti & Craighero, 2004). Subsequent neuroimaging studies have provided evidence of a similar action representation or ‘mirror system’ in humans, consisting of the Premotor and Posterior Parietal cortices, (for examples, see Rizzolatti et al., 1996; Buccino et al., 2001; Iacoboni, Woods, Brass, Bekkering, Mazziotta & Rizzolatti, 1999) as well as some proposed contribution from the Superior Temporal Sulcus (Blakemore and Frith, 2005). These data both provide further evidence of a coupling between perception and action, and also demonstrate that the observation of another agent’s action can activate the motor system of the observer.

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[1] From here on ‘motor stimuli’ are defined as moving or static images of the hand.

Several human behavioural studies have demonstrated that observing movements performed by another agent can modulate motor performance, positing that the observation of action activates the same motor system used in action execution through a homologous mirror system; this has been demonstrated using simple intransitive movements (Kilner, Paulignan and Blakemore, 2003; Kilner, Hamilton and Blakemore, 2007; Stanley, Gowen and Miall, 2008; Gowen, Stanley and Miall 2008) as well as more complex goal orientated actions such as manual prehension (Castiello, Lusher, Mari, Edwards, & Humphreys, 2002; Castiello, 2003; Edwards, Humphreys and Castiello, 2003; Dijkerman and Smit, 2007; Griffiths and Tipper, 2009). For example, Edwards et al. (2003) used motion tracking to record the actions of participants following the observation of either a congruent or incongruent action. Each trial began with the participant observing a priming action, which consisted of the experimenter reaching to and grasping an object. After a brief period in which their vision was occluded, the participant was required to perform a grasping action to an object in the same location as observed in the priming event. However, the target object they grasped would either be the same size as the object observed in the priming event (congruent priming) or of a different size (incongruent priming). The data showed that prime congruency affected motor planning; the observation of congruent priming actions led to earlier occurrences of peak reach velocity and peak grasp aperture compared to the observation of incongruent priming actions. In a further condition in which participants observed either a congruent or incongruent object alone (without action), only effects on time to peak grasp aperture were present. This suggests that while the observation of a congruent *target object* alone was sufficient to provide priming for grasp preparation, observation of a congruent *action* may lead to further movement facilitation (i.e. a significantly earlier time to peak velocity). These data demonstrate that action observation can attune the observer’s motor system to the subsequent performance of a congruent action, and that while observing a target object alone can have some priming effects on grasping performance, observing the target object accompanied by a grasping action may lead to additional priming effects.

The presence of distractor objects during the observation of a grasping action has also been demonstrated to influence performance of subsequently executed actions in which no distractor is present. Castiello (2003) conducted a study in which participants would observe the actions of either a human or robot model performing a manual prehension task. Previous studies had shown that the presence of a distractor object can modulate grasping performance, as the representation of the distractor interferes with the action programmed to the target object (see Castiello, 1999). In this study, it was hypothesised that observing a model perform an action in the presence of a distractor would lead to priming effects on subsequent performance, even if the distractor object was removed prior to participants performing their actions. Participants observed a priming event in which the model grasped a sphere, which was presented either alone or in the presence of a distractor object of an identical or smaller size relative to the target. After a brief period in which the participant’s vision was occluded, they were then required to grasp the target sphere, always doing so in the absence of any distractor objects. The data revealed that the amplitude of the participant’s maximal grip aperture was affected by the observation of a human model, being smaller when they had observed the model grasp the target object in the presence of a small distractor compared to both other conditions. This effect was absent when a robotic model was used to demonstrate the action (and also when human models imitated the movements of the robot), indicating that the effects were not due to the presence or absence of distractor objects, but rather due to observing the normal kinematics of a human model with the intent to grasp the target object (see also Castiello et al., 2002).

While the studies of Edwards et al. (2003) and Castiello (2003) demonstrated effects of sequential action observation on motor planning, data using concurrent action observation have revealed effects on late execution kinematics. Dijkerman and Smit (2007) manipulated object size congruency in a concurrent action execution task. Participants grasped a cube of a fixed size while observing the experimenter perform grasping or pointing actions. The experimenter would either perform a pantomimed action to empty space (in the baseline condition), or act towards a congruently sized cube (identical to the participant’s cube), a smaller cube, or a larger cube. Observing the experimenter concurrently grasping a larger object led to interference in the participant’s own movement, as their grip aperture increased significantly compared to when they observed the pantomime grasping and congruent grasping conditions. This modulation of grip aperture was not present when the participant observed the experimenter perform pointing actions, suggesting that specific kinematic aspects of the observed action led to the interference effect.

While these studies focussed on the grasp component of the prehensile action, a recent series of experiments by Griffiths and Tipper (2009) examined the effects of action observation on the reach component. The experiments involved two participants alternately grasping target objects, allowing the effects of observing another person’s reaching actions to be examined on the subsequent trial. In some conditions, participants were required to reach over an obstacle placed between their hand and the target object. Experiments in which the participants sat opposite each other, alternately grasping the same target object revealed that observing their counterpart perform a reaching action while reaching over an obstacle did not prime the movement paths of participants. However, effects were revealed in later experiments which decreased the distance between participants. These experiments found an effect of action observation when participants observed an action which avoided an obstacle which was placed along the reach path for their own actions; when a participant observed a reaching action performed over an obstacle, their subsequent reaching actions simulated the action they had observed, showing higher reach trajectories compared to conditions in which they had previously observed a reaching action performed in the absence of an obstacle. This effect persisted even when the participants sat adjacent to one another, suggesting that it was not reliant on the obstacle being placed in the participant’s own movement path, but rather that the avoided obstacle needed to be presented within their own peripersonal space in order to affect their movement. This study was the first to demonstrate action simulation effects for the reach trajectory of a prehensile action.

These studies highlight a number of interesting avenues for research. Primarily, the nature of the observed action or movement is a key factor which requires further examination. The previous studies reviewed above have manipulated goal directed aspects of observed actions, examining the effects of the observed goal on the observer’s own executed kinematics. This is likely due to the precedent set by the original studies in primates, which have shown that the activity of mirror neurons was modulated by an interaction between the observed movement and objects, rather than observed kinematics alone (di Pellegrino, 1992; Gallese et al., 1996, Rizzolatti et al., 1996). For example, the modulation of grip aperture demonstrated by Dijkerman and Smit (2007) was due to the observed grasp aperture rather than the observed target object, as illustrated by the absence of effects in the pointing condition. Therefore, the modulation of performance was due to observing the goal of the action; grasping the target object. Similarly, Griffiths and Tipper (2009) elicited effects using the goal directed action of avoiding an obstacle by placing it in the observed reach path. The experiment presented here examined whether the observation of non-goal directed movement kinematics could modulate action execution. Our hypothesis was that the modulation effects would not be goal directed, but rather based on observation of movement kinematics (similar to the effects shown for intransitive movements examined in studies of motor contagion; see Blakemore & Frith, 2005 for a review). That is, compared to the observation of normal (congruent) reaching actions, observation of reaching actions that follow an exaggeratedly high (incongruent) movement trajectory should modulate the participant's performance, and their actions should take on aspects of the observed movement such as an increased reach height trajectory.

Further modifications to the experimental design were made to test two other avenues raised by the literature review. Firstly, while Edwards et al's. (2003) study of sequential action observation demonstrated effects on motor planning, Dijkerman and Smit (2007) showed that concurrent action observation led to effects on motor execution kinematics. This suggests that the observation of action using these distinct timing modalities may lead to different effects, but to date no studies have directly compared them. The investigation reported here examined both sequential and concurrent action observation, providing a single dataset with which to compare the effects of these timing modalities. It was hypothesised that sequential action observation would lead to a change in participant's motor planning, leading to modulatory effects on their reaching actions spanning the entire duration of the movement they performed. Alternatively, it was theorised that concurrent action observation may only lead to effects on later phases of the participant's action, as visual information from the observed movement would not be available during the early phases of the participant's action. In order to examine this, the participant's reach height was examined at multiple phases of their reaching movement. Secondly, while several studies have demonstrated that action observation can affect performance, there have been few systematic investigations of the effects of different interpersonal viewpoint. The majority of studies have presented the experimenter in a fixed position (Castiello et al., 2002; Castiello, 2003, Edwards et al., 2003; Dijkerman & Smit, 2007). The series of experiments conducted by Griffiths and Tipper (2009) examined action observation from a number of viewpoints, but did not directly compare the effects of observing actions from different viewpoints in the same set of experimental data. While some studies have compared egocentric and allocentric viewpoints (Gianelli, Dalla Volta, Barbieri, & Gentilucci, 2008), no literature has systematically examined whether there is a distinction between observed actions performed at different (allocentric) locations. The study presented here examined the effects of manipulating the position of the experimenter, moving them between opposite and side on positions.

2.3 Materials and Methods

2.3.1 Participants

Eight participants (six female) aged 23-33 took part in the study. All were right handed with normal or corrected to normal vision, and were naïve to the purpose of the study. Procedures were approved by the School of Sport and Exercise Sciences, University of Birmingham Ethics Committee. All participants gave written informed consent prior to their involvement in the study.

2.3.2 Experimental Equipment

Figure 2-1 illustrates the experimental set up. Participants sat at a table covered with a black cloth, and observed actions performed live by a 23 year old male experimenter. A circular (25mm diameter) reference marker was placed 50mm from the table edge in front of the participant. The centre of this reference marker was 300mm from the centre of the target object; a hollow plastic cylinder (white in colour, height 54mm, diameter 54mm, weight 19g). A similar arrangement was provided for the experimenter, with reference markers both directly opposite and perpendicular to the participant, equidistant from an identical target object. The distance between the participant and experimenter's objects (distance between observed action target and executed action target) was 450mm.

All data was recorded using 14mm diameter reflective markers placed on the wrist of the participant and experimenter, and on top of each target object. Movements of these markers were recorded at 120Hz using an eight camera infra-red Vicon system (Vicon MX) calibrated with millimetre accuracy.

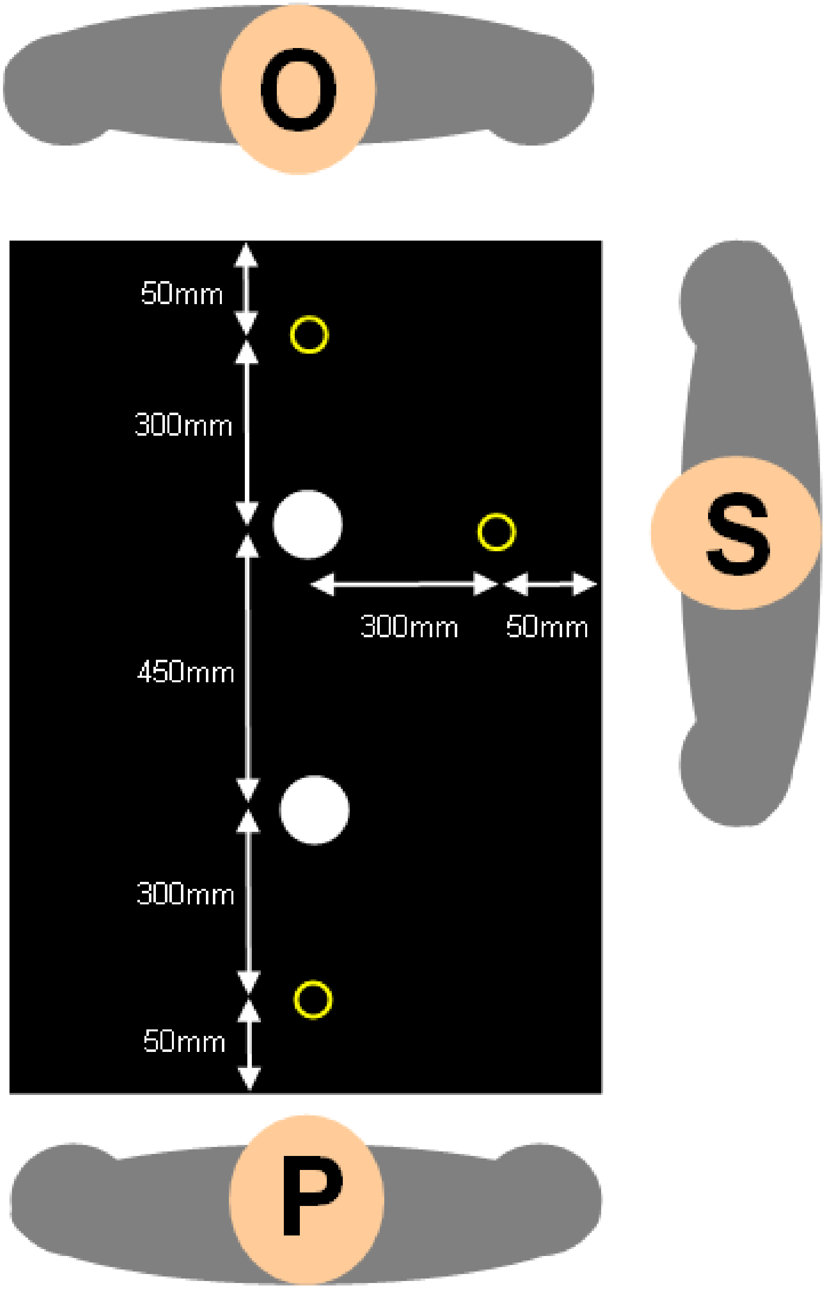

Figure 2-1: Illustration of the experimental set up. The participant (P) sat in a fixed position, while the experimenter sat in either an Opposite (O) or Side on (S) position. Small open circles represent the starting reference markers, while large filled circles represent the target object.

2.3.3 Design and Procedure

Independent variables were tested using a pseudo-random block design. Each block of the experiment consisted of 20 trials in which the experimenter's reaching actions were presented in a random order. Trials began with the participant and experimenter each holding a circular reference marker. Throughout the experiment, participants were required to perform normal reaching and grasping actions. However, in each trial they would observe either a congruent (normal) reaching action, in which the experimenter reached directly to the target object in a natural manner, or an incongruent (high) reaching action, in which the experimenter reached towards the target object using an exaggeratedly high movement trajectory (as though reaching over an obstacle). Therefore, as the participants were always instructed to perform normal reaching and grasping actions, only characteristics of the *observed* movements were manipulated as independent variables.

Timing was fixed within separate trial blocks. In sequential blocks, participants first observed the movement of the experimenter, then looked at their own target object and initiated their own action only once the experimenter's hand had returned to the starting reference marker. In concurrent blocks, the participant performed their actions in unison with the experimenter, attempting to initiate their movement and grasp their object at the same time as the experimenter (participants were instructed to observe the experimenter's action and attend to their own target object using their peripheral vision). Experimenter position was also fixed within blocks, with the experimenter sitting either directly opposite or to the right side of the participant throughout each block. Prior to each block, participants performed practice trials until they were proficient in performing the required task. The experiment consisted of four blocks which were counterbalanced across participants. Each participant completed 80 trials in total.

2.3.4 Analysis

For the analysis of reach height trajectory a 3x2x2x2 repeated measures ANOVA was employed with the independent variables of temporal phase (trials were temporally normalised, then the height of the participant's wrist was examined at the frames closest to the 25%, 50% or 75% phases of the reaching action), observed reach congruency (congruent 'normal' reach or incongruent 'high' reach), timing (sequential or concurrent), and experimenter position (opposite or side on). Participant reach height was recorded using a reflective marker placed on the wrist, and was measured relative to the table surface.

2.4 Results

2.4.1 Data Reduction

A number of trials were not included in the analyses; 30 trials were removed due to prolonged marker occlusion and problems in the reconstruction process preventing dependent variable analysis. A further 14 trials were removed as outliers (values lying more than 3 standard deviations from the mean). Therefore, 93% of all trials collected were analysed.

2.4.2 Data Analysis

Figure 2-2 illustrates the data for participant reach height trajectory. For the analysis of reach height trajectory, Mauchly's test indicated that the assumption of spheriphicity had been violated, and was therefore corrected using Greenhouse-Geisser estimates of sphericity. The results revealed a significant main effect for the temporal phase of the reaching action (F[2,14] = 7.19, $p < 0.05$). This effect showed that participant reach height trajectory increased at the midpoint of movement, then reduced toward the end of the movement (Mean: 25% phase = 95mm, 50% phase = 99mm, 75% phase = 84mm, SEM: 7.19mm vs 5.99mm vs 4.82mm). The analysis also revealed a reliable main effect of reach congruency, (F[1,7] = 9.22, $p < 0.05$). This showed that participant reaching actions were relatively low when they observed congruent ‘normal’ reaching actions, and were comparatively higher when they observed incongruent ‘high’ reaching actions (Mean: congruent ‘normal’ reach = 91mm, incongruent ‘high’ reach = 94mm, SEM 5.42mm vs 5.87mm). There were no significant main effects for timing, (F[1,7] = 2.35, $p = 0.17$) or position (F[1,7] = 3.55, $p = 0.10$), and no interactions of statistical significance (e.g. temporal phase by reach congruency by timing: F[2,14] = 0.41, $p = 0.67$).

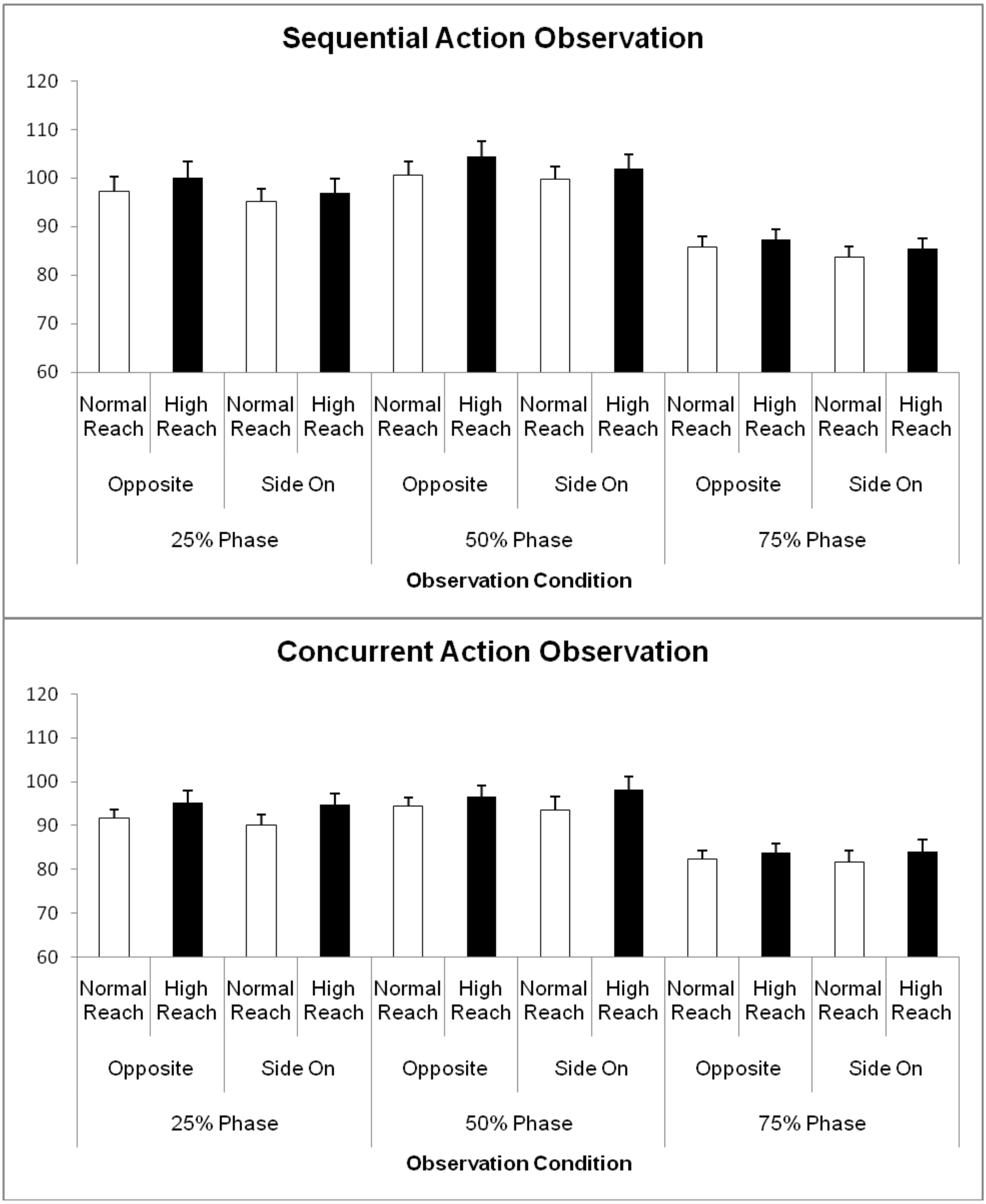

Figure 2-2: Data for participant reach height. Upper and lower panels present data for sequential and concurrent action observation respectively. Error bars show the average within participant standard error of the mean.

2.5 Discussion

As hypothesised, the comparison between the observation of congruent ‘normal’ reaching actions and incongruent ‘high’ reaching actions revealed a modulation of the participant movement performance. In comparison to the observation of congruent ‘normal’ reaching actions, participants performed actions which were higher in trajectory (greater maximum wrist height) when they observed incongruent ‘high’ reaching actions. This was consistent with previous data examining the observation of congruent and incongruent actions (Castiello et al., 2002; Castiello, 2003; Edwards et al., 2003; Dijkerman & Smit, 2007; Griffiths and Tipper, 2009). As participants were instructed to perform normal reaching actions throughout the experiment, our data suggest that specific kinematic aspects of the observed movement were automatically imitated by the observer.

While the study presented here demonstrates effects similar to those found by Griffiths and Tipper (2009), a disparity between these two datasets provides an interesting point for discussion. Griffiths and Tipper (2009) found effects on reach trajectory which were limited only to conditions in which the obstacle being avoided during the observed reaching action was presented within the peripersonal space of the observer. The participant did not have to avoid the obstacle themselves, nor did it have to be placed in the path they would later use when reaching to their target object, but they were affected by observed actions which avoided the obstacle when it was presented within their reaching space. In contrast, the actions performed by the experimenter in the study presented here occurred well outside of the extent of participant action space. When considered from a neurophysiological perspective, it is conceivable that this difference could be due to differential firing of mirror neurons. While early single cell recording studies in the primate brain suggested that the distance from which an action was observed had no effect on the firing properties of mirror neurons (Gallese et al., 1996), a recent study has demonstrated differences in firing activity for actions observed from different relative distances. Caggiano, Fogassi, Rizzolatti, Thier and Casile (2009) recorded the activity of 105 mirror neurons in area F5. Of these neurons, 28 demonstrated stronger firing activity when actions were presented to the monkey in peripersonal space, and 27 showed a preference for encoding actions presented in extrapersonal space, with the remaining 50 demonstrating no differences in their firing rate for the presentation of actions at different distances. Although the number of neurons examined which demonstrated preferences for peripersonal and extrapersonal space was comparable, this does not rule out the possibility that when considered across the whole brain, a majority of mirror neurons may show preferable firing activity for the observation of actions in extrapersonal or peripersonal space, and future research may enlighten this issue.

An alternative explanation for the differences occurring between the study presented here and the study of Griffiths and Tipper (2009) would be the differences in the rationality of the observed actions across the two experiments. While Griffiths and Tipper (2009) presented participants with an explicit reason to employ a higher reach trajectory (to achieve the goal of avoiding an obstacle), the study presented here offered no such explicit reason for the experimenter to perform actions with a high reach trajectory. Several behavioural and brain imaging studies demonstrate a distinction between rational and irrational movements (Gergely, Nadasdym Csibra and Biro, 1995; Gergely et al., 2002, Brass et al., 2007). Work with preverbal infants has shown an ability to evaluate the rationality of an agent's goal-directed action (Gergely et al., 1995), and has also revealed a preference for imitation of irrational actions when it is explicitly clear that a more rational alternative has been avoided intentionally (Gergely et al 2002). In the latter study, the authors propose the spurning of a rational action may infer that the alternative method employed may be in some way advantageous in achieving the intended goal. Following this, Brass et al. (2007) demonstrated differential activation of the Superior Temporal Sulcus when adult participants observed the same action in different contexts affecting its plausibility (such as using the knee to push a button when the hands were occupied compared to observing the same action when the hands were free). These differences in processing may explain why the effects reported here remained present even outside of peripersonal space, especially as the human Superior Temporal Sulcus is frequently associated with the human mirror system (see Miall, 2003; Blakemore and Frith 2005).

Modulation of the discharge of mirror neurons in primates has been demonstrated to occur in response to specific goal directed actions, rather than to intransitive movements (Gallese et al., 1996, Rizzolatti et al., 1996). However, action observation studies with humans have demonstrated that the observation of simple movement kinematics with no explicit goal can modulate performance (Kilner et al 2003, Kilner et al 2007, Gowen et al 2008, Stanley et al 2008), a phenomenon known as motor contagion. As mentioned in Chapter 1, this led Blakemore and Frith (2005) to propose a mirror system for action observation composed of at least three levels; a low level where mirroring effects from observing simple biological movements occur (the level at which motor contagion effects would arise), a higher level at which specific goal directed actions are mirrored (the level involving the eponymous mirror neurons), and a further theoretical level at which the intentions of others are mirrored. Therefore, some of the differences between our findings and those of Griffiths and Tipper (2009) could arise from different aspects of the mirror system being activated. In the study presented here it is not readily apparent whether the action observation effects occurred due to a modulatory effect occurring at a high level of this proposed system, driven by the participants attempting to imitate the *motor intention* of the experimenter (in a similar manner to the effects described by Castiello, 2003, and in accordance with Gergely et al., 1995;2002) or at a lower level being driven by the participants imitating the *motor kinematics* of the experimenter. However, both these possible explanations propose that the effects observed occurred on a different level to those of Tipper and Griffiths (2009), as their goal-directed approach of having the observed model avoid an obstacle would theoretically activate the intermediate, goal directed aspect of this system. Regardless of the level at which the modulation occurs, the automatic imitation effects from observing the experimenter's reaching actions revealed during the experiment presented here are consistent with previous literature (Castiello et al., 2002; Castiello, 2003; Edwards et al., 2003; Dijkerman and Smit 2007, Griffiths and Tipper, 2009).

While our study may present movement based, kinematically driven effects rather than action based, goal directed effects, the data does not necessarily challenge the goal directed theory of imitation suggested by Bekkering, Wohlschlager and Gattis (2000). The goal directed theory suggests observed actions are broken down then recomposed by the observer, who will attend to key goals (such as the target object) but neglect aspects of lesser importance (such as the specific movement kinematics used to achieve those goals) when demands are placed on cognitive resources. In the study presented here, the goal (grasping the same target object) remained constant, allowing for more cognitive resources to be directed to the observed movement kinematics. To truly test this hypothesis, future studies could use the findings presented here while manipulating cognitive load to further examine effects on action priming.

The data presented illustrate an important point to consider in relation to the action observation literature previously discussed, highlighting the issue that effects of action observation are generally small in magnitude. A large difference between the experimenter's reaching trajectories (recording of experimenter kinematics throughout the study revealed a difference in experimenter wrist height between congruent 'normal' reaching actions and incongruent 'high' reaching actions of approximately 70mm) led to a small, but significant modulation of participant's reach height (a mean difference of approximately 3mm). While these modulatory findings were small in size, they are similar to the magnitude of the differences seen in previous studies examining grasp priming (Castiello et al., 2002; Castiello, 2003; Edwards et al., 2003; Dijkerman and Smit, 2007) and therefore it could be proposed that this is due to the experimental task; manual prehension is perhaps one of the most robust and over-learned skills available to examine, and therefore may be resistant to experimental manipulation. However, studies of motor contagion have shown similar modest effects when participants performed experimental tasks they were likely to be far less familiar with (see Kilner, Paulignan, & Blakemore, 2003; Kilner, Hamilton & Blakemore, 2007). Together these data suggest that the goal-directed model proposed by Bekkering et al. (2000) requires further testing using motion tracking, as this provides an approach more sensitive to the subtle and often minute changes demonstrated in the action observation literature.

In terms of the other independent variables examined, the action observation effects presented here occurred regardless of the different timing modalities employed. It had been assumed that viewing an entire action before moving would allow for modification of motor planning (Edwards et al., 2003), while observing ongoing action would only allow for modification of kinematics during execution (Dijkerman & Smit 2007). If this had been the case, it would have been expected that the data would show a significant difference for the timing modality employed during the early phase of the movement, as the motor planning effects would modulate sequential action execution from the outset of the participant’s movement, while concurrent action execution would only modulate participant performance once visual feedback of the reaching action occurred (presumably during the later phases of the action). In the study presented here, the reach height effects persisted across all timing conditions regardless of the different movement phases examined, and there was no significant interaction between the factors of temporal phase and observed reach type. A post-hoc analysis examining the timing of the initial phase (25% temporal phase) of the participants’ reaching actions provides an explanation for this finding. The only reliable effect revealed by this analysis was a significant main effect of participant reach ($F[1,7] = 28.15$, $p < 0.001$), showing that participant movements were fractionally slower when they observed reaching actions performed with an incongruent ‘high’ reaching action compared to a congruent ‘normal’ reaching action (Mean: 283ms vs 287ms, SE: 20.43 vs 20.68). Importantly, as no significant effects of timing were apparent ($F[1,7] = 0.05$, $p = 0.84$), the data revealed that the average time at which the 25% phase of the reach component occurred was 285ms into the reaching movement. As a number of studies estimate the delay in using visual feedback to modulate ongoing action execution is in the order of 100-300ms (e.g. Savelsbergh, Bootsma and Whiting, 1991; Miall, Weir and Stein, 1985; Desmurget and Grafton, 2000; Saunders and Knill, 2003; Saunders and Knill 2005), it is therefore possible that participant performance could have already been modulated by visual feedback at this temporal phase in the concurrent action observation conditions. While a detailed analysis of the initial 100ms of the participants' reaching actions could examine the differences between sequential and concurrent action observation, limitations due to the sampling frequency of the motion capture system used in this study prevent such an investigation from being conducted using this data set in a reliable manner. It is therefore left to future studies to further examine whether differences between sequential and concurrent action observation can be reliably observed.

