

# **A BEHAVIOURAL EXAMINATION OF THE PROPERTIES OF THE ACTION OBSERVATION SYSTEM**

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## SUMMARY

The aim of this doctoral work is to examine the proposed properties of the Action Observation System (AOS) using the behavioural paradigm of movement interference effect. A review of the research literature of the AOS shows that it is primarily proposed to be:

1. AUTOMATIC,
2. UNMEDIATED, and
3. SPECIFIC

I examine the above properties by designing experiments that can systematically test each of the properties. I also develop a measure of motor interference more sensitive than variance or standard deviation which have been more commonly used thus far.

This thesis consists of six chapters, three of which present behavioural data, a general introduction (CHAPTER 01) and a general discussion (CHAPTER 06).

Chapter 02 provides a theoretical framework of the proposed properties of the AOS based on research literature with a particular focus on motor interference. CHAPTER 03 presents behavioural data from an experiment that attempted to replicate the findings of Kilner et al. (2007). CHAPTER 04 presents behavioural data from a set of two related experiments that, i) developed a more sensitive measure of motor interference and ii) examined the effects of observing “Dot” and “Video (human)” stimuli on motor interference when diagonal movements are observed and executed. CHAPTER 05 presents the findings from an experiment that examined the effect of observational viewpoint on the AOS and measured the effect via motor interference. CHAPTER 06 re-examines the properties of the AOS based on the results of the

experiments described in Chapters 03, 04 and 05, as well as based on other existing literature. I conclude with an appendix on how action might be represented in the AOS.

## STATEMENT

I hereby declare that the work has not been submitted for a higher degree to any other university or institution. The experiments described in this thesis have been performed with approval from Macquarie University Human Research Ethics Committee (Approval Number: xxx)

Signature:

$$x \cdot U(x) = j$$

Date: 12 April 2014

## DEDICATION

This doctoral thesis is dedicated to four people who made it possible – A/Prof. Mark Williams, Dr. Jason Friedman, A/Prof. Anina Rich and Ms. Lesley McKnight. I offer my gratitude to you.

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# **CHAPTER 1: GENERAL INTRODUCTION**

# CHAPTER 01: GENERAL INTRODUCTION

## I. INTRODUCTION

Human beings are social animals. We live in a dynamic and complex world where we act and interact. We seldom live in isolation, and if we are forced to do so, we imagine interacting with humans and other creatures and objects – we create and recreate experiences in our mind. While language is an important and a common way to communicate, we express and understand actions and intentions even without the spoken language. We not only plan and execute actions of our own, we also perceive the actions of others, all in a dynamic and cluttered environment. It is therefore not surprising that the human brain has evolved systems to observe and understand others' actions and use that information to interact with them.

Recent decades have seen a surge in research on how we act and understand actions. How do we understand the goals of other people's actions and then infer the intentions behind those actions such that we can plan our own action responses? What are neural systems that underlie the cognitive processes involved in action understanding? Glimpses of answers to these questions have been emerging from the fields of neurophysiology, cognitive neuroscience, artificial intelligence, clinical neuroscience, etc. Technological advances in the fields of neuroimaging and electrophysiology have aided our forays into the world of action understanding. Carefully designed behavioural and psychophysical studies have also been key to understanding cognitive processes such as action understanding, and by extension, understanding the neural substrates underlying these processes. Psychophysics has been defined as "the analysis of perceptual processes by studying the effect on a

subject's experience or behaviour of systematically varying the properties of a stimulus along one or more physical dimensions" (Bruce, Green, & Georgeson, 1996). Psychophysical studies are providing deep insights about action understanding using various behavioural variables such as reaction times and analysis of trajectories of arm movements. It is the aim of my doctoral work to employ psychophysical paradigms to know how we understand others' actions when we observe them.

The main aims of my doctoral thesis are:

To review the recent research on the Action Observation System focussing particularly on motor interference effects in order to isolate the proposed fundamental properties of the Action Observation System.

1. To test the validity of the underlying assumptions by designing experiments that employ the movement interference effect paradigm.
2. To discuss the fundamental properties of the Action Observation System based on the results of my experiments and compare them to evidence from research literature, and find out which theory or theories are best supported by the evidence.

In this first chapter, the Action Observation System (AOS) and its role in motor cognition are described. It begins with a summary of the early research on motor cognition. The discovery of MIRROR NEURONS in the brain of non-human primates and their possible functions are described, followed by a global view of the AOS in the human brain.

## II. EARLY RESEARCH ON MOTOR COGNITION

The history of modern neuroscience could well be the history of motor control leading to the concept of motor cognition. Some of the earliest research in neurophysiology focused on localising different functions of the brain to specific regions of the brain. One of the most famous examples of this attempt at localisation is that of Pierre Paul Broca, who in 1862 showed that a stroke patient who could not speak (he could only say the word “tan”) could however, understand language, had suffered from a lesion of the left frontal lobe. After observing similar effects of this lesion in other patients, Broca concluded that the left frontal lobe was responsible for generating articulate speech and this region has since been known as Broca’s area (FIGURE 1). Carl Wernicke who was studying stroke patients shortly after Broca published his findings, showed that patients who suffered from lesions around the area where the temporal and parietal lobes met in the posterior part of the left hemisphere, could speak but they made no sense. This region is known as the Wernicke’s area (FIGURE 1). Broca’s findings supported the prominent theory that brain function was localised in different areas.

Some of the major support for this “localisation theory of brain function” came from studies on muscle excitability. Gustav Fritsch stimulated the brain surfaces of live frogs and dogs using electricity resulting in very characteristic movements in the hind legs and neck. In 1870, Eduard Hitzig, working with Fritsch, showed that applying electricity to specific brain regions led to very specific muscular contraction in dogs, leading to the understanding of the brain region that plans, controls and executes voluntary movements, known as the MOTOR CORTEX (FIGURE 02).

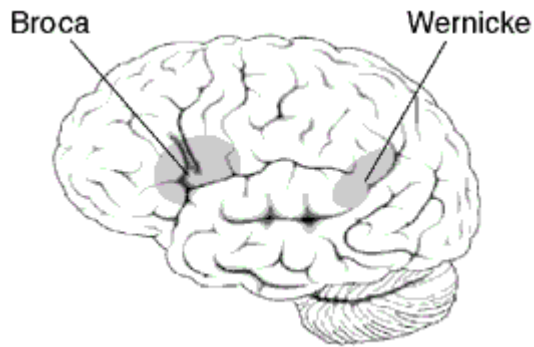


FIGURE 1: Approximate location of Broca's region and Wernicke' area in the human brain [<http://www.nidcd.nih.gov/health/voice/pages/aphasia.aspx>]

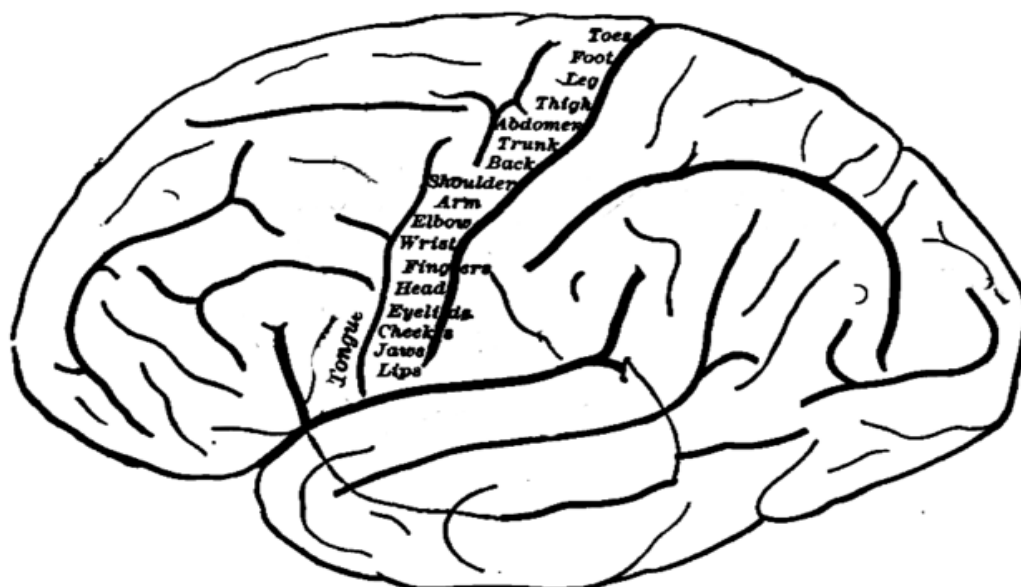


FIGURE 2: Representation of body parts along the central sulcus in a topography of human motor cortex [Stephen Walter Ranson, WB Saunders. (1920). *Anatomy of the Nervous System*]

The idea that the planning, controlling and executing of voluntary movements was the only role of motor cortex was strengthened by “sensorimotor theory of action

generation". According to this theory actions are simply reactions to external stimuli. The deafferentation experiments of Mott and Sherrington (1885) provided the most convincing evidence in support of this theory. Mott and Sherrington cut the sensory nerves in the arm of a monkey, a process known as deafferentation, such that no sensory signals passed to the monkey's brain. They found that the monkey not only lost all sensation of that limb but also stopped using it. In order to explain this observation, they proposed that movements were initiated by and based on the sensory aspect of spinal reflexes. They concluded that the monkeys could not use the limbs because the sensory aspect of the spinal reflexes were destroyed. This explanation was soon generalised to explain all kinds of movements. This theory renegaded the motor cortex solely to the function of initiating and generating movements.

An alternative to the "sensorimotor theory of action generation" was put forward by Charlton Bastian in 1897. His theory of 'kinesthetic images' stated that every movement left a trace in the form of an 'image' which was then stored in the motor cortex, such that it could be revived every time that movement needed to be executed. William James also supported the theory of kinesthetic images (James, 1890). He claimed that these kinesthetic images represented a "mental conception" of actions, such that these "conceptions" or "ideas" could be transformed into an action whenever it had to be executed.

Hugo Liepmann (1900), who coined the term 'apraxia' to denote all problems of action generation, put forward his idea of 'movement formula'. He suggested that the

movement formula were units of action and that were partial representations of both an action and its goal. Every sub-movement that comprised a movement had its own formula such that each sub-movement added up hierarchically to generate the complete movement. For example, in the course of the final movement of picking up a mug from a table, there are many sub-movements such as the bending of the arm, positioning the wrist and the palm in the most optimal fashion, and the grip of the fingers, and each sub-movement has a formula. According to Liepmann, movement formulae entails a space-time representation of movements that is stored in the left parietal lobe (Liepmann, 1905). For a movement to be executed, formula or space-time representation plan has to be retrieved and this information must be passed on to the primary motor cortex via many cortical (R. C. Leiguarda & Marsden, 2000; Liepmann, 1905). Therefore, every movement is comprised of all partial representations of submovements that will add up to form the complete representation when the movement is finally executed. Nikola Bernstein called these formulae or representations ‘internal models’ (1935).

There was a resurgence of the concept of ‘kinesthetic images’ in the 1980s and 1990s when technology caught up with experimental science such that computer simulations could be run to test various models. Michael Arbib (1981) named Bernstein’s internal models ‘motor schemas’ in order to emphasize their hierarchical nature. These schema were recursive entities that could be broken down into individual components such that goals could be nested in one another. For example, some of the higher-level goals of picking up the proverbial coffee mug from a table could be to “drink coffee to stay alert”, or to “enjoy a mug of coffee in solitude/with a friend”. Some of the lower-level goals could be to “reach” for the mug and “grasp” it



at the handle. Grasping, in turn, could have a still lower level of goals such as “close fingers around the handle”. Each of these nested goals would have to be assembled in near-spontaneous fashion in order to be of any use at all in the process of motor cognition.

The nested or hierarchical nature of actions suggested that action was not only a simple execution of motor commands but also a “representation” of those commands at the level of goals. Neurophysiological recordings of the monkey brain led to the discovery of neurons that respond to both an action and the observation of this action - so-called ‘mirror neurons’. These recordings demonstrated that the motor cortex was indeed involved in action representation. It also showed that action representation might involve goal representation in a hierarchical manner.

### III. MIRROR NEURONS IN NON-HUMAN PRIMATES

Mirror neurons are a special kind of visuomotor neurons that are found in area F5 of the monkey premotor cortex (FIGURE 03). These neurons discharge when the monkey performs a particular action as well as when it observes another individual perform the same action - the individual can be another monkey or a human being (Di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996a). Two kinds of visuomotor neurons have been identified area F5 of a monkey - canonical and mirror. The canonical neurons fire in response to the mere presentation of an object, whereas the mirror neurons fire only when there is object-directed action (Rizzolatti & Luppino, 2001). The mirror neurons respond when there is an interaction between an effector (hand or mouth) and an object. Mere mimicking an action or the mere

presentation of an object is not sufficient to evoke a response from the mirror neurons. Mirror neurons also do not respond to non-object-directed or intransitive actions.

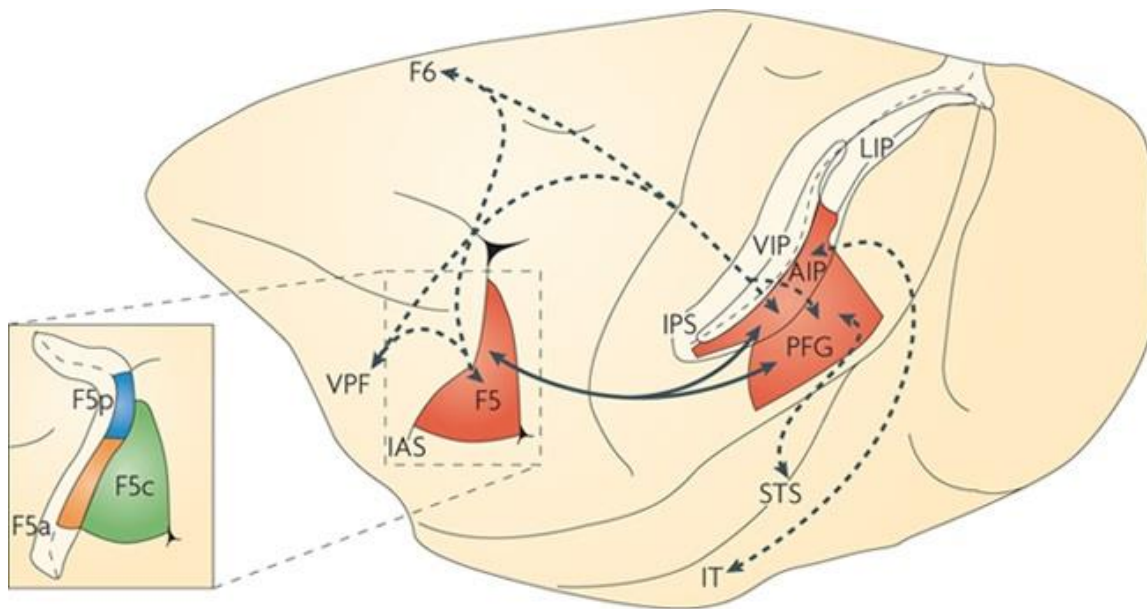


FIGURE 03. Brain of a macaque monkey in which mirror neurons were first discovered. The areas in which mirror neurons were found to be mainly concentrated are area F5, area 7b and STS (superior temporal sulcus) [Rizzolatti, G. & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nature Reviews Neuroscience*, 11, 264-274. doi:10.1038/nrn2805]

Mirror neurons exhibit a great degree of generalization in their responses (Rizzolatti & Luppino, 2001). It does not matter if the object towards which an action is directed is of significance to the monkey or not - mirror neurons fire with the same intensity when the object in question is food or a geometric solid. They are not affected whether a human hand or a monkey grasps an object or whether the action occurs

near to the monkey or far from it. They also do not seem to be influenced by reward - they fire with the same intensity whether the experimenter grasps food and gives it to the subject monkey or another monkey in the same room. These neurons seem to be concerned with object-direction actions alone.

