

**NEUROBEHAVIOURAL REPRESENTATIONS  
OF OBSERVED ACTION VIEWPOINT**

by

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## 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.

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**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 Gallese 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 (Umiltà 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 themselves 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 pollicis (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 interosseus. This pattern of modulation reflected the activity in the muscles when they were used to perform the observed actions (i.e. the opponens pollicis was used only in the performance of grasping actions, while the first dorsal interosseus 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; Gallese 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; Gallese 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 hemisphere. 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<sup>1</sup> can prime subsequent action (Craighero, Fadiga, Umiltà, & 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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<sup>1</sup>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**

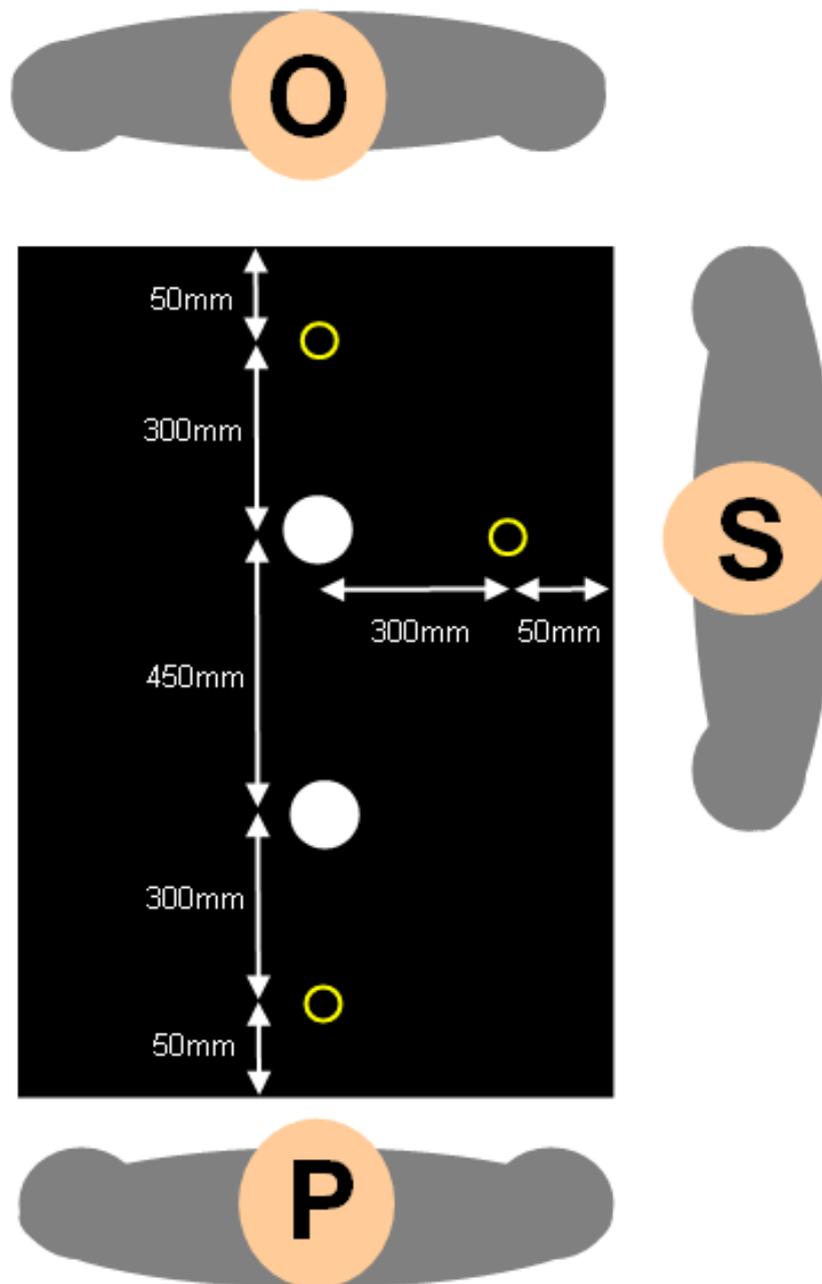
### **2.3.1 Participants**

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**

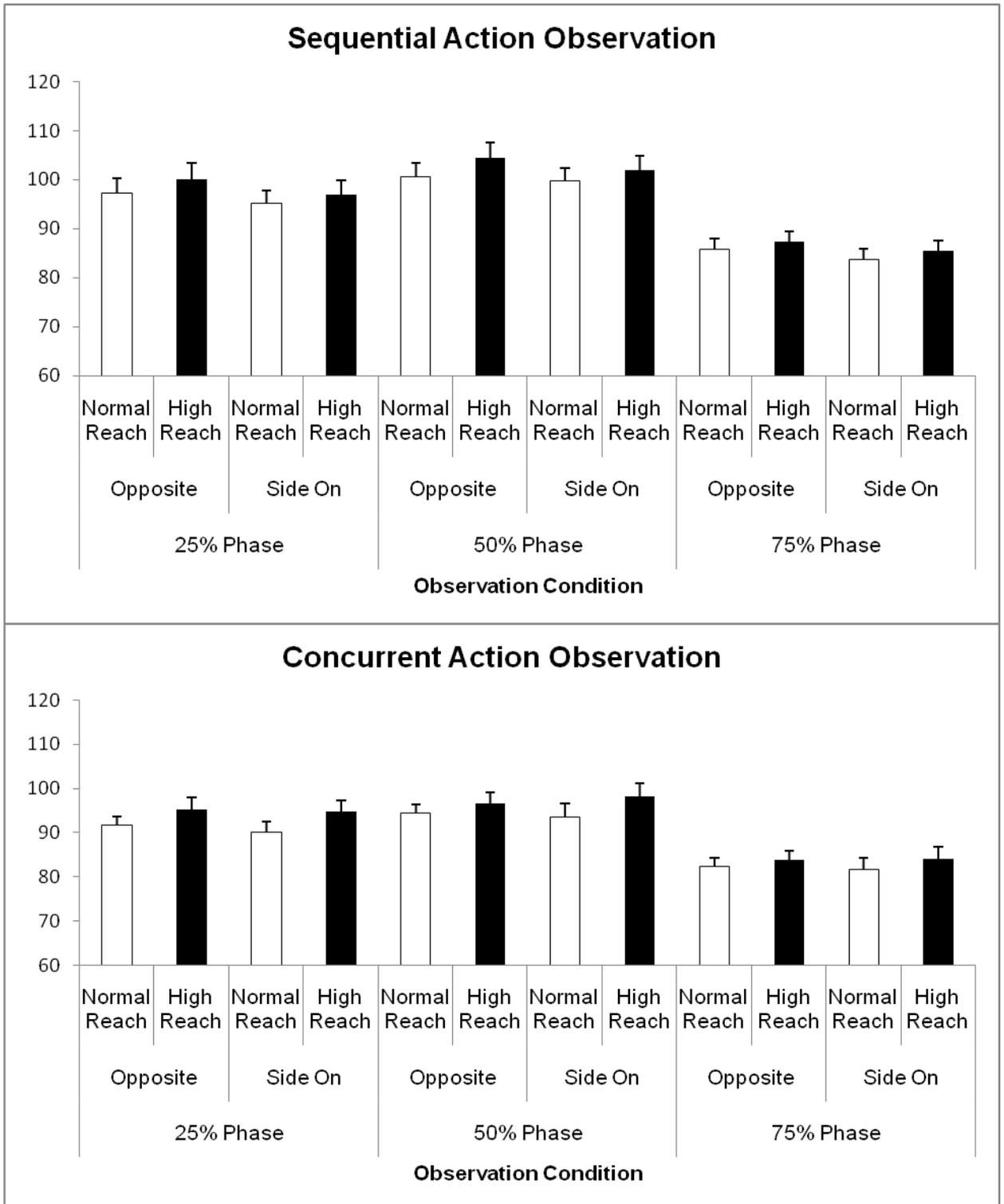
### **2.4.1 Data Reduction**

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 sphericity 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, Nadasdy 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, Wohlschlagel 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

































































































































































































































































