The analysis conducted also revealed that the effects of action observation demonstrated during this study occurred regardless of the position of the experimenter relative to the participant. Previous studies comparing actions observed from an egocentric frame of reference to an allocentric viewpoint (similar to our 'opposite' position) have shown preferences for a compatible egocentric viewpoint (Gianelli et al., 2008; Vogt et al., 2003). The authors suggest the improved performance was due to the greater congruency between the observed egocentric viewpoint and the observer's own natural viewpoint. As the study presented here effectively compared the observation of two incongruent positions (or perhaps more accurately an incongruent and neutral position when considering the relative spatial direction of the observed movements), the data presented are consistent with this proposal. Griffiths and Tipper (2009) conducted a series of experiments across which the position of the experimenter differed, but reported no differences dependent on the experimenter's location – only the position of the target obstacle the experimenter was required to avoid had any effect on the participant. While differences in brain activity when observing grasping actions from an egocentric or allocentric viewpoint have recently been demonstrated (Shmuelof & Zohary, 2008), it remains to be seen whether there is such a distinction between the observation of actions observed from different allocentric positions. These data may suggest that observed stimuli are interpreted in terms of whether they are egocentrically framed or allocentrically framed, but that there are no distinctions for different viewpoints within these overall perceptual frameworks.

In conclusion, the study presented here replicates and extends the findings of Griffiths and Tipper (2009). While they used an implicit, goal directed approach to manipulate the observed reach trajectory, the study presented here employed an explicit, movement based approach. The explicit nature of the observed task in this study could be responsible for the effects extending to a range outside of the observer's peripersonal space, and different aspects of the mirror system may well be activated by these two similar yet distinct approaches to modulating observed reach trajectories. In summary, the observation of the experimenter's action led to a small yet significant modulation of participants' reaching performance. These effects are attributed to activity occurring at the level of the mirror system which deals with either movement kinematics or intentions, as opposed to the intermediate level at which action goals are considered, though further experimentation is required to truly discern at which level these mirroring effects occur.

CHAPTER 3:

FACILITATION AND INTERFERENCE EFFECTS OF VIEWPOINT ON CONCURRENT ACTION AND OBSERVATION

3.1 Abstract

Previous studies have demonstrated that observed movements can interfere with the concurrent execution of movements. These studies have generally attributed interference effects to incongruence between the observed and executed movements. The study here examined different aspects of observed and executed movement congruency. Participants performed simple arm movements using one of two tasks, and observed the experimenter perform movements varied by their task and spatial congruency. Movements of the participant and experimenter were recorded using motion capture, and the dependent measure of spatial error was calculated from fingertip position. The data revealed that specific kinematic aspects of the observed movements were incorporated into the observer’s own movements. Importantly, the observation of the same movement kinematics led to interference or facilitation effects depending on the viewpoint of the observer and the task they performed. The data are discussed in terms of previous studies, which suggest that low level properties of observed movements can modulate participant performance.

3.2 Introduction

As presented in the previous chapter of this thesis (Chapter 2), a number of human behavioural studies have demonstrated that observing actions performed by others can modulate the observer's performance of motor tasks. Evidence of such effects can be seen in studies that focussed on interference in visual coordination of movement (e.g., Schmidt, Carello & Turvey, 1990; Kilner, Paulignan and Blakemore, 2003; Bouquet, Gaurier, Shipley, Toussaint and Blandin, 2007, Kilner, Hamilton and Blakemore, 2007; Stanley, Gowen and Miall, 2007; Gowen, Stanley and Miall, 2008; for a review see Blakemore and Frith, 2005). For example, in Schmidt et al (1990), a number of experiments were conducted in which pairs of participants performed sinusoidal leg movements in an anterior/posterior direction, moving both in tandem with their partner and in time with an auditory metronome. In one condition, participants were required to move in symmetrical phase with their partner (so the participants' limbs were in matching phases of the movement cycle, with similar patterns of agonist and antagonist activity), while a further condition required participants to move in alternative phase (so their limbs were in opposite phases of the movement cycle). When the metronome pacing the movements played at low frequencies (between 0.6 – 1.2Hz), participants were able to coordinate their movements with a relatively low level of timing error. However, when the metronome played at higher frequencies (between 1.4 – 2.2Hz), movements performed in alternative phase became unstable; participants would make more timing errors, leading them to shift towards moving in the (more stable) symmetrical phase. As previous studies had demonstrated similar effects for phasing when participants moved in time with themselves (Kelso, 1984), the authors concluded that the same principles underlie both between and within participant phasing. This data provided evidence of the principle that observing other people's actions can modulate the activity of the motor system.

Since this study, several investigations have employed similar tasks to examine the effects of action observation at a behavioural level. Using a paradigm comparable to Schmidt et al. (1990), Kilner et al. (2003) had participants perform sinusoidal arm movements in either the horizontal or vertical plane. While performing these movements the participants would concurrently observe either the movements of a human experimenter, the movements of a robotic arm, or complete a baseline condition in which they observed no movement. In the experimenter and robot arm conditions, the observed agent would move either in a congruent direction or in an incongruent (orthogonal) direction to the participant. The observation of congruent movements had no effect on the movements of the participant when compared to the baseline condition. However, observation of incongruent actions being performed by the experimenter led to interference in the participants' movements, which showed greater variance than in the baseline condition. Interestingly, the observation of incongruent robotic arm movements had no effect on performance. They suggested the effect was not simply due to the increased demands on attention (resulting from observing a target moving in an incongruent direction), but rather was driven by either the observation of a human actor performing the movements due to some shared conspecific process, or the observation of biological motion, perhaps due to its inherent variability in contrast to the fixed and highly repeatable movements of the robotic arm.

To address this issue, Bouquet et al. (2007) conducted a series of experiments to specifically examine whether the observation of a human actor was essential to drive the interference effect, or whether the effect was simply due to observed movement variance. In the first experiment, participants were split into two groups, with one group replicating the interference task of Kilner et al. (2003) in time with a human model, and the second group performing the same task while observing pre-recorded videos of the same model. The data revealed that both the observation of the live modelled 3D movements and pre-recorded 2D movements elicited similar interference effects, with greater variability being present in participant movements when they observed incongruently directed movement. In a later experiment, a group of participants observed the motion of a dot stimulus representing either human (biologically valid) pre-recorded movement or an artificial (biologically invalid) movement generated by a computer. The data revealed that the interference effect occurred both when observing incongruently directed, biologically valid and biologically invalid dot motion stimuli, though the variance in participants' performed movements was greater when observing biologically valid stimuli. As the biologically valid stimuli presented dot motion with more variability in the error plane, this suggested the presence of a bottom-up effect of stimulus content on participant performance.

Other experiments also examined the effects of manipulating the agency of the observed movement (Kilner et al., 2007; Stanley et al., 2007; Gowen et al., 2008). For example, Kilner et al. (2007) manipulated both the velocity profile and agency of the observed action. In one condition, participants observed video stimuli depicting humans performing forearm movements in either a horizontal or vertical direction (similar to the task employed by Kilner et al., 2003), and were instructed to observe the index finger of the actor. These stimuli were edited to show either minimum jerk kinematics (i.e. retained the natural biological velocity profile of the actor's movement by starting slowly, showing a smooth acceleration to a peak velocity to the midpoint, then decelerating slowly), or artificially generated, constant velocity kinematics. In further conditions these minimum jerk and constant velocity stimuli were converted to mask the agency of their origin: the movement of the actor's finger was represented as a white ball shown against a blue background (similar to the dot motion stimuli employed by Bouquet et al., 2007). Participants observed the movement of the stimuli while simultaneously performing movements of the forearm in either a congruent or incongruent direction. The data revealed that observing the actor perform movements in an incongruent direction with minimum jerk (biologically valid) kinematics led to interference in the participants’ movements when compared to a baseline condition of performing movements while observing a static fixation cross. Conversely, observation of the actor moving with artificially generated constant velocity (biologically invalid) kinematics had no effect on the participant compared to baseline. These data suggested that the interference effect arose from the observation of incongruently directed minimum jerk (biologically valid) kinematics, rather than being due to observing a human agent performing them. However, when participants observed the stimuli which simply depicted the motion of the fingertip as a ball of white light moving against a blue background, the observation of both minimum jerk (biologically valid) and constant velocity (biologically invalid) kinematic profiles caused interference in the participants’ movements (similar to the findings of Bouquet et al., 2007). The authors proposed that the ball stimuli did not present participants with enough information to discriminate whether the observed movement represented biological or non-biological movement, and therefore both were processed in the same manner.

Stanley et al. (2007) examined this notion further by manipulating the attributed agency of a moving dot. As well as completing the interference task with an experimenter (as in Kilner et al., 2003), participants were required to move their arm while observing the movement of a white dot projected against a black background. These dot stimuli depicted either the pre-recorded (biologically valid) kinematics of an experimenter, or a (biologically invalid) computer generated movement with a constant velocity profile. Participants were split into two groups, and while each group saw both the biological and non-biological dot movements within the same testing session, one group was told all movements of the observed dot represented pre-recorded human kinematics, while the second group was informed that all movements of the dot depicted computer generated trajectories. The results revealed that the attributed agency of the dot was a key factor in causing interference effects; when participants moved in an incongruent direction to the dot, only the group who believed the movements depicted (biologically valid) human kinematics showed an interference effect, while observing the same stimuli had no effect on the group who believed that all of the movements they observed were computer generated (biologically invalid). They suggested that the participants who believed the actions were human generated (biologically valid) would covertly imagine a human performing the corresponding action that would cause the observed movement trajectory, which in turn led to the interference effect. As well as this top-down effect of agency belief, there were effects resultant from the motion of the observed stimulus; participant movement variability increased when observing human (biologically valid) movements compared to computer generated (biologically invalid) movements, regardless of congruency and agency beliefs. This effect was similar to the results of Bouquet et al. (2007), and was attributed to an automatic bottom-up effect resultant from the increased level of error-plane variability present in the biological movement profiles (see also Gowen et al., 2008).

It can be summarised from these studies that the observation of movements attributed to another person can interfere with concurrent action execution, and that low level properties of these movements can exert automatic bottom-up effects that modulate movement performance. While it is clear that the interference effect described in the previous studies was due to incongruence between the observed and executed movements, the level at which this effect occurs has not yet been examined. For example, the interference effect may be due to the incongruence between the manner in which the movements were produced (task congruency), the incongruence of the relative spatial directions of the observed and executed movements (direction congruency), or a combination of both of these factors. Therefore, the study presented here aimed to examine these issues. Introducing a new type of movement task (articulation of the shoulder and the elbow) provided the opportunity to manipulate task congruency for the observed and executed movements. It was hypothesised that the effect would still be apparent in these new movement types, due to the similarity of their nature to the movements used in previous studies (see Kilner et al., 2003; 2007, etc; interference effects from action observation have also been demonstrated in more complex movements such as manual prehension, as examined in greater detail in Chapter 2). Varying the position of the experimenter relative to the participant also allowed manipulation of the relative spatial direction congruency of observed and executed movements. It was hypothesised that both task congruency and direction congruency would modulate the performance of the participant’s movements; observing movements being performed using an incongruent movement task or incongruent movement direction to those being executed would lead to a greater level of error in performed movements.

3.3 Materials and Methods

3.3.1 Participants

The study examined the performance of 14 participants (eight female) aged 23-35. All participants were right handed with normal or corrected to normal vision. The study was approved by the School of Sport and Exercise Sciences, University of Birmingham Ethics Board. All participants gave written informed consent prior to their involvement.

3.3.2 Experimental Equipment and Setup

The participant and experimenter were required to stand upright and perform sinusoidal movements using their right arm. The participant always stood in the same location within the testing laboratory, while the relative position of the experimenter was manipulated; they stood either directly opposite the participant at a distance of 2.00m, or to the participant's right side at a distance of 1.75m. This discrepancy in distance ensured that the approximate midpoint of the experimenter's movements remained at a consistent distance of 1.75m from the participant (see Figure 3-1, lower panel).

Movements were recorded using an eight camera infrared motion tracking system (Vicon MX, Vicon), calibrated to millimetre accuracy prior to each testing session. Reflective markers were attached to the participant and experimenter's index finger nail, and the tracker recorded movements of these markers at a frequency of 120Hz. An auditory metronome (frequency 1Hz) was used to set the pace of the performed movements. The metronome was played aloud through speakers in the baseline conditions, or through earphones to the experimenter alone during experimental conditions.

3.3.3 Design and Procedure

During the experiment, participants were required to perform either an anterior or lateral movement task. Anterior movements were performed by moving the arm at both the shoulder and the elbow, while keeping the index finger in line with the sagittal plane of the body (see

Figure 3-1, upper panel for an illustration). Therefore, anterior movements consisted of two segments; one in which the finger moved away from the body, and another in which it moved back towards the body. Lateral movements were performed in a manner similar to previous studies (see Kilner et al., 2003; Stanley et al., 2007; Gowen et al., 2008), with the participant making sinusoidal movements at the shoulder while keeping the elbow in a fixed position (see Figure 3-1, middle panel for an illustration). Lateral movements also consisted of two segments, one taking the fingertip from a position on the right of the body to the left of the body, and another returning the fingertip from the left to the right.

In experimental conditions participants performed one of the two movement tasks while concurrently observing the movements of a 22 year old male experimenter, who would also perform one of the two movement tasks. In baseline conditions, the experimenter would hold their hand in a static position[2] (corresponding with the approximate position of the midpoint of their movements), while the participant performed their assigned movement task. Movement segments were completed at a frequency of 1Hz. In experimental conditions, timing was achieved either by moving in time with the experimenter (the experimenter established their own timing by moving in time with an auditory metronome played over earphones so as to be audible only to them), while in the baseline conditions timing was achieved by having the participant move in time with the same metronome played over a set of speakers. Therefore, due to the capture rate of the motion tracking system, approximately 120 positions of the index fingertip were recorded (i.e., XYZ coordinates) for each movement segment.

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[2] Post Hoc analysis revealed the average displacement of the experimenter’s finger during the baseline conditions was 2mm. The experimenter stood either directly opposite or side on to the participant (one position for each of the 2 times the respective baseline condition was completed) in accordance to the varying of their position during the experimental trials.

In experimental conditions, task congruency was manipulated by having the experimenter perform either the same or the opposite movement task to the participant. Direction congruency (the relative spatial direction matching of the movements performed by the experimenter and participant) was manipulated by having the experimenter stand either directly opposite or side on to the participant. As it was hypothesised that the observation of these movements would lead to modulation of performance, the experimenter kept their eyes closed in all conditions in order to avoid being influenced by the movements of the participant.

Prior to the beginning of the experimental session, participants were provided with an opportunity to practice performing both the anterior and lateral movement tasks in time with an auditory metronome until they were proficient in timing their movement segments. Participants then completed the baseline conditions, randomised for order within block. The participant then completed the experimental conditions. The experimenter remained in the same position relative to the participant throughout each block, and experimenter position was counterbalanced across conditions. Within each experimental block, trials were randomised. Before each trial, the participant was instructed in which direction to perform their movements, and therefore, which movement type they were required to perform. In the experimental conditions participants were also informed of the direction in which the experimenter would move prior to each trial.

The eight experimental and two baseline conditions examined during the experiment are presented in Figure 3-1 (lower panel). Each trial consisted of the participant performing 36 movement segments. Of these, 30 segments were used in the analysis; the initial five segments were discarded from the analysis in order to give the participant chance to establish consistent timing with the experimenter, and the final movement segment was discarded as some participants would end the movement prematurely. Each trial type was completed twice, giving a total of 60 movement segments per condition.

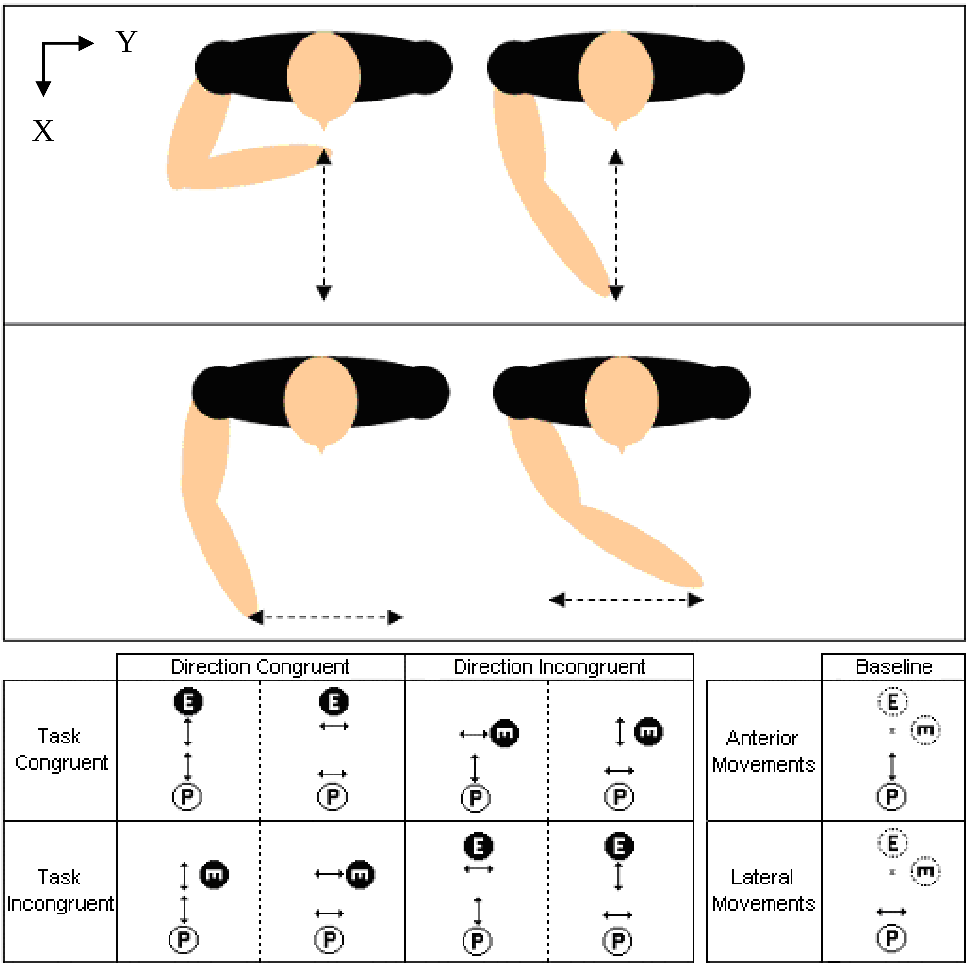

Figure 3-1: Upper and Middle panels illustrate the manner in which anterior and lateral movements were performed, respectively. Each illustrates the starting position and direction of movement for one movement segment. When performing anterior movements, participants moved in the X direction while attempting to minimise movement in the Y direction, and vice versa for lateral movements. Lower panel depicts the experimental and baseline conditions. Circles containing the letter E represent the experimenter - black filled circles show conditions in which the experimenter performed movements, while white dashed circles show the possible positions of the experimenter in the baseline conditions, in which their hand remained static. Open circles containing the letter P represent the participant. For each experimental condition (bottom panel, left), the left inset shows the participant making anterior movements, while the right inset shows them making lateral movements.

3.3.4 Data Analysis

The dependent variable of spatial error was calculated using the position of the participant's fingertip. The standard deviation of the participant's movement in the plane orthogonal to the intended direction (the Y plane during anterior movements and the X plane during lateral movements, effectively the 'error' direction) was calculated for each movement segment. The mean average of the standard deviation was then calculated for each trial type. This method for calculating spatial error in the participant's movement is similar to the methods previously used (see for example Stanley et al., 2007).

The independent variables used in the study were participant movement type (lateral or anterior), direction congruency (direction congruent or direction incongruent) and movement congruency (movement congruent or movement incongruent). The dependent measure used was the spatial error (mean standard deviation of movement in the orthogonal 'error' direction, measured in mm) in the participant's movement. The data were analysed using a 2x2x2 repeated measures ANOVA (see section 3.4.2). As the baseline conditions did not fit into this initial analysis, a separate ANOVA using the same 2x2x2 structure was conducted in which each condition was examined in comparison to its respective baseline. 'Spatial Error from Baseline' was calculated by subtracting the spatial error recorded in the respective baseline condition from each experimental condition, effectively providing a positive value if spatial error increased from baseline and a negative value if spatial error decreased from baseline (see section 3.4.3).

3.4 Results

3.4.1 Data Reduction

A number of movement segments were not included in the analyses conducted. A total of 296 movement segments were removed from the analysis. Of these trials, 248 were removed due to marker occlusion which prevented dependent variable analysis, and a further 48 movement segments were removed from the dataset as outliers (values lying more than 3 standard deviations from the mean). Therefore, a total of 8104 movement segments (96% of all collected) were analysed.

3.4.2 Spatial Error

Figure 3-2 presents the data for the analysis of the spatial interference in participants' movements. The analysis of spatial error revealed a significant main effect of movement type (F[1,13] = 31.29, $p < 0.001$), which showed that participants performed anterior movements with less spatial error than lateral movements (Mean: anterior movements = 14mm, lateral movements = 39mm, SEM: 2.37mm vs 3.65mm). A significant main effect of direction congruency was also present (F[1,13] = 21.05, $p < 0.001$). This effect revealed that participants performed movements with less spatial error when they observed the experimenter perform congruently directed movements compared to incongruently directed movements (Mean: congruent direction = 25mm, incongruent direction = 29mm, SEM: 1.96mm vs 2.31mm). The main effect of task congruency was not significant (F[1,13] = 2.63, p = 0.13).

The analysis also revealed several significant interactions. A significant interaction between movement type and direction congruency (F[1,13] = 31.33, $p < 0.001$) was analysed using two separate repeated measures ANOVAs for movement type (anterior vs. lateral). In this analysis, anterior movements showed no effect of direction congruency (F[1,13] = 0.31, $p = 0.59$), while for lateral movements there was a significant effect for direction congruency (F[1,13] = 10.28, $p < 0.01$), with congruently directed movements showing less spatial error than incongruently directed movements (Mean: congruent direction = 27mm, incongruent direction = 29mm, SEM 1.26mm vs 1.56mm). A significant interaction between task congruency and direction congruency (F[1,13] = 10.59, $p < 0.01$) was also revealed, and was analysed using two ANOVAs for task congruency (congruent task vs incongruent task). However, this analysis revealed no significant differences in direction congruency for the task congruent condition (F[1,13] = 2.72, $p = 0.12$) or the task incongruent condition (F[1,13] = 1.87, $p < 0.20$). The final significant interaction was a three-way interaction between all factors analysed (F[1,13]= 7.61, $p < 0.05$). This interaction was analysed by splitting conditions into four separate ANOVAs for movement type and task congruency. Only the ANOVA for lateral, task incongruent conditions showed a significant direction congruency effect (F[1,13] = 57.78, $p < 0.001$), revealing that participant movements showed less error when they were performed in a congruent direction compared to an incongruent direction (Mean: direction congruent = 34mm, direction incongruent = 46mm, SEM 3.50mm vs 3.40mm). None of the other ANOVAs conducted revealed significant effects (anterior, task congruent F[1,13] = 0.49, $p = 0.50$; anterior, task incongruent F[1,13] = 0.13, $p = 0.73$; lateral, task congruent: F[1,13] = 2.80, $p = 0.12$). The interaction between movement type and task congruency was not of statistical significance (F[1,13] = 0.87, $p = 0.37$).

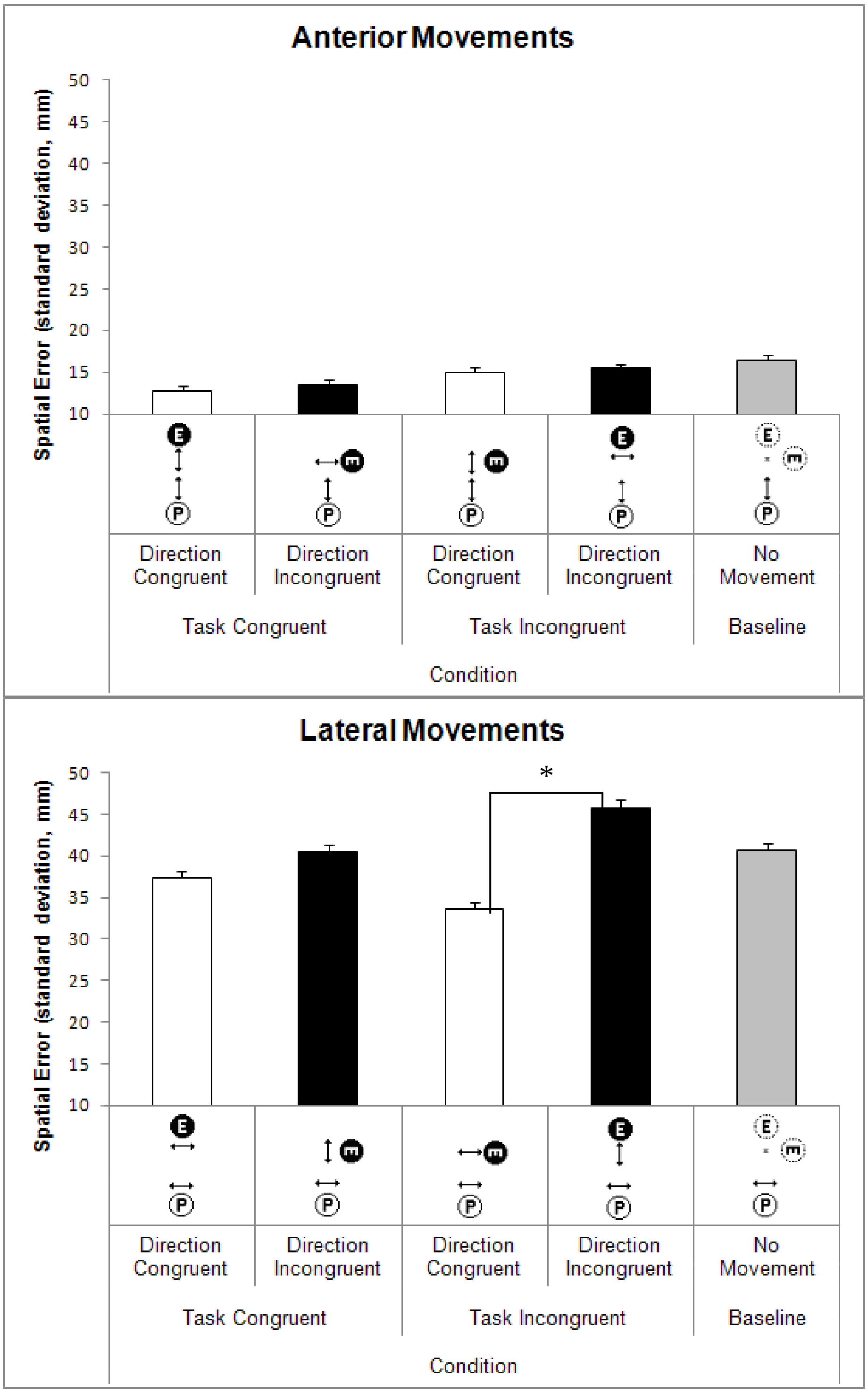

*Figure 3-2: Upper panel shows participant spatial error for anterior movements, Lower panel depicts participant spatial error for lateral movements. Baseline conditions are included for comparison. Error bars represent mean within participant standard error. * Indicates significance at the p<0.05 level.*

3.4.3 Spatial Error Relative to Baseline

A further analysis of the data was conducted in order to compare each condition with its respective baseline. The analysis revealed a significant main effect of direction congruency ($F[1,13] = 21.95$, $p < 0.001$), with participants making movements with less error when observing movements performed in a congruent direction compared to an incongruent direction (Mean: congruent direction = -4mm, incongruent direction = 0mm, SEM: 1.54mm vs 1.17mm). No significant main effects of movement type ($F[1,13] = 0.09$, $p = 0.77$) or task congruency ($F[1,13] = 2.67$, $p = 0.13$) were revealed in this analysis. However, several significant interactions were revealed. A significant interaction between movement type and direction congruency ($F[1,13] = 30.44$, $p < 0.001$) was analysed using two separate ANOVAs for movement type (anterior vs. lateral). Within this interaction analysis, anterior movements revealed no significant effects of direction congruency ($F[1,13] = 0.31$, $p = 0.59$), while the analysis of lateral movements did reveal a significant effect of direction congruency ($F[1,13] = 10.28$, $p < 0.01$). This demonstrated that direction congruent movements showed lower spatial error compared to baseline than direction incongruent movements (Mean: direction congruent = -11mm, direction incongruent = -8mm, SEM: 2.86mm vs 2.09mm). A significant interaction between task congruency and direction congruency was also revealed ($F[1,13] = 10.59$, $p < 0.01$), and was analysed using two separate ANOVAs for task congruency (congruent task vs incongruent task). This analysis of direction congruency revealed no significant differences for the task congruent condition ($F[1,13] = 2.72$, $p = 0.12$) or the task incongruent condition ($F[1,13] = 1.87$, $p < 0.20$). For the congruent task, there was no significant effect of direction congruency ($F[1,13] = 2.63$, $p = 0.13$), but for the incongruent task there was a significant effect of direction congruency ($F[1,13] = 44.38$, $p < 0.001$). This effect demonstrated that direction congruent movements had less spatial error compared to baseline than direction incongruent movements (Mean: congruent direction = -7mm, incongruent direction = 5mm, SEM: 2.86mm vs 2.09mm).