Mirror neurons are classified as "broadly congruent" and "strictly congruent" based on the functional relationship between their visual and motor properties (Gallese et al., 1996). The broadly congruent mirror neurons do not require that they observe exactly the same action that they code for (e.g., they may code for precision grip but they fire even when observing a power grip as long as the action is directed towards an object). The strictly congruent mirror neurons require that the action observed is the exactly the same as the action that they motorically code for.

Most of the early studies on mirror neurons were performed on regions that represented hand actions. But soon other regions of the monkey began to be investigated for the presence of mirror neurons. One study looked at the neurons present in the lateral region of F5 where they mostly represent mouth actions (Ferrari et al., 2003). It was found that about 25% of neurons that they studied exhibited mirror properties. The mirror neurons in this region were classified based on the visual stimuli that triggered them - ingestive and communicative mirror neurons. The ingestive mirror neurons fired to actions related to ingestive functions like grasping food with the mouth, sucking the food, or breaking it. They formed about 80% of all the mouth mirror neurons studied. About one third of these mirror neurons were strictly congruent and the others were broadly congruent. The

communicative mirror neurons fired with when they observed a communicative mouth action such as lip smacking. But they also functioned as ingestive mirror neurons because they fired when the monkey performed any ingestive action. They are, therefore, at the crossroads between a motorically significant action that has survival benefits and a communicative action that may have a higher-level survival benefit. Some research shows that communicative gestures have their origins in ingestive actions in evolution (MacNeilage, 1998). Seen this way, the communicative mouth mirror neurons may be displaying a vestigial relationship to the ingestive role these neurons may have played in evolution

Neurons that respond to observed actions are not restricted to area F5. They are also found in the cortex of superior temporal sulcus (STS) (FIGURE 01) (Jellema et al., 2000, 2002; Perrett et al., 1990). Some of the movements that elicit response from the STS are moving the arms, bending the torso, turning the head, and walking. A small subsection of neurons in the STS fire when observing goal-directed hand movements. STS and area F5 differ in comparison on two counts:

1. the STS codes for a greater number of movements than area F5 - this may be so because the output of STS reaches the entire ventral premotor region and not simply area F5; and
2. the STS does not show motor properties.

Finally, the rostral part of the inferior parietal lobe, an area known as area also responds to observation of action (FIGURE 01) (Fogassi et al., 1998; Gallese et al., 2002). Area 7b receives input from the STS and sends output to the ventral premotor

cortex (that includes area F5). About 90% of the neurons in this region respond to sensory stimuli, but about half of them also show motor properties (Fogassi et al., 1998; Gallese et al., 2002; Hyvarinen, 1982). These neurophysiological recordings show that “mirror neurons” in the motor cortex are involved not only in action execution but also respond to action observation. Further investigations focused on the possible function of mirror neurons, as well as their homologues in the human brain.

#### IV. POSSIBLE FUNCTIONAL ROLES OF MIRROR NEURONS IN NON-HUMAN PRIMATES

What might be the functional role of these mirror neurons in monkeys? Two hypotheses have been put forward:

- 1) mirror neurons are essential for action understanding (Rizzolatti et al., 2001); and
- 2) mirror neurons mediate imitation (Jeannerod, 1994)

Rizzolatti et al. propose a simple mechanism for the manner in which mirror neurons mediate action understanding (Rizzolatti et al., 2001). Every time an individual observes an action performed by another individual, the neurons that code for that particular action in the observer's premotor cortex are activated. The automatic motor resonance between observed actions and the neurons that code for those actions if executed by the observer leads to the transformation of visual information into motor knowledge. The researchers concede, though, that the mirror neuron mechanism alone may not be responsible for action understanding. While mirror neurons may be involved in imitation, it cannot be the main function of mirror

neurons because imitation is present only in humans and some apes (Tomasello & Call, 1997).

In order to further elucidate the properties of the mirror neuron circuit in monkeys, researchers proposed that for the mirror neurons to be involved in action understanding, they should fire in situations where the monkey does not see the actual action being performed but it has sufficient clues to generate a mental representation of the action being performed by the experimenter (Umiltà et al., 2001). Towards this end, Umiltà et al. tested the mirror neurons in two conditions - "full vision" and "hidden vision". In the "full vision" condition, the monkey could fully see the object-directed action; in the "hidden condition", the monkey could not see the final part of the object-directed action. Food was placed behind a screen such that the monkey saw it being placed. It was found that mirror neurons that discharged when observing the final part of the action to grasp food placed behind a screen were the same as those that discharged when the last part of the action was hidden from its view. Miming the action in full vision and hidden vision did not elicit the discharge of mirror neurons. This led the researchers to conclude that it was understanding of the action performed by the experimenter that caused the mirror neurons to fire.

Mirror neurons discharge even in response to auditory cues (Köhler et al., 2002). In this experiment, the monkey either saw a paper being ripped or heard the sound of a paper being ripped without actually seeing the action. About 15% of the neurons fired both when observing the action and when hearing the sound associated with that

action without actually seeing it. When asked to perform the action, 29 of the 33 studied neurons that showed selectivity to visual and auditory cues were involved in the motor task. This results of this study showed that mirror neurons were sensitive not only to action-related visual stimuli but also to auditory stimuli.

There is general consensus among scientists that the mirror neurons are related to action understanding (Rizzolatti, Fogassi, & Gallese, 2001; Rizzolatti et al., 1999; Rizzolatti, & Sinigaglia, 2010). This then formed the basis for developing hypotheses about the way in which action understanding in humans might be supported by a similar system.

## V. ACTION OBSERVATION SYSTEM IN THE HUMAN BRAIN

Based on the role that mirror neurons play in monkeys, many researchers (Rizzolatti, Fogassi, & Gallese, 2001; Rizzolatti et al., 1999; Rizzolatti, & Sinigaglia, 2010) expected to find a neural circuit with the “action observation-action execution” property in the human brain.. This neural circuit is known as the Action Observation System (AOS) and is believed to underlie action understanding. fMRI, TMS, and behavioural studies aided in the localisation of AOS and explored the various roles it played in the realms of action understanding and motor cognition.

Action understanding is a complex and multi-layered process that requires the coordination of many parts of the brain, from motor to memory. Consistent with this, many brain imaging studies show that action observation activates a large number of regions encompassing the cortical regions that are predominantly motor in nature,

frontal, temporal, occipital and parietal visual areas (Buccino et al., 2001; Decety et al., 2002; Grezes et al., 1998, 2001, 2003; Iacoboni et al., 1999; Rizzolatti et al., 1996b). The regions that constitute the core AOS are the rostral part of the inferior parietal lobule, the posterior part of the inferior frontal gyrus and the lower part of the precentral gyrus (Rizzolatti and Craighero, 2004) (FIGURE 05). Studies on comparative anatomy along with brain imaging suggest that superior frontal sulcus and the superior precentral sulcus represent a homologous region to the monkey arcuate sulcus (Rizzolatti et al., 2002; Rizzolatti and Arbib, 1998).

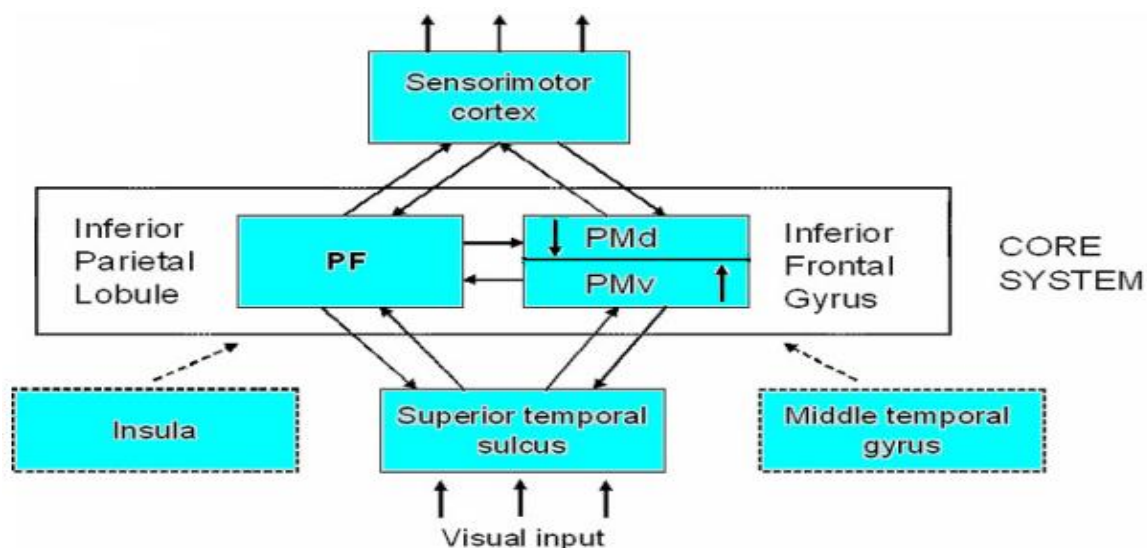


FIGURE 05. This schematic shows the brain areas that comprise the core AOS and the extended AOS. Abbreviations: PMd – dorsal premotor cortex, PMv – ventral premotor cortex, PF – Inferior parietal lobule, homologue of area 7b of monkey brain, [Pineda, J. (2008). Sensorimotor cortex as a critical component of an 'extended' mirror neuron system: Does it solve the development, correspondence, and control problems in mirroring? *Behavioral and Brain Functions* 47(4) doi:10.1186/1744-9081-4-47]



The first indirect neurophysiological evidence of the activation of the motor system when observing actions in the absence of overt action dates back to the 1950s.

Gastaut, and Bert (1954) showed through EEG recordings that there was a desynchronisation of the “mu-rhythm” not only when actions were executed but also when observing others perform actions. This finding was later confirmed by EEG recordings (Altschuler et al., 1997, 2000) and MEG data (Hari et al., 1998). More direct evidence for the presence of AOS came from Transcranial Magnetic Stimulation (TMS) and fMRI. Various experiments over the last three decades have investigated the functions of the AOS.

TMS is a non-invasive method that is used to cause activity in specific parts of the brain. This activity is generated by a rapidly changing magnetic field as electromagnetic induction induces weak electric currents. A TMS study showed that transitive and intransitive actions led to an increase in the Motor Evoked Potentials (MEPs - these evoked potential are correlated with motor excitability and are recorded from muscles are stimulation of motor cortex) when participants had to observe an experimenter grasp objects (transitive actions) or execute meaningless gestures (intransitive actions) (Fadiga et al., 1995). In the control condition participants had to detect the dimming of a small spot of light; further control was done by presenting 3-D objects which do not engage the AOS. The motor cortex corresponding to the right hand and arm muscles was stimulated during action observation. The increase in MEPs corresponded to the muscles that the participants would have used to execute those movements. This result shows that observing actions stimulates the muscles that would be used if those actions are executed.

Although the motor system might be active when we observe actions, we do not involuntarily execute movements of others. Thus, Baldiserra et al. (2001) hypothesised there may be an inhibitory mechanism, perhaps in the spinal cord, to prevent such mimicry. They used a reflex that can be elicited by simulating a nerve with an electrical current, known as a H-reflex. The magnitude of the H-reflex evoked in the extensor and flexor muscles of participants was influenced by observing another individual opening and closing his hand. The study showed that the magnitude of H-reflex in flexors increased when “hand opening” was observed and decreased when “hand closing” was observed. On the other hand, the size of H-reflex in extensors increased when “hand closing” was observed and decreased when “hand opening” was observed. This showed that there was an inhibitory mechanism in the spinal cord that prevented the execution of observed actions.

#### A. ACTION OBSERVATION SYSTEM AND IMITATION

Functionally, the AOS has been implicated in action understanding and imitation, observational learning, gestural communication and evolution of speech. The finding that action execution and action observation seem to rely on the same neural substrate led to a series of investigations on the role of AOS in imitation. For example, in one fMRI study, Iacoboni et al. (1999) examined the brain activity of participants under two conditions – “observation only” and “observation-execution”. Under the “observation only” condition, participants watched a finger movement, a cross on an empty background, and a cross on a stationary finger, but did not execute any movements of their own. Under the “observation-execution” condition, participants watched a finger movement and imitated the same movement as fast as they could. The results showed a greater activity in the “observation-execution”

condition than in any other “observation only” condition in these areas: the right STS, the right parietal operculum, the right anterior parietal region and the left pars opercularis of the IFG. In a subsequent study, Broca’s area was also found to be important for the imitation of goal-directed actions (Koski et al., 2002). This finding supports the argument that action observation and action imitation share a neural substrate.

## B. ACTION OBSERVATION SYSTEM AND LANGUAGE

Based on evidence that Broca’s area was part of the AOS (Buccino et al., 2008; Rizzolatti, & Arbib, 1998; Heiser et al., 2003), and because speech is considered to be a motor act (Lieberman, & Mattingly, 1985), Rizzolatti and Arbib (1998) postulated that the AOS is involved in gestural communication and evolution of speech. Support for this view has come from TMS studies demonstrating an increase in the excitability of the hand motor cortex both during spontaneous speech and reading (Meister et al., 2003; Tokimura et al., 1996). Further evidence comes from a recent study on the role of AOS in language. Zarr et al. (2013) had participants read blocks of sentences where every sentence in a block described movement of objects in a direction toward or away from the reader. Following every reading-based block, adaptation to the read sentences was measured as prediction time error by asking the participants to predict the end-point of videotaped actions. There was disruption in the prediction of actions due to the adapting sentences but (a) only for the videotapes of biological motion; and (b) only when there was a match between the effector in the videos and that used in the sentences (e.g., the leg or the hand). This results suggests that there is a link between the AOS and language.