The three-way interaction between all factors analysed was also found to be statistically significant (F[1,13]= 8.34, p < 0.05), and analysed using four separate ANOVAs for movement type and task congruency. The ANOVA for lateral, task incongruent conditions revealed a significant effect of direction congruency (F[1,13] = 57.78, p < 0.001), which demonstrated that participants performed movements with less spatial error compared to baseline for congruently directed movements compared to incongruently directed movements (Mean: congruent direction = -7mm, incongruent direction = 5mm, SEM: 2.86mm vs 2.09mm). None of the other ANOVAs revealed significant effects (anterior, task congruent F[1,13] = 0.49, p = 0.50; anterior, task incongruent F[1,13] = 0.13, p = 0.73; lateral, task congruent: F[1,13] = 2.80, p = 0.12). The interaction between movement type and task congruency was not of statistical significance (F[1,13] = 0.89, p = 0.36).

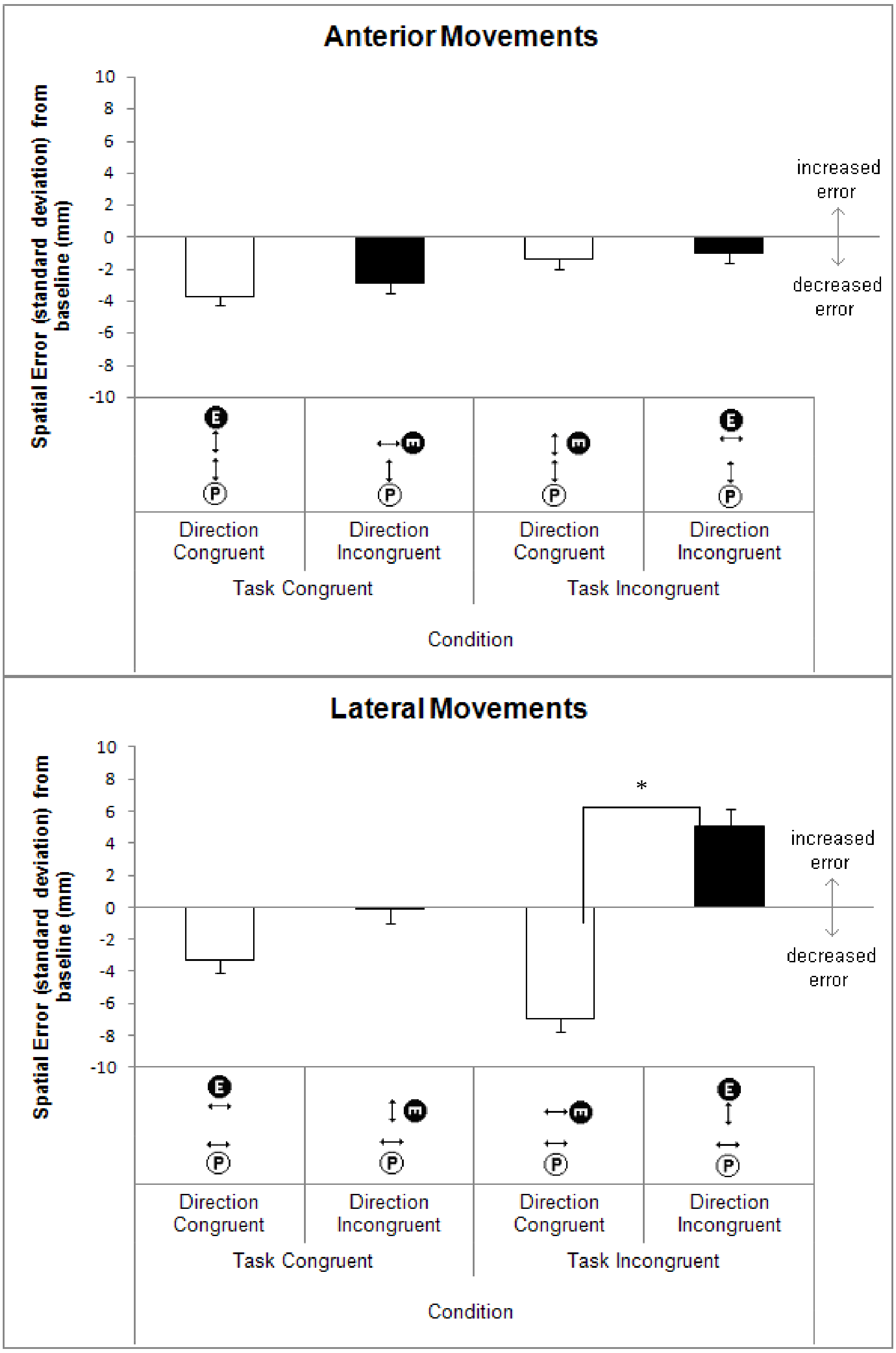

Figure 3-3: Analysis of spatial interference compared to baseline. Positive values show increases in error, negative values show decreases. Upper panel shows data for anterior movements, lower panel shows lateral movements. Error bars represent mean within participant standard error. Indicates statistical significance at the p<0.05 level.*

3.5 Discussion

The study presented here examined what the effects of observing simple movements were on the execution of performing movements in a similar manner. Using two distinct types of movement (lateral movements which allowed articulation at one joint, and anterior movements which allowed articulation at two) we modulated observed task congruency and direction congruency in order to examine the effects these factors had on movement execution. The data revealed that only movements performed using the lateral movement task were affected by action observation, and only when observing the experimenter perform the incongruent, anterior movement task.

The data demonstrate that anterior movements were performed with a lower level of error than lateral movements, as evidenced from the significant main effect for movement type in the analysis of spatial error. This effect was not apparent in the analysis of spatial error relative to baseline, as each movement type was compared to a different relative baseline. The analyses conducted revealed that none of the experimental conditions in which the participant performed anterior movements differed from baseline. The level of error for anterior movements performed by the participant was similar across all conditions, suggesting a ceiling level of performance had been achieved. This can likely be attributed to the greater level of control that was allowed by articulating at two joints (anterior movements) as opposed to allowing articulation at only one (lateral movements). This would also explain why action observation did not affect anterior movements – participants simply had too great a level of control over the performance of their anterior movements to be affected by the observation of another movement.

The results demonstrated that when performing lateral movements, the observation of movements performed using an incongruent task (anterior movements) in an incongruent direction interfered with the ability to execute actions. This increase in error compared to baseline performance was in accordance with previous studies (See Kilner et al., 2003; Stanley et al., 2007). However, the analyses also revealed that contrary to our hypothesis, when participants performed lateral movements, the observation of a movement performed using an incongruent task in a congruent direction showed a significant *decrease* in the level of movement error compared to the baseline condition. This facilitation effect was unexpected, as the results of previous studies had suggested that observing movements performed in a congruent direction would not be different to baseline performance (Kilner et al., 2003; Kilner et al., 2007). Furthermore, as only interference effects have been demonstrated in previous studies, the effect has often been labelled as ‘the interference effect’ (Stanley et al., 2007; Gowen et al., 2008, see also Blakemore and Frith, 2005). A further point for discussion is that there were no corresponding performance modulation effects when participants observed the corresponding lateral movement conditions during their own performance of lateral movements (i.e. lateral movement, task congruent conditions). Previous studies provide a logical explanation for these effects. The findings of Stanley et al. (2007) and others (see Bouquet et al., 2007; Gowen et al., 2008) suggested that increasing the variability of observed stimuli can lead to increased error in participant performance, presumably due to an automatic bottom up effect of stimulus content. In order to further examine this, a post hoc analysis was conducted on the movements performed by the experimenter. The analysis revealed that the experimenter performed their movements with similar levels of error to those of the participants for each movement type; that is, anterior movements of the experimenter showed significantly lower levels of spatial error than their lateral movements[3]. This would explain the apparently paradoxical facilitation effect revealed when participants observed anterior, direction congruent movements when performing lateral movements; the participants' own executed lateral movements took on aspects of the observed anterior movement, including a lower level of error in the intended direction of movement. Conversely, this may also explain why the observation of lateral movements had no effect on participant movement execution; the level of error in the observed lateral movement was too great to cause any modulation of the participant's action, regardless of direction congruency. High error, lateral movements would show relatively large level of movement in both the intended and erroneous directions, while low error, anterior movements would be more concentrated in one direction, leading to bottom-up modulation of performance.

Such a proposal also fits within (and possibly extends) the goal directed theory of imitation suggested by Bekkering et al. (2000), which proposes that observed actions are broken down into their constituent elements, then reconstructed and imitated according to their perceived hierarchical importance. This approach suggests that the key components of the observed action (such as the target object to be acted to, or the hand observed to be moving) thought to be of high importance are retained by the observer and therefore imitated, while components of lesser importance (such as movement paths taken) are generally deemed to be of lesser importance and therefore neglected. In the study presented here, while the movements performed by the participants and experimenter were not goal directed in the traditional sense (i.e. they lacked a target object with which to interact), they were not lacking in purpose;

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[3] The experimenter's anterior movements (M = 9mm, SD = 3.27mm) showed significantly less spatial error than their lateral movements (M = 28mm, SD = 5.13mm) when analysed using a paired samples t test (t = -28.23, $p < 0.001$).

participants were explicitly instructed that the aim of their movements was to perform each segment with minimal deviation in the orthogonal error direction. Therefore, when considering the cues that participants would attend to when observing the actions of the experimenter, two factors related to this key instruction were the direction of the experimenter's movement (manipulated via direction congruency), and the magnitude of any experimenter movement in the error direction (which would be high for observed lateral movements, and low for observed anterior movements). This latter factor suggests that the observation of the experimenter performing lateral movements would therefore be less compelling than the observation of anterior movements, not due to the manner in which the movement was produced or the congruency between the observed and executed tasks, but because of the kinematic properties and relative level of error in each movement type as discussed above. Therefore, it appears that observing the same type of movement from different viewpoints can lead to different modulatory effects depending on the task being performed; interference effects will arise when the observed movement direction conflicts with the direction of an executed movement (direction incongruent condition), while facilitatory effects arise when the observed movement occurs in a spatially congruent direction to a performed movement (direction congruent condition).

Initially, it may appear that the finding that task congruency did not modulate movement performance is in contradiction to previous findings; Brass, Bekkering and Prinz (2001) found that observed movement *type* had a greater influence on participants than observed movement *direction* for a simple finger movement task. However, this can be explained by a number of differences in the experimental paradigms employed between this data and the present study. While the participants in Brass et al. (2001)'s study were responding to a choice reaction time task, participants in the study presented here were instructed to perform a particular movement, and therefore prompted in which direction to move prior to each trial. In addition, participants in the presented study were instructed to observe the fingertip of the experimenter throughout their performed movement; an instruction to observe the movement of the hand has been provided in studies using similar experimental tasks (see for example Kilner et al., 2003), and is consistent with data suggesting that observers tend to focus on the movement of the hand during the observation of arm movements (Mataric and Pomplun, 1998). It is likely that maintaining fixation on the experimenter's fingertip may have been a key factor in driving the effects revealed, as previous data suggests that spatial attention is required for action observation effects to occur (Bach, Peatfield and Tipper, 2007). Therefore, in the study presented here it can be assumed that focusing attention on the manner in which the observed movement was performed (movement type, task congruency) was deemed to be of lower priority than focusing attention on the observation of the trajectory and relative spatial direction of the observed finger (direction congruency), potentially explaining why no significant effects of task congruency were apparent in the analysis.

An obvious issue to address is that the study presented here did not attempt to examine the effects of congruency relative to the muscles used to perform the different tasks. As this study focused on manipulating the direction of the movements relative to the observer by always matching the direction of movement according to the egocentric location of the participant, it was not possible to match the exact phases of the motor program used to generate the movements. However, it is likely that this factor would only play a small role in any effects revealed. Previous studies have demonstrated that movements employing both in and out of phase movement tasks are effective in eliciting interference effects (comparison of horizontal movements, effectively performed out of phase, and vertical movements, effectively performed in phase, revealed no differences in Kilner et al., 2003) and there is data to suggest that effects are more reliable when observed actions are presented out of phase compared to in phase (observation of horizontal, out of phase movements revealed reliable interference effects in Stanley et al., 2007). Furthermore, as Schmidt et al. (1990) demonstrated that participant error increased while observing movements performed at incongruent points in the movement phase, it would appear that the approach adopted in the experiment presented here would actually be more likely to elicit the effects we aimed to examine. Finally, the frequency at which participants performed movements in the study presented here was relatively low (1Hz), while interference effects related to phase shifting are generally not observed until higher movement frequencies are attained (1.4Hz and upwards; see Schmidt et al., 1990).

In conclusion, the data presented here revealed effects of movement observation on concurrent movement execution. This effect was driven by specific kinematic aspects of the observed action (in particular the spatial direction of the movement), as opposed to the manner in which the movement was performed (movement type) or the congruency between the observed and executed movement tasks (task congruency). A key point is that observing the same movement being performed from different viewpoints led to either facilitation or interference in the performance of the participant’s movement, depending on the spatial direction congruency of the observed movement.

CHAPTER 4:

EFFECTS OF OBSERVED VIEWPOINT ON MOVEMENT PRIMING

4.1 Abstract

Action priming studies have demonstrated that the presentation of motor stimuli can modulate participant performance in motor tasks. Relatively few studies have examined whether the viewpoint from which these motor stimuli are observed can lead to further modulation of these effects. Three experiments using a simple finger priming task were designed to examine this via the recording of participant reaction times and response errors. Experiment 1 revealed that participants responded faster and made fewer errors when stimuli depicted actions from a viewpoint congruent with the observer's own natural vantage point, and greater performance for mirror matching when observing movements from a viewpoint consistent with observing somebody directly opposite. Experiment 2 revealed these effects were unlikely to result from the congruency between the positions of the participant's own hand when making the motor response and the observed stimulus viewpoint. Experiment 3 demonstrated that decreasing the congruency between the observed viewpoint and the participant's natural vantage point only led to modulation of performance when the rotation of the observed hand was greater than 90˚. The data are discussed in terms of previous action priming studies.

4.2 Introduction

As presented in the earlier chapters of this thesis (Chapters 1-3), a number of studies have demonstrated that the presentation of either a visual or motor stimulus can prime subsequent action (for examples see; Brass, Bekkering, Wohlschlager and Prinz, 2000; Brass et al., 2001; Craighero et al., 1996; Craighero, Bello, Fadiga and Rizzolatti, 2002; Edwards et al., 2003; Frischen, Loach and Tipper, 2009; Symes et al., 2008; Tucker and Ellis, 1998; Vainio, Tucker and Ellis, 2007). For example, Craighero et al. (1996) required participants to perform grasping actions to a bar hidden within a circular chamber. This bar could be set to either a 45˚ clockwise or anticlockwise angle, and participants were instructed as to the bar's orientation prior to each trial. Participants sat in front of a computer monitor and first observed a fixation cross while holding a switch with a pinch grip. The colour of the cross acted as a go signal – once it changed, participants were required to release the switch and grasp the hidden bar as quickly as possible. Furthermore, the go signal was accompanied by the appearance of a priming stimulus around the fixation cross; this could be a neutral circle, or a rectangle in an orientation congruent or incongruent to the orientation of the bar to be grasped. The data revealed that participant response times were significantly faster when the priming stimulus was a rectangle congruent with the orientation of the bar compared to the incongruent and neutral stimuli. This suggested that the congruency between the visual properties of the observed stimulus and the required response led to a priming effect on participant performance.

Evidence that observation of motor stimuli can lead to priming effects has also been provided. Brass et al. (2000) examined the effects of movement (and to a lesser extent, symbolic and spatial) priming cues in a simple finger movement task. This series of experiments involved participants observing pre-recorded video clips depicting a left hand at rest on a table. The participant’s own right hand was positioned in front of the monitor (so as to mirror the image of the observed hand), and movements of their index and middle fingers were recorded using motion tracking. In the first experiment, participants completed two conditions in which they responded to either observed finger movements or symbolic cues. In the finger movement condition, participants were required to directly match the observed finger movement, raising their index finger in response to the observation of the on screen hand raising its index finger, and raising their middle finger in response to the observation of the on screen hand raising its middle finger. For experimental trials, an additional symbolic cue (the number ‘1’ for the index finger and ‘2’ for the middle finger for congruent trials, and vice versa for the incongruent trials) would appear in the space between the index and middle finger of the observed hand, while in the baseline condition the finger movements would be presented alone. In the symbolic cue condition, participants were required to initiate their finger movements in response to the symbolic cue - the number ‘1’ indicated they should respond with their index finger, and the number ‘2’ indicated they should respond with their middle finger. The symbolic cue was presented either alone (baseline trials), or accompanied with a congruent or incongruent finger movement (for congruent and incongruent trials respectively). The results demonstrated that participants responded faster in the finger movement condition than the symbolic cue condition, suggesting that participant performance was directly modulated by the observation of motor stimuli. Furthermore, the appearance of congruent or incongruent symbolic cues had no effects on performance in the finger priming condition. Alternatively, in the symbolic cue condition the appearance of a congruent finger movement led to a facilitation of participant performance, while the appearance of an incongruent finger movement interfered with participant performance. These data suggested that participant performance was modulated by the observation of finger movements, even when (in the case of the symbolic cue condition) these movements were irrelevant to the task being performed. In a second experiment, symbolic cues were replaced by a spatial cue consisting of an ‘x’ superimposed over the nail of either the index or middle finger. For baseline trials in the spatial cue condition, an ‘x’ would appear over either the index or middle fingernail, but both fingers remained motionless. For congruent or incongruent trials, the ‘x’ would appear over the moving or stationary finger respectively. The results of this experiment revealed that participants were faster when responding to the finger movement condition than the spatial cue condition. Furthermore, in the finger movement condition the appearance of spatial cues only led to interference in participant performance, with participant response times increasing when incongruent spatial cues were presented. In the spatial cue condition, the appearance of congruent or incongruent finger movements led to facilitation or interference in participant performance respectively. The data from these experiments demonstrated that the observation of motor stimuli primed participants to perform congruent movements, and led to improved participant performance when compared to the observation of symbolic or spatial cues.

Craighero et al. (2002) also showed evidence that the observation of motor stimuli can prime participant performance. They modified their original paradigm (Craighero et al., 1996) to examine participant responses to the observation of stimuli depicting hand actions. In an initial experiment, participants performed reaching and grasping actions to a bar hidden in a circular chamber. The orientation of this bar could be set to either a 45° clockwise or 45° anticlockwise angle, and participants were instructed as to the orientation of the bar prior to each trial. The go signal to initiate the movement was the presentation of a stimulus on the computer screen. The stimuli depicted '...images of the right hand as seen in a mirror' (Craighero et al, 2002) (effectively the same as observing somebody directly opposite perform the movement with their left hand), with one picture showing the hand in a position consistent with the action required to grasp the 45° clockwise bar, while the other picture was consistent with the action required to grasp the 45° anticlockwise bar; therefore, each stimulus could be congruent or incongruent depending on the grasping action required. The data revealed that participant response times were significantly faster when they were presented with a hand stimulus congruent with their required response, compared to when they were presented with stimuli depicting actions incongruent with their required response. A second experiment then revealed that this effect could be modulated by the orientation of the observed hand. The previously used stimuli depicting the right hand in a mirrored orientation (effectively as though observing a person opposite perform the required grasping action with their *left* hand) were compared with similar stimuli depicting the same hand posture with the view rotated by 180° (consistent with the participant observing a person in their own current position performing the grasping action with their *left* hand). These data revealed a preference for the observation of the mirror-matched stimuli, as participant response times were faster for these original stimuli than to the newly introduced rotated stimuli. Together, these data demonstrated that the observation of motor stimuli led to priming effects on subsequent motor performance, and that the viewpoint from which the stimulus was observed can further modulate these effects.

Other data to show that the viewpoint of the observed stimuli can modulate visuomotor priming was presented by Vogt et al. (2003). The study used a similar paradigm to the previous experiments conducted by Craighero et al. (1996; 1998; 2002), with participants being instructed on a trial-by-trial basis to grasp a horizontally or vertically orientated bar. Participants performed the grasping action following the appearance of one of four priming stimuli, consisting of pictures of hands. These stimuli were varied by congruency and perspective. Stimuli depicted a hand performing a grasping action either congruent or incongruent with the response required to grasp the horizontally or vertically orientated bar. In terms of perspective, ‘own perspective’ stimuli were consistent with the participant observing their own right hand perform a grasping action, while ‘other perspective’ stimuli were consistent with observing the left hand of person directly opposite grasping the bar (or as though observing a mirror image of the participant’s own hand perform the action). Prior to the beginning of each trial, participants would observe one of three fixation conditions; a simple fixation cross alone, or a fixation cross superimposed on a picture of a hand shown from an ‘own perspective’ or ‘other perspective’ view in a neutral position (corresponding to the starting position of the hand of the participant). The data revealed similar priming effects to the study of Craighero et al. (2002), but that the perspective of the observed hand and the fixation condition further modulated these effects. When participants fixated on neutral hand postures prior to the go signal, congruency effects were only present for ‘own perspective’ stimuli. However, when participants observed a fixation cross prior to performing their movements, congruency effects were only present for stimuli depicting hands in the ‘other perspective’. The authors hypothesised that this could have been due to the immediacy of the required response, as the sudden appearance of ‘own perspective’ stimuli would rarely occur in natural conditions, meaning that participants would therefore be unfamiliar with responding to them in a rapid manner. A second experiment was undertaken in order to examine this hypothesis, using the same experimental set up as the initial experiment. Participants began each trial fixating on a colour hand shown in a neutral posture from either the ‘own perspective' or 'other perspective'. After this, a colour prime picture would be shown for a fixed interval (0ms, 200ms, 400ms or 600ms) after which the prime picture would change from colour to grayscale, providing the go signal for the participant to perform their action. This experiment revealed congruency effects only for the observation of 'own perspective' stimuli. These data suggest that participants display a preference for responding to stimuli which are presented from viewpoints congruent with their own vantage point (see also Gianelli et al., 2008).

Studies of visuomotor priming have demonstrated that visual and motor stimuli can prime participant performance, and that modulation of these priming effects can occur when participants observe actions from different viewpoints. The data reviewed here demonstrate such priming effects, and also present data which examine the effects of the viewpoint from which an action is observed, and to some extent, the identity of the hand performing the action. To clarify, Craighero et al. (2002) presented participants with visual stimuli depicting '...images of the right hand as seen in a mirror'; it is of interest to note that this description effectively describes images of the *left* hand, and that an alternative way to classify these stimuli would be as images of the left hand of a person directly opposite the participant. As participants performed their grasping action with their right hand, the identity of the observed hand was therefore incongruent with the response required (i.e. they responded with their *right* hand while observing a *left* hand). This issue was further compounded in the second experiment, which introduced rotated images of the initial stimuli. These newly introduced rotated stimuli depicted a hand shown from a viewpoint consistent with the participant performing the action with their own *left* hand. Again, as participants performed all responses with their *right* hand, the observed stimuli were therefore incongruent with the manner (i.e.

regarding hand identity) in which participants were required to perform the task. Furthermore, the complication that the observed hand stimuli were effectively consistent with observing either one’s own hand or the hand of another person was not addressed. While Vogt et al. (2003) began to address this issue (using stimuli which clearly depicted actions from either the ‘own perspective’ or ‘other perspective’ viewpoints), their ‘own perspective’ stimuli only presented a right hand, while their ‘other perspective’ stimuli only presented a left hand. Therefore, these studies did not systematically investigate any potential interactions between observed hand viewpoint and observed hand identity.

These examples highlight inconsistencies in the previous action priming literature. Of primary interest is the unresolved issue of whether observed action viewpoint will modulate participant performance. This is particularly important at present as data from neuroimaging have recently revealed differences in brain activity for the observation of movements performed from different viewpoints (Shmuelof and Zohary, 2008), though this has not yet been thoroughly examined at the behavioural level. Therefore, a series of experiments examining this issue are presented here. The aim of the first experiment was to examine whether the observation of movements consistent with movements performed by either oneself or another person would modulate participant performance. To address a further issue with the previous literature, this experiment also examined whether the identity of the observed hand (whether the hand observed to act was a left or right hand) would modulate participant performance. The findings of this experiment led to further questions that were addressed in two follow up experiments. Experiment 2 aimed to examine whether the congruency between the observed hand viewpoint and participant hand posture would modulate responses and Experiment 3 examined how a gradual manipulation of the congruency between the observed hand viewpoint and the participant’s own natural vantage point would modulate responses.

4.3 Experiment 1: Observed Hand Identity

This experiment aimed to examine whether observed hand viewpoint (orientation of the observed hand relative to the participant) and observed hand identity (left or right hand) could modulate participant responses. As previous studies have shown a preference for viewpoints congruent with the observer’s own vantage point (Vogt et al., 2003; Gianelli et al., 2008), it was hypothesised that the priming effect of observing an action would be greater for these types of stimuli. This would result in participant responses being fastest when they observed movements from a viewpoint consistent with their own natural vantage point (a rotation of 0˚ relative to the participant) compared with a viewpoint incongruent with their own natural vantage point (180˚ rotation relative to the participant). It was also hypothesised that the factors of observed hand viewpoint and observed hand identity would interact. When observing actions from the 0˚ viewpoint, it was hypothesised that participants would respond faster when responding to stimuli depicting a right hand compared to a left hand (as the observed right hand responses would be highly congruent with the participant’s own responses, all made with the right hand). Conversely, it was hypothesised that when observing movements from the 180˚ viewpoint, participant responses would be slower when responding to observed movements made by a right hand compared to a left hand (due to the mirror-like congruency between the observed left hand and the participant’s right hand).

4.3.1 Materials and Methods

4.3.1.1 Participants

A single group of 30 undergraduate students (19 Male, aged 18-23) from the School of Sport and Exercise Sciences at the University of Birmingham participated in the study. All were right handed with normal (or corrected to normal) vision, and naive to the purposes of the study. All procedures were reviewed by the school ethics committee prior to the experiment, and informed consent was obtained from all participants prior to their participation.

4.3.1.2 Experimental Equipment and Setup

Prior to the experiment, a series of videos depicting the right hand of a female model were recorded and edited into a series of video stimuli. These stimuli were presented using DMDX presentation software (Forster and Forster, 2003) on a Dell Precision 8400 computer with a 17inch CRT monitor.

Figure 4-1 illustrates the video clip stimuli created for the experiment. The stimuli were created so as to be similar to the stimuli used in previous studies of motor priming (see Brass et al., 2000; 2001). These stimuli were edited so that the movement durations were identical in each clip. Each clip began with a static image depicting the hand at rest against a black table surface, with the index and middle fingers raised. This image was presented for 560ms, and was then followed by a series of images lasting for 60ms which showed either the index or middle finger moving downwards towards the table surface. A final image presented the finger that had moved at rest on the table surface, and was shown for 560ms.

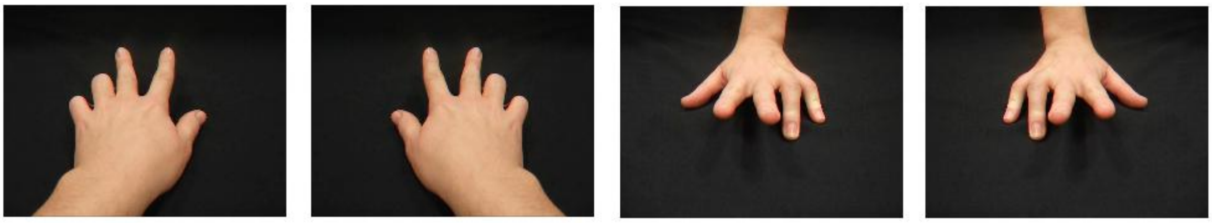

Figure 4-1: Examples of experimental stimuli from Experiment 1. From left to right: Left hand, 0° viewpoint; right hand, 0° viewpoint; left hand, 180° viewpoint, right hand, 180° viewpoint. Each image depicts the starting frame for each condition. All stimuli were created using a right hand, then copied and horizontally flipped during editing to create identical stimuli depicting a left hand. A total of eight stimuli were created for the experiment due to the combinations of different hands (left or right), viewpoints (0° or 180°) and finger movements (index or middle) used in the experiment.

4.3.1.3 Design and Procedure

Participants were instructed that they would observe a series of video clips, and should respond to them as quickly and as accurately as possible. Participants made all responses with their right hand using a computer keyboard positioned directly in front of the screen, and were required to press ‘F’ with their index finger if the video clip showed movement of the index finger, and ‘H’ with their middle finger if they observed a middle finger movement. Participants were given a brief practice period (eight trials) before the experimental data was collected. Each of the eight video clips was presented 10 times during the experiment, resulting in a total of 80 trials (20 per condition).

4.3.1.4 Data Analysis

Data was analysed using a 2x2 repeated measures ANOVA. The independent variables examined were observed hand viewpoint (0˚ or 180˚) and observed hand identity (left or right). Two dependent variables of response time (ms) and response error (percentage of incorrect responses) were analysed.

4.3.2 Results

4.3.2.1 Data Reduction

For the response time analysis 114 trials were removed, including 93 trials where participants responded incorrectly, 3 in which they failed to respond and 18 outliers (responses lying further than 3 standard deviations from the mean). Hence 95% of trials were examined. For the response error analysis, the percentage of incorrect responses for each condition (including trials where participants did not respond) was examined.

4.3.2.2 Response Times

Figure 4-2 illustrates participant response times. The repeated measures ANOVA revealed a significant main effect for observed hand viewpoint (F[1,29] = 142.63, $p < 0.001$) with participant responses being faster for the 0˚ viewpoint condition than the 180˚ viewpoint condition (Means: 0˚ viewpoint = 464ms, 180˚ viewpoint = 520ms, SEM: 9.83ms vs 11.38ms). The main effect for observed hand identity was not statistically significant (F[1,29] = 3.02, $p = 0.09$). The analysis also revealed a significant interaction between the factors of observed hand viewpoint and observed hand identity (F[1,29] = 45.20, $p < 0.001$). This interaction was analysed using separate paired samples t-tests (Bonferroni corrected critical $\alpha = 0.025$) for the different viewpoint conditions. This analysis revealed a significant effect for the 0˚ viewpoint (t[29] = 6.148, $p < 0.001$), with participants responding slower to left hand stimuli (Mean = 489ms, SD = 54.72ms) compared to right hand stimuli (Mean = 438ms, SD = 62.01ms), and a significant effect for the 180˚ viewpoint (t[29] = -3.94, $p < 0.001$), with participants responding faster to the left hand stimuli (Mean = 504ms, SD = 72.67ms) than to right hand stimuli (Mean = 536ms, SD = 59.12ms).

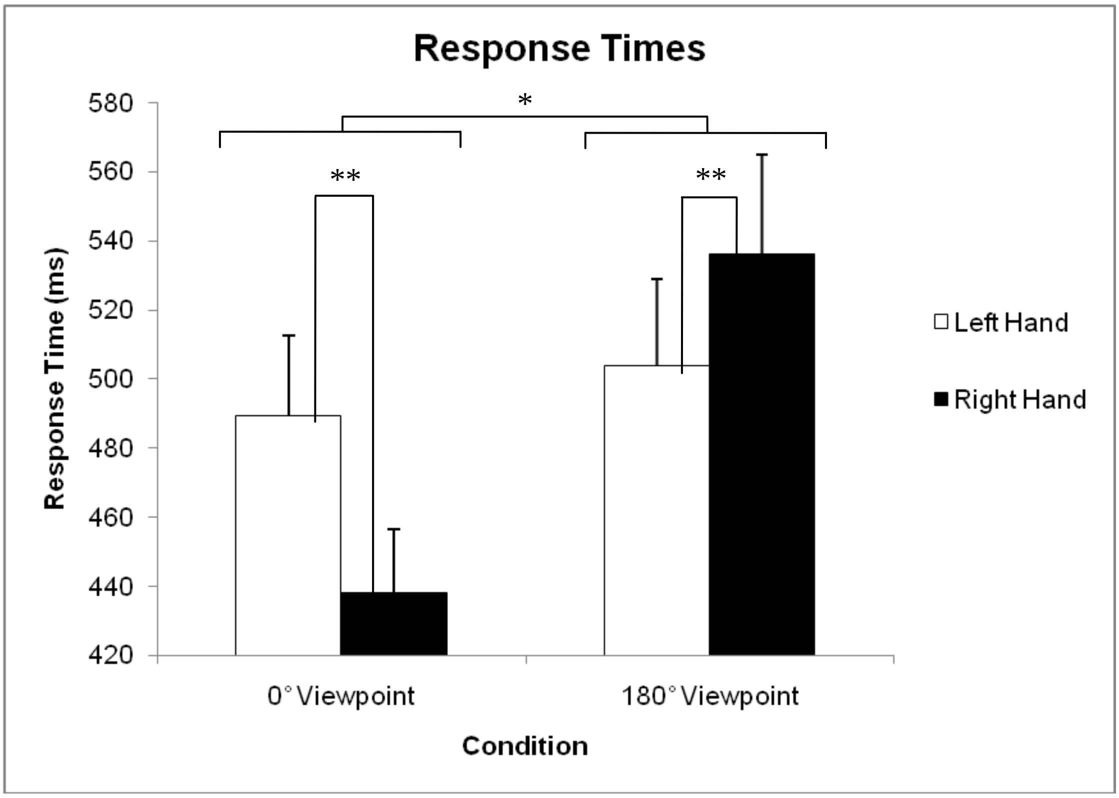

*Figure 4-2: Participant response times for Experiment 1. Error bars show mean within participant standard error. * Indicates significant main effect (p < 0.001) . ** Indicates statistically significant t-score (p < 0.001).*

4.3.2.3 Response Errors

Figure 4.3 depicts the data for the participant response errors. The ANOVA revealed a significant main effect of observed hand viewpoint ($F[1,29] = 9.89$, $p < 0.01$). This effect revealed that participants made significantly fewer errors when responding to observed hand stimuli for the 0˚ viewpoint than for the 180˚ viewpoint (Means: 0˚ viewpoint = 4.3%, 180˚ viewpoint = 6.8%, SEM: 0.91% vs 1.26%). There was no significant main effect of observed hand identity ($F[1,29] = 0.05$, $p = 0.83$). However, the data did reveal a significant two-way interaction ($F[1,29] = 22.42$, $p < 0.001$). The significant interaction was analysed using two paired samples t-tests (Bonferroni corrected critical $\alpha = 0.025$) for each observed hand viewpoint condition. The t-test for the 0˚ viewpoint was statistically significant ($t[29] = 4.51$, $p < 0.001$), revealing that participants made more errors when responding to left hand stimuli (Mean = 8.5%, SD = 10.0%) compared to right hand stimuli (Mean = 0.2%, SD = 0.9%). The t-test for the 180˚ viewpoint was also statistically significant ($t[29] = -4.18$, $p < 0.001$), revealing that participants made fewer errors when responding to left hand stimuli (Mean = 2.8%, SD = 3.9%) compared to right hand stimuli (Mean = 10.8%, SD = 11.6%).

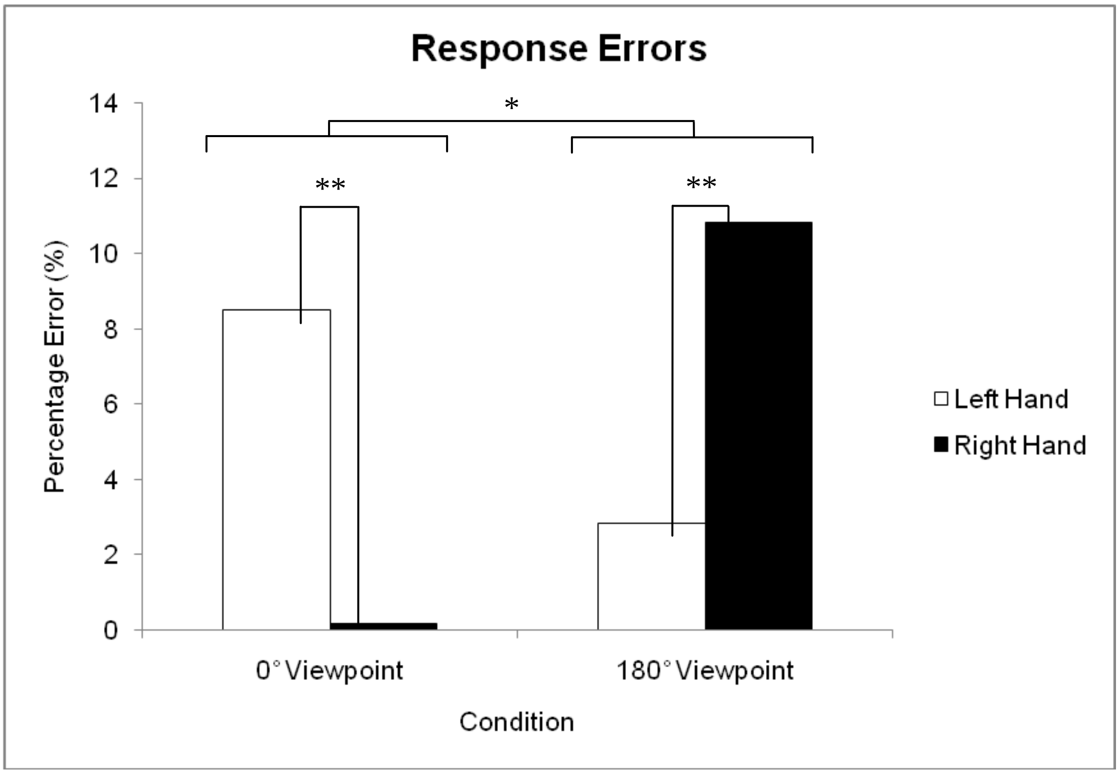

*Figure 4-3: Participant response errors for Experiment 1. * Indicates significant main effect (p < 0.001). ** Indicates statistically significant t-score (p<0.001).*

4.3.3 Discussion

In this experiment, the viewpoint of observed actions was manipulated to examine whether there was a preference for the observation of movements from a viewpoint congruent with the observer’s natural vantage point. In addition, the identity of the observed hand was manipulated in order to examine whether there would be a preference for anatomical matching in viewpoints consistent with the vantage point of the participant, and mirror matching for viewpoints consistent with observing another person sitting directly opposite the participant.

The data for both response times and incorrect responses revealed that as hypothesised, participant performance was faster and more accurate when movements were observed from a 0˚ viewpoint compared to a 180˚ viewpoint. This is consistent with previous studies (Vogt et al., 2003; Gianelli et al., 2008) which have suggested a preference for viewpoints consistent with those of the participant’s own natural vantage point due to the congruency between the observed movement and the required response. As also hypothesised, a significant interaction between observed hand viewpoint and observed hand identity revealed that participants demonstrated a preference for anatomical matching in the 0˚ condition (i.e. greater levels of performance when observing the right hand stimuli), and a preference for mirror matching in the 180˚ condition (i.e. greater levels of performance when observing the left hand stimuli). This is consistent with data from both behavioural and neuroimaging studies (Vainio, Tucker and Ellis, 2007; Craighero et al., 2002; Shmuelof and Zohary, 2008), which suggest a preference for anatomical matching of actions when observed from a viewpoint congruent with the natural vantage point of the observer, and a preference for mirror matching when observing movements of the hand of an actor as though positioned directly opposite the observer. Data from Craighero et al. (2002) suggest that this is due to the spatial congruency between the location of the observed finger movement and the required finger response.

4.4 Experiment 2: Hand Posture Congruency

The data from Experiment 1 revealed that the greater the level of congruency between the observed hand movement and the participant's own vantage point, the greater their levels of performance in the task. However, due to the design of the initial study it was not possible to determine whether this effect was due to the congruency of the observed movement with the participant's own vantage point, or the congruency between the observed movement and the participant's own hand posture. Experiment 2 examined this relationship by changing participant hand posture. It was expected that if the participant hand posture was a contributory factor in their performance, manipulating the congruency between their hand posture and observed movements would lead to modulatory effects on performance, and an experiment to examine this proposal was devised.

4.4.1 Materials and Methods

4.4.1.1 Participants

Participants were 16 postgraduate students from the School of Sport and Exercise Sciences at the University of Birmingham, aged 22-35. All were right handed and had normal (or corrected to normal) vision. Participants were naive to the purpose of the study. All procedures were approved by the school ethics committee, and participants gave informed consent prior to their participation.

4.4.1.2 Experimental Equipment and Setup

Procedures for the creation and presentation of stimuli were the same as in Experiment 1 (see section 4.3.1.2). The video stimuli for this experiment depicted the hand from either a 0˚ or 90˚ viewpoint (see figure 4-4). Note that only video clips of right hands were used in Experiment 2. The experimental setup was the same as in Experiment 1 with the exception that participants made responses using a computer mouse, the orientation of which varied between two positions (0˚ or 90˚).

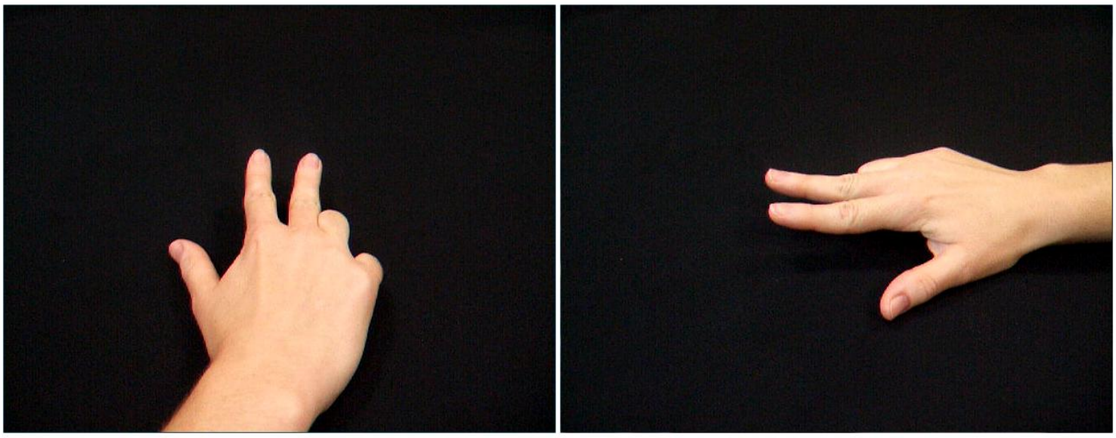

Figure 4-4: Observed viewpoint conditions (left panel: 0˚, right panel: 90˚) in Experiment 2. Participant hand posture was varied in a 2x2 design to either match or differ from the observed hand. Note that only videos depicting right hands were used. A total of 4 stimuli were used in the experiment due to the combinations of observed hand viewpoints (0˚ or 90˚) and finger movements (index or middle).

4.4.1.3 Design and Procedure

Participants were instructed to observe a series of video clips presented on a computer screen, and respond to them as quickly and as accurately as possible using a computer mouse. Participants made their responses by pressing the left mouse button with their index finger if the video depicted index finger movement, and the right mouse button with their middle finger if they observed movement of the middle finger. Participants completed two blocks of trials, and the mouse was fixed to the table in front of the computer monitor in one of two positions at the beginning of each block. This meant that when the participant held the mouse, their hand would be in either a 0˚ posture or a 90˚ posture, allowing for the manipulation of congruency between participant hand posture and the observed hand viewpoint depicted in the video stimuli. Participants were given a brief practice (four trials) at the beginning of each block before completing the experimental conditions. In each block, all four video clips were presented 10 times. Therefore, participants completed a total of 80 trials in the experiment (split between 2 blocks of 40 trials each), with a total of 20 trials being completed for each condition.

4.4.1.4 Data Analysis

Data was analysed using a 2x2 factor repeated measures ANOVA, with the factors of observed hand viewpoint (0˚ or 90˚) and participant hand orientation (0˚ or 90˚). The dependent variables of response time (ms) and response errors (percentage error) were analysed using separate ANOVAs.

4.4.2 Results

4.4.2.1 Data Reduction

In the analysis of participant response time, a total of 21 trials were removed from the analysis. This included 12 trials in which the participant made an incorrect response, and 9 outliers (response times lying more than 3 standard deviations from the mean). This left 98%

of all trials collected to be examined. In the analysis of participant error a percentage score was calculated for each condition.

4.4.2.2 Response Times

Figure 4-5 presents the data for participant response times. The repeated measures ANOVA revealed no significant main effects for observed hand viewpoint (F[1,15] = 0.42, p = 0.54) or hand orientation (F[1,15] = 1.02, p = 0.33). The interaction between these factors was also not of statistical significance (F[1,15] = 0.02, p = 0.88).

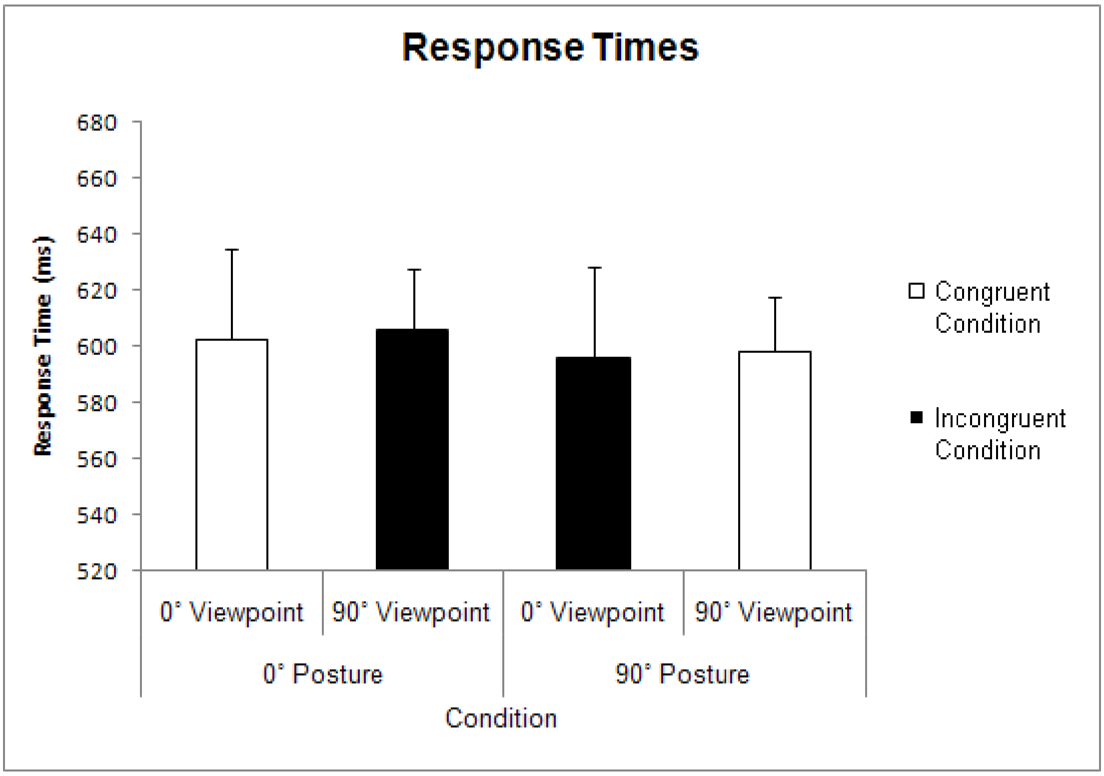

Figure 4-5: Participant response times for Experiment 2.

4.4.2.3 Response Errors

Figure 4-6 depicts participant response errors. The repeated measures ANOVA revealed no significant main effects of observed hand viewpoint (F[1,15] = 2.46, p = 0.14) or participant hand posture (F[1,15] = 1.00, p = 0.33). The interaction between these factors was also not statistically significant (F[1,15] = 0.24, p = 0.63).

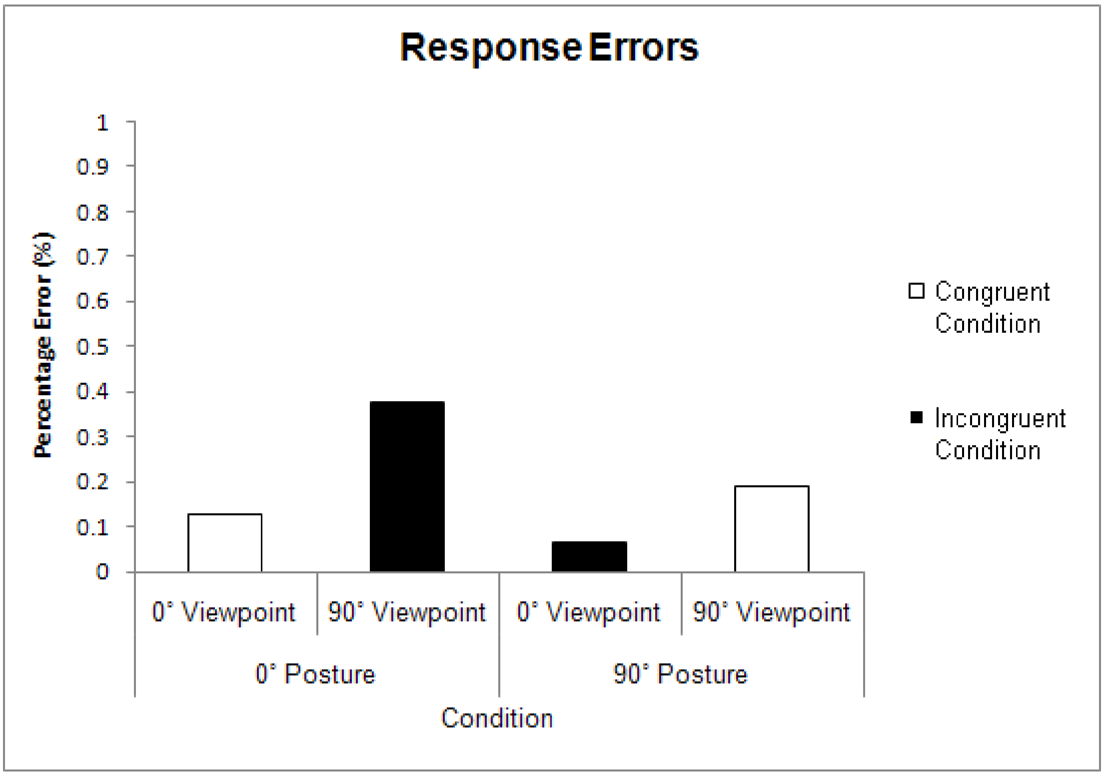

Figure 4-6: Participant response errors for Experiment 2.

4.4.3 Discussion

Experiment 2 examined whether participant responses to finger movements observed from different viewpoints were affected by their own hand posture. The data revealed that altering the posture of the participant's hand had no effect on their response times or response accuracy. This suggests that the congruency between the state of the participant's own motor system and the movements they observe appears to be of no consequence to their performance in this task.

4.5 Experiment 3: Observed Hand Viewpoint

The data from Experiment 1 revealed that participant performance was greatest when participants observed movements from a viewpoint congruent with their own natural vantage point (0˚ viewpoint) compared to a less compatible viewpoint (180˚ viewpoint). Experiment 3 therefore examined the effect of systematically manipulating the congruency between the participant's own natural vantage point and the viewpoint from which they observed movements. It was hypothesised that participant performance would progressively decrease as the rotation of the observed movement viewpoint increased relative to the 0˚ viewpoint.

4.5.1 Materials and Methods

4.5.1.1 Participants

The same 16 participants from Experiment 2 completed Experiment 3 (see section 4.4.1.1 for details).

4.5.1.2 Experimental Equipment and Setup

Figure 4-7 illustrates the video clip stimuli used in Experiment 3. Experimental stimuli were created in the same manner as the previous experiments (see Experiment 1 for details). The experimental setup was the same as in Experiment 2.

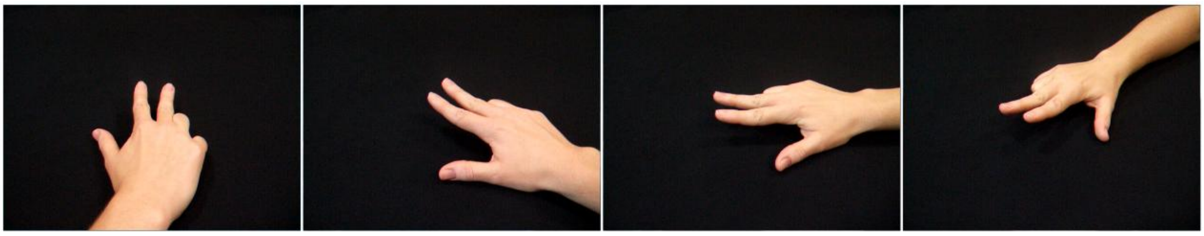

Figure 4-7: Examples of the experimental stimuli shown in Experiment 3. From left to right: 0˚, 45˚, 90˚ and 135˚ observed viewpoint conditions. A total of 8 stimuli were used due to the combinations of observed hand viewpoints and finger movements (index or middle).

4.5.1.3 Design and Procedure

Participants were instructed to observe video clips presented on screen, and respond to these video clips as quickly and as accurately as possible. Participants held a computer mouse in their right hand, which was fixed in a position central to the screen. If they observed movement of an index finger, participants were required to respond by pressing the left mouse button with their index finger, while if they observed the movement of a middle finger, participants responded by pressing the right mouse button with their middle finger. A practice period was provided (8 trials) before participants completed the main experiment. Each video clip was presented 10 times, leading to a total of 80 trials for the experiment (20 trials per condition).

4.5.1.4 Data Analysis

Data was analysed using a repeated measures ANOVA examining observed hand viewpoint (0˚, 45˚, 90˚ or 135˚). The dependent variables of participant response time (ms) and response errors (percentage of incorrect responses) were analysed in separate ANOVAs based on this structure.

4.5.2 Results

4.5.2.1 Data Reduction

Data were prepared separately for the two dependent variables analysed. For the analysis of participant response times, a total of 30 trials were removed from the analysis, including 18 trials in which the participant responded incorrectly and 12 outliers (trials in which the response time lay more than 3 standard deviations from the mean). This left 98% of all trials collected in the analysis. For the analysis of response errors, a percentage score was calculated for each condition.

4.5.2.2 Response Times

Figure 4-8 presents data for participant response times. The repeated measures ANOVA analysis revealed a significant effect of observed hand viewpoint (F[3,45] = 23.38, p < 0.001). Bonferroni corrected pairwise comparisons revealed that participant performance was significantly slower for the 135˚ viewpoint condition (Mean = 671ms, SEM = 13.34ms) than for the 0˚ viewpoint (Mean = 613ms, SEM = 9.89ms), 45˚ viewpoint (Mean = 624ms, SEM = 13.17ms), and 90˚ viewpoint (Mean = 622ms, SEM = 13.06ms); 0˚ vs 135˚ (t [15] = -57.85, p < 0.001) 45˚ vs 135˚ (t [15] = -46.53, p < 0.001), 90˚ vs 135˚ (t [15] = -48.23, p < 0.001). No other pairwise comparisons revealed statistically significant effects (p > 0.73).

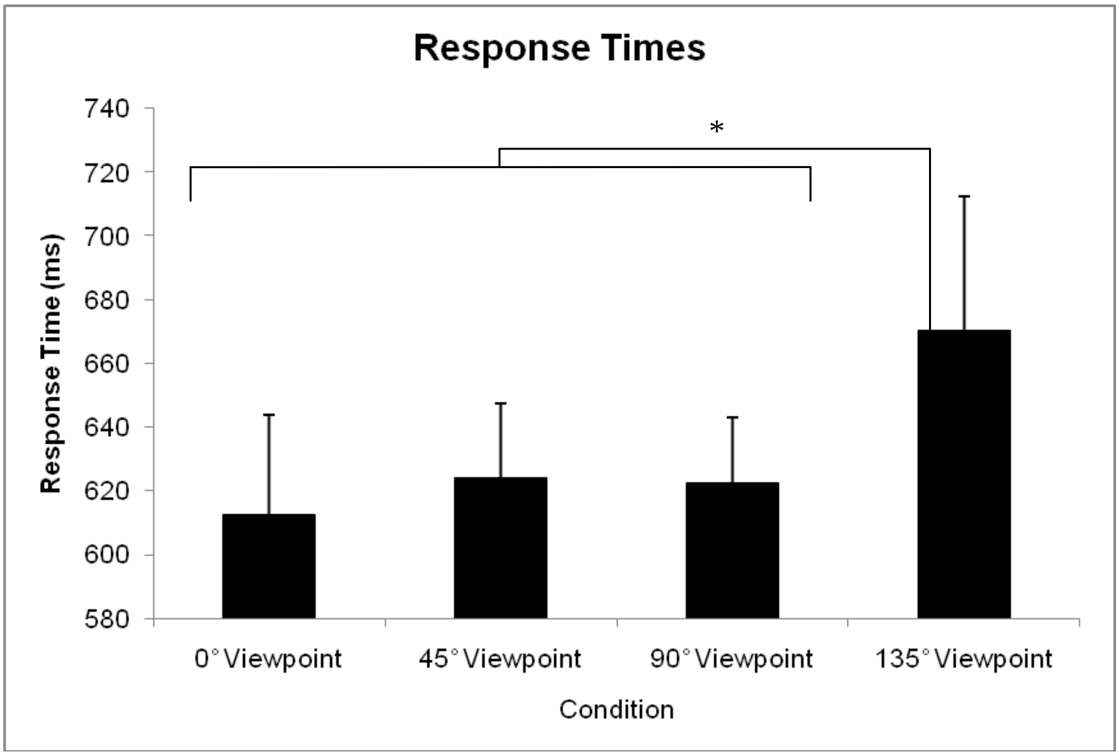

*Figure 4-8: Participant response times for Experiment 3. * Indicates statistically significant t score at the p < 0.001 level.*

4.5.2.3 Response Errors

Figure 4-9 illustrates the data for participant response errors. A repeated measures ANOVA revealed that there was no significant main effect of observed hand viewpoint (F[3,45] = 2.76, p = 0.09).