### C. ACTION OBSERVATION SYSTEM AND SENSORIMOTOR EXPERIENCE

Automatic imitation is the tendency of people to repeat observed actions because they are automatically primed to do so (Heyes, 2010). The strength of this priming depends on the correspondence between the observed motor acts and the existing motor plans (Prinz, 1997). A different kind of priming occurs with prior practice and prior knowledge. In a recent study, EEG was used to investigate the hypothesis that priming could be reversed (Quandt and Marshall, 2014). There were three groups of participants who watched videos of a model grasping, reaching and lifting two objects while EEG was simultaneously recorded. Each group received different information about the weight difference between the two objects: (i) A lengthy sensorimotor experience manipulating the objects; (ii) a short sensorimotor experience manipulating the objects; or (iii) no sensorimotor experience, only written info about the weights of the two objects. All the groups of participants then observed the videos again. For the first two groups of participants who had extended or brief sensorimotor experience with the two objects, the EEG response was differentially sensitive to the estimated weight of the objects. The group of participants who received only written information showed no differential effects, leading the researchers to conclude that priming via prior action execution modulates action observation. Action observation and action execution therefore influence each other in a bidirectional manner.

Marshall et al. (2013) found that infants also demonstrate a bidirectional link between action observation and action execution, suggesting these processes develop very early on in the development of the brain. They gave 14-month-old infants sensorimotor experience with lifting objects of different weights while recording mu-

rhythms using EEG. There was a differential hemispheric response to lifting lighter and heavier objects. Further, the EEG responses were sensitive to “expected object weight” based on the previous sensorimotor experience. When the infants observed an experimenter reach out to the previously-manipulated objects, the EEG responses corresponded to the “expected object weight” even before the object was actually lifted. Thus, prior knowledge and learning have an influence on how the motor system responds to observed actions and understands the actions presumably via the AOS.

#### D. ACTION OBSERVATION SYSTEM AND THE “ASSOCIATIVE SEQUENCE LEARNING (ASL) THEORY

The evidence for a bidirectional link between action observation and action execution provides support for the “Associative Sequence Learning (ASL) theory” of Cecilia Heyes (Cook et al., 2010; Catmur and Heyes, 2013; Heyes, 2013). According to this theory, sensorimotor learning plays an inductive role in the development of the fronto-parietal Action Observation Network. It stands in opposition to the Hebbian learning theory, which states that sensorimotor experience plays only a facilitative role in development of the AOS. According to the ASL, sensorimotor experience is a necessary condition in the development of the AOS such that it forges the motor maps that correspond with action observation and action execution. In contrast, the Hebbian theory postulates that the mapping would occur visually without any need for learning or experience; sensorimotor experience merely tunes or modifies the AOS, such that there is a greater or lesser correspondence between the motor plans of observed and executed actions. The two theories therefore make opposing predictions for the role of sensorimotor experience in learning.

According to the ASL theory (Catmur and Heyes, 2013; Heyes, 2013), the development of the AOS depends not only on how close together two motor events occur (CONTIGUITY) but also on the predictive relationship of the two motor events (CONTINGENCY). This theory predicts that there is greater associative learning when one event, E2, occurs after an event E1, such that they form a contiguous pair. It also predicts that the learning decreases when E2 occurs in the absence of E1. Therefore, the mapping between observed and executed motor acts is influenced by, i) time – how far apart in time do the motor acts occur, and ii) how often do they appear together such that the appearance of one event predicts the appearance of the next.

The mapping between observed and executed actions may not be explained Hebbian associations. These associations can form for all kinds of events, including events that may not have any causal relationship at all. As an example, a musician flexing his fingers before playing his instrument can create a Hebbian association: the musician may flex his fingers before performing any number of tasks. However, flexing is repeatedly followed by playing, establishing a Hebbian relationship. In this sense, Hebbian learning is “promiscuous” for it cannot lead to the formation of reliable link between motor acts of observed and executed actions. Even though the act of flexing is always followed by the act of playing the instrument, flexing the fingers cannot form a causal relationship with playing. For deeper learning to occur, contiguity is a necessary but insufficient condition – contiguity has to be accompanied by contingency. Therefore, Hebbian accounts of learning cannot account for the mapping between observed and executed motor acts.

In summary, the Action Observation System (AOS) is the proposed neural substrate underlying the cognitive processes of action understanding. Action observation and action execution are linked in a bidirectional manner such that observation and execution influence each other. This bidirectional link between perception and action is strengthened by sensorimotor experience. Such experience, as explained by the theory of “Associative Sequence Learning”, strengthens the mapping between observed and executed actions.

The aim of this chapter was to provide a global view of the AOS. In the second chapter, I review the recent research on the Action Observation System (AOS) focussing particularly on automatic imitation and motor interference effects. Chapter 02 will conclude with my derived main properties of the AOS and the outline for the experimental chapters of the thesis.

**CHAPTER 2: THE PROPERTIES  
OF THE ACTION  
OBSERVATION SYSTEM – A  
THEORETICAL FRAMEWORK**



## CHAPTER 02: THE PROPERTIES OF THE ACTION

### OBSERVATION SYSTEM – A THEORETICAL FRAMEWORK

The aim of this chapter is to review the literature on the Action Observation System (AOS), particularly with respect to automatic imitation and motor interference, and discuss the proposed fundamental properties of this system. Although these properties have been examined and explained in different papers, this is the first time they have been drawn together to provide a reference framework to design experiments that study the AOS. Although many of the global roles of the AOS have been studied using neuroimaging and electrophysiological techniques, behavioural studies illustrate the finer properties of the AOS. Due to the complexity of the system, there are still many debates about these properties that will be highlighted in the following sections.

#### I. AUTOMATIC IMITATION

Automatic imitation is a kind of stimulus-response compatibility (SRC) effect (for example, the Simon effect (Simon, & Wolf, 1963)) in which the task-irrelevant action stimuli modulate the reaction times (speed) and/or accuracy of performance in a given task (Heyes, 2011). According to Heyes (2011), automatic imitation is the propensity to copy observed actions even when they are not relevant to a given task. The term ‘automatic imitation’ implies that this particular kind of imitation is ‘direct’ and ‘automatic’, that is, it occurs without any volitional control of the observer (Heyes, 2011).

It has been proposed that the Action Observation System mediates automatic imitation (Longo et al., 2009). Researchers suggest that the Action Observation

System links the perception and execution of action in a 'direct' manner, i.e., without the mediation of higher-level cortical processes (Gallese et al., 1996; Gallese, & Goldman, 1998; Rizzolatti, Fogassi, & Gallese, 2001; Rizzolatti et al., 1996; Rizzolatti et al., 1999). This mapping between perception and execution of actions is known as motor resonance (Uithol et al., 2011; Buccino, Rinkofski, & Riggio, 2004). When people see an action that is qualitatively similar to the motor plans of actions present in their motor repertoire, they are automatically primed to repeat them as the motor plans for the observed actions are simulated due to motor resonance (Prinz, 1997). The strength of this priming depends on the correspondence between the observed motor acts and the existing motor plans (Prinz, 1997). This mapping is believed to be strengthened with experience and practice of actions, thereby lending credence to the "Associative Learning Theory" (Catmur & Heyes, 2013; Heyes, 2013) outlined in Chapter 01.

The most direct link between automatic imitation and the neural Action Observation System (which is studied using neuroimaging rather than behavioural methods) comes from studies that show that action observation leads to a selective activation of the muscles involved in that action (Fadiga, Fogassi, Pavesi & Rizzolatti, 1995; Strafella & Paus, 2000). Berger and Hadley (1975) gave evidence that participants show more electromyographic (EMG) activity in the arm when they observe arm wrestling actions than when they observe stuttering actions, and *vice versa*.

One study directly the Action Observation System with automatic imitation (Catmur, Walsh, & Heyes, 2009). The human IFG is suggested to be homologous with area F5

of monkeys, where mirror neurons were initially discovered (Rizzolatti, & Arbib, 1998). Catmur et al. (2010) used a repetitive-Transcranial Magnetic Stimulation (rTMS) protocol, where a continuous stimulation of theta-bursts disrupts the functioning of IFG during an automatic imitation task. In this experiment, the Posterior Parietal Cortex (PPC) was stimulated as a control, and in a baseline condition no stimulation was given during the performance of the task. Participants made an outward (abduction) movement of either the index finger or the little finger of their right hand in response to a coloured dot (orange dot—index response; purple dot—little response). An image of an index- or little-finger abduction movement was used as the task-irrelevant cue, and was presented at the same time as the coloured dot. The size of the automatic imitation effect was calculated by subtracting RTs in imitatively compatible trials (index stimulus – index response, or little stimulus – little response) from RTs in imitatively incompatible trials (index stimulus – little response or little stimulus – index response). The results showed that the theta-burst rTMS of the left IFG completely eliminated the effect of automatic imitation in the imitatively compatible trials relative to the baseline. Theta-burst rTMS of the PPC showed no such effect on either the imitatively compatible or the imitatively incompatible trials. These results thus provide the first possible evidence that the Action Observation System mediates automatic imitation and that automatic imitation can be used a behavioural index of the Action Observation System.

The evidence suggests that automatic imitation is i) mediated by the Action Observation System (Catmur et al.2009); and ii) is a useful behavioural index of the properties of the Action Observation System (Longo et al., 2009; Press, Bird, Flach,

& Heyes, 2005; Stanley, Gowen & Miall, 2007; van Schie, van Waterschoot & Bekkering, 2008).

#### A. DISSOCIATING THE EFFECT OF AUTOMATIC IMITATION FROM SPATIAL COMPATIBILITY

Many studies point out that the effect of automatic imitation might be no different from the effect of spatial compatibility (Aicken, Wilson, Bertenthal, Longo & Kosobud, 2006; Jansson, Wilson, Williams & Mon-Williams, 2007). It is likely that a propensity to act in the same relative position as the stimulus (spatial compatibility) has been confounded with a propensity to generate a topographically similar action, i.e. to produce imitatively compatible' responses (Catmur, & Heyes, 2011) or 'movement compatible' responses (Brass et al., 2001). For example, in the Stuermer et al., (2000) experiment, participants observed and executed movements in which the opening movement chiefly consisted of an upward movement, and the closing movement consisted of a downward movement. Therefore, faster responses in compatible than incompatible trials may have been due to an urge to open the hand when observing hand opening (automatic imitation), or to move upwards when observing an upwards stimulus (spatial compatibility). However, many studies have dissociated the effect of automatic imitation from spatial compatibility (Chong, Cunnington, Williams & Mattingley, 2009; Bertenthal et al. 2006; Leighton & Heyes, 2010; Bach et al., 2007). There is, however, evidence from other studies that these factors can be dissociated. This is discussed in the following section, reviewing different types of grips, finger movements, and hand/mouth movements

## 1. POWER GRIP VERSUS PRECISION GRIP

Chong et al. (2009) showed that automatic imitation of power/precision grip is not caused by left-right spatial compatibility. This experiment employed a 'go-no go' procedure. During the go trial, participants were informed at the beginning of the trial by a numerical stimulus whether they were to execute a precision grip or power grip with their right hand. After a variable interval, an image of either a left or a hand in power or precision grip was presented in third-person view. The image specified whether a power or a precision grip should be made. Reaction of movement initiation was faster when the stimulus and response were compatible (power grip stimulus – power grip response vs precision grip stimulus – precision grip response) than when the stimulus and response were incompatible (power grip stimulus – precision grip response or *vice versa*). The effect of automatic imitation was no greater for observing spatially compatible stimuli than incompatible stimuli (left hand stimulus), than when they were spatially incompatible (right hand stimulus). These results show that the effect of observed movements on imitation and or/action execution is the result of automatic imitation rather than spatial compatibility.

## 2. FINGER MOVEMENTS

Bertenthal et al., (2006) measured the effect of observing fingers movements on a choice reaction-time task. The priming effects of imitative and spatial stimuli were tested in combination, in opposition, and independently. It was found that both spatial compatibility and imitation contributed to the priming effects. However the priming effects due to imitation declined during the course of study whereas the priming effect due to spatial compatibility remained constant. This finding suggests

that observed movements exert a priming effect that wears off over time due to familiarity with the stimulus (response facilitation effect).

### 3. HAND/MOUTH MOVEMENTS

Leighton and Heyes (2010) showed that mouth open/close and hand/mouth compatibility effects were due to automatic imitation rather than up-down or left-right spatial compatibility. For example, mouth opening responses were quicker when participants observed mouth opening than when they observed mouth closing stimuli. This effect was no different for observing the mouth stimuli that were rotated such that the lips moved in a horizontal rather than a vertical plane. Likewise, initiation of hand movements was faster when participants observed irrelevant hand movements than when they observed the irrelevant mouth movements. This effect was no different when the hand was on table and when it was presented in front of the mouth. These results show that there is mapping between observed and executed movements such that these motor maps are automatically simulated on action observation. Such simulation is observed as automatic imitation, which is used as a measure of Action Observation System's motor resonance function.

Evidence for the 'automatic' resonance property of the Action Observation System comes from examining automatic imitation. In the studies on automatic imitation (Leighton & Heyes, 2010; Chong, Cunnington, Williams, & Mattingley, 2009; Bertenthal et al. 2006; Longo et al., 2009), it is not likely that the participants *intended* to be influenced by the task-irrelevant stimuli. In fact, they are usually instructed not to respond to the task-irrelevant stimuli. For example, in the hand

opening/closing experiment of Stuermer et al. (2000), participants are instructed to respond to colour cues of the hand stimuli and *not* to respond to the opening and closing actions of the hand stimuli. In spite of such instructions, the RT difference between compatible and incompatible trials is generated by the task-irrelevant stimulus, i.e. to the opening or closing actions of the hand stimuli. Effect of automatic imitation is found in experiments where the task-irrelevant stimuli are located in a spatially distinct location than the task-relevant stimuli (Leighton, & Heyes, 2010; Brass et al., 2000; Catmur, & Heyes, 2011). In these experiments, participants were told that they did not have to attend to these spatially distinct task-irrelevant stimuli. The apparent simulation of motor plans occurs even when the participants do not *intend* to direct their attention to the irrelevant stimuli, suggesting that it happens involuntarily.

The automatic imitation effects occur when i) participants have been instructed not to respond to the stimuli (task-irrelevant) that generate the effects; ii) they are not needed by the instructions to attend to the positions where the task-irrelevant stimuli appear; and iii) their response to the task-irrelevant stimuli interferes with the actual performance. These findings are consistent with the proposal that the Action Observation System, which mediates the automatic imitation effect, is mostly independent of the intention of the actor-observer (Rizzolatti et al., 1996; Grafton et al., 1996; Decety, 1997; Grezes, Costes, & Decety, 1998). Therefore, I propose that the two of the main properties of the Action Observation System are that it is:

- i)       AUTOMATIC - motor plans of the observed actions are simulated automatically at the same time of action observation and without any

volitional control of the observer as long as the motor plans are already in the observer's motor repertoire; and

- ii) UNMEDIATED - motor plans of the observed actions are simulated automatically at the same time of action observation and without any cognitive effort required from the observer.

## II. MOTOR INTERFERENCE

In the last section, I examined how automatic imitation may be linked to the Action Observation System. I also pointed out two main properties of the Action Observation System that could be inferred from studies on automatic imitation. In this section, I present another effect known as the movement interference effect and explore the ways in which it can shed light on the properties of the Action Observation System.

Motor interference occurs when the motor system is primed to move in the direction and manner of observed movements (presumably via the mechanism of automatic imitation) but is 'forced' to move in a different fashion due to task requirements (Blakemore & Frith, 2005; Wilson & Knoblich, 2005). This motor interference can be measured behaviourally via its manifestation as the movement interference effect – observed actions that interfere with simultaneously executed incongruent actions (Kilner, Paulignan, & Blakemore, 2003; Kilner, Hamilton, & Blakemore, 2007; Gowen, Stanley, & Miall, 2008; Craighero et al., 1996).



Automatic imitation suggests that imitating an observed movement is easier than responding to verbal instructions or other symbolic instructions because of the mapping between observed and executed actions. Brass et al. (2000) examined whether observing finger movements had a stronger congruency effect on execution of finger movements in comparison to spatial and symbolic cues. The results showed that participants initiated their finger movements faster if asked to imitate finger movements than when they responded to spatial and symbolic cues. They found that observing finger movements had a strong congruency effect on movement observation, whereas spatial and symbolic cues had no such congruency effect. Observing incongruent finger movements interfered with the executed finger movements – there was higher reaction time for initiating movements when observing incongruent finger movements than when observing congruent finger movements. These results suggest that observing incongruent movements interferes with executed movements because of the automatic simulation of motor plans of observed movements. They also support the claims that the Action Observation System is both automatic and involuntary and unmediated by the cognitive efforts of the observer-actor.

#### A. MEASURING THE EFFECT OF BIOLOGICAL VS NON-BIOLOGICAL MOTION ON THE ACTION OBSERVATION SYSTEM BY MOVEMENT INTERFERENCE

Human beings live in a dynamic social environment, which requires that they quickly decode the movements made by other human beings, understand the goals of those movements and respond to them (Fogassi et al., 2005; Gallese, & Goldman, 1998; Wilson, & Knoblich, 2005; Ramnani & Miall, 2004; Kilner et al., 2004). It is because

of this requirement that perception of biological motion is important for action understanding. Sensitivity to biological motion is also important in the context of imitation. It has been found that biological cues elicit faster responses non-biological spatial cues (Iacoboni et al., 1999; Brass et al., 2000; Bertenthal, Longo, & Kosobud, 2006). Biological movements are also imitated faster than non-biological stimuli even if they are kinematically matched (Tai et al., 2004; Biermann-Ruben et al., 2008; Biermann-Ruben et al., 2008; Jonas et al., 2007; Jonas et al., 2007; Kesslet et al., 2006). It is therefore possible that the Action Observation System shows a preferential sensitivity to observing biological motion.

In addition to the two properties of the Action Observation Network, i.e., it is AUTOMATIC and UNMEDIATED, it is further proposed that the Action Observation System's resonance function is SPECIFIC to the observation actions with biological kinematics (Bouquet et al., 2007; Di Dio et al., 2013; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Decety, & Grèzes, 2006; Gallese, & Goldman, 1998; Perani et al., 2001).

Developmental studies show that sensitivity to biological motion occurs as early as 18 months. Meltzoff (1995) found that 18-month-old infants finished tasks if human adults demonstrated them but not if a mechanical device showed them the same task. Another study looked at the influence of human versus mechanical actions on the execution of those actions by infants (Moriguchi et al., 2012). This study involved 6-month-old infants who were involved in a search task. The infants watched the hiding of an object at location A. One group looked at a human hand search for the

object, and another group of infants saw a mechanical hand search for the object. In both conditions, the search was successful. In another condition, the object was placed at another location B and the infants searched for the object. It was found that infants were more likely to search for the object in location A if they had watched a human hand search there then if they had seen a mechanical hand. These studies demonstrate that the Action Observation System might be selectively sensitive to biological motion from infancy onwards.

Consistent with the findings from infants, adults also show specific effects from biological motion. Castiello et al., (2000) showed that movement components such as time to reach peak velocity and maximum grip aperture were influenced by the prior observation of a human model perform grasping objects of same or different sizes, but not when observing a robotic arm do the same. Kilner et al. (2003) found that there was interference in executed horizontal or vertical movements from simultaneously observing incongruent horizontal or vertical arm movements only when participants observed a human model make movements, and not when a robot performed the same movements. These findings support the argument that the Action Observation System might be selectively sensitive to biological motion.

In a PET study (Tai et al, 2004), participants observed manual grasping actions performed by a robot and by a human model. Observing a human model elicited activation in the left premotor cortex, something that was absent when observing robotic movements. This finding supported the hypothesis that the Action Observation System was sensitive to observing biological motion alone.

Movement interference studies show that i) observing an incongruent movement interferes with the simultaneous execution of another movement; ii) the interference is most likely the result of a conflict of observed incongruent motor plans that are automatically simulated upon observing actions and the motor plans of the executed action. Although there is some evidence that the AOS might be more sensitive to observation of biological motion, as we will discuss next, this issue is far from resolved.

#### DEBATES ABOUT THE SPECIFIC SENSITIVITY OF THE ACTION OBSERVATION SYSTEM TO BIOLOGICAL MOTION

There are a number of potential issues with the interpretation that the sensitivity of the AOS is specific to biological motion. In the studies that compare human movements with robotic movements (Kilner et al., 2003; Castiello et al., 2000), it is possible that the interference is found because of “human-bias” – the stronger perceptual link with actions of humans than of non-human actors (Press et al., 2007), rather than reflecting biological specificity. Kilner et al., (2007) addressed this issue in their study. They compared the effect of observing a human or an abstract stimulus like dot on movement interference. The human (in a video) and the dot moved with either a natural (minimum-jerk) velocity profile or a constant velocity profile. They found that observed incongruent human (video) movements only interfered with executed movements in the natural velocity profile condition whereas there was movement interference for observing incongruent dot movements for both the natural and constant velocity profile conditions. This finding suggests

that the “form” of the observed movements may also play a role in the perception of those movements.<sup>1</sup>

There is neuroimaging evidence that the brain distinguishes real and virtual hand actions. Perani et al., (2001) showed that there were different neural correlates for observing real and virtual hand actions in an fMRI study. They investigated whether different visuomotor and perceptual processes were engaged for observing real hand actions and observing of 3D virtual reality hand actions. Participants passively observed grasping actions of geometrical objects made by a real hand or by 3D and 2D virtual reality hand reconstructions. It was found that only real hand actions in natural environments activated a visuospatial network that included the right posterior parietal cortex, which is believed to be part of the Action Observation System. Lateral and mesial occipital regions were engaged during the observation of virtual reality hand actions, which do not constitute the Action Observation System. This study suggests that movement kinematics and the form of observed effector might conjointly engage the Action Observation System.

Press et al., (2005) further examined the effect of the “form” of observed movements on movement interference. In one experiment, participants were asked to perform a specific movement (e.g. opening their hand) when a human or robotic hand presented a compatible (opened) or an incompatible movement (closed). It was found that there was automatic imitation for both human and robotic stimuli – the

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<sup>1</sup> Kilner, Paulignan, and Blakemore (2003) and Kilner, Hamilton and Blakemore (2007) are the two studies key to this thesis. These two studies will be critically analysed in Chapter 03 of the thesis. Only the general findings are mentioned in this chapter. The methodological issues are addressed in Chapter 03.

compatible stimulus cue caused a fast initiation of the specified movement when compared to the compatible stimulus cue. However, observing a human hand had a greater effect on the performance than the robotic hand. This suggests that the Action Observation System may not be exclusively specific to observed biological motion but that it might be sensitive to non-biological as well, although not as strongly as for biological motion.

The role of “form” of the observed stimulus and its relation with movement kinematics was investigated by Longo and Bertenthal (2009). They looked at the automatic imitation of movements stimulated by observing a virtual, computer-generated hand perform specific finger movements. This stimulus was the same across all conditions, but some participants were instructed that they would be observing short clips of “computer-generated model of a hand”, whereas other participants were given no such information regarding the virtualness of the hand. Participants performed finger movements specified in a task as they simultaneously observed either what they were told was the virtual hand or the same clip without being given any information about it. There was a significant lowering of automatic imitation, measured as reaction time of movement initiation, in the group of participants whose attention had been drawn to the virtualness of the hand. This result suggests that there may not be a direct one-to-one link between movement kinematics and the Action Observation System. Just as the form of the effector plays a role along with the kinematics, this study proposes that the “belief” about the effector also influences the AOS.

Despite an apparent bias towards stronger effects from biological stimuli, the picture is unclear as to whether this reflects a true specificity for processing biological motion. In addition, factors such as ‘belief’ about the biological nature and the velocity profiles also seem to influence the response. The varied results about the effect of biological vs non-biological motion as well as the form of the observed stimuli on the Action Observation Network need to be examined further. Towards that end, in Chapter 03, I critically analyse the two key studies on movement interference effect - Kilner, et al., (2003, 2007), and, and present the findings of my experiment that attempted to replicate the results of the Kilner et al., (2007) study. I analyse the shortcomings of the methodology of Kilner et al., (2007) in the light of my replication study in Chapter 03. In Chapter 04, I present the findings from two experiments whose aims were i) to develop a measure of movement interference more sensitive than the commonly used variance or standard deviation; and ii) to study the effect of the “form” of the observed stimuli conjointly with their movement kinematics on movement interference. In Chapter 05, I present the results of the study that examined the effect of observational viewpoint on movement interference. I re-examine the three proposed properties of the Action Observation Network (viz., Automatic, Unmediated and Specific) as understood by measuring movement interference in the light of research literature and my own experimental findings.

# **CHAPTER 03: EXPERIMENT 1**

## **– A REPLICATION STUDY**



## CHAPTER 03: EXPERIMENT 3.1 – A REPLICATION STUDY

### I. INTRODUCTION

We are constantly interacting with the world while observing the actions of others. The interaction between what we observe and how we perform an action gives valuable insights into the system that supports action understanding. The movement interference effect is the measurable interference of simultaneously observed movements on executed movements that are qualitatively different from the observed movements (Kilner, Paulignan, & Blakemore, 2003; Kilner, Hamilton, & Blakemore, 2007). This objective measure can therefore provide an index of the shared representation of observer and executed actions in the Action Observation System (AOS). In this chapter, I present the key studies examining the overlap between action observation and action execution based on the movement interference effect paradigm, and an experimental replication to test the properties of the Action Observation System (AOS).

The theories of motor resonance suggest that there is overlap between action execution and perception of action via observation (Buccino et al., 2004; Gallese, & Goldman, 1998; Rizzolatti et al., 1999; Uithol et al., 2011; Zentgraf et al., 2011). Kilner et al., (2003) hypothesised that observed incongruent movements must interfere with simultaneously executed movements by virtue of this overlap. They also suggested that this interference effect measured as variance in executed movements, would be a measure of this parity between action observation and action execution. They also wanted to find out if this interference effect could be measured

only for observing a human being execute incongruent movements or even for observing a robot perform simultaneous incongruent movements.

Participants made sinusoidal arm movements in the horizontal or vertical plane as they observed a robotic arm or a human execute similar horizontal or vertical movements. The observed movements could be either congruent (movements in the same plane as those made by the participants – observed and executed horizontal or vertical movements) or incongruent (movements in the opposite plane as those made by the participants – observed horizontal and executed vertical movements or *vice versa*). In a baseline condition, the participants moved their arms either in the horizontal or the vertical direction without observing any movements. An Optotrak 3020 recording system was used for recording the arm movement data, and variance in the movement was used as an index of interference to the executed movement.

The results showed that the variance when observing human incongruent movements was greater than the variance when observing congruent movements, demonstrating a motor inference effect. In addition, the variance in horizontal movements differed from the variance in vertical movements irrespective of whether the observed movements were congruent or incongruent and whether the participants observed a human or a robot. In general, there was greater variance for executing horizontal movements than for vertical movements. The results showed that there was greater variance when observing a human make incongruent arm in comparison with baseline movements. There was no significant difference between the variance in baseline condition and for observing a robot make either congruent

or incongruent movements and for observing a human execute congruent movements. This study shows that there is an overlap between action observation and action execution. This overlap generates interference when observing movements incongruent to executed movements at the same time.

Kilner et al. (2003) did not find any interference to executed movements when observing a robot make incongruent movements. Robotic movement differs from human movement in two main ways – i) robotic movement has different movement kinematics than that of human movement, particularly with respect to its velocity profile, and ii) the robot looks very different from a human – the “form” of the robot differs from the “form” of a human as facial expressions are absent in a robot. It is possible that the physical differences in the stimuli interfered with executed movements rather than the simulation of motor plans of observed incongruent movements.

Another possible issue with this experiment is that there were very few trials per condition, raising the possibility that there would be insufficient data to detect subtle effects. Eight participants made ten sinusoidal arm movements in every trial (one movement comprised of starting at either left corner, moving to the right corner and coming back to the same position in case of horizontal movements, and starting at the bottom point, moving to the top and returning to the start position in case of vertical movements). There were eight conditions in the experiment (Congruency – Congruent and Incongruent, Observed Effector - Human and Robot, and Movement Direction – Horizontal and Vertical). In addition, there were two baseline conditions

in which participants executed either Horizontal or Vertical movements without observing anything. Participants performed only two trials per condition such that there were only 200 trials per participant in the experiment. Therefore, the experimental power may be too low to detect the subtle effects of movement interference.

Kilner et al., (2007) addressed some of the above concerns in another experiment. This experiment looked at the issue with movement kinematics in a more rigorous and controlled manner as compared the experiment in which the effect of human and robot movements on the Action Observation System (AOS) was studied (Kilner et al., 2003).

Human arm movements differ from robotic movements in many ways, kinematics being the most significant difference between the two. Human arm movements are typically described as having a bell-shaped 'minimum jerk' (MJ) trajectory (Flash & Hogan, 1985), where the movement begins slowly, shows smooth acceleration and then slowly decelerates (Rizzolatti, Fogassi, & Gallese, 2001). This is in contrast to the instantaneous acceleration to maximum velocity at the start of the movement, and an instantaneous deceleration to rest at the end of the movement characteristic of a constant velocity movement (FIGURE 01). Robotic movements are movements are governed by Newton's laws, whereas the trajectory of human arm movements is constrained by arm dynamics and deviates from a linear path, such that the derivative of acceleration (jerk) is minimized over the movement (Abend et al., 1982). Therefore there are significant differences between human movements that

trace a 'minimum jerk' trajectory and objects that display constant velocity movements like robots.