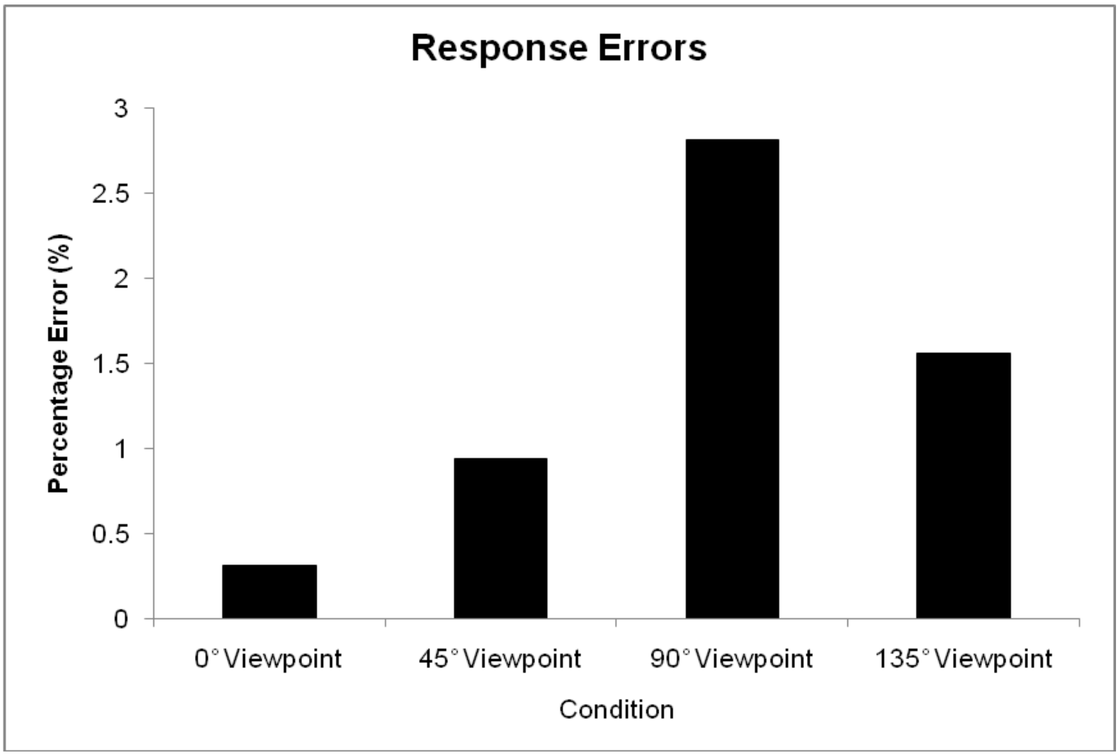

Figure 4-9: Participant response errors for Experiment 3.

4.5.3 Discussion

In this experiment, the viewpoint from which movements were observed was systematically manipulated by rotating the position of the observed hand. When compared to a condition congruent with the participant's own viewpoint (0˚ viewpoint), participant response times to conditions with only slight levels of rotation (45˚ and 90˚ viewpoints) showed no significant differences. However, observing movements at more extreme rotations (135˚ viewpoint) led to a decrease in participant performance. It is noteworthy that while the movements viewed at the 0˚, 45˚ and 90˚ viewpoints all presented movements that the participant could potentially perform themselves, the movements viewed in the 135˚ viewpoint presented movements which could only feasibly be performed by another person. This result may suggest that there is a perceptual boundary between movements that a person could perform themselves and movements that could only be performed by another person.

4.6 General Discussion

The overarching aim of the study presented in this chapter was to examine whether the viewpoint from which an action is observed can modulate participant performance. Across three experiments, participants performed a simple finger movement imitation task in response to a series of observed motor stimuli shown from different viewpoints. Experiment 1 examined the effects of observing actions from two different viewpoints, one consistent with the observer's own natural vantage point, the other consistent with observing the movements of a person positioned directly opposite. This experiment also examined whether the identity of the observed hand would interact with the viewpoint from which it was observed. The second experiment examined whether manipulating the spatial congruency between the observed and executed movements would modulate participant performance, and the third experiment systematically examined the effects of small increments in the observed viewpoint angle on participant responses.

In accordance to the main hypothesis that the viewpoint from which an action is observed should modulate participant performance, modulatory effects of observed hand viewpoint were revealed in Experiments 1 and 3. When considering the results for all three experiments, the data showed that when participants observed motor stimuli from viewpoints consistent with positions their own hand could be observed from (i.e. 0˚, 45˚ and 90˚ viewpoints) their performance was faster than when they observed stimuli which depicted hand actions outside the range of their natural performance (i.e. 135˚ or 180˚ viewpoints). In addition, there were no differences in performance for actions observed within the range of their own hand viewpoint (i.e., the 0˚, 45˚ and 90˚ viewpoints). This is consistent with previous studies which have demonstrated that participant performance is improved when imitating movements shown from a viewpoint consistent with actions that they themselves could perform (Vogt et al., 2003; Gianelli et al., 2008). Furthermore, the respective anatomical and mirror matching processes revealed for the 0˚ viewpoint and the 180˚ viewpoint in Experiment 1 are consistent with both previous behavioural and neuroimaging data (Vainio et al., 2007; Craighero et al., 2002, Shmuelof and Zohary, 2008).

These data appear to suggest that viewpoint switches between ‘self’ and ‘other’ representations at a particular angle. This was shown in Experiment 3, where there were no modulations in performance when comparing the 0˚, 45˚ and 90˚ viewpoints, but all of these viewpoints differed from the 135˚ viewpoint. As noted previously, the 0˚, 45˚ and 90˚

viewpoints all showed movements that the participant could potentially perform themselves, while the 135° viewpoint presented movements that could only be performed by another person. This finding could represent a perceptual boundary which exists between the movements that a person can perform themselves and the movements of another person. This could explain the difference in performance for the viewpoint stimuli, as movements observed from the 135° viewpoint are effectively removed from the motor repertoire of the observer, leading to an increase in the processing time required for participants to respond to them. Such an explanation is also consistent with previous studies of action observation examining higher level functions such as selective attention, which have shown that participants are to some degree influenced by the frame of reference they observe an action to be performed from (Frischen et al., 2009). The notion that the observed stimuli were processed in terms of actions that the participant could either perform themselves or would have to observe another person perform could also potentially explain why no modulatory effects were revealed in Experiment 2; as both types of observed motor stimuli were consistent with movements that the participant could perform themselves (regardless of the current state of their motor apparatus), they were processed in the same manner.

The findings of the study presented here could be interpreted in terms of agency, with responses to observed movements which could be performed by the participant being faster than responses to observed movements which could only have been performed by another person. It is of interest to consider whether this represents a facilitatory effect (i.e. observing stimuli consistent with movements the participant could perform themselves *improves* their performance) or an effect due to interference (i.e. observing stimuli consistent with movements only another person could perform *interferes* with their performance). While it is sometimes difficult to ascertain whether modulatory effects are due to facilitation, interference, or a mixture of both these effects, data from previous studies suggest that the effects revealed in the study presented here are likely to be caused by interference. Brass et al., (2000) demonstrated that the observation of incongruent finger movement stimuli led to interference effects on participant performance. This can likely be attributed to a high level of performance in the task, as participants appeared to perform at a ceiling level, preventing potential facilitatory effects of the observed motor stimuli, but allowing for a decrease in performance during the observation of incongruent motor stimuli. As the stimuli employed in the study presented here were based on the stimuli originally created by Brass et al., (2000), it is likely that the effects revealed show a similar interference with movement performance when observing actions from incongruent viewpoints, rather than a facilitation of performance for congruent stimuli (see also Blakemore and Frith, 2005).

In conclusion, the data from this series of experiments reveal that participant performance in a simple visuomotor priming task was modulated by the viewpoint from which movements were observed. More specifically, when participants observed movements from a viewpoint consistent with movements they could perform themselves, their responses were faster compared to when they observed movements from a viewpoint consistent with movements that could only be performed by another person. This suggests that observed movements seen from a viewpoint consistent with movements that the participant could perform themselves required less processing compared to when they observed stimuli from a viewpoint consistent with observing the movements of another person. This effect appears to be primarily driven by the congruency between the participant’s natural vantage point and the viewpoint of the observed stimuli, as only differences between stimuli which could be attributed to observing either oneself or another person were revealed. As previous studies have demonstrated differences in brain activity during the observation of egocentrically and allocentrically framed actions, there is scope for further investigation of such effects using neuroimaging techniques. That is, in order to ascertain whether a perceptual boundary exists between observing movements which could be performed by the observer and movements that could only be attributed to observing another person. This will be addressed in the next chapter (Chapter 5).

CHAPTER 5:

DOES OBSERVING ACTIONS FROM DIFFERENT VIEWPOINTS LEAD TO A GRADUAL OR CATEGORICAL SHIFT IN BRAIN ACTIVITY?

5.1 Abstract

Recent fMRI studies have demonstrated differences in brain activity when movements are observed from egocentric or allocentric viewpoints, suggesting action observation effects are modulated by agency. However, as no paper has systematically examined the effects of manipulating the observed viewpoint of an action, it has not been possible to discern at what point the agency of an observed stimulus changes. As a consequence, it is not apparent whether the change in perceived agency is reflected in a sudden or gradual change in neural activity. Therefore, the study presented here aimed to replicate and extend the work of previous experiments, examining whether activity in the Premotor and Parietal areas of the brain is modulated by observing actions from different viewpoints. Participants observed grasping actions performed from several different viewpoints, achieved by incrementally rotating the position of the hand through positions 0˚, 45˚, 90˚, 135˚ and 180˚ relative to the observer. Main contrasts revealed that stimuli successfully elicited activity in Premotor and Parietal areas, and that observing actions from any of the viewpoints examined consistently led to activity in the left Superior Parietal Lobule; activity was also revealed in the right Superior Parietal Lobule when the viewpoint was consistent with the participant's own natural vantage point (0˚ of rotation). These data are discussed in terms of previous studies which infer that bilateral brain activity during the observation of action reveal stronger representations of observed actions.

5.2 Introduction

As described in more detail in the introductory chapter of this thesis (Chapter 1), single cell recording studies have demonstrated the existence of mirror neurons in primate Premotor area F5 and the Parietal cortex area PF (Di Pellegrino et al 1992; Gallesse et al 1996; Rizzolatti et al 1996; Gallese et al., 2002; Fogassi et al., 2005; for a review see Rizzolatti, Fabbri-Destro and Cattaneo, 2009). Following the discovery of mirror neurons in primates, several neuroimaging studies have demonstrated the existence of a similar motor representation system for action observation in the human brain. Early evidence of this system was provided by a study which used positron emission topography (PET) to examine the representations of grasping actions (Rizzolatti et al., 1996). During this study, brain activity was recorded when participants observed an experimenter grasp objects with their right hand (grasping observation condition), and also when the participant observed the object alone with no accompanying action (object observation condition). Activity occurring during the grasping observation condition was then contrasted with the activity occurring during the object observation condition, exposing the areas of the brain which responded to the observation of goal directed actions (and effectively removing unrelated activity due to the observation of objects). This contrast revealed increases in blood flow to areas in the left hemisphere, including the Inferior Frontal Gyrus (Broca’s area), and the Superior Temporal Sulcus. As the Inferior Frontal Gyrus is often considered to be the human homologue of primate area F5, and the Superior Temporal Sulcus of the monkey has strong links with areas F5 and PF, the authors suggest their activation in this instance was likely to reflect the activity of a human mirror system.

Since Rizolatti et al's (1996) study, a number of other neuroimaging investigations have examined the effects of different visual stimuli on the human mirror system. Buccino et al. (2001) had participants observe a series of pantomimed, non object orientated (i.e. intransitive) and object directed actions, including foot actions such as pushing down on the brake pedal of a car, hand actions such as reaching and grasping, and mouth actions such as biting and chewing. Observation of both pantomimed and object directed actions revealed a somatotopic activation of the Premotor cortex in accordance to the classic motor homunculus. When participants observed actions directed to objects, additional activity occurred in the Parietal lobe, which again was arranged in a somatotopically organised manner. These data demonstrated that the observation of both pantomimed (intransitive) and object based (goal directed) movement kinematics activated the human mirror system, and that the area activated was dependent on the effector observed.

While several studies have examined the stimuli and conditions to which the human mirror system responds (such as to object directed actions or intransitive movements, or to the part of the body performing the movement), other studies have examined what the role of the human mirror system might be (e.g. purposes for which the system may have evolved). One suggestion is that the mirror neuron system may provide a neural substrate by which the observer can imitate other people, allowing actions to be learned via observation. Evidence supporting this claim was provided by Iacoboni et al., (1999). They conducted an fMRI study in which participants were required to respond to the observation of different action cues by performing a simple lifting movement of their index or middle finger. During the study, participants were presented with imitative, symbolic or geometric stimuli. Imitative stimuli depicted a hand lying prone on a table, and after a short delay the index or middle finger would be raised; participants were required to respond to imitative cues by directly matching the observed finger movement themselves. Symbolic stimuli presented a static image of the same hand, with a cross appearing over the finger the participant was required to lift. Finally, geometric stimuli presented the participant with a gray background against which a cross would appear to the left or right, indicating which finger the participant should respond with. The data revealed that BOLD activity was greater in Broca’s area (the left frontal operculum), the right Anterior Parietal region, and the right Parietal Operculum when participants responded to the imitative cues, as shown when activity in the symbolic stimuli condition was compared to the imitative condition, and when activity in the geometric condition was compared to the imitative condition. Even when the activity from the symbolic and geometric conditions was grouped together, their combined activity was still less than that of the imitative condition. The greater responses occurring in human mirror system areas when participants responded to imitative cues led the authors to suggest that this activity represented a cortical mechanism for human imitation.

In a related fMRI study, Buccino et al. (2004a) examined the effects of imitative learning on brain activity. A group of musically naive participants were required to perform a finger positioning task using the head of a guitar. In an imitation condition, participants first observed a video clip of a guitar chord being played repetitively by an expert guitarist, then after a brief pause were required to imitate the guitar chord, placing their fingers on the fretboard in a configuration consistent with playing the chord themselves. In a non-imitation condition, participants would observe the same guitar chord being played, but then after a brief pause would perform a non-imitative action (such as grasping and releasing the guitar neck, rhythmically covering or gently scratching the fretboard). An event related design was used to measure differences in brain activity that corresponded to different phases within the trial. First, a cue event consisting of the presentation of a coloured square indicated to the participant which type of action to perform (e.g. a green square indicated an imitation trial; a red square indicated a non-imitation trial). The cue was followed by Event 1, in which participants observed a stimulus video clip (i.e. a guitar chord being played). Event 2 then presented participants with a blank blue screen; for the last second in Event 2, a fixation cross the same colour as the initial cue appeared to remind the participant of the type of trial to perform. Depending on the condition, the data collected during Event 2 therefore reflected activity underlying the participant’s preparation of an imitative or non-imitative action. In Event 3, the participants performed either an imitative or non-imitative response, again depending upon the condition. The data revealed that while brain activity was similar during the execution of imitative and non-imitative actions (Event 3), the activity occurring during the observation of action (Event 1) and the preparation of a response (Event 2) was modulated by the different experimental conditions (whether the participant was required to perform an imitative or non-imitative action). When observing guitar chords (Event 1) with the intent to imitate them, as well as activity in the occipital and temporal lobes, there was strong activity in brain areas traditionally associated with the human mirror system. This included bilateral (but greater left) Inferior Parietal Lobule activity extending to the Superior Parietal Lobule, and Premotor activity in the Inferior Frontal Gyrus and Precentral Gyrus. While there was a similar pattern of activity when participants observed the same stimuli with the intent to perform a non-imitative action, the activity was lesser in both strength and volume. When preparing an action (Event 2) involving the imitation of a previously seen action chord, there was strong activity in areas similar to those active in Event 1. However, when preparing a non imitative action, while the pattern of activity was similar, the strength of activations was low, being almost the same as that at rest. The stronger activity in mirror system areas revealed for the imitative compared to non-imitative conditions suggests that this system plays a role in the imitation of actions and possibly provides evidence that the system may play a role in the imitative *learning* of actions. The data also suggest that the activity of the human mirror system can be modulated by the intention of the observer; that is, the intention to selectively imitate the observed action.

Other experimental evidence supporting the notion that the mirror system can be modulated by top down effects comes from a study that manipulated the viewpoints from which actions were observed. Shmuelof and Zohary (2008) conducted a study in which participants observed video clips of a left or right hand reaching for and grasping objects from an egocentric viewpoint (as though the hand performing the action belonged to the observer) or an allocentric viewpoint (as though the hand belonged to a person sitting opposite the observer). When participants observed movements performed from the egocentric viewpoint, activity in the anterior Superior Parietal Lobule was greater in the hemisphere contralateral to the hand observed than in the ipsilateral hemisphere. Conversely, when participants observed movements performed from the allocentric viewpoint, activity in the anterior Superior Parietal Lobule was greater in the hemisphere ipsilateral to the observed hand compared to the activity in the contralateral hemisphere. Therefore, in the egocentric viewpoint the activity matched the pattern of activation that would occur when the participant executed the action themselves, while in the allocentric viewpoint the opposite pattern of changes in the BOLD signal occurred. The authors explained this mirror-like congruency in terms of automatic imitation – when imitating the movements of a person positioned opposite, it is intuitive for the observer to match actions observed to be made by a left hand using their own right hand (as though looking in a mirror), which would primarily involve the use of the left hemisphere. For this to occur, a top down (non-conscious) selection effect would be required to determine whether the viewpoint of the action corresponded with that of the observer, or another person. Following selection, the nature of the observed stimulus would presumably lead to automatic imitative motor processes (i.e. as in Stanley et al., 2007). It is of interest to note that while this study revealed effects corresponding to the agency of the observed stimuli, as only two viewpoints were examined it was not possible to ascertain what would occur at perceptual boundaries; in other words, there was no way to examine at which point ‘egocentric’ (or self) stimuli became ‘allocentric’ (other person) stimuli, or at which point the selection of the appropriate limb changes from an anatomical to a mirror matching process. Similarly, the question of whether these changes in representation occur in a gradual manner or in a categorical manner (note that the data from Chapter 4 support the latter suggestion), has not been examined.

Other than the paper by Shmuelof and Zohary (2008), no other papers have considered measures of observed action viewpoint in fMRI analyses. However, this question has been addressed to some extent in studies examining mental imagery. For example, Ruby and Decety (2001) conducted a PET imaging study in which participants had to imagine motor tasks (e.g. imagining the use of objects such as a razor which was presented on screen, or imagining the performance of verbally described tasks). Participants were instructed to generate mental images of the action being performed from either an egocentric (“first person perspective”, as though observing themselves perform the action from their own natural vantage point) or allocentric (“third person perspective”, as though observing an experimenter perform the action from a “three-quarters view”) viewpoint. Activity during both conditions was compared to a baseline condition; for object observation, the baseline condition involved the passive observation of a set of objects not used in the imagery conditions, and for auditory descriptions the baseline condition consisted of descriptions of landscapes not including humans or animals. Imagining egocentric actions led to increased activity in the left Inferior Parietal Lobe, Precentral Gyrus and Supplementary Motor Cortex, while imagining allocentric actions revealed increases in activity of the Left Precentral Gyrus and Superior Frontal Gyrus, as well as right Inferior Parietal Lobule activity. Therefore, the agency of the imagined actor affected participant Inferior Parietal Lobule activity in a manner consistent with studies using visual observation (Shmuelof and Zohary, 2008); the differences in brain activity were likely due to selection based on agency, as the instructions provided to participants explicitly stated to imagine the action being performed by either themselves or another person.

The studies discussed above consider the role of the human mirror system in the imitation and learning of actions. These data suggest that motor areas involved in action execution are primed by the observation of action, and this activation primes the execution (imitation) of the same action. However, this account differs subtly from other proposals suggesting the mirror system may play a role in movement prediction (Miall, 2003), which would facilitate co-operative movements (see Newman-Norlund, van Schie, van Zuijlen and Bekkering, 2007), or in the understanding of the intentions of others (Blakemore and Frith, 2005). These proposals are prevalent in the action observation literature, and it is possible that the mirror system could be involved in all of these potential roles. At a basic level the mirror system may facilitate the automatic imitation of observed actions, but this does not mean it cannot provide a utility for other processes, such as facilitating movement prediction and allowing the observer to understand the intentions of others.

While studies of action observation and motor imagery have demonstrated modulatory effects of action viewpoint on brain activity, they have primarily examined the differences between actions presented from an egocentric viewpoint (congruent with the action being performed by the observer) or an allocentric viewpoint (congruent with the action being performed by another person in a fixed position). However, it is possible to present movements from different viewpoints within these two ranges, which itself may lead to automatic bottom-up modulations of mirror system activity driven by stimulus content. As previous evidence demonstrates that both top down and bottom up effects can modulate mirror system activity, it is therefore of interest to systematically examine the effects of changing the viewpoint from which an action is observed in order to ascertain whether small differences in stimulus content can modulate these effects. In the study presented here, observed action viewpoint was manipulated by rotating the observed hand at 45˚ increments in order to examine both when an observed action shifted from being represented egocentrically to being represented allocentrically, as well as to examine whether any low-level modulations due to the particular angle the hand was presented from would modulate these effects. It was hypothesised that the observation of action would lead to activity in areas associated with the human mirror system. Furthermore, based on data from Chapter 4, it was hypothesised that mirror system activity would differ for egocentric agency (0˚, 45˚ and 90˚ viewpoints) compared to allocentric agency (135˚ and 180˚ viewpoints).

5.3 Materials and Methods

5.3.1 Participants

BOLD fMRI measurements were collected from 10 participants (6 female, ages 22-26). All participants were right handed, had normal or corrected-to-normal vision, and were naive to the purposes of the study. Participants were screened for contraindications prior to scanning sessions. Experimental procedures were approved by the local ethics committee, and participants gave written informed consent prior to their participation.

5.3.2 Experimental Equipment and Setup

Video clips were recorded with a digital camera and later edited (using Edit Studio 5, Puremotion, USA) to have a fixed duration of 2 seconds. During the experiment, timing and display of stimuli was controlled by ‘Presentation’, a programme used for psychological experiment stimulus delivery (Neurobehavioral Systems). During the experiment participants observed the stimuli projected onto a screen behind the scanner via a mirror attached to the head coil.

5.3.3 MRI Data Acquisition

Functional MR data were acquired with a 3T Phillips scanner via echo-planar imaging (EPI) using an 8-channel parallel head coil. For each experimental run, 58 T2*-weighted echo planar images were collected (TR = 2.5s). Whole brain coverage was achieved with 44 slices (voxel size 3x3x3mm, acquisition matrix 80 x 80, FOV 240 x 240 x 132). Structural images were collected using T1-weighted images (voxel size 1x1x1mm).

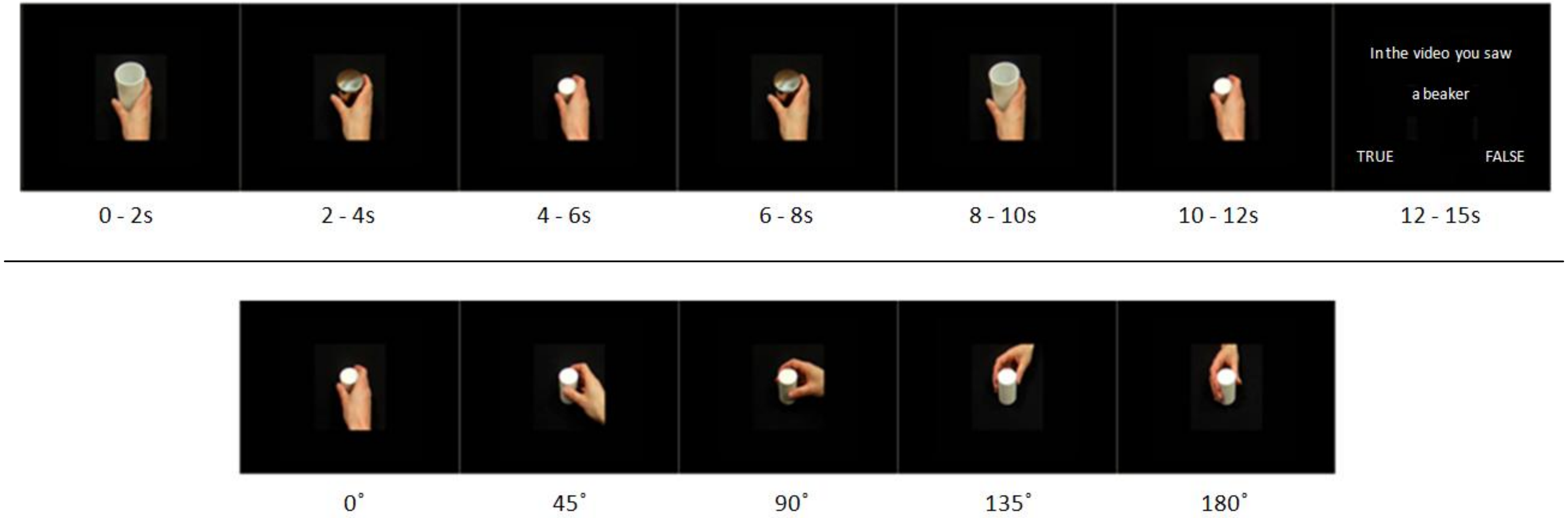

Figure 5-1: The upper Panel provides an example of the timeline for an experimental sequence. A blank screen was presented prior to each sequence. The sequence lasted 12 seconds overall, and was composed of 3 individual clips repeated twice in a random order. These clips depicted different objects (0-2s: a beaker, 2-4s: a salt cellar, 4-6s; a cylinder) being grasped, in this case by a hand which appeared in the 0° viewpoint. At the end of some blocks (1/3 chance), a question regarding the last video clip would appear (12-15s in the example above), and participants were required to respond to this with a button press (in the example provided the correct answer would be false, as the last video clip in the block depicts the cylinder). Lower panel provides examples of the different viewpoint conditions shown during the experiment.

5.3.4 Design and Procedure

Participants completed a total of 10 runs, each lasting approximately two and a half minutes. Each run consisted of six blocks of videos. Each block presented an uninterrupted sequence of the video stimuli (shown from one viewpoint) lasting for 12 seconds, created by presenting three different video clips repeated twice in a pseudo-random order (see Figure 5-1 for an example of a single block). Each video clip depicted an object (a cylinder, salt cellar or beaker) positioned at the centre of the screen. In control blocks, the video clips presented the object alone (with no accompanying action). In experimental conditions, the right hand of a female model would reach into the visible area of the clip, grasp the object, release it and move back out of shot. Therefore, for each experimental block the hand would reach in from a fixed angle relative to the participant (giving the different viewpoints of 0˚, 45˚, 90˚, 135˚ or 180˚), grasp the object, release it and then move back out of view a total of six times. In order to maintain participants' attention, a question regarding the last video clip seen would sometimes appear at the end of a block (questions were presented randomly following two of the six blocks in each run, and remained on screen for 3 seconds). These questions all took the format "In the video you saw..." (e.g. "In the video you saw the salt cellar") and required a true or false response from the participant, made using a button box held in the right hand. Blocks were separated by 12 seconds of blank screen, allowing adequate time for the recovery of the BOLD response between blocks.

5.3.5 Data Analysis

Data pre-processing, processing and analysis were all performed using the FMRIB software library (FSL; FMRIB, Oxford). Slice timing was corrected prior to processing, and volumes were motion corrected and realigned to the middle volume of the run using MCFLIRT. BOLD signals were high pass filtered using a Gaussian-weighted filter, and spatially filtered with a 6mm FWHM kernel.

Six explanatory variables were associated with each of the experimental conditions (objects being grasped from the viewpoints of 0˚, 45˚, 90˚, 135˚ and 180˚) as well as the control condition (objects presented alone). Question conditions were also modelled, and consequently all activation levels were calculated relative to the unmodelled (baseline) condition of observing a blank black screen. Prior to the main analyses, data pre-processing was conducted to examine and collate the data from each participant. First level analysis was conducted on each of the separate runs for each participant, and several contrasts were created to explore activity during the different experimental conditions (see below for details). For second level analysis, contrasts were combined for each participant based upon the first-level analysis using a fixed effects treatment of variance. Third level analysis compared this second level analysis across all participants and was combined using a mixed effects treatment of variance (FLAME 1 + 2).

5.3.5.1 Common Areas of Activation

This third level analysis examined which areas of the brain were responsive to the observation of action stimuli, regardless of the viewpoint. Using contrast masking, the contrast [OBS > BAS] revealed areas of the brain which showed greater activity during action observation conditions (i.e. OBS: 0˚, 45˚, 90˚, 135˚ and 180˚) compared to the unmodelled baseline condition (BAS) of observing a black screen.