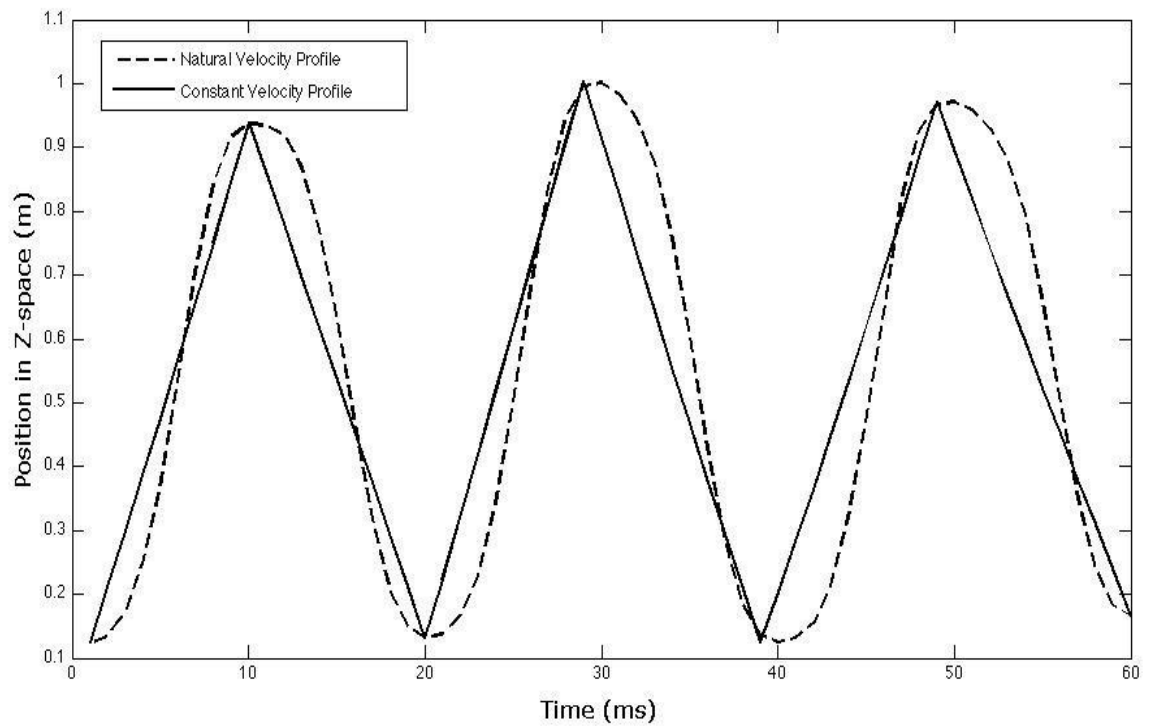


FIGURE 01. Graphs of movements with Natural Velocity (dashed line) and Constant Velocity (solid line) profiles.

Kilner et al. (2007) examined the potential sources for differences in the movement interference effect between humans and abstract stimuli like a ball moving on the screen on the Action Observation System (AOS). A high-speed video camera was used to film a human model make arm movements and the footage was altered to create a video with arm movements with a constant velocity profile. Therefore, there were two kinds of human videos: one video showing normal, biological (MJ) arm movement and another showing the human arm moving with constant velocity (CV)

motion. Another set of videos were created where the human arm movement was replaced with a white ball moving on a black screen with the same movement kinematics as in the two human arm videos, such that there were two more videos - ball moving with MJ velocity profile and ball moving with a constant velocity (CV) profile. Participants made sinusoidal arm movements while observing the videos of a ball or a human arm that moved either in the same direction (congruent) or tangential (incongruent) to the participants' own movements. Here, as in the earlier experiment (Kilner et al., 2003), participants observed and executed either horizontal or vertical movements.

Kilner et al., (2007) predicted that there would be interference to executed movements when participants observed the human arm make incongruent MJ movements relative to congruent trials unlike the Kilner et al., (2003) study where they compared the congruent and incongruent trials to the baseline condition. If this interference was based solely or primarily on the form of the effector, there should be no interference for observing a ball make either MJ or CV movements. In contrast, if the interference depended on kinematics rather than form, both a human and a ball moving with an MJ profile should cause interference, but there should be no effect of either moving with a CV profile.

Similar to the findings of the previous study, there was interference to simultaneously executed movements when observing the human arm video with a MJ velocity profile, but not a human with a CV profile. In case of the ball, however, there was interference irrespective of the movement kinematics of the ball. The

experimenters concluded that movement interference effect was driven primarily by the observation of biological motion rather than the artificiality of the effector.

This study poses a problem with respect to the direction of executed movements. In the earlier study that looked at human versus robot movements (Kilner et al., 2003), the variance of executed movements was significantly greater for executing horizontal than vertical movements. In their next study (Kilner et al., 2007) which looked at the effect of human (in a video recording) versus a ball, the variance of executed movements was significantly greater for executing vertical than horizontal movements. There was a main effect of Movement Congruency, where observing incongruent movements interfered more with executed movements than observing congruent movements. There were two significant interactions – between Movement Congruency and Movement Direction, and between Movement Congruency and Velocity Profile. Due to the significant interaction between Movement Congruency and Movement Direction, they investigated the effects separately for horizontal and vertical movements. The results of this analysis showed that all the significant main effects and interactions were found only for the movements executed in the vertical direction. All their inferences about the Action Observation System were based on these partial results. They state that the experimental design might have led to this difference, but it is hard to accept that explanation for the selective bias towards vertical executed movements: The experimental structure between the Kilner et al., (2003) and the 2007 study is similar in all aspects except that the manipulation of form of the observed effector (human versus ball) and movement kinematics (minimum jerk versus constant velocity profile) was better controlled for than in

Kilner et al, (2003) experiment. Therefore, the results of this experiment, and their interpretations thereof, are not convincing.

The following experiment is an attempt to replicate the results of Kilner et al (2007). The fact that interference effects were found only when executing movements in the vertical direction and not in the horizontal direction made me cautious about accepting their conclusions about the AOS. In particular, there seems no good theoretical reason why one should see effects in one plane but not the other if the effect reflects automatic activation of the AOS. The movement interference effect, however, has been used as an effective paradigm in other studies investigating the Action Observation System (AOS) (Blakemore, & Frith, 2005; Brass et al., 2000; Brass, & Heyes, 2005; Prinz, 1997; Stanley, Gowen, & Miall, 2007; Wohlschlaeger and Bekkering, 2002). Therefore I wanted to re-examine the primary hypothesis of Kilner et al., (2007) by replicating their study and attempt to clarify the issue raised by the selective interpretations with respect to direction of executed movements. This has theoretical implications on predictions about the properties of the AOS and how it engages in action understanding. It also formed the basis for a more robust experiment presented in Chapter 04.



## II. EXPERIMENTAL METHODS

### PARTICIPANTS

Twelve healthy, right-handed participants took part in the study (mean age = 24; number of males 8; number of females = 4). Informed written consent was obtained from each participant according to the policies of the Macquarie University Human Research Ethics Committee.

### STIMULI

Participants observed video recordings of the experimenter making either Horizontal or Vertical movements (FIGURE 02). Horizontal movements started near the midpoint between the body and the screen at the left corner of the frontal plane and moved horizontally across to the right corner of the plane and returned to the starting point. Vertical movements started at the near the midpoint between the body and the screen at the bottom of the frontal plane and moved vertically upwards to the top of the plane and returned to the starting point.

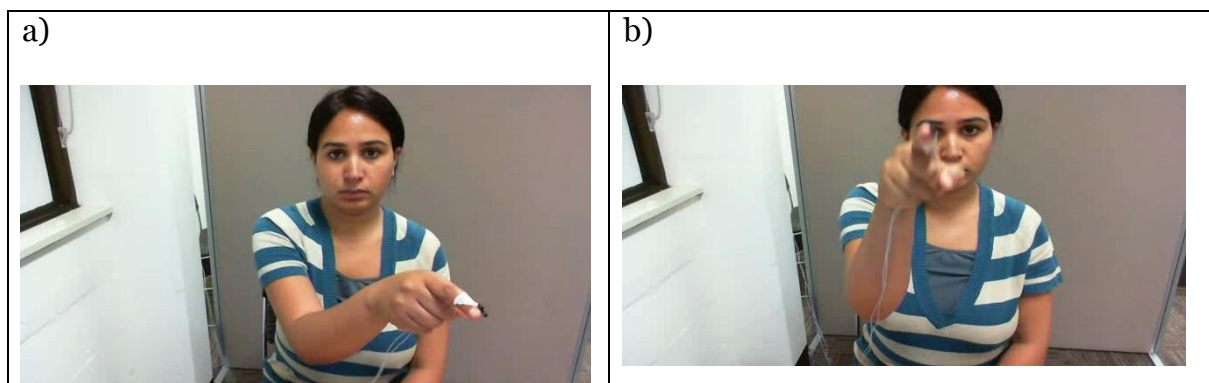


FIGURE 02. Images of (a) Horizontal Movement (b) Vertical Movement

To generate the stimuli, a webcam (Microsoft LifeCam) was used to record right arm movements made by the experimenter at 30 Hz. The movement of the hand was

simultaneously tracked with an Optotrak Certus Motion Capture System (Northern Digital Inc.) at 200 Hz sampling rate by placing two small markers (infrared light emitting diodes or LEDs) on the index fingertip of her right hand. Programs written in MATLAB (The Mathworks Inc.) were used to determine the frame numbers required to generate videos at 15 Hz with approximately constant velocity (CV). The original videos were resampled to 15 Hz to generate the natural velocity (NV) videos, so that both the CV and NV videos had the same number of frames and sample rate, and the peaks and troughs of the movements coincided.

To generate 'dot' stimuli, a 2X2 matrix of white squares on a black background was created. Based on the frame numbers generated for NV and CV videos, the position of the fingertip was calculated from the Optotrak data at those frames. The “dot” movement was derived from the fingertip movements, and hence both the video and the “dot” comprised of exactly the same movement kinematics.

## EXPERIMENTAL DESIGN

Participants sat in a quiet, dark room at a table with a LCD touchscreen (70 X 39 cm, 1360 X 768 pixels, 60 Hz) placed approximately 70 cm in front of them. Hand movements were recorded using the same setup as described in the 'Stimuli' section.

Each trial started with the participants tapping on the right foot pedal placed under the table at a position convenient to each subject. A central fixation dot appeared on the screen after the participants tapped the pedal, followed by a beep after 1 second.

The participants were instructed to place their fingertips about 15 cm away from the middle left or bottom centre of the screen over the table surface as the starting point.

Instructions for the movement to be executed appeared on the screen at the beginning of each block, and the participants executed only one kind of movement in each block – either Horizontal or Vertical. The movements alternated between blocks. There were eight blocks per session – four blocks for Horizontal movements and four blocks for Vertical movements. The participants were not given specific instructions to move synchronously, but they did synchronise their movements with the observed movements by the time they performed a few trials in the first block.

The stimulus (video or dot), appeared on the screen 1 second after the beep. The participants performed three full movement cycles per trial while simultaneously observing the stimulus on the screen. For horizontal movements, one full movement cycle comprised a rightward movement to the middle right corner of the screen and one leftward movement to the starting position at the middle left corner of the screen when executing horizontal movements. For vertical movements, one full movement cycle comprised an upward movement to the top corner of the screen and one downward movement to the starting position at the bottom corner of the screen.

The executed movements were either congruent or incongruent with the observed movements. In the congruent condition, the participants observed and executed movements in the same direction (e.g., both observed and executed movements were either Horizontal or Vertical), while in the incongruent condition, the observed and executed movements were in different directions (e.g., observed movement was

Horizontal and executed movement was Vertical or *vice versa*). The following conditions were presented with four repetitions each per block in a randomised order: Observed Effector (Dot versus Human) X Movement Congruency (Congruent versus Incongruent) X Velocity Profile (Natural Velocity versus Constant Velocity).

## DATA ANALYSIS

Programs written in MATLAB were used to analyse the data. The first two blocks of the experiment were discarded during the analysis for each subject as they were considered practice blocks. The first rightward and the last leftward movement of each trial for horizontal executed movements, and the first upward and the last downward movement of each trial for vertical executed movements were discarded in order to account for errors in initiation and termination of movements, such that the analysis comprised of two movement cycles (e.g., two upward and two downward movements), and the movement data was segmented into these four parts based on peaks in the velocity profile. Trials with more than 5% of the data missing due to occlusion of both the markers on the fingertip were also excluded. Missing data points were interpolated using spline interpolation for the rest of the trials. Mean variance in perpendicular distance ( $\text{mm}^2$ ) of the individual movement trajectories was used as the measure of movement interference.

## RESULTS

A 2X2X2X2 repeated measures ANOVA was performed using SPSS. The four factors were Movement Congruency (Congruent versus Incongruent), Movement Direction (Horizontal versus Vertical), Observed Effector (Dot versus Human), and Velocity Profile (Natural Velocity versus Constant Velocity).

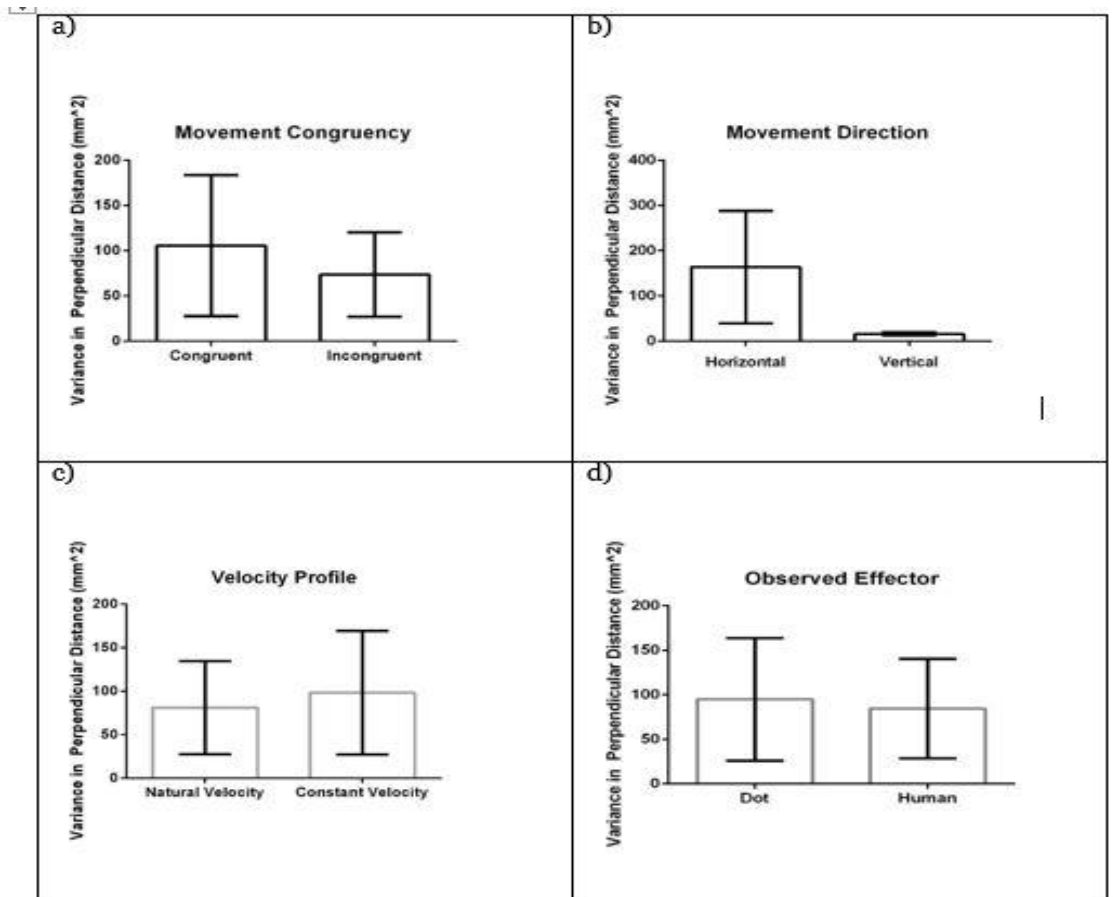


FIGURE 03. a) The mean variance in perpendicular movement execution for congruent and incongruent trials across all conditions; b) The mean variance in perpendicular movement execution for making horizontal and vertical movements across all conditions; c) The mean variance in perpendicular movement execution for observing natural and constant velocity profile trials across both human and dot effectors d) The mean variance in perpendicular movement execution for observing natural and constant velocity profile trials across all conditions

FIGURE 03 gives the variance in perpendicular distance for each of the factors. The repeated measures ANOVA showed no main effect of Movement Congruency  $F(1,11) = 1.043$ ,  $p = 0.329$ ; Movement Direction  $F(1,11) = 1.431$ ,  $p = 0.257$ ; Velocity Profile  $F(1,11) = 0.939$ ,  $p = 0.353$ ; or Observed Effector  $F(1,11) = 0.613$ ,  $p = 0.450$ .

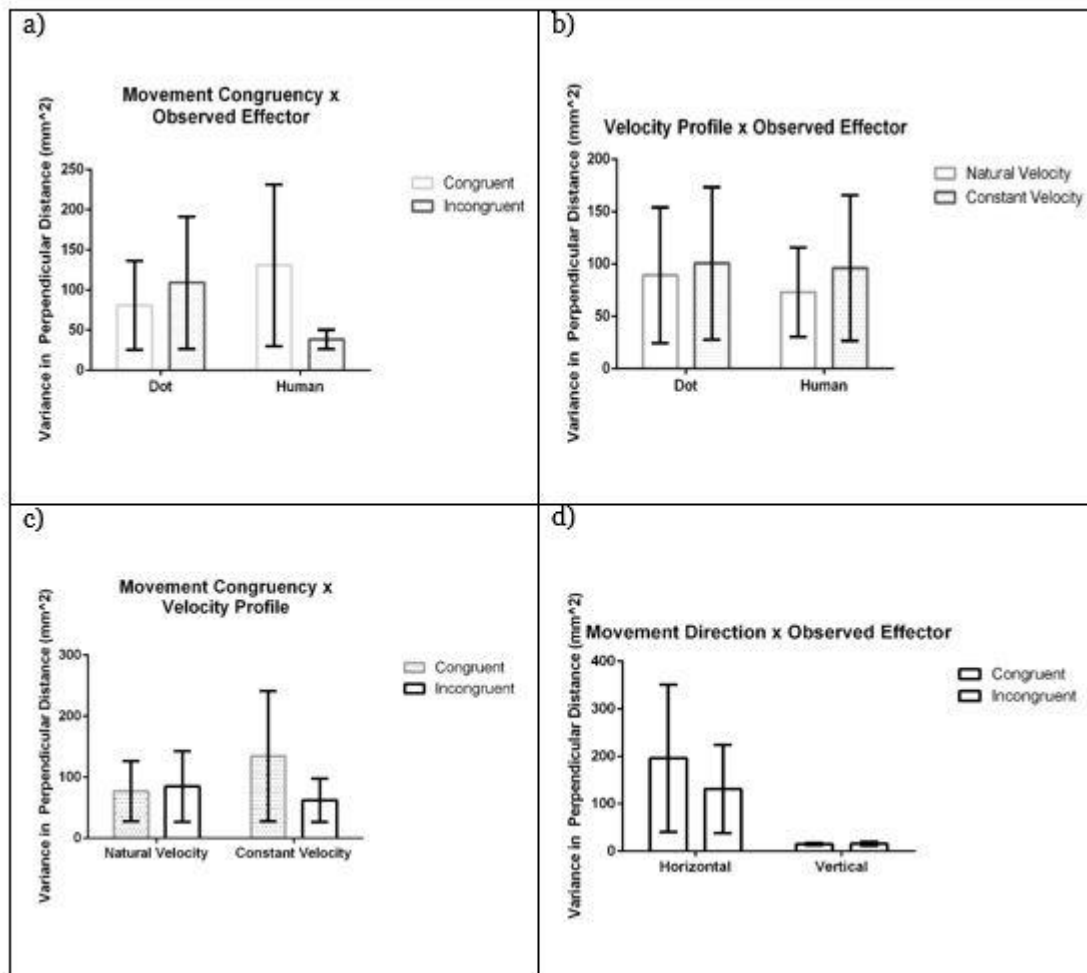


FIGURE 04. The mean variance in perpendicular movement execution for key interactions: a) Observing human and dot movements that are either congruent or incongruent with the executed movements; b) Observing human and dot movements with either natural (NV) or constant velocity (CV); c) Observing movements with natural (NV) or constant velocity (CV) profiles that are either congruent or incongruent to executed movements; d) Observing movements that are either congruent and incongruent with horizontal and vertical executed movements.

FIGURE 04 gives the variance in perpendicular distance for the key interactions - Movement Congruency X Observed Effector  $F(1,11) = 1.061$ ,  $p = 0.325$ ; Velocity Profile X Observed Effector  $F(1,11) = 0.345$ ,  $p = 0.569$ ; Movement Congruency X Velocity Profile  $F(1,11) = 0.993$ ,  $p = 0.340$ ; Movement Congruency X Movement Direction  $F(1,11) = 1.087$ ,  $p = 0.320$ . None of the two, three, or four way interactions were significant (all  $p > 0.3$ ).

### III. DISCUSSION

The aim of this study was to replicate the reported motor interference effects of Kilner et al. (2003, 2007). Using a careful design, I failed to find any significant interference effects of observing either a human movement or a dot movement, regardless of whether the movement kinematics matched biological motion or not. It is also possible that the large 4-way ANOVA could not detect the subtle differences in movement interference because of a lack of power. In my replication study, there were 12 participants and 256 trials per participant for eight conditions. There was no baseline condition either. My replication study certainly has more power than the Kilner et al., (2003) experiment and has almost the same total number of trials as the Kilner et al., (2007) experiment.

Although one must be extremely cautious in interpreting null results, the variance between Kilner et al.'s two previous studies does raise concerns about the robustness of their results. First, in the Kilner et al (2003) study, the variance of executing horizontal movements was significantly greater than the variance of executing vertical movements. Also, there were only 200 trials per participant across all

conditions including the baseline condition. It is possible that the power was too low to detect significant effects.

Second, in the Kilner et al (2007) study, contrary to the results of their earlier experiment (Kilner et al., 2003), the variance in executive vertical movements was significantly greater than the variance in executing horizontal movements. Even though they found a main effect of Observer Effector, they fail to mention the size of that effect in terms of the actual variance in executed movements for observing a human versus a ball. There were two significant interactions – between Movement Congruency and Movement Direction, and between Movement Congruency and Velocity Profile. Due to the significant interaction between Movement Congruency and Movement Direction, they investigated the effects separately for horizontal and vertical movements. The results of this analysis showed that all the significant main effects and interactions were found only for the movements executed in the vertical direction.

It is not clear as to why they analysed the data for Horizontal and Vertical directions independently when a paired-sampled t-test would have sufficed. It is hard to accept the interpretations of the study solely based on the results of a partial effects of vertical executed movements. The authors acknowledge that there is variability between the two previous studies in spite of using the same observed and executed movements (horizontal and vertical). This variability needs to be explored by designing a more robust experiment.

In the following experimental chapter, I explored the ambiguity in the effect of movement direction on motor interference further. Since there were no significant



main effects or interactions in the replication study, I modified the paradigm to explore the effects of movement interference when observing and executing diagonal movements in the frontal plane. I also looked for a measure more sensitive than variance in perpendicular direction to study the movement interference effect.

**CHAPTER 04: DEVELOPING A  
SENSITIVE MEASURE OF MOTOR  
INTERFERENCE AND THE ROLE OF  
OBSERVED EFFECTOR ON MOTOR  
INTERFERENCE**

# CHAPTER 04: DEVELOPING A SENSITIVE MEASURE OF MOTOR INTERFERENCE AND THE ROLE OF OBSERVED EFFECTOR ON MOTOR INTERFERENCE

## I. INTRODUCTION

Movement interference studies have shown that observing or even imagining incongruent movements interferes with simultaneously executed movements (Kilner, Paulignan, & Blakemore, 2003; Kilner, Hamilton, & Blakemore, 2007; Gowen, Stanley, & Miall, 2008; Craighero et al., 1996). While these studies have demonstrated the involvement of the motor regions of the brain in action perception, the conditions under which this involvement can occur is far from clear. One potential explanation for the variability of the results in the two Kilner et al. studies (2003, 2008) and the previous chapter is the use of quite different movements (vertical and horizontal) – there was greater variance of executing horizontal movements in the 2003 study, whereas there was greater variance of executing vertical movements in the 2008 study. In the 2008 study, Kilner et al., reported their interpretations based on the effect of executing vertical directions also, thereby creating a bias in the interpretation. In the previous chapter, I failed to replicate either effect, possibly due to lack of power. In order to resolve this ambiguity in the effect of movement direction on motor interference, in these next experiments, I modified Kilner et al.'s experimental design by changing the direction of the observed and executed movements. In Experiment 1, all participants observed both 'Dot' and 'Video' (human) stimuli. It is possible that participants observing 'Video' (human) movements may have imagined these movements when observing 'Dot' stimuli as well. In Experiment 2, the issue of the spill-over of stimuli due to

imagination is resolved. The first group of participants observed only 'Dot' stimuli and the second group of participants observed only 'Video' stimuli. I predicted that Experiment 02 will clarify how the Action Observation System (AOS) might be affected by the observed effector.

Vertical and horizontal movements differ greatly in their kinematics. According to Atkeson and Hollerbach (1985), the 'inward' and 'outward' trajectories of horizontal movements are nearly straight and not significantly different from each other.

However, an 'upward' vertical movement is more curved than a 'downward' vertical movement that is nearly straight like the horizontal movement trajectories. Thus, it is possible that in the previous movement studies, all of which contrasted vertical and horizontal movements, this variance in kinematics might mask other more subtle effects of congruency. There is another specific kinematic difference between vertical and horizontal movements - vertical movements are categorised as free-arm movements, whereas horizontal movements are classified as compliant motion (Brady et al., 1982). According to Brady et al., (1982), vertical movements are more natural than horizontal movements because they are less constrained kinematically than horizontal movements. Compliant motion such as a horizontal movement has fewer degrees of freedom, which is seen as the nearly straight-line of its trajectory.

One novel alternative is to use diagonal movements reaching to the left vs the right. These movements are much more similar with respect to biomechanical constraints, just heading in different directions. Thus, we might be able to see more compelling

and robust effects of watching an incongruent vs congruent motion while executing diagonal movements.

Using these diagonal movements should provide a more sensitive measure for examining the key predictions of the experiment. First, I hypothesised that there should be interference on observing incongruent relative to congruent trials, evidenced by greater variability in angle of executed movement trajectory. Second, I predicted this effect would only be seen for observing movements with a natural velocity profile because most behavioural studies show that the Action Observation System is preferentially engaged by observing biological movements (Kilner et al., 2003; Ulloa, & Pineda, 2007; Bouquet et al., 2007). The angles made by movement trajectories with respect to global horizontal coordinates in the frontal plane were used as the measure of interference when observing movements incongruent to the executed movements. Angle of movement trajectories was chosen instead of commonly used measures such as variance and standard deviation to provide a more sensitive measure of movement interference. Diagonal movements are closer to each other with respect to biomechanics and they naturally produce an angle in the frontal plane. Although the magnitude of the effect measured as angle may be small, I predicted that it would be less masked by subtle differences in producing left and right movements (unlike the grossly different horizontal and vertical movements). It may also be able to detect subtle differences in movements that measures like standard deviation and variance may miss.

## EXPERIMENT 4. 1: DEVELOPING A MORE SENSITIVE MEASURE OF THE MOTOR INTERFERENCE EFFECT

In this experiment, I presented dot and video stimuli similar to those presented in the previous chapter, but using diagonal movements. In Experiment 4.1, these different stimuli were presented within a single experimental run and determined if angle made by movements was a more sensitive measure than variance in movements. Even though variance was used by Kilner et al. (2003, 2007) to measure the movement interference effects, it is possible that the use of horizontal and vertical movements may have masked the actual effects of movement interference. Horizontal and vertical movements are kinematically very different from each other (Atkeson, & Hollerbach, 1985). Kilner et al. (2003, 2007) reported contradictory results of the execution of horizontal and vertical movements in both their studies suggesting that they may not be able to accurately measure movement interference. Diagonal movements were used instead of horizontal and vertical movements since diagonal movements are biomechanically more similar to each than horizontal and vertical movements are.

## EXPERIMENTAL PROCEDURES

### PARTICIPANTS

Twelve healthy, right-handed participants took part in the study (mean age = 18.67; number of males = 7; number of females = 5). Informed written consent was obtained from each participant according to the policies of the Macquarie University Human Research Ethics Committee.

## STIMULI

Participants observed video recordings of the experimenter making either Diagonal to Right or Diagonal to Left movements (see FIGURE 01). Diagonal to Right movements started at the bottom left corner of the frontal plane (0,0 of the coordinate system) and moved diagonally across to the top right corner of the plane (1,1 of the coordinate system) and returned to the starting point. Diagonal to Left movements started at the bottom right corner of the frontal plane (1,0 of the coordinate system) and moved diagonally across to the top left corner of the plane (0,1 of the coordinate system) and returned to the starting point. Each stroke was approximately 60 cm long and took approximately 0.6 seconds.