5.3.5.2 Contrasts for Activity at Different Viewpoints

Further third level contrast analyses examined the effects of observing an action from different viewpoints. This was achieved by comparing the different action observation conditions with the control (CON) condition of observing objects with no actions. This resulted in the following five contrasts: [000 > CON], [045 > CON], [090 > CON], [135 > CON] and [180 > CON], which were all explored at the whole brain level.

5.3.5.3 Contrasts for Agency

Chapter 4 revealed effects dependent on the viewpoint from which an action was observed. Participant responses were faster when they observed actions they could perform themselves (‘egocentric’ actions) when compared with actions that could only be performed by another person (‘allocentric’ actions). Four contrasts were designed in order to examine whether similar effects were revealed in neural processing for egocentric agencies (viewpoints 0˚, 45˚ and 90˚) and allocentric agencies (viewpoints 135˚ and 180˚). The first contrast, [EGO > CON] revealed areas of the brain which showed greater activity for the observation of actions which were egocentrically framed compared to the control condition. The second contrast, [ALLO > CON] revealed areas of the brain which showed greater activity for the observation of actions which were allocentrically framed compared to the control condition. The contrast [EGO > ALLO] revealed areas of the brain which showed greater responses to egocentric stimuli compared to allocentric stimuli, while the contrast [ALLO > EGO] revealed areas showing greater activity for allocentric stimuli compared to egocentric stimuli.

5.3.5.3 Region of Interest Analysis: Superior Parietal Lobule and Previous Maxima

In order to gain a more comprehensive understanding of the activity revealed at the whole brain level, further exploratory Region of Interest (ROI) analyses were conducted on the data examining brain areas associated with the mirror system. Shmuelof and Zohary (2008) previously reported that activity in the anterior Superior Parietal Lobule was modulated by the viewpoint from which actions were observed. Therefore, a mask of the Superior Parietal Lobule was created for each hemisphere of the brain, and activity occurring in this region was examined using ROI analyses based on the five contrasts comparing activity from different viewpoints (i.e. [000 > CON], [045 > CON], [090 > CON], [135 > CON] and [180 > CON]). While Shmuelof and Zohary (2008) report activity local to the anterior Superior Parietal Lobule, it is difficult to objectively define this area using standard brain atlases. Therefore, small regions of interest (6x6x6 cubes of MNI space) centered on the locations of previous maxima reported by Shmuelof and Zohary (2008) were created to allow for more intricate examination of Superior Parietal Lobule activity. The locations of these regions of interest are presented in Table 5-1. As the coordinates originally stated by Shmuelof and Zohary (2008) were presented in Talairach space, a non-linear transformation was applied to convert them to values in MNI space (Brett, 2002). The data collected from each ROI analysis was examined using a 2x5 repeated measures ANOVA, with factors of hemisphere (left or right) and viewpoint (0˚, 45˚, 90˚, 135˚ or 180˚). The dependent measure was the percentage change in the BOLD signal.

Table 5-1:Coordinates for ROI analyses for local maxima identified by Shmuelof and Zohary (2008).

	TAL			MNI		
Area for Local Maxima	X	Y	Z	X	Y	Z
Egocentric, contralateral hand preference						
Left anterior Superior Parietal Lobule	-32	-45	52	-32	-49	54
Right anterior Superior Parietal Lobule	26	-49	65	26	-54	68
Allocentric, ipsilateral hand preference						
Left anterior Superior Parietal Lobule	-36	-55	54	-36	-59	56
Right anterior Superior Parietal Lobule	28	-47	62	28	-52	65

5.3.5.5 Region of Interest Analysis: Brodmann Areas

To further examine changes in BOLD activity during the study, region of interest analyses were conducted on the five contrasts comparing the different action observation conditions to the control condition. Five masks were created for this analysis. Three masks examined activity in areas traditionally associated with the human mirror system, which included Broca’s area (BA44), the Premotor Cortex (BA6), and the Inferior Parietal Lobule (area PF). Two further masks examined the Motor Cortex (BA4a and BA4p), which was chosen for examination due to its traditional role in the production of movements. Activity in these areas were compared using a 2x5 repeated measures ANOVA with factors of hemisphere (left or right) and viewpoint (0˚, 45˚, 90˚, 135˚ or 180˚).

5.4 Results

Average head movement for all participants across all ten runs was 0.14mm (maximum value of 1.03mm). This was deemed acceptable and so consequently data from all 10 participants were used in the analysis. Note that all data analysis presented in this chapter was originally performed in MNI space; the Talairach coordinates reported are provided for reference purposes, and were calculated using a non-linear transformation (Brett, 2002).

5.4.1 Common Areas of Activation

The contrast [OBS > BAS] revealed activity in brain areas for the observation of action from all viewpoints examined (see Figure 5-2). As well as activation of primarily visual areas, activity was also revealed in Premotor and Parietal areas. In the left hemisphere, Premotor activity occurred in the Paracingulate Gyrus, Precentral Gyrus and Supplementary Motor Cortex, while Anterior Intra-Parietal Sulcus activity was revealed in the Superior Parietal Lobule. In the right hemisphere, Premotor activity was revealed in the Postcentral Gyrus, Supplementary Motor Cortex and Superior Frontal Gyrus.

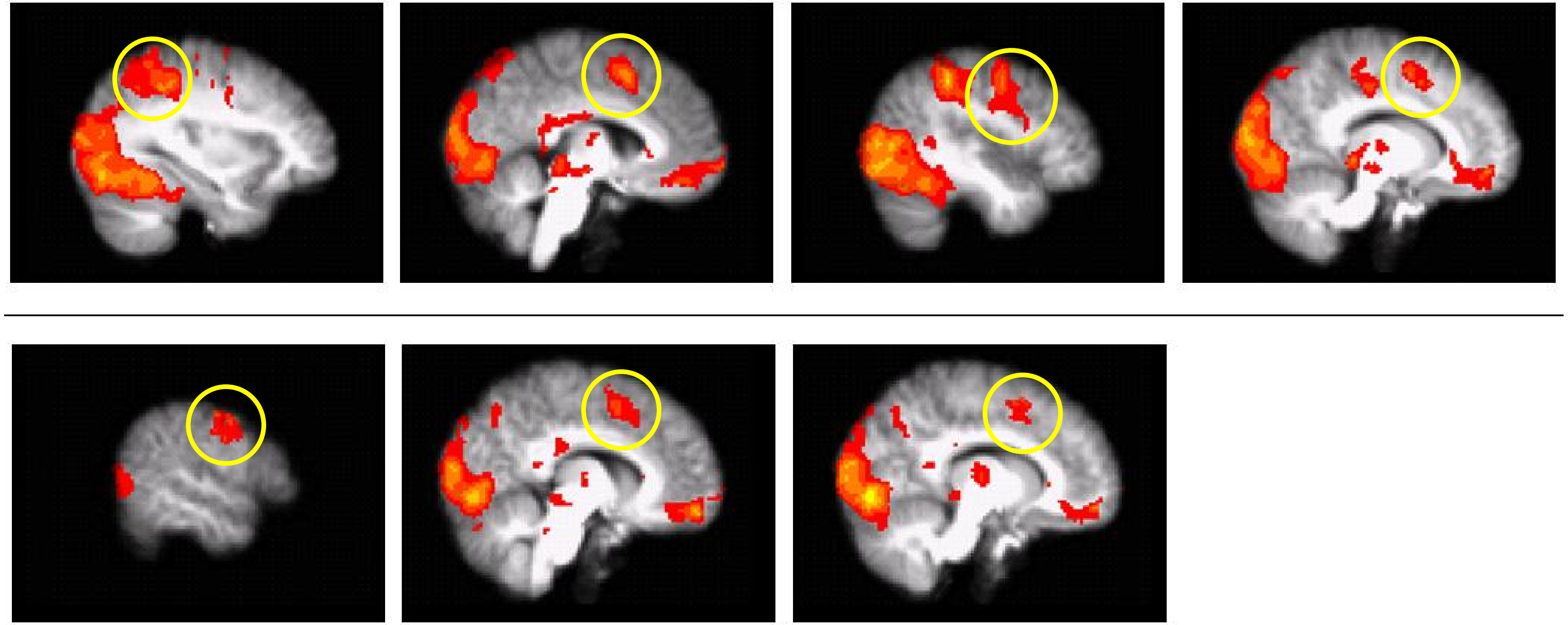

Figure 5-2: Significant activations in Premotor and Parietal brain areas for the contrast [OBS > BAS] as revealed by contrast masking. Upper panel shows left hemisphere activations for (from left to right) the Superior Parietal Lobule, Paracingulate Gyrus, Precentral Gyrus and Supplementary Motor Cortex. Lower panel shows right hemisphere activations for (from left to right) the Postcentral Gyrus, Supplementary Motor Cortex and Superior Frontal Gyrus. Coordinates of the activations shown are presented in Table 5-2.

Table 5-2: Areas active for the contrast [OBS > BAS] as revealed by contrast masking.

** Denotes activity in Premotor and Parietal areas according to the Julich atlas.*

Area for Local Maxima	Z Score	TAL X	TAL Y	TAL Z	MNI X	MNI Y	MNI Z
[OBS > BAS] Left Hemisphere							
Postcentral Gyrus	5.53	-44	-35	46	-44	-38	48
Occipital Pole	5.37	-8	-94	18	-8	-98	14
Thalamus	5.22	-18	-29	0	-18	-30	-2
Lateral Occipital Cortex	5.13	-46	-76	0	-46	-78	-4
Superior Parietal Lobule*	4.58	-32	-41	43	-32	-44	44
Paracingulate Gyrus*	4.34	-4	12	47	-4	10	52
Precentral Gyrus*	4.12	-44	-2	42	-44	-4	46
Frontal Medial Cortex	4.12	-12	50	-11	-12	52	-10
Supplementary Motor Cortex*	3.97	-12	6	48	-12	4	52
Frontal Pole	3.88	-8	54	-9	-8	56	-8
[OBS > BAS] Right Hemisphere							
Lingual Gyrus	6.23	14	-80	-1	14	-82	-6
Lateral Occipital Cortex	5.30	48	-73	7	48	-76	4
Frontal Pole	4.76	8	54	-14	8	56	-14
Precentral Gyrus	4.11	61	-2	35	62	-4	38
Postcentral Gyrus*	3.87	57	-6	44	58	-8	48
Supplementary Motor Cortex*	3.72	8	8	49	8	6	54
Cingulate Gyrus	3.56	4	-24	25	4	-26	26
Superior Frontal Gyrus*	3.39	12	14	42	12	12	56

5.4.2 Contrasts for Activity at Different Viewpoints

The contrasts [000 > CON], [045 > CON], [090 > CON], [135 > CON] and [180 > CON] revealed activity occurring during the observation of actions performed from separate, specific viewpoints. All contrasts revealed activity in the Superior Parietal Lobule. However, this activity occurred bilaterally only for the contrast [000 > CON], while in all other contrasts examined, Superior Parietal Lobule activity was constrained to the left hemisphere alone (See Figure 5-3). Local maxima for these activations are reported in Tables 5-3 to 5-7, which also report brain activity revealed in other regions.

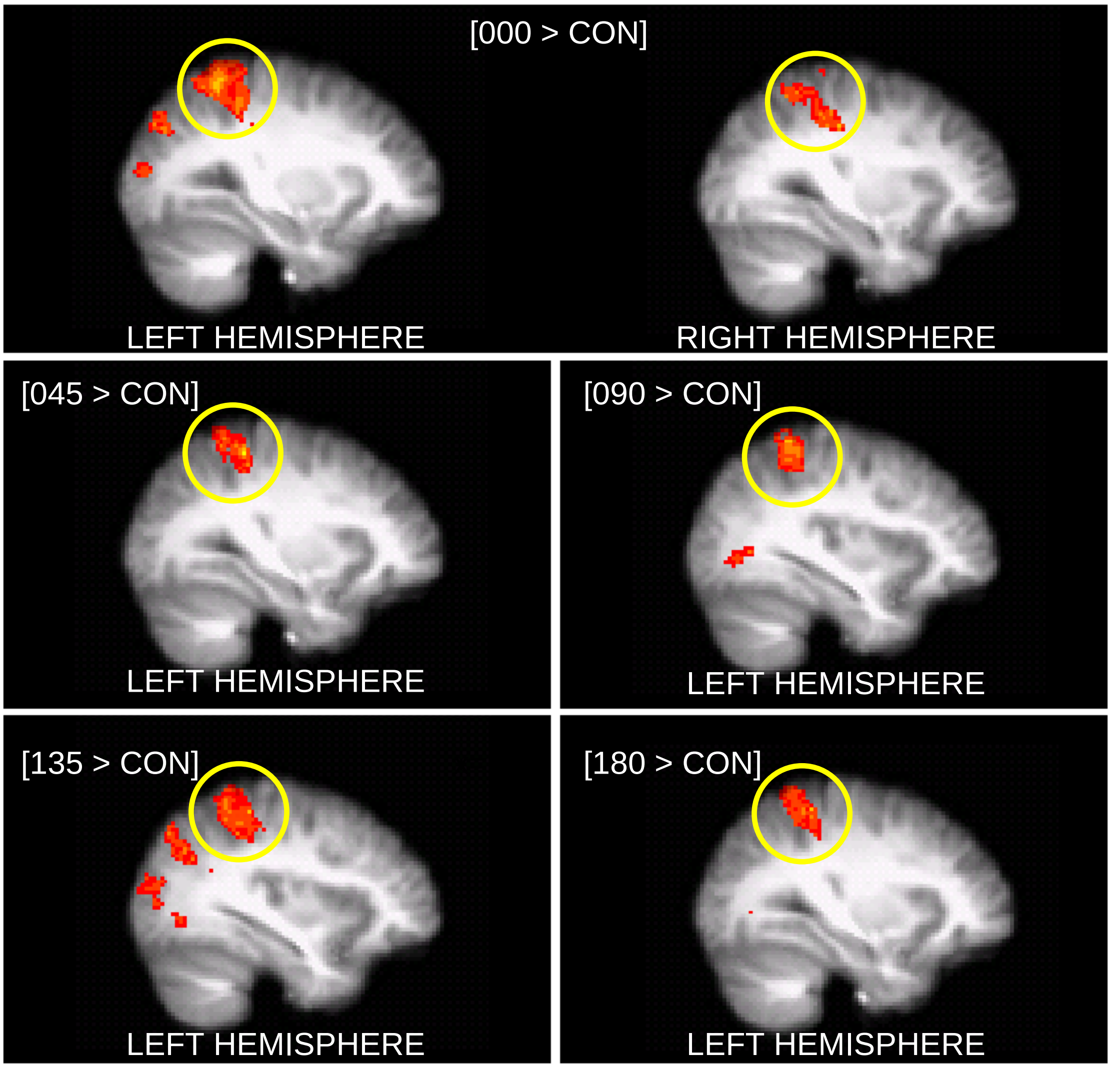

Figure 5-3: Significant activity in the Superior Parietal Lobule for the action observation viewpoint contrasts (see Tables 5-3 to 5-7 for coordinates of local maxima). Top panel shows bilateral activation, which occurred for the [000 > CON] contrast alone. Other panels show left hemisphere activity: Middle left panel [045 > CON], middle right panel [090 > CON], bottom left panel [135 > CON] and bottom right panel [180 > CON].

*Table 5-3: Areas active for the contrast [000 > CON]. * Denotes activity in Premotor and Parietal areas according to the Julich atlas.*

		TAL			MNI		
Area for Local Maxima	Z Score	X	Y	Z	X	Y	Z
[000 > CON] Left Hemisphere							
Lateral Occipital Cortex	4.94	-44	-65	12	-44	-68	10
Supracalcarine Cortex	4.33	-2	-85	12	-2	-88	8
Superior Parietal Lobule*	4.21	-28	-51	48	-28	-50	60
Postcentral Gyrus*	4.08	-39	-35	46	-30	-38	48
[000 > CON] Right Hemisphere							
Lateral Occipital Cortex	4.82	44	-69	18	44	-72	16
Middle Temporal Gyrus	4.25	50	-54	3	50	-56	0
Postcentral Gyrus*	4.15	32	-23	38	32	-26	40
Superior Parietal Lobule*	3.68	25	-36	52	26	-40	54

*Table 5-4: Areas active for the contrast [045 > CON]. * Denotes activity in Premotor and Parietal areas according to the Julich atlas.*

		TAL			MNI		
Area for Local Maxima	Z Score	X	Y	Z	X	Y	Z
[045 > CON] Left Hemisphere							
Postcentral Gyrus*	5.37	-30	-34	53	-30	-38	56
Superior Parietal Lobule*	4.40	-32	-44	56	-32	-48	58
Lateral Occipital Cortex	4.40	-48	-68	9	-48	-70	6
Middle Temporal Gyrus	4.10	-42	-56	6	-42	-58	4
Occipital Pole	4.03	-2	-86	34	-2	-90	32
Cuneal Cortex	3.55	-8	-85	19	-8	-88	16
[045 > CON] Right Hemisphere							
Lateral Occipital Cortex	4.57	55	-62	7	56	-64	4

*Table 5-5: Areas active for the contrast [090 > CON]. * Denotes activity in Premotor and Parietal areas according to the Julich atlas.*

		TAL			MNI		
Area for Local Maxima	Z Score	X	Y	Z	X	Y	Z
[090 > CON] Left Hemisphere							
Lateral Occipital Cortex	5.08	-48	-66	9	-48	-68	6
Superior Parietal Lobule*	4.23	-34	-40	54	-34	-44	64
Lingual Gyrus	4.22	-6	-72	-3	-6	-74	-8
Occipital Fusiform Gyrus	3.69	-18	-76	-11	-18	-78	-18
[090 > CON] Right Hemisphere							
Lateral Occipital Cortex	4.12	51	-69	13	52	-72	10

*Table 5-6: Areas active for the contrast [135 > CON]. * Denotes activity in Premotor and Parietal areas according to the Julich atlas.*

		TAL			MNI		
Area for Local Maxima	Z Score	X	Y	Z	X	Y	Z
[135 > CON] Left Hemisphere							
Lateral Occipital Cortex	5.40	-48	-67	11	-48	-70	8
Lingual Gyrus	4.65	-6	-76	-1	-6	-78	-6
Postcentral Gyrus*	4.43	-34	-32	53	-34	-36	56
Occipital Pole	4.22	-24	-86	36	-24	-90	34
Superior Parietal Lobule*	4.08	-36	-36	50	-36	-42	52
Cingulate Gyrus	3.88	-2	-42	15	-2	-44	14
Precuneous Cortex	3.68	-6	-52	14	-6	-54	12
[135> CON] Right Hemisphere							
Lateral Occipital Cortex	4.01	46	-58	0	46	-60	-4
Precuneous Cortex	3.70	6	-52	15	6	-54	14
Middle Temporal Gyrus	3.63	48	-56	3	48	-58	0
Cingulate Gyrus	3.62	4	-46	15	4	-48	14

*Table 5-7: Areas active for the contrast [180 > CON]. * Denotes activity in Premotor and Parietal areas according to the Julich atlas.*

		TAL			MNI		
Area for Local Maxima	Z Score	X	Y	Z	X	Y	Z
[180 > CON] Left Hemisphere							
Lateral Occipital Cortex	5.30	-48	-67	11	-48	-70	8
Superior Parietal Lobule*	4.20	-30	-36	55	-30	-40	58
Angular Gyrus	4.04	-46	-57	16	-46	-60	14
Cingulate Gyrus	3.79	-2	-44	15	-2	-46	14
Parahippocampal Gyrus	3.77	-2	-41	0	-2	-42	-2
Middle Temporal Gyrus	3.67	28	-69	-12	28	-70	-18
[180 > CON] Left Hemisphere							
Lateral Occipital Cortex	4.92	48	-73	9	48	-76	6
Occipital Fusiform Gyrus	4.19	22	-70	-5	22	-72	-10
Lingual Gyrus	4.19	12	-78	-5	12	-80	-10
Cingulate Gyrus	3.57	4	-44	15	4	-46	14

5.4.3 Contrasts for Agency

The contrasts [EGO > CON], [ALLO > CON], [EGO > ALLO] and [ALLO > EGO] allowed for the examination of perceived action agency on participant brain activity. The rationale for these contrasts was based on the data presented in Chapter 4 (Experiments 1 and 3). Therefore, the egocentric viewpoints grouping ("EGO" contrasts) consisted of actions viewed from 0˚, 45˚ and 90˚, while the allocentric viewpoints grouping ("ALLO" contrasts) consisted of actions viewed from 135˚ and 180˚.

The activations revealed by the contrast [EGO > CON] are presented in Table 5-8. Activity was revealed in several areas of the left hemisphere classically associated with the human mirror system, including the Superior Parietal Lobule and several Premotor areas (see Figure 5-4). For the contrast [ALLO > CON] (see Table 5-9), the data revealed some activity in left hemisphere Premotor areas (see Figure 5-5), but did not reveal activations of the Superior Parietal Lobule.

For the contrast [EGO >ALLO] (see Table 5-10), activity in left hemisphere areas traditionally associated with the human mirror system was demonstrated in the Superior Parietal Lobule and the Precentral Gyrus (see Figure 5-6). However, the contrast [ALLO > EGO] (See Table 5-11), revealed no activity in areas of the brain traditionally associated with the human mirror system.

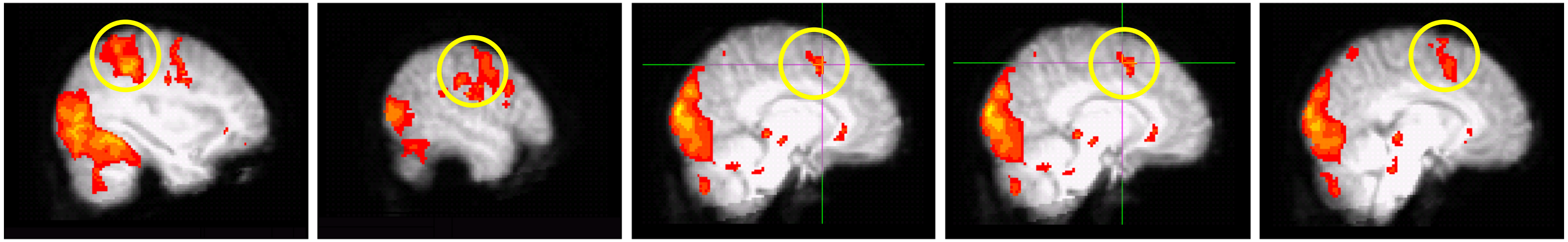

Figure 5-4: Significant activations in Premotor and Parietal brain areas for the contrasts [EGO > CON]. Panels shows left hemisphere activations for (from left to right) the Superior Parietal Lobule, Supramarginal Gyrus, Paracingulate Gyrus, Supplementary Motor Cortex and Superior Frontal Gyrus. Coordinates for the activations shown are presented in Table 5-8.

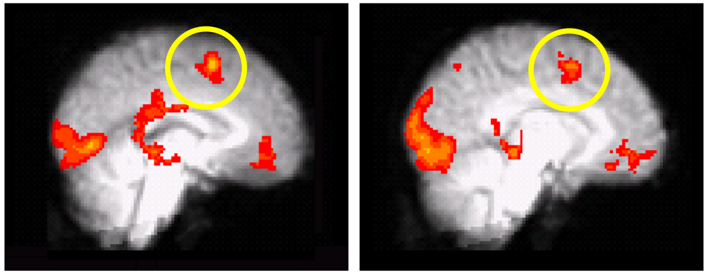

Figure 5-5: Significant activations in Premotor brain areas for the contrasts [ALLO > CON]. Panels show left hemisphere activations for (from left to right) the Supplementary Motor Cortex and Cingulate Gyrus. Coordinates for these activations are presented in Table 5-9.

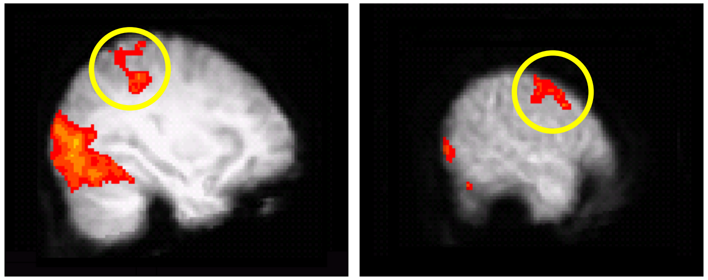

Figure 5-6: Significant Activations in the Premotor and Parietal brain areas for the contrast [EGO > ALLO]. Panels show left hemisphere activations for (from left to right) the Superior Parietal Lobule and the Precentral Gyrus. Coordinates for these activations are presented in Table 5-10.

*Table 5-8 Areas active for [EGO > CON]. * Denotes Premotor and Parietal activity.*

		TAL			MNI		
Area for Local Maxima	Z Score	X	Y	Z	X	Y	Z
[EGO > CON] Left Hemisphere							
Lateral Occipital Cortex	5.68	-44	-79	11	-44	-82	8
Occipital Pole	5.54	-8	-96	17	-8	-100	14
Superior Parietal Lobule*	4.80	-32	-41	43	-32	-44	44
Postcentral Gyrus	4.45	-46	-34	53	-46	-38	56
Supramarginal Gyrus*	4.26	-51	-22	31	-52	-24	32
Thalamus	4.70	-20	-29	0	-20	-30	-2
Pallidum	3.85	-16	6	2	-16	6	-2
Putamen	3.74	-20	8	1	-20	8	2
Insular Cortex	3.65	-20	12	-2	-20	12	-2
Frontal Pole	3.89	-30	48	-14	-30	50	-14
Frontal Occipital Cortex	3.66	-24	35	-5	-24	36	-4
Subcallosal Cortex	3.51	-2	23	1	-2	24	2
Paracingulate Gyrus*	3.87	-10	14	45	-10	12	50
Supplementary Motor Cortex*	3.81	-10	6	48	-10	4	52
Superior Frontal Gyrus*	3.57	-6	12	49	-6	10	54
[EGO > CON] Right Hemisphere							
Lingual Gyrus	5.48	16	-78	-5	16	-80	-10
Brain-Stem	3.72	6	-31	-3	6	-32	-6
Hippocampus	3.61	24	-22	-7	24	-22	-10
Thalamus	3.58	22	-29	5	22	-30	4

*Table 5-9 Areas active for [ALLO > CON]. * Denotes Premotor activity.*

Area for Local Maxima	Z Score	TAL X	TAL Y	TAL Z	MNI X	MNI Y	MNI Z
[ALLO > CON] Left Hemisphere							
Lateral Occipital Cortex	5.60	-48	-69	11	-48	-72	8
Temporal Occipital Cortex	5.01	-34	-51	-16	-34	-52	-22
Postcentral Gyrus	4.98	-34	-35	46	-34	-38	48
Supplementary Motor Cortex*	4.81	-2	10	49	-2	8	54
Cingulate Gyrus*	3.21	-8	8	38	-8	6	42
[ALLO > CON] Right Hemisphere							
Lingual Gyrus	5.43	8	-78	1	8	-80	-4
Cingulate Gyrus	4.04	2	41	-4	2	42	-2
Paracingulate Gyrus	3.97	4	40	-9	4	42	-8
Frontal Pole	3.63	10	56	-8	10	58	-6

*Table 5-10 Activity for contrast [EGO > ALLO]. * Denotes Premotor and Parietal activity.*

		TAL			MNI		
Area for Local Maxima	Z Score	X	Y	Z	X	Y	Z
[EGO > ALLO] Left Hemisphere							
Occipital Pole	5.93	-6	-92	19	-6	-96	16
Lateral Occipital Cortex	5.35	-22	-86	25	-22	-90	22
Superior Parietal Lobule*	3.88	-30	-36	48	-30	-40	50
Postcentral Gyrus	3.72	-36	-34	53	-36	-38	56
Precentral Gyrus*	3.86	-55	7	31	-56	6	34

Table 5-11 Areas active for the contrast. [ALLO > EGO].

Area for Local Maxima	Z Score	TAL X	TAL Y	TAL Z	MNI X	MNI Y	MNI Z
[ALLO > EGO] Left Hemisphere							
Lateral Ventricle	3.98	-22	-44	11	-22	-46	10
Caudate	3.87	-16	-16	21	-16	-18	22
[ALLO > EGO] Right Hemisphere							
Thalamus	3.92	8	-25	1	8	-26	0
Cingulate Gyrus	3.84	18	-40	8	18	-42	6
Lateral Ventricle	3.84	10	-28	16	10	-30	16
Intracalcarine Cortex	4.02	16	-68	9	16	-70	6
Precuneous Cortex	3.98	4	-56	10	4	-58	8
Cuneal Cortex	3.77	18	-65	24	18	-68	22
Lateral Occipital Cortex	3.71	14	-74	44	14	-78	44

5.4.4 Region of Interest Analysis: Superior Parietal Lobule

As Shmuelof and Zohary (2008) previously demonstrated that the Superior Parietal Lobule was sensitive to the viewpoint from which an action is observed, this analysis first examined the Superior Parietal Lobule for each hemisphere, and then considered activity in this area based on the location of previously identified maxima. When examining the Superior Parietal Lobule in each hemisphere, a significant effect of hemisphere was revealed ($F[1,9]=14.51$, $p < 0.01$). This effect demonstrated a significantly greater change in the BOLD signal for the left hemisphere compared to the right (Mean: left hemisphere = 0.13%, right hemisphere = 0.05%, SEM: 0.17% vs 0.27%). The main effect for viewpoint failed to achieve statistical significance ($F[4,36] = 2.90$, $p = 0.12$), and the interaction between hemisphere and viewpoint was also not of statistical significance ($F[4,36] = 3.82$, $p = 0.07$). This data is presented in Figure 5-7.