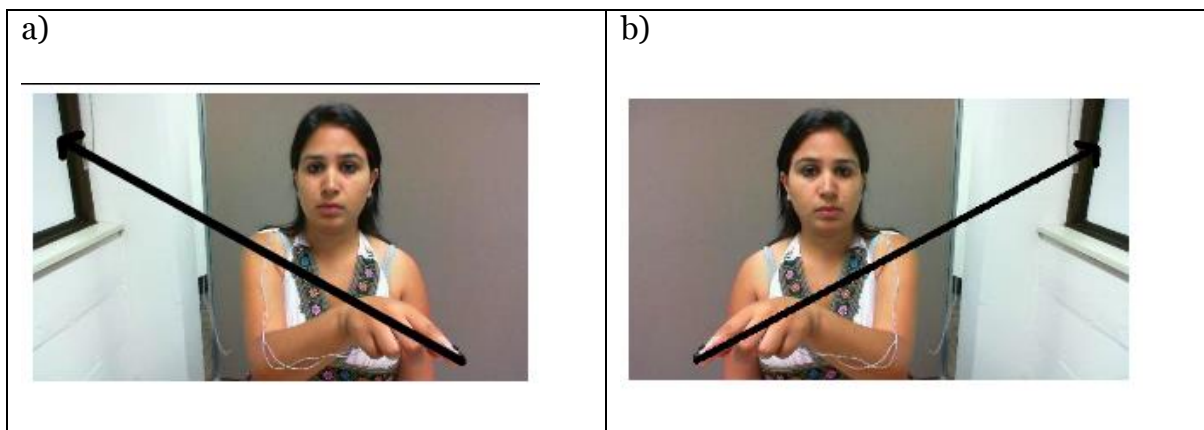


FIGURE 01. Observed videos. a) Diagonal to Left movement b) Diagonal to Right movement

To generate the stimuli, a webcam (Microsoft LifeCam) was used to record movements made by me with my right arm at 30 Hz. The movement of the hand was simultaneously tracked with an Optotrak Certus Motion Capture System (Northern Digital Inc.) at 200 Hz sampling rate by placing two small markers (infrared light

emitting diodes or LEDs) on the index fingertip of her right hand. Programs written in MATLAB (The Mathworks Inc.) were used to determine the frame numbers required to generate videos at 15 Hz with approximately constant velocity (CV). The original videos were resampled to 15 Hz to generate the natural velocity (NV) videos, so that both the CV and NV videos had the same number of frames and sample rate, and the peaks and troughs of the movements coincided (see FIGURE NO 1. FROM CHAPTER 03).

To generate 'dot' stimuli, a 2X2 matrix of a white square on a black background was created. Based on the frame numbers generated for NV and CV videos, the position of the fingertip was calculated from the Optotrak data at those frames. The “dot” movement was derived from the fingertip movements, and hence both the videos and the “dot” comprised of exactly the same movement kinematics.

## EXPERIMENTAL DESIGN

Participants sat in a quiet, dark room at a table with a LCD touchscreen (70 X 39 cm, 1360 X 768 pixels, 60 Hz) placed approximately 70 cm in front of them. Hand movements were recorded using the same setup as described in the 'Stimuli' section.

Each trial started with the participants tapping on the right foot pedal placed under the table at a position convenient to each subject. A central fixation dot appeared on the screen after the participants tapped the pedal, followed by a beep after 1 second. The participants were instructed to start movements at about 15 cm away from the left bottom or right bottom of the screen over the table surface. The stimulus (video



or dot) appeared on the screen 1 second after the beep (FIGURE 02). The participants performed three full movement cycles per trial while simultaneously observing the stimulus on the screen. One full movement cycle comprised an upward movement to the top corner of the screen and one downward movement to the starting position at the bottom corner of the screen. Instructions for the movement to be executed appeared on the screen at the beginning of each block, and the participants executed only one kind of movement in each block – either Diagonal to Right or Diagonal to Left. The movements alternated between blocks. There were eight blocks per session – four blocks for Diagonal to Right movement and four blocks for Diagonal to Left movement. The participants were not given specific instructions to move synchronously, but they synchronised their movements with the observed movements by the time they performed a few trials in the first block.

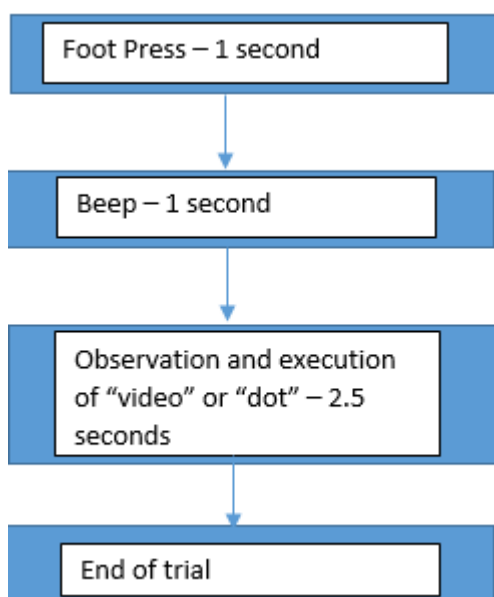


FIGURE 02. Time course of the trial structure

The participants always executed one movement (within a block). The observed movement could be congruent or incongruent with the executed movement for that block (varying on a trial by trial basis). In the congruent condition, the participants

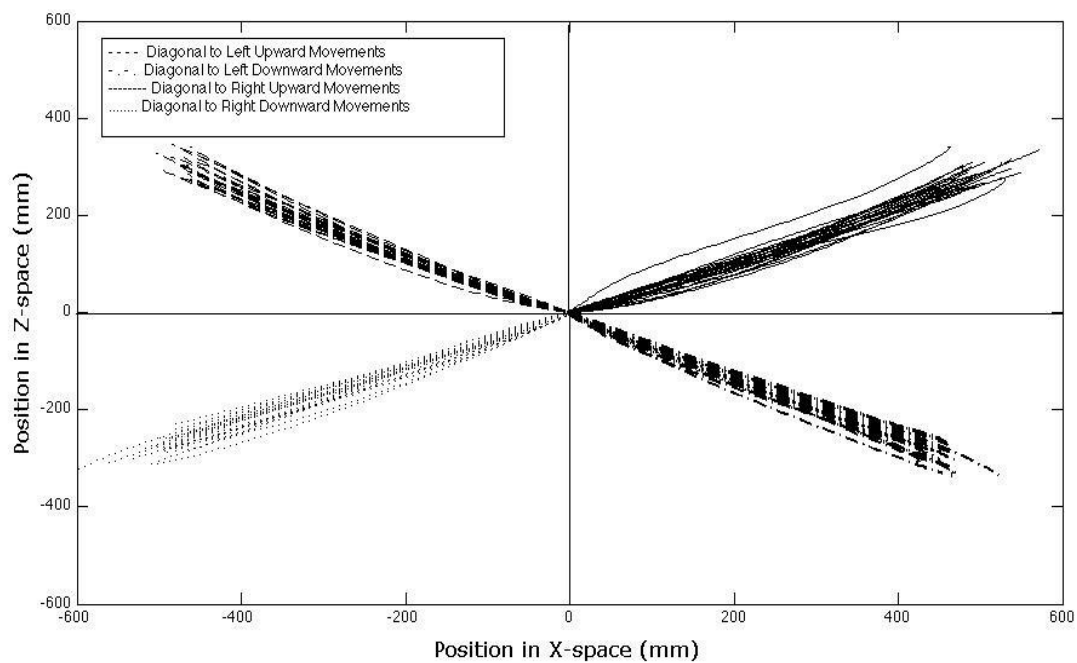
observed and executed movements in the same direction (e.g. both observed and executed movements were either Diagonal to Left or Diagonal to Right.). In the incongruent condition, the observed and executed movements were in different directions (e.g. observed movement was Diagonal to Right and executed movement was Diagonal to Left and vice versa.) The following conditions were presented with four repetitions each per block in a randomised order: Observed Effector (Dot versus Human) X Movement Congruency (Congruent versus Incongruent) X Velocity Profile (Natural Velocity versus Constant Velocity).

## DATA ANALYSIS

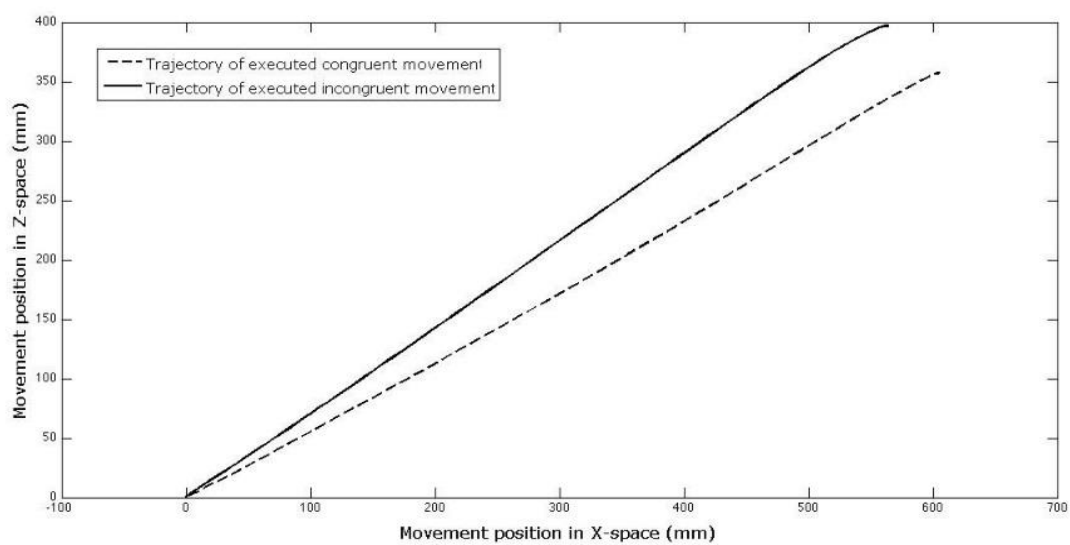
Programs written in MATLAB were used to analyse the data. The first two blocks of the experiment were discarded during the analysis for each subject as they were considered practice blocks. The first upward and the last downward movement of each trial were discarded in order to account for errors in initiation and termination of movements, such that the analysis comprised of two movement cycles (i.e. two upward and two downward movements), and the movement data was segmented into these four parts based on peaks in the velocity profile. Trials with more than 5% of the data missing due to occlusion of both the markers on the fingertip were also excluded. Missing data points were interpolated using spline interpolation for the rest of the trials.

The angle of the movement in the frontal plane was calculated as the angle between the position at each time point (relative to the start point) and a vector pointing towards the right. The angle was used as the measure of interference. All movement

trajectory angles were shifted to the positive first quadrant such that they were all within the range 0 degrees to 90 degrees. This facilitated averaging and comparing of angles made by upward and downward movements in both the left and right diagonal directions (FIGURE 03). Angles were averaged across segmented movements and then across trials for each condition. With this formulation, the greater the interference from observing incongruent movements, the greater the angle of the executed movement, as would be the case if the movement trajectory was shifted to the direction of the observed movement.



a)



b)

FIGURE 03. Trajectories of Diagonal to Right and Diagonal to Left movements segmented and angles of congruent and incongruent movements compared with each other.

a) Segmented trajectories of Diagonal to Right and Diagonal to Left movements. The four trajectories analysed per trial were segmented into upward and downward movements. The trajectories are plotted in X-Z space (X being the left-right position and Z being the height (up-down position) of each movement); b) Trajectory of executed movement shifted when executing a congruent and an incongruent movement. Trajectories of congruent movements (dashed line) and incongruent movements (solid line) were shifted so that they started at the same point (0,0) for Diagonal to Right movements.

## RESULTS AND DISCUSSION

A 2X2X2X2 repeated measures ANOVA was performed using SPSS. The four factors were Movement Congruency (Congruent versus Incongruent), Movement Direction (Diagonal to Right versus Diagonal to Left), Observed Effector (Dot versus Video), and Velocity Profile (Natural Velocity versus Constant Velocity).

There was a significant main effect of Movement Congruency ( $F(1,11) = 5.232$ ,  $p = 0.043$ ), no other significant main effects (all  $P > 0.1$ ), and a significant three-way interaction between Movement Congruency, Movement Direction, and Observed Effector,  $F(1,11) = 5.475$ ,  $p = 0.039$ . The four-way interaction was not significant,  $F(1,11) = 0.070$ ,  $p = 0.796$ , hence the data in FIGURE 04 is collapsed across the Velocity profile conditions.

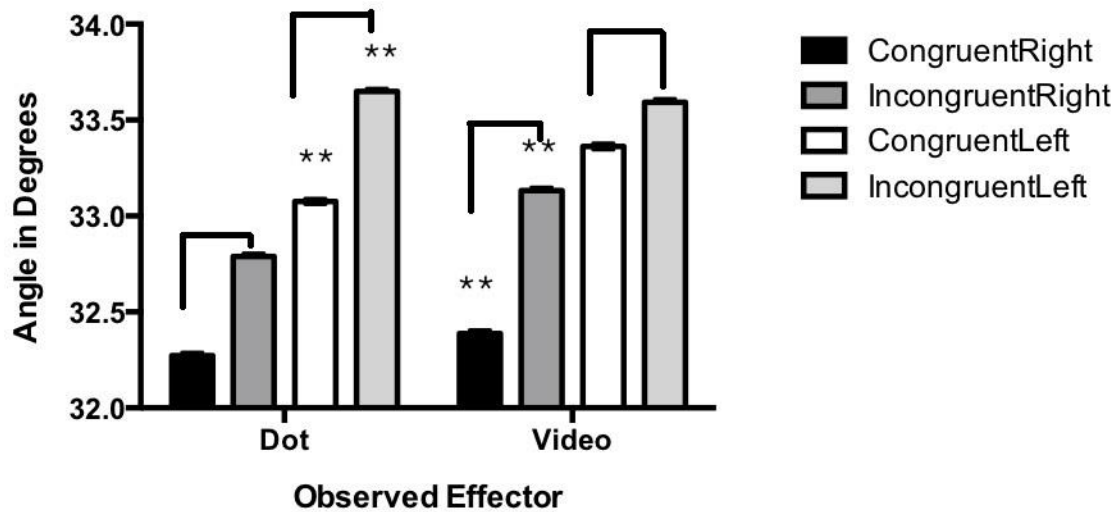


FIGURE 04. Mean angle in degrees (measure of motor interference) for participant movements while observing either a Dot or Video (human) moving in a congruent or incongruent diagonal direction. Note these data are collapsed across the natural vs constant velocity as this was not involved in any significant effects (\*\* Indicates the significant pairs)

FIGURE 04 illustrates the source of the three way interaction. Post-hoc paired t-tests confirmed that when observing the “Dot”, the angle was significantly greater for executing Diagonal to Left movements in incongruent relative to congruent conditions  $t(11) = -2.270$ ,  $p = 0.044$ . In contrast, when observing the “Video”, the angle was significantly greater for executing Diagonal to Right movements in incongruent conditions relative to congruent conditions  $t(11) = -2.474$ ,  $p = 0.031$ .

The results of this experiment demonstrate a significantly greater interference when observing incongruent diagonal movements on executed movements than when

observing congruent diagonal movements. These results show that angle of executed movements are an effective measure of movement interference. The pattern of interference was not clear though. The difference in movement interference due to observed effector and the kinematics it entails may be masked by the carry-over effects of observing the “Video” and ‘Dot’ in a randomised manner. For example, during the “Dot” condition, participants may actually be imagining the movements. It is also possible that there are some effects of the relative difficulty of executing the Diagonal to Left vs Right movements. Diagonal to Left movements require that the wrist and arm be flexed which might generate a greater angle when executed. To examine these issues more closely, in Experiment 4.2, we separated the effector type between two groups – one group observed only the “Dot” stimuli with all other conditions remaining the same as in Experiment 4.1, and the second group observing only the “Video” with all other conditions remaining the same as in Experiment 4.1.

## II. EXPERIMENT – 4.2: DETERMINING THE EFFECT OF OBSERVING HUMAN VERSUS ABSTRACT DOT MOVEMENTS ON MOTOR INTERFERENCE

As videos are visually more detailed and interesting than a dot moving on the screen, the significant results in the previous experiment may reflect a carry-over of the videos on the dot conditions. That is, the participants may be imagining the videos when watching the dot conditions well. Here, I split the observed effectors between two groups. One group of participants observed only the video (human) effector, while the other group of participants observed only the dot effector. Experiment 4.1 showed that angle was a more sensitive measure of motor interference and that it could detect subtle differences in movement trajectory. In Experiment 4.2, first, I

predicted that there should be interference on observing incongruent relative to congruent trials, evidenced by greater variability in angle of executed movement trajectory. Second, I predicted that there will be an effect of observing a human and that there may not be an effect of observing a dot.

#### 4.3.1 EXPERIMENTAL PROCEDURES

##### PARTICIPANTS

Two groups each comprising twelve healthy, right-handed participants took part in the study (mean age = 19; number of males = 4; number of females = 8). Informed written consent was obtained from each participant according to the policies of the Macquarie University Human Research Ethics Committee. One group of participants watched only the 'Dot' stimulus while the second group of participants watched only the 'Video' stimulus.

##### STIMULI

The 'Dot' and the 'Video' stimuli were identical to Experiment 1.

##### RESULTS

A 2X2X2 repeated measures ANOVA was performed separately using SPSS for the two groups with Observed Effector 'Dot' and 'Video'. The within-subjects factors for each of the two groups were Movement Congruency (Congruent versus Incongruent), Movement Direction (Diagonal to Right versus Diagonal to Left), and Velocity Profile (Natural Velocity versus Constant Velocity).



## RESULTS FOR OBSERVING THE DOT EFFECTOR

No factors or interactions were significant for the group observing only the 'Dot' movements. This finding supports my hypothesis that there might have been a carry-over of videos even in the dot trials in Experiment 1.

## RESULTS FOR OBSERVING THE VIDEO (HUMAN) EFFECTOR

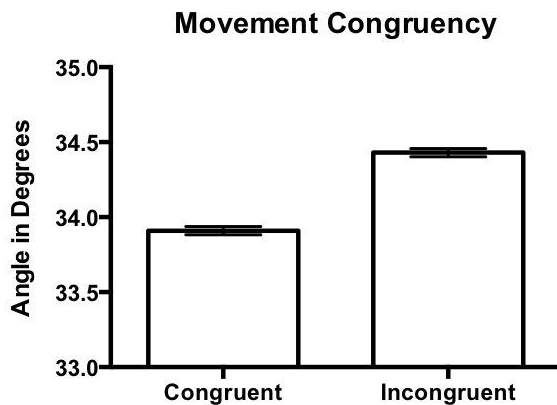


FIGURE 05. Mean angle in degrees (measure of motor interference) for participant movements while observing movements in a congruent or incongruent diagonal direction across all conditions.

FIGURE 05 gives the mean angle in degrees for participant movements while observing movements in a congruent or incongruent diagonal direction across all conditions. The repeated measures ANOVA showed a main effect of Movement Congruency ( $F(1,11) = 4.992$ ,  $p = 0.043$ ). The angle of movement was significantly greater for observing incongruent movements (mean =  $34.42^\circ$ ) compared to congruent movements (mean  $33.91^\circ$ ).

The repeated measures ANOVA showed a main effect of Movement Direction  $F(1,11) = 11.361$ ,  $p = 0.06$ . The angle of movement was significantly greater when executing Diagonal to Left movements (mean =  $35.23^\circ$ ) compared to Diagonal to Right movements (mean =  $33.11^\circ$ ).

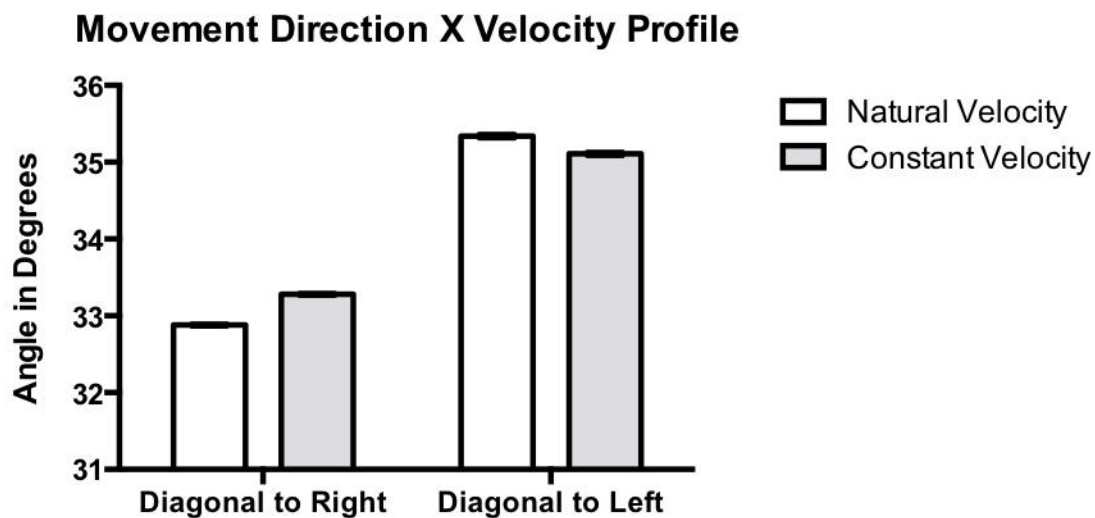


FIGURE 06. Mean angle in degrees for participant movements while observing movements with either natural velocity (NV) or constant velocity (CV) profile in a congruent or incongruent diagonal direction.

FIGURE 06 gives the mean angle in degrees for participant movements while observing movements with either natural velocity (NV) or constant velocity (CV) profile in a congruent or incongruent diagonal direction. The repeated measures ANOVA showed an interaction between Movement Direction and Velocity Profile,  $F(1, 11) = 9.968$ ,  $p = 0.009$  (FIGURE ). The paired t-tests showed that there was a differential effect of Velocity profile only when executing Diagonal to Right movements -  $t(11) = -2.635$ ,  $p = 0.023$  - such that there was a greater angle when

observing Constant Velocity Profile movements than Natural Velocity Profile movements.

#### IV. DISCUSSION

The aim of Experiment 4.1 was to develop a measure of motor interference more sensitive than variance or standard deviation and to use movements less kinematically different than horizontal and vertical movements, such as diagonal movements. Using a robust design, I showed that the angles produced by the trajectory of arm movements are a sensitive measure of motor interference. The results Experiment 1 show that there is a greater variability in angle when observing incongruent movements as compared to congruent movements irrespective of the velocity profile of observed movements. The effect of observed dot or video (human) stimuli was, however, not entirely clear. In particular, the difference in the direction of the movement based on the type of effector may reflect carry-over effects of observing the “Video” in alternating blocks with seeing the ‘Dot’ condition. It is also possible that the relative difficulty of executing the Diagonal to Left vs Right movements affects the variability in angle. To investigate these issues more closely, in Experiment 4.2, I separated the effector type between two groups.

In Experiment 4.2, one group of participants observed only the ‘Dot’ effector and the second group observed only the ‘Video (human)’ effector. As there might not be enough power in the experiment to run a 4-way ANOVA with the observed effector as the between-subjects factor, I analysed the two effector groups separately. There were no main effects or significant interactions for observing the ‘Dot’ effector. For the ‘Video’ effector, consistent with the results of Experiment 4.1, there was greater variability in angle for observing incongruent movements compared to congruent

movements. There was also a greater variability in angle for executing Diagonal to Left movements than for Diagonal to Right movements. Also, there was a greater angle when observing Constant Velocity Profile movements than Natural Velocity Profile movements but only when executing Diagonal to Right movements.

The influence of directionality of the executed movement is interesting because Kilner et al., (2003, 2007), also found an asymmetry in both their movement interference effect studies. In their first study (Kilner et al., 2003) where they used a model and non-humanoid robot as stimuli, they found that executing horizontal movements generated a greater variance than executing vertical movements across all conditions. In the second study (Kilner et al., 2007), they found that executing vertical movements generated a greater variance than executing horizontal movements across all conditions. Therefore, the results about direction of executed movements were the exact opposite of those in the Kilner et al., (2003) study.

A possible cause for this effect of directionality of executed movements may arise from the intrinsic differences in kinematic features of the individual movements (Atkeson, & Hollerbach, 1985). According to Atkeson and Hollerbach, 'inward' and 'outward' horizontal movements are nearly straight and not significantly different from each other. However, an 'upward' vertical movement is more curved than a 'downward' vertical movement, which is again nearly straight like both the horizontal movements. The strong effect of executing Diagonal to Left movements may be the result of a mix of such kinematic patterns. Making an upward diagonal movement towards the left requires a wrist flexion that is not needed as much for either the

downward diagonal movement or both upwards and downwards Diagonal to Right movements. This flexion may have added to the greater angle that was observed when participants executed Diagonal to Left movements.

Contrary to many previous studies that posit that the fp-AON is preferentially sensitive to the observation of biological motion (Kilner, Hamilton, & Blakemore, 2007; Perani et al., 2001; Grezes et al., 2001; Gowen et al., 2010), the above experiments did not show any differential effect of velocity profile on movement interference. In the case of Experiment 4.1, Velocity Profile was neither a main effect nor did it interact with any other factor. In Experiment 4.2, it only interacted with Movement Direction for the group of participants that observed the “Video” stimulus alone, which could be explained by the significant main effect of Movement Direction. The paired t-test results are hard to interpret because of the big difference in the angles between Diagonal to Left and Diagonal to Right movements.

Another possible reason for not obtaining any main effect of Velocity Profile in the experiments could be the relatively low frame rate for the video used (15 frames per second). It is known that we “fill in” between frames if we do not observe them, and it is plausible that we fill in the frames according to typical laws of human movement (Johansson, 1973; Saygin et al., 2004). Thus, even in the constant velocity condition the regions involved in the perception of biological motion such as Superior Temporal Sulcus (STS), fill-in for the missing frames because they are temporally very close to each other. This could lead to a masking of the effect of velocity profile on motor interference.

In the set of videos used in this experiment, participants always observed Diagonal to Left movements executed in the “mirror” view and Diagonal to Right movements executed in the “specular” view. In terms of observational viewpoint, the experimenter was recorded making Diagonal to Right movement with her right arm, which appeared to the participant as Diagonal to Left movements from the participant's point of view, known as the SPECULAR VIEW. The specular view video was flipped such that the experimenter now appeared to the participants as making Diagonal to Right movements from the participant's mirror point of view, known as the MIRROR VIEW. In this video, the experimenter appeared to make movements with the left arm, just as the participant would appear when making movements with the right arm in front of a mirror. Therefore, Diagonal to Right movements were always observed in mirror view and Diagonal to Left movements were always observed in specular view. It is possible that this observational viewpoint had an effect on movement congruency that was seen as the interaction between Movement Congruency, Movement Direction and Observed Effector in the experiment where dot and video stimuli were shown in a single experimental run. When observing a video, greater angle was found for observing incongruent movements (in mirror view only) when the participant executed Diagonal to Right movements. When observing a dot, greater angle was found for observing incongruent movements when the participant executed Diagonal to Left movements. Since there could no effect of observational viewpoint in case of such abstract stimulus as a dot moving on the screen, the greater angle for executing Diagonal to Left movements could be an effect of Movement Direction.

Could this viewpoint bias the results of the experiments such that Movement Direction emerges as a significant factor? Human beings interact with other human beings in social settings. Most of our interactions occur with others in the third-person view or “specular” view, making it the more “learned” experience. Would there be greater interference from observing movements in the “specular” view irrespective of the direction of observed movement simply because it is the view we are more conditioned to? These questions are addressed in Chapter 05.

## **CHAPTER 05**

Sista, U. S., Friedman, J., Williams, M.A., (submitted). This chapter has been submitted to *Neuropsychologia* as “Effect of Mirror versus Specular View on the Action Observation Network”



# CHAPTER 05: EFFECT OF OBSERVATIONAL VIEWPOINT ON THE ACTION OBSERVATION SYSTEM

## I. SUMMARY

In this current research we used the movement interference effect paradigm to study the effect of observational viewpoint on executed movements when simultaneously observing either congruent or incongruent movements. This paradigm has been shown to be an effective behavioural measure of the functioning of the fronto-parietal Action Observation Network (Brass et al., 2000; Wolhschlager, & Bekkering, 2002; Kilner et al., 2003, 2007). Right-handed participants observed movements in two views, MIRROR and SPECULAR. Mirror view was like watching oneself make right-handed movements in the mirror; Specular view was like watching a third-person facing oneself make right-handed movements. Based on studies on automatic imitation we predicted that there would be greater interference for observing incongruent movements in the specular view if motor plans for observed right-handed movements are automatically simulated. We found the opposite effect – greater interference was generated for observing incongruent movements in the mirror view compared to congruent movements in the mirror view. This finding is in line with studies on imitation which show that we have a preference for imitating movements seen in mirror view. This preference may be employed to infer the goal of an action and imitate that action when handedness is not important, e.g., in a social context such as in our current study.

Keywords: Action Observation Network, Movement Interference Effect,  
Observational Viewpoint

## II. HIGHLIGHTS