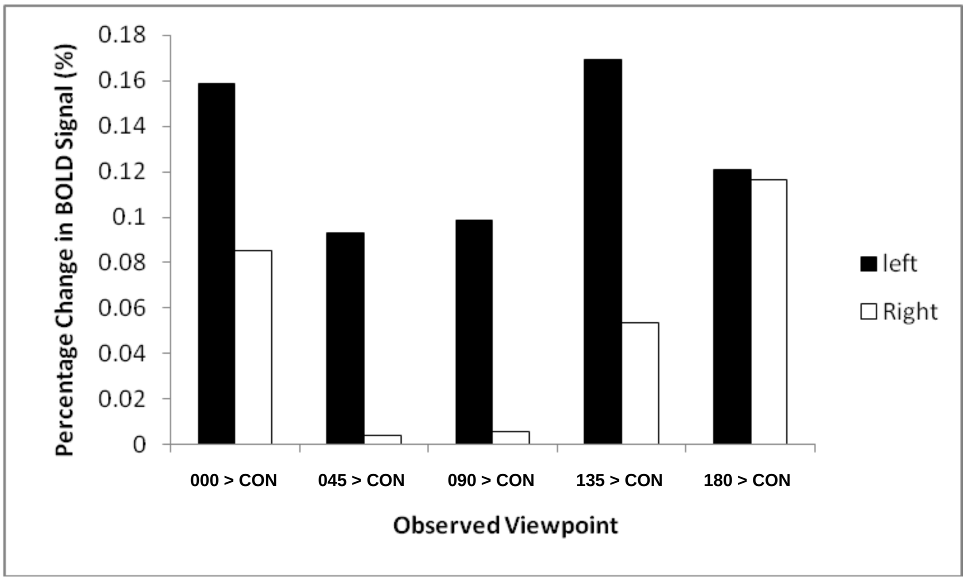

Figure 5-7: Changes in regional blood flow to the Superior Parietal Lobule.

Figure 5-8 presents the data for the analysis of Superior Parietal Lobule areas based on the local maxima reported by Shmuelof and Zohary (2008) which showed a preference for contralateral hand activity during the observation of action from an egocentric viewpoint (i.e. consistent with the 0° viewpoint presented in this study). This analysis revealed a significant main effect of hemisphere (F[1,9] = 8.70, $p < 0.05$), with the change in BOLD signal to the left hemisphere being greater than the change found in the right hemisphere (Mean: left hemisphere = 0.23%, right hemisphere = 0.08%, SEM: 0.04% vs 0.04%). The main effect of viewpoint was not statistically significant (F[4,36] = 3.24, $p = 0.10$), nor was the interaction between hemisphere and viewpoint (F[4,36] = 3.97, $p = 0.07$).

Figure 5-9 presents the data for the analysis of Superior Parietal Lobule areas identified by Shmuelof and Zohary (2008) which previously demonstrated a preference for ipsilateral hand activity during action observation from an allocentric viewpoint (consistent with the 180° viewpoint presented in this study). This analysis initially revealed a main effect for viewpoint (F[4,36] = 8.05, $p < 0.05$). However, no significant differences were apparent when the effect was analysed using pairwise comparisons with a Bonferroni interval adjustment. The main effect of hemisphere was not of statistical significance (F[1,9] = 0.48, $p = 0.51$), neither was the interaction between hemisphere and viewpoint (F[4,36] = 0.38, $p = 0.51$).

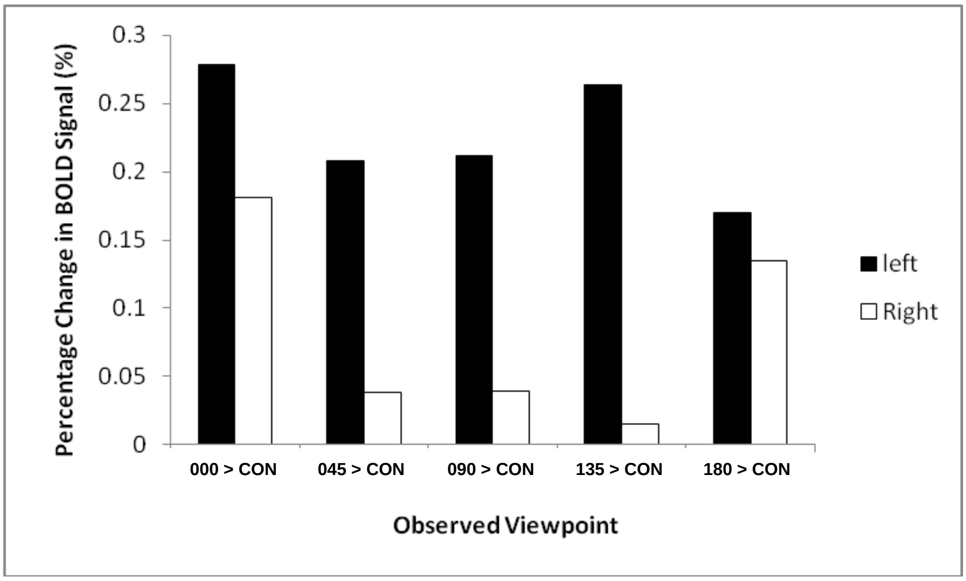

Figure 5-8: Changes in regional blood flow to the Superior Parietal Lobule areas previously revealed to show a preference for the contralateral hand viewed from an egocentric viewpoint. Areas examined in each hemisphere are based on coordinates identified by Shmuelof and Zohary (2008).

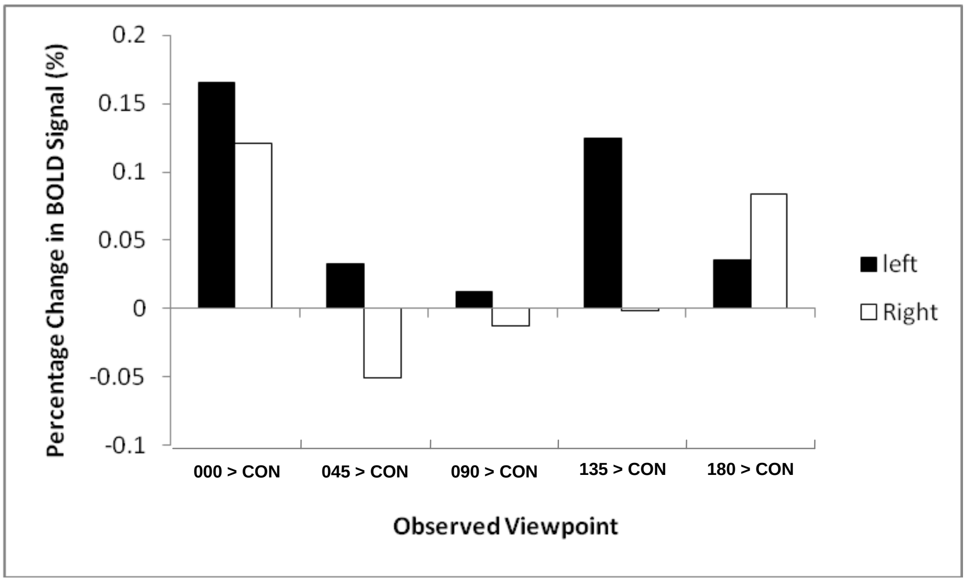

Figure 5-9: Changes in regional blood flow to the Superior Parietal Lobule areas previously revealed to show a preference for the ipsilateral hand viewed from an allocentric viewpoint. Areas examined in each hemisphere are based on coordinates identified by Shmuelof and Zohary (2008).

5.4.5 Region of Interest Analysis: Brodmann Areas

This analysis examined a number of areas of the brain defined by the Brodmann atlas (with areas traditionally associated with the human mirror system considered first). Repeated measures ANOVA analysis of activity occurring in Broca's area (BA44; see Figure 5-10) revealed no significant main effect of hemisphere ($F[1,9] = 3.24$, $p = 0.11$), or viewpoint ($F[4,36] = 0.65$, $p = 0.65$), and no significant interaction between these factors ($F[4,36] = 0.18$, $p = 0.94$). Similarly, the analysis of the Inferior Parietal Lobule (area PF; see Figure 5-11) revealed no significant main effects of hemisphere ($F[1,9] = 0.57$, $p = 0.47$) or viewpoint ($F[4,36] = 1.10$, $p = 0.43$), and no interaction between the two factors ($F[4,36] = 0.33$, $p = 0.85$). However, the analysis of the Premotor Cortex (BA6; see Figure 5-12) revealed a significant main effect of hemisphere ($F[1,9] = 26.39$, $p < 0.01$). This effect revealed that the percentage change in BOLD signal to the left hemisphere was greater than the percentage change in BOLD signal to the right hemisphere (Mean: left hemisphere = 0.013%, right hemisphere = -0.034%, SEM 0.033% vs -0.034%). There was no significant main effect of viewpoint ($F[4,36] = 0.53$, $p = 0.27$), and no significant interaction between hemisphere and viewpoint ($F[4,36] = 0.86$, $p = 0.54$).

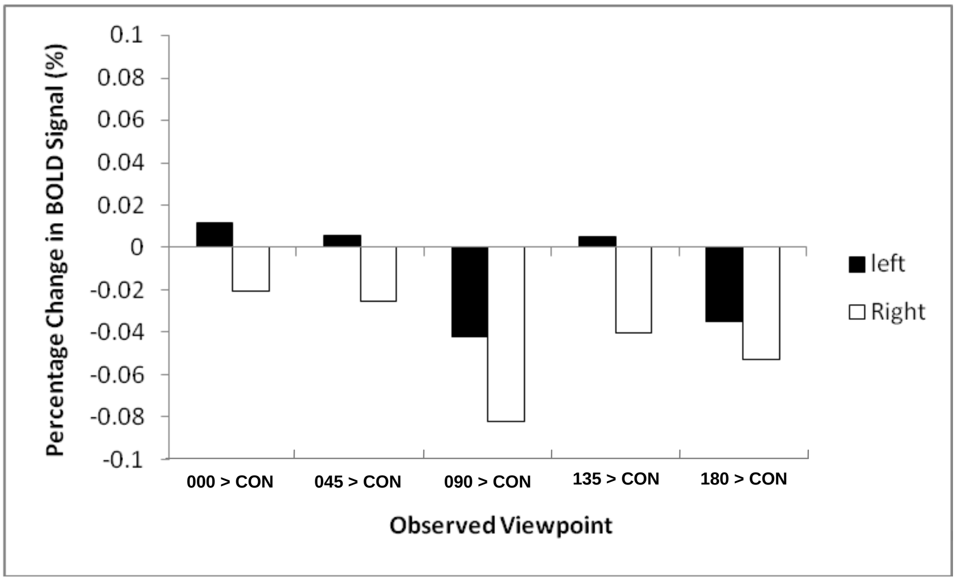

Figure 5-10: Changes in regional blood flow for Broca's area (BA44).

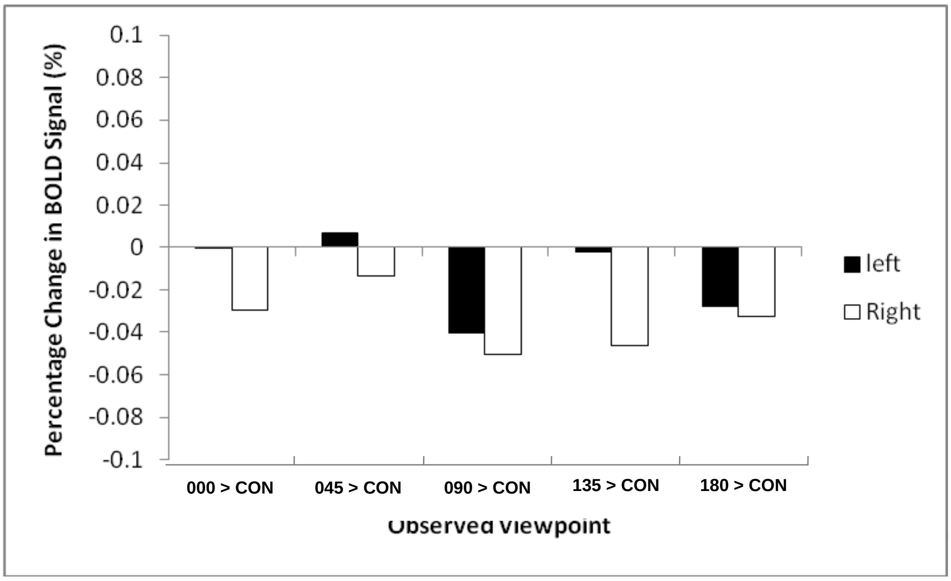

Figure 5-11: Changes in regional blood flow for the Inferior Parietal Lobule (PF).

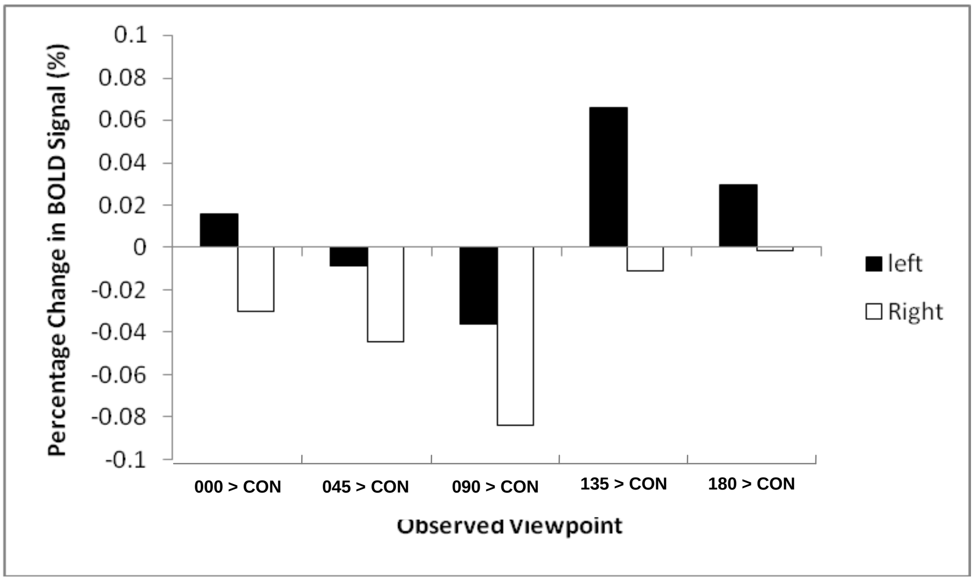

Figure 5-12: Changes in regional blood flow for the Premotor Cortex (BA6).

For the analysis of the Motor Cortex, the analysis of BA4a (see Figure 5-13) revealed a significant main effect of hemisphere ($F[1,9] = 12.07$, $p < 0.01$), with the percentage change in BOLD signal to the left hemisphere being greater than the percentage change in BOLD signal to the right hemisphere (left hemisphere = 0.031%, right hemisphere = -0.012%, SEM: 0.029% vs 0.028%). No significant main effect of viewpoint ($F[4,36] = 2.12$, $p = 0.20$) or significant interaction between the factors of hemisphere and viewpoint ($F[4,36] = 1.59$, $p = 0.29$) occurred. The analysis of BA4p (see Figure 5-14) also revealed a significant main effect of hemisphere ($F[1,9] = 8.48$, $p < 0.05$), with greater changes in the BOLD signal occurring in the left hemisphere than the right (Mean: left hemisphere = 0.021%, right hemisphere = -0.011%, SEM: 0.021% vs 0.013%). Again, no significant main effect of viewpoint ($F[4,36] = 1.85$, $p = 0.24$) or interaction between hemisphere and viewpoint ($F[4,36] = 2.07$, $p = 0.20$) was present.

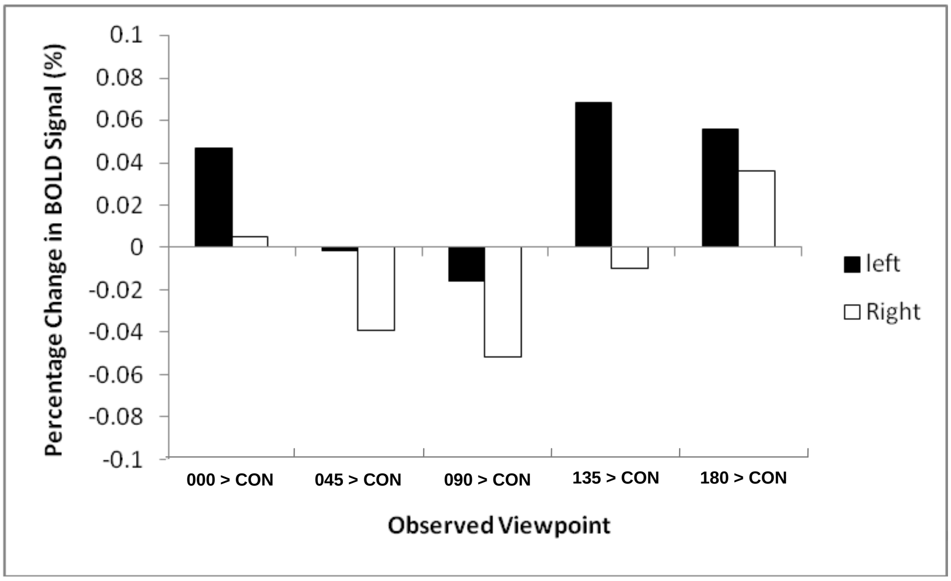

Figure 5-13: Changes in regional blood flow for the Motor Cortex (BA4a).

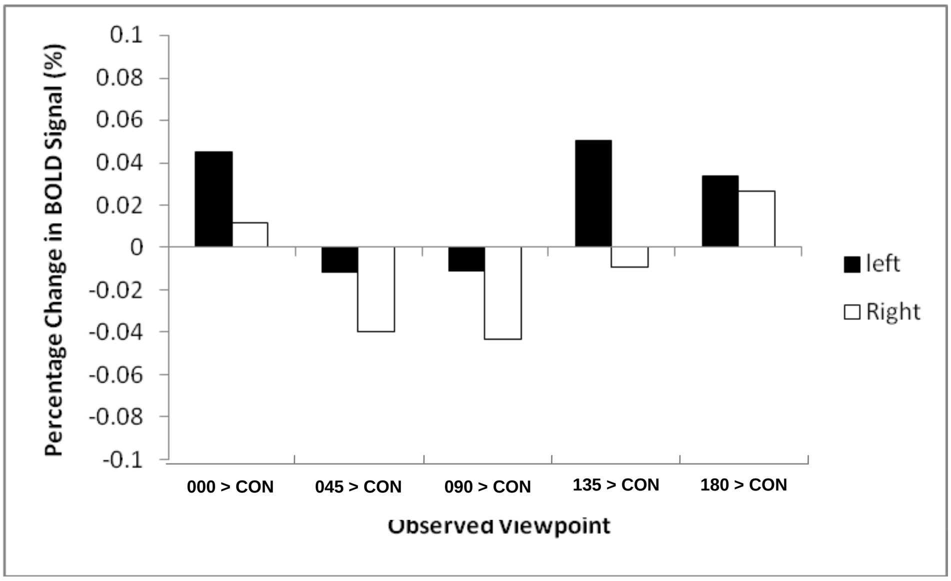

Figure 5-14: Changes in regional blood flow for the Motor Cortex (BA4p).

5.5 Discussion

Previous human neuroimaging studies have demonstrated activity in the Premotor and Parietal cortices during the observation of action (for examples see Buccino et al., 2001; 2004a: 2004b; Shmuelof and Zohary, 2008), and while recent studies have demonstrated that this activity can be modulated by the viewpoint from which actions are observed, only a small selection of viewpoints have been examined. The aim of the study presented here was to examine whether the viewpoint from which an action is observed modulates brain activity. While it was first hypothesised that the observation of action would lead to activity in the Premotor and Parietal regions, the main focus of the study was to examine whether this activity was modulated by the viewpoint from which actions were observed. Several analyses were conducted at both the whole brain and region of interest level in order to test the hypothesis and fully understand the data. The results presented here not only demonstrate significant activation of areas in the human brain classically associated with the mirror system, but also reveal differences in the activity for the hemispheres of the brain dependent on the viewpoint from which actions are observed, and differences in activity dependent on the agency of the observed actions.

The initial analysis examined common areas of activation during action observation at the whole brain level, contrasting activity for all action observation conditions with the activity occurring during the unmodelled baseline (the contrast [OBS > BAS]). This revealed significant activity in the Premotor Cortex and Superior Parietal Lobule during the observation of action. The activation of these areas in response to the observation of actions was consistent with data from primate neurophysiology and human neuroimaging. Single cell recording studies have demonstrated the existence of mirror neurons in primate Premotor

Cortex area F5 (di Pellegrino et al., 1992; Rizzolatti et al., 1996; Gallesse et al., 1996) and primate Parietal area PF (Rizzolatti et al., 2001; Fogassi et al., 2005) in response to action observation and execution. The Premotor and Parietal areas active in the study presented here are often considered to be the human homologues of primate areas F5 and PF (for a review see Rizzolatti et al., 2009). Furthermore, the activations revealed were consistent with previous studies in humans (Buccino et al., 2001; 2004a; 2004b; Shmuelof and Zohary, 2008) which have been attributed to the human mirror system. Together, these data strongly suggest that the Premotor and Parietal activity revealed in the study presented here represent activation of the human mirror system.

The analyses of activity for actions observed from different viewpoints compared to the control condition ([000 > CON], [045 > CON], [090 > CON], [135 > CON] and [180 > CON]) all revealed significant activity in the Superior Parietal Lobule. This activity was predicted prior to the experiment based on previous data; Shmuelof and Zohary (2008) recently demonstrated activity in the anterior Superior Parietal Lobule during action observation, and suggested that activity in this area was sensitive to the viewpoint from which actions were observed. In the study presented here, the contrast analyses all revealed activity occurring in the left hemisphere. This finding could be attributed to the video stimuli used in this study, as they all depicted actions performed by a right hand. However, it is noteworthy that the contrast for the 0˚ viewpoint ([000 > CON]) elicited *bilateral* Superior Parietal Lobule activity. This data may suggest the presence of a stronger representation for actions presented from the 0˚ viewpoint compared to other observed movements. This interpretation is consistent with previous neuroimaging studies which have attributed bilateral activations of the Parietal Lobe to the presence of stronger representations of observed actions (Buccino et al., 2004b). A further contrast analysis which grouped the observed actions in terms of agency, examining differences between egocentric actions (0˚, 45˚ and 90˚ viewpoints) and allocentric actions (135˚ and 180˚ viewpoints), revealed significant Superior Parietal Lobule activity for the observation of egocentric actions, but not for the observation of allocentric actions. This suggests that greater mirror system activity occurred in the egocentrically framed conditions. Such a proposal is also supported by behavioural evidence, which demonstrate improved performance when actions are observed from a viewpoint consistent with the observer's natural vantage point compared to other viewpoints (see for example Vogt et al., 2003; Gianelli et al., 2008; Experiments 1 and 3 of Chapter 4). Together, these data may suggest that a stronger representation exists for actions observed from a viewpoint consistent with the observer's own natural vantage point compared to other viewpoints.

In order to further understand how brain activity differed in correspondence to the changes in viewpoint, a series of region of interest (ROI) analyses were conducted. These analyses concentrated on the areas associated with the mirror neuron system as demonstrated in a previous study (Shmuelof and Zohary, 2008), examining the activity of the Superior Parietal Lobule. The data revealed only significant main effects of the hemisphere examined, indicating greater activity in the left hemisphere compared to the right hemisphere (effectively demonstrating the same effect as revealed for the analysis at the whole brain level). The ROI analysis based on Brodmann areas revealed similar findings, with significant effects in the Premotor Cortex (BA6) and motor system areas (BA4a and BA4p) showing greater activity occurring in the left hemisphere compared to the right hemisphere. This effect was consistent with the previous findings and can be most likely explained by the experimental stimuli depicting movements performed by the right hand. Perhaps a more surprising result was the finding that no significant differences occurred in Broca's area or area PF, which have both been suggested to be part of the human mirror system in previous studies (Buccino et al., 2001; 2004a). A possible explanation for this could be the size of the areas examined relative to the size of the activations occurring within them. For example, Broca's area is classically associated with the production of speech (see Binkofski and Buccino, 2004), and it has only recently been revealed that a small section of this area also contains a representation of the hand (see Buccino et al., 2001; Binkofski and Buccino, 2004). Therefore, it is possible that any activity in response to the observation of the hand stimuli presented in this study was of too small a magnitude to cause an overall change in the BOLD activity for this area, as the analyses consider the average activity of all of the voxels within the defined area (for more on this issue see Poldrack, 2007). An alternative analysis would be to select regions of the brain that are smaller in volume and correspond more directly to the area of interest, such as creating a mask specifically based on the hand representation within Broca's area. However, at present, these volumes are not pre-determined for analyses, and would therefore require their manual selection (which may lead to subjective differences). The concept that only small areas of a particular brain region may be sensitive to the stimuli in the study presented here could explain why the trends for greater activity in the 0˚ and 180˚ viewpoints revealed in the ROI analysis of the Superior Parietal Lobule failed to achieve statistical significance. Data from Shmuelof and Zohary (2008) suggest that it is the *anterior* portion of this brain region which is sensitive to observed action viewpoint, but as it is difficult to define this region subjectively using standard brain atlases, the main analysis conducted in the study presented here considered this area as a whole. In an attempt to address this, areas based on the maxima previously identified by Shmuelof and Zohary (2008) were used to create small ROI masks for a more detailed analysis of small areas of the Superior Parietal Lobule. However, this analysis again only demonstrated trends in activity which were not of statistical significance. Therefore, while the analysis at the whole brain level suggests that there are different patterns of activation in the Superior Parietal Lobule for the different hemispheres of the brain during action observation, the ROI analyses conducted provided no further evidence that the activity which occurred in these contrasts was modulated by the viewpoint from which an action was observed.

When considering the data presented in this study in relation to the data provided by Shmuelof and Zohary (2008), there are several issues worthy of discussion. Shmuelof and Zohary (2008) reported bilateral activity in the Superior Parietal Lobule when participants observed actions from an egocentric viewpoint or allocentric viewpoint (consistent with the 0˚ viewpoint and 180˚ viewpoints as presented in this study). The data presented here partially replicate this finding, with the observation of action from the 0˚ viewpoint evoking bilateral activation in the Superior Parietal Lobule. However, only the left Superior Parietal Lobule was active during the other observed viewpoint conditions (45˚, 90˚, 135˚ and 180˚) in the study presented here. Furthermore, the data of Shmuelof and Zohary (2008) suggested a crossover interaction, with a preference for activity in the contralateral Superior Parietal Lobule for actions observed from an egocentric viewpoint, and a preference for activity in the ipsilateral Superior Parietal Lobule for actions observed from an allocentric viewpoint. In the study presented here, ROI analyses revealed no such interaction; only a significant main effect was revealed, demonstrating that the change in BOLD signal to the Superior Parietal Lobule in the left hemisphere was greater than the change in BOLD signal to the right hemisphere. The differences could be explained by the types of stimuli used in the two experiments; Shmuelof and Zohary (2008) examined only two viewpoints, but did so using stimuli depicting actions of both the left and right hand, while the study presented here examined five viewpoints, but only presented actions performed by the right hand. As the data presented here suggest that right hand stimuli activate the Superior Parietal Lobule in both hemispheres when seen from a 0˚ viewpoint, but only the left hemisphere when seen from all other viewpoints examined, it may be of interest to examine whether observing left hand stimuli from a 180˚ viewpoint would activate both hemispheres of the brain, but when viewed from other viewpoints only activate the right hemisphere. This could potentially explain both the data presented in the study here and the data of Shmuelof and Zohary (2008).

Another notable difference between the study presented here and the study of Shmuelof and Zohary (2008) is the choice of control conditions. While the study presented here controlled for canonical circuit activity (activations in response to the observation of graspable objects; see Grezes, Armony, Rowe and Passingham, 2003) by using a control condition in which objects were presented to participants with no accompanying action, Shmuelof and Zohary (2008) used scrambled versions of their object grasping clips as a control. Therefore, the data provided by Shmuelof and Zohary (2008) may contain additional activity unrelated to the observation of action due to activations of the canonical system, which would explain some of the discrepancies between their data and the study presented here. As the study presented here controlled for canonical activity, the data presented in this study represents activations due to the observation of action alone.

In summary, the data presented here suggest that observing actions from different viewpoints can lead to the activation of different areas of the brain. Bilateral Superior Parietal Lobule activity was revealed at the whole brain level when actions were observed from the 0˚

viewpoint, while activity was limited to the left Superior Parietal Lobule for all other viewpoints examined. This suggests that stronger representations exist within the brain for actions observed from the 0° viewpoint compared to the other viewpoints examined, and is consistent with previous data suggesting a preference for actions to be observed from a viewpoint consistent with our own natural vantage point compared to other viewpoints. Furthermore, while the observation of egocentric actions led to activation of the left Superior Parietal Lobule, no such activations were present for the observation of allocentric actions. Therefore, future studies aiming to use action observation for modulating or improving performance should present observed actions from a viewpoint congruent with the participant's own natural vantage point, as the data presented here suggest there are stronger representations for egocentrically framed actions compared to allocentrically framed actions.

CHAPTER 6:

GENERAL DISCUSSION

6.1 Introduction

The central aim of this thesis was to examine whether the viewpoint from which an action is observed would modulate behavioural performance and brain function. Together, the studies described in the four empirical chapters demonstrate that combining evidence from behavioural studies with data acquired using neuroscientific techniques can help to establish a more comprehensive understanding of how the viewpoint from which an action is observed can affect the observer’s motor performance and brain activity. The final chapter of this thesis will provide an overview of the empirical data presented in the thesis. The strengths and limitations of the thesis will be discussed, and then potential directions for future research will be proposed.

6.2 Summary of Results

The first empirical chapter of this thesis (Chapter 2) used motion capture to examine participant performance in a manual prehension task. A multitude of previous behavioural studies have demonstrated that the observation of action can modulate participant performance in manual prehension tasks (Castiello et al., 2002; Castiello, 2003; Edwards et al., 2003; Dijkerman and Smit, 2007; Griffiths and Tipper, 2009). In turn, these studies were informed by data from neuroscience which demonstrate common coding for the observation and execution of action (di Pellegrino et al., 1992, Gallese et al., 1996; Rizzolatti et al., 1996; Rizzolatti et al., 2001; Fogassi et al., 2005). The experiment presented in Chapter 2 aimed to examine three factors. The principle theme of the investigation was to examine whether the observation of incongruent movement kinematics could modulate participant performance, while further aspects examined the effects of the timing of the action observation paradigm, and the viewpoint from which the action was observed. The data revealed that participant reach trajectories were modulated by the observation of incongruent reaching actions; observing the experimenter reach to an object with a high reach trajectory led to an increase in the height of the reaching action of the participant, compared to when they observed a normal reaching action. This effect occurred regardless of whether the participant's actions were performed sequentially or concurrently with those of the experimenter, and was also unaffected by the viewpoint from which the experimenter's action was observed.

The finding that manual prehension tasks can be modulated by action observation is consistent with previous studies (Castiello et al., 2002; Castiello, 2003; Edwards et al., 2003; Dijkerman and Smit, 2007; Griffiths and Tipper, 2009). The finding that the prehension task itself was not affected by observed action viewpoint may be due to the choices of viewpoints used in the study. For example, previous behavioural studies have revealed differences between viewpoints consistent with the natural vantage point of the observer and other viewpoints (see Vogt et al., 2003; Gianelli et al., 2008), but have not directly examined whether differences exist between different viewpoints incongruent with the natural vantage point of the observer, the main aim of the viewpoint intervention in this study. The finding that there were no differences between the viewpoints from which the experimenter was observed could potentially be explained by a system which uses separate representations for egocentrically and allocentrically framed actions, but does not distinguish between actions presented from different viewpoints within these overall categories. It was also possible that the task chosen could be insensitive to manipulation, as the goal directed nature of the grasping task reduced any potential effects due to spatial incongruence between the participant and experimenter. As the effects of reach height revealed in the study were due to the relative spatial direction congruency of movements of the participant and experimenter, the next empirical chapter of the thesis was devised to further examine the effects of direction congruency on participant performance.

The second empirical chapter of this thesis (Chapter 3) again used motion capture to record participant kinematics during a similar manipulation of action observation to that presented in the preceding chapter, with participants executing simple arm movements while observing similar movements from different viewpoints. Previous studies have demonstrated that the performance of this task can be modulated by action observation (Kilner et al., 2003; Bouquet et al., 2007; Kilner et al., 2007; Stanley et al., 2007; Gowen et al., 2008), and these studies are again informed by the neuroscience literature (di Pellegrino et al., 1992, Gallese et al., 1996; Rizzolatti et al., 1996; Rizzolatti et al., 2001; Fogassi et al., 2005). In the experiment presented in Chapter 3, congruency between the movements of the participant and experimenter was manipulated across two levels; task congruency was manipulated via the performance of different arm movements, and direction congruency was manipulated by changing the position of the experimenter relative to the participant.

The data from Chapter 3 revealed a modulation of participant performance when the direction congruency of the movements was manipulated. Critically, this effect was itself modulated by the viewpoint from which the observed action was seen, and the effects were driven by the spatial direction congruency of the observed movements. As expected based on the findings of previous studies (Kilner et al., 2003; Bouquet et al., 2007; Kilner et al., 2007; Stanley et al., 2007; Gowen et al., 2008), when participants observed a movement in an incongruent direction to their own, it interfered with their performance. However, when participants observed movements in a congruent direction to their own, it led to a facilitation of performance, an effect which has not previously been reported in studies using such paradigms (this is discussed further below). The findings of Chapter 3 were consistent with and expanded the findings presented in Chapter 2, as both chapters demonstrated effects of relative spatial congruency. However, the data in Chapter 3 also show that the viewpoint from which an action was observed could modulate the effects of action observation. In order to further examine the effects of observed action viewpoint, further behavioural experiments using a greater range of viewpoints were conducted in Chapter 4.

The third empirical chapter of this thesis (Chapter 4) again examined action observation effects elicited from participants viewing simple movements, this time using computer based response time measurements. Studies using such paradigms have previously demonstrated effects of action observation on participant response times (Brass et al., 2000; Brass et al., 2002; Symes et al., 2008; Tucker and Ellis, 1998; Vaino et al., 2007; Bach et al., 2007). Chapter 4 presented three experiments in which the ability of participants to match simple finger movements observed from different viewpoints was examined. Experiment 1 revealed that both the viewpoint from which an action was observed and the identity of the hand observed to act modulated participant performance. For stimuli seen from a viewpoint congruent with looking down at their own hand, participants responded fastest when their required response anatomically matched the observed movements. However, for stimuli seen from a viewpoint congruent with looking at another person positioned directly opposite the participant, responses were fastest when the required response was a mirror match for the observed movement. Experiment 2 revealed no differences when the congruency between the observed stimulus and participant hand posture was manipulated, suggesting that this effect was not affected by the current state of the participant’s own motor system. Experiment 3 revealed that participants were faster to respond when the observed stimuli presented movements that they could potentially perform themselves, and slower when they observed movements performed by a hand in a position which they could not naturally or comfortably adopt themselves.

The data revealed in Experiment 1, which demonstrate greater performance for anatomically matched stimuli when observing actions from a viewpoint congruent with the participant's natural vantage point, and greater performance for mirror matched stimuli when the observed action viewpoint was congruent with observing a person sitting opposite, is consistent with the findings of a recent fMRI study (Shmuelof and Zohary, 2008). Furthermore, consistent modulatory effects of observed action viewpoint were revealed in Experiment 1 and Experiment 3. These effects revealed that participants were faster to respond to stimuli showing actions from viewpoints consistent with movements they could themselves perform in comparison to actions seen from viewpoints consistent with observing other people. This data is consistent with previous studies which have suggested that observing actions from a viewpoint congruent with the natural vantage point of the observer is advantageous (Vogt et al., 2003; Gianelli et al., 2008). As the findings of Experiment 1 were consistent with the findings of a previous fMRI study (Shmuelof and Zohary, 2008), an fMRI experiment was devised in order to examine whether the consistent effects of observed action viewpoint demonstrated in Experiments 1 and 3 could also be demonstrated at a neural level.

The final empirical chapter (Chapter 5) of the thesis used functional magnetic resonance imaging to examine whether the viewpoint from which an action is observed modulates brain activity. Actions were observed from five different viewpoints, with several contrasts being conducted comparing brain activity during action observation to brain activity during the observation of control or baseline conditions. An initial contrast comparing brain activity during action observation to brain activity during the baseline condition revealed that Premotor and Parietal areas of the brain traditionally associated with the human mirror system were activated during action observation. Contrasts comparing each of the five viewpoints used to the baseline condition revealed activity in the left Superior Parietal Lobule; activity was also revealed in the right Superior Parietal Lobule when participants observed actions from a viewpoint congruent with their own natural vantage point. When brain activity was grouped depending on whether participants considered the observed stimuli to be actions that they could perform themselves (‘egocentric’ actions) or actions that they would attribute to another person (‘allocentric’ actions), the data revealed that Superior Parietal Lobule activity was greater for the observation of egocentric actions. The findings presented in Chapter 5, which demonstrate that the viewpoint from which an action is observed can modulate mirror system activity, are consistent with previous studies which have examined the differences between participant brain activity when observing actions from different viewpoints (Shmuelof and Zohary, 2008). Furthermore, the data provide a logical extension of the data provided in Chapter 4, demonstrating that participant brain activity was modulated depending on whether participants considered the actions they observed to be movements they could potentially perform themselves, or movements that they attributed to other people.

An interesting point to consider regarding the behavioural studies presented in this thesis (Chapters 2, 3 and 4) is the nature of the effects revealed. Previously, it had been suggested that action observation effects primarily show that the observation of action interferes with participant performance (see Blakemore and Frith, 2005). The majority of effects presented in the behavioural chapters of this thesis are likely to be consistent with this hypothesis. Chapter 2 examined the effects of observing a congruent condition (observing a normal reaching action) compared to an incongruent condition (observing a high reaching action), and found a modulation of participant reach kinematics consistent with the incongruent action interfering with their action (i.e. a higher reach height when observing high reaching actions, even though they were instructed to perform normal reaching actions throughout the experiment). Similarly, an interference effect was present in Chapter 3, with the data for one condition revealing an increase in participant movement error when they observed movements in an incongruent direction to the movements they were required to perform. In Chapter 4 there was no true baseline condition against which to compare conditions, making it difficult to directly determine whether the effects of action observation were due to interference or facilitation. However, as previous experiments using similar paradigms have suggested that their effects are due to observed movements interfering with participant performance (Brass et al., 2000; 2001), it is likely that the effects presented in Chapter 4 are also due to interference effects.

The reason for the prevalence of interference effects in the behavioural action observation literature is likely due to the tasks performed. In most studies, participants are familiar with the movements they perform (e.g. the manual prehension task used in Chapter 2), or the movements are very simple in nature (e.g. the tasks used in Chapters 3 and 4), suggesting the presence of ceiling effects. Furthermore, studies which have examined the effects of action observation when participants learn a novel task have demonstrated the presence of both interference and facilitation effects (Mattar and Gribble, 2005; Brown, Wilson and Gribble, 2009). Similar effects were present in Chapter 3 of this thesis, with both interference and facilitation effects being present in different conditions. Together, these data suggest that in some cases, particularly when the task is novel or initial performance is relatively poor, that action observation can lead to both interference and facilitation effects. It is also possible that this data may have implications for rehabilitation; in situations where the normal performance of the motor system has been impaired (i.e. performance is not close to ceiling levels to begin with), action observation may be useful to help improve performance in motor tasks, and has already been demonstrated to have beneficial clinical applications (Ertelt et al., 2007).

To summarise, the data presented in the empirical chapters of this thesis provide an answer to the hypothesis posed in the introductory chapter. The data presented here demonstrate that the viewpoint from which an action is observed can modulate participant motor performance and brain activity.

6.3 Strengths and Limitations

The primary strength of this thesis lies in its use of both behavioural and neuroscientific techniques, as the advantages of one compensate for the limitations of the other. The behavioural methods used in Chapters 2, 3 and 4 provide data regarding participant motor responses to observed movements, allowing for the presentation of data with both high spatial accuracy (Chapters 2-3) and high temporal accuracy (Chapter 4). However, the use of behavioural techniques alone would mean that the proposed neural effects of observed actions could only be inferred. In contrast, fMRI provides data regarding the brain structures active during action observation, but is limited by the tasks that can be performed in the scanner, as well as having relatively poor temporal accuracy. Therefore, the use of these complementary techniques provides a holistic approach to the aims of the thesis, allowing for a greater opportunity to compare and contrast data from behavioural studies in context with the neuroscientific evidence underlying their design. There are however, a number of limitations specific to each experimental paradigm used in the thesis, and these issues are examined further below.

Chapter 2 presented data from a manual prehension task in which participants observed the actions of an experimenter positioned either directly opposite or side on to them, but did not present an action in which the participant and experimenter performed movements in similar relative spatial directions (i.e. if the participant and experimenter had sat side by side, both their actions would have been directed in a ‘forwards’ direction relative to the participant). The experimental paradigm was specifically designed to examine two ‘allocentric’ viewpoints, as previous studies have generally only compared one egocentric with one allocentric viewpoint (Vogt et al., 2003; Gianelli et al., 2008; Shmuelof and Zohary, 2008). However, as no differences were revealed between the two allocentric viewpoints examined, the addition of a third viewpoint with congruent spatial direction components may have provided useful data to determine whether this was due to the presence of a single generalised representation for all allocentrically framed actions, or was caused by the incongruence between the observed and performed movements.

In Chapter 3, in which participants performed simple arm movements, no effects of task congruency were revealed. This may have been due to an experimental instruction given to the participants. Participants were required to fixate on the fingertip of the experimenter while observing their movements, which may have emphasised the experimental manipulation of direction congruency while simultaneously decreasing the perceived importance of task congruency. Previous studies have demonstrated that for action observation effects to occur, spatial attention needs to be directed towards the relevant effector involved (Bach et al., 2007). However, even if no particular visual fixation instruction had been provided to the participants before the experiment, it is still likely that they would have directed their gaze towards the experimenter’s hand (Mataric and Pomplun, 1998).

In Experiment 2 of Chapter 4, participants were presented with stimuli that were either congruent or incongruent with the current posture of their own hand. However, the spatial positioning of the stimuli remained somewhat incongruous, as in some conditions visuomotor transformations were required to match the observed hand posture to the participant’s current hand posture. It is possible that effects of hand posture congruency may have been revealed if the participant had responded to the movements by placing their hand behind a screen (so that the observed hand movements were directly spatially matched with the movements they were required to perform). While previous experiments using apparatus which presented actions in positions spatially congruent with the required responses have revealed no effects of such spatial congruency manipulations (Vogt et al., 2003), there is still scope to further examine whether such experimental manipulations would reveal additional congruency effects.

Chapter 5 required participants to observe grasping actions performed from different viewpoints, and attributed activity of Premotor and Parietal regions of the brain to activations of the human mirror system. Due to time limitations, it was not possible to acquire data from participants as they physically performed grasping actions themselves, meaning that activation maps revealed from both observed and executed performance could not be directly compared. However, as a wealth of evidence has previously demonstrated that similar regions of the brain are activated during the observation and execution of action (for a review see

Rizzolatti et al, 2001), it is still likely that the activations revealed can be attributed to the human mirror system. The addition of data examining participant brain activity during action execution may have provided further insight into the activity revealed during action observation.

6.4 Future Directions

The data presented in this thesis was collected using a number of different techniques ranging from the behavioural measures of motion tracking and response time measurement to the neuroscientific analysis of brain activity using fMRI. Therefore, there are a multitude of distinct directions that future research based upon this work could pursue. The ideas proposed in this section will therefore focus on three possible approaches. First, studies employing a behavioural approach (similar to the experiments presented in Chapters 2-4 of this thesis) will be discussed. Secondly, experiments based on neuroscientific approaches (similar to Chapter 5 of this thesis) will be considered. Third and finally, an approach combining both behavioural measurements and techniques from neuroscience will be advocated.

6.4.1 Behavioural Experiments

The data from the empirical chapters of this thesis (Chapters 2-5) are consistent with the notion that observed actions are processed in terms of agency, with actions that could be performed by the observer being processed in a different manner to actions that could only naturally be performed by other people. This notion could be further explored using behavioural paradigms. For instance, in an extension of the paradigm used in Experiment 1 of Chapter 4, participants could be presented with movements from a 0˚ viewpoint or a 180˚ viewpoint. Additional stimuli could vary the distance at which these movements are observed, presenting them at positions beyond the peripersonal space of the observer. This would allow the opportunity to examine whether the agency effects revealed rely on the ability of the participant to potentially perform the observed movement themselves. As found in Chapter 4, Experiment 1, it would be expected that when responding to the stimuli positioned within the peripersonal space of the observer, participants would respond faster to the 0˚ viewpoint stimuli than to the 180˚ viewpoint stimuli (as participants could potentially perform the movements in the 0˚ viewpoint stimuli themselves). However, if potential agency is the key to the effects revealed, participant responses would not distinguish between the two types of viewpoint stimuli when they occurred outside of their peripersonal space (as participants could not potentially perform either of these movements themselves).

It should also be noted that the majority of studies reviewed in the earlier chapters of this thesis (Chapters 1-5) have primarily examined basic functions of the human mirror system, such as investigating the influence of observing the actions of others on movement performance in the short term. It is proposed that future studies examining the effect of observed action viewpoint could extend on this foundation by examining functions of the mirror system that are related to classic effects found within participants, as this would provide further evidence that observing the actions of others involves the same processes as executing actions oneself. An example of such an effect is presented in the study of Mattar and Gribble (2005), in which participants learned to perform a motor task in novel environment through observing the actions of others. In this study, participants moved a cursor presented on screen to different target locations by interacting with a robotic arm. In a preliminary session, participants performed the cursor movement task using the robotic arm in a normal environment. Participants were then assigned to one of three groups. One group observed a video of an actor learning to perform the cursor movement task with the robotic arm exerting a clockwise force field to their movements. A second group observed a similar video clip in which an actor learned to perform the cursor movement task with the robotic arm applying a counter clockwise force field to their movements. The final group acted as a control group and simply rested for a time equal to the duration of the video clips observed by the other groups. All participants then performed the cursor movement task again, but this time the robotic arm applied a clockwise force field to their movements. Participant movements were analysed in terms of the curvature of their movements, and this was found to be influenced by the group to which they had been assigned. Participants who had observed the actor learning to move in a clockwise (i.e. congruent) forcefield showed less curvature in their movements than the control group, while participants who had observed the actor learning to move in a counterclockwise (i.e. incongruent) forcefield showed more curvature in their movements compared to the control group. These data suggested that participants were able to learn how to perform actions in a novel environment by observing the actions of others, and such paradigms could easily be manipulated to examine whether observing actions from different viewpoints can modulate such effects, particularly when it is considered that clockwise movements must be considered relative to the viewpoint of the observer. For example, an actor learning to perform the task in a clockwise forcefield could be recorded using two cameras, one filming from a viewpoint consistent with the actor’s viewpoint (so that the direction of forcefield appeared to push their movements in a *clockwise* direction) and the other from a similar position but below the participant (so that the direction of the forcefield appeared to push them in a *counter clockwise* direction). Groups of participants could then be shown one of two different videos of the actor learning in the forcefield, and their ability to learn from these videos could be assessed by having them perform the task themselves. Even though both groups would observe the same task being performed, it would be hypothesised that the group who observed the learning video from the viewpoint of the observer would outperform the group who saw the other video, due to the relative spatial incongruence of the movements in the latter condition.

6.4.2 Neuroscientific Experiments

The neuroscientific techniques of TMS and fMRI have already been discussed in earlier sections of this thesis (see Chapters 1-5), and there are several potential ways in which these techniques could be used to examine the effects of observed action viewpoint in studies of action observation.

TMS is a technique which has previously been used in action observation studies. Fadiga et al., (1995) reported that the observation of action can lead to modulations of corticospinal excitability. Using single pulse TMS, the excitability of the motor system during the observation of actions (such as those presented in Chapters 2-5 of this thesis) could be probed. In an extension of the data presented in Chapter 3, MEPs could be collected during the observation of the same action seen from different viewpoints. In a further proposed experiment, participants could observe a continuous arm movement task (similar to the task presented in Chapter 3), in which the observed actor would sometimes stop their movement unexpectedly. By comparing conditions in which MEPs were elicited during the observation of action and where they were recorded shortly after the actor stopped their movements unexpectedly, it would be possible to examine whether the motor system responds to bottom-up stimulus content (in which case MEP amplitude would be modulated only when participants observed an experimenter moving), or uses a predictive mechanism to estimate the activity to be performed by the observed actor (in which case MEPs would continue to be modulated even when observed movements stopped unexpectedly).

In addition to TMS, advanced fMRI methods could also be explored. As presented in the first chapter of this thesis, a recent fMRI study has used repetition suppression to provide strong evidence of the existence of mirror neurons in the human Inferior Frontal Gyrus (Kilner et al., 2009). In this study, a special grasping apparatus was used. Participants either performed different types of grasping actions using the apparatus (pulling a ring with their index finger or grasping another object), or observed a video clip of these actions being performed. It was revealed that when participants performed a particular type of grasping action then observed it (or vice versa), activity in the Inferior Frontal Gyrus was reduced compared to conditions in which they performed and observed different actions (or vice versa). These data suggested that the Inferior Frontal Gyrus contains neurons which fire in response to both the execution and the observation of actions, and that their firing patterns were attenuated when the same stimulus was repeated, regardless of whether it was executed or observed (i.e. the expected firing pattern of mirror neurons). Future studies could easily adapt the viewpoint from which actions are observed to examine whether this effect persists for different viewpoints. The data provided in this thesis suggest that repetition suppression effects would be revealed when viewing actions from a variety of viewpoints congruent with movements that the participant could perform themselves, and may also occur for a variety of viewpoints congruent with movements that the participant could not perform themselves, but would not occur when viewpoints presenting actions from these two distinct frames of reference were presented together. This would help provide further evidence that observed actions are encoded in terms of their egocentric and allocentric properties, and help provide a more detailed understanding of the neural populations underlying this activity.

6.4.3 Behavioural Neuroscience Experiments

While the data presented in this thesis distinguish between the use of behavioural and neuroscientific techniques, a strong approach that future studies could employ would be to combine these two methodologies. Combining these two types of research has provided a number of methodologically strong studies, allowing the examination of not only the performance of the participant, but also the neural activity underlying it.

While TMS was primarily developed as a tool for neurophysiological assessment (Barker, Jalinous and Freeston, 1985), the approach taken by studies using this methodology can be adapted for studies of behavioural neuroscience. For instance, Wassermann, Pascual-Leone and Hallett (1994) conducted a neurophysiological investigation using single pulse TMS to map the areas of the cerebral hemisphere which evoked MEP responses in muscles of the hand and shoulder. This mapping paradigm was later used to examine the effects of learning a new motor skill on the plasticity of the Motor cortex (Pascual Leone, Nguyet, Cohen, Brasil-Neto, Cammarota and Hallett, 1995). Participants performed a simple keyboard playing task, playing a sequence of keys in time with an auditory metronome for two hour periods each day for a week. Each day, the representation of the long finger flexor muscles of the hand (used to perform the task) were mapped using single pulse TMS both before and after the training period. Over the course of a week, the cortical representation of these muscles increased in size (i.e. an increase in the area of the brain that when stimulated would elicit activity in the muscles used to perform the task), and the threshold level of TMS required to activate them decreased. Of particular relevance to this thesis is the finding that similar changes in the underlying representations of the muscles used to perform the task occurred when participants performed a motor imagery task instead of physically performing the task. As action imagery and action observation have been demonstrated to elicit similar activity in the human mirror system (Guillot, Collet, Nguyen, Malouin, Richards and Doyon, 2009), it would be of interest to examine whether action observation would elicit similar changes in the representation of muscles used to perform fine motor skills. The paradigm could be further adapted to examine whether observing the action from a viewpoint congruent with the participant performing it themselves would lead to additional improvements in performance compared to observing the action from a viewpoint incongruent with the participant performing it themselves.

A further application of single pulse TMS is to evoke small contractions in target muscles, leading to movements which can be measured via motion tracking techniques. Classen, Liepert, Wise, Hallett and Cohen (1998) demonstrated that single pulse TMS could be used to elicit small movements which fell predominantly in one of two directions; stimulation of the Motor cortex area innervating the thumb led primarily to either abduction or adduction movements. Further examination revealed that brief periods of physical training could lead to a reversal of the direction of these movements – for example, if stimulation of the Motor cortex of a participant predominantly led to abduction movements, having them perform voluntary adduction movements for a short time led to a shift in the preferred direction of movement elicited via stimulation. Later studies demonstrated that similar changes could be induced by periods of observational training (Stefan et al., 2005), as well as practice combining both action execution and action observation (Stefan, Classen, Celnik and Cohen, 2008). Such paradigms could be further adapted to examine the relative contributions of task and spatial direction congruency for movement observation paradigms. Once the initial direction of TMS induced thumb movements was found, participants could observe videos of the same type of movement presented in a different *direction* (i.e. if TMS elicited thumb abduction movements in an *upwards* direction, participants could observe a video of thumb abduction movements occurring in a *downwards* direction). It is hypothesised that the data would be consistent with the spatial direction congruency effects revealed in Chapters 2 and 3 of this thesis. The direction of thumb movements elicited from the participant would change according to the *direction* of the movements seen in the video (i.e. *upwards abduction* movements would change to *downwards adduction* movements), even though the *type* of movement observed would remain unchanged (i.e. participants would always observe abduction movements – only their relative direction would matter).

While single pulse TMS can be used to assess corticospinal excitability transiently, repetitive TMS (rTMS) and the associated technique of Theta Burst Stimulation (TBS) can be used to generate longer lasting modulations in brain activity. For example, low frequency (1Hz) rTMS and continuous TBS can be used to inhibit the activity of areas of the brain, a finding which has led to a number of ‘virtual lesion’ studies using these techniques (Brown, Wilson and Gribble, 2009; Galea, Albert, Ditye and Miall., 2010). For example, as Mattar and Gribble (2003) had previously demonstrated that the observation of action can modulate motor learning (see above), Brown et al. (2009) examined whether such effects could be modulated by disrupting brain areas involved in motor learning. As in the previously established paradigm, participants first moved an onscreen cursor to different targets by manipulating a robotic arm in a normal environment. Participants then observed a video of an actor learning to perform the same task with the robotic arm applying either a clockwise or counterclockwise force field to their movements, or in the control condition observed no learning video. Depending on the experimental condition to which participants had been assigned, they then either had rTMS applied to their Motor cortex, or simply rested. Finally, all participants performed the cursor movement task again with the robot arm applying a clockwise force field to their movements. When participant movement curvature was examined, the groups who received no rTMS showed learning similar to the previous experiment (Mattar and Gribble, 2003), with participants who observed learning in a clockwise (i.e. congruent) forcefield showing less curvature in their movements than control participants, and participants who had observed learning in the counterclockwise (i.e. incongruent) forcefield showing greater movement curvature than the control group. Additionally, it was revealed that the rTMS treatment interfered with these effects. For clockwise (i.e. congruent) observational learning, participants who received rTMS showed *greater* movement curvature than participants who had received no stimulation, revealing that the stimulation had interfered with the beneficial effects of observing a congruent motor learning video. Conversely, for anticlockwise (i.e. incongruent) observational learning, participants who received rTMS showed *less* movement curvature than participants who had received no stimulation, demonstrating that the stimulation had interfered with the detrimental effects of observing an incongruent motor learning video. These data demonstrate that the Motor cortex is involved in learning via action observation, highlighting the benefits of using an experimental approach which combines both behavioural measurements and neuroscientific techniques. Such paradigms could easily be adapted to examine the effects of interfering with the function of areas of the mirror system, and videos depicting actors filmed from different viewpoints could examine the effects of observed action viewpoint on motor learning (see above for further details of the importance of viewpoint on clockwise movements).

Inhibitory brain stimulation techniques can also be used to examine the connectivity between different areas of the brain. A recent study has used TBS in a particularly elegant manner, demonstrating an improvement in motor learning when a brain area which normally competes for resources during memory consolidation was suppressed. Galea, Albert, Ditye and Miall (2010) examined the relative contribution of *declarative* learning (the ability to *verbally recall* a sequence of numbers) and *procedural* learning (the ability to *physically perform* the same sequence of numbers expressed as movements) to the improvement of the performance of a motor skill. Participants were tested using a Serial Response Time Task (SRTT), after which continuous TBS was applied to either a control site (the occipital cortex), or to an area of the brain involved in the consolidation of *declarative* learning (the left or right Dorsolateral Prefrontal Cortex). When SRTT performance was retested eight waking hours later, participants in the control group showed no improvement in their response times for the SRTT. However, participants who had their ability to consolidate declarative knowledge inhibited via TBS showed an improvement in their response times when performing the SRTT. These data suggest that by reducing the activity of brain areas involved in the consolidation of *declarative* aspects of the task, areas involved in *procedural* consolidation were afforded additional resources, leading to the improvement in response times. Such paradigms could be adapted to examine whether a similar competition suppression mechanism occurs within the different areas of the human mirror system, or to simply suppress the activity of areas of the mirror system during action observation to examine the effect this had on subsequent behavioural measures of participant performance.

6.5 Conclusion

The central aim of this thesis was to examine whether the viewpoint from which an action is observed can modulate the behavioural performance and neural responses of participants. The data presented in the empirical chapters of this thesis answer this question by presenting data consistent with the notion that observed actions are processed in terms of agency. Participants appear to have stronger representations of actions that are egocentrically framed (i.e. actions that they could perform themselves) than actions that are allocentrically framed (i.e. actions that could only naturally be performed by another person). The data also suggest that the relative spatial direction kinematics of a movement are given preference over the manner in which the movement itself is actually performed (i.e. that direction congruency has greater effects on action observation than task congruency). Future research should focus on further examining these effects of agency and spatial direction kinematics using methods from both behavioural studies and neuroscience in order to build a more comprehensive understanding of the behavioural responses of participants and the neural activity underlying them.

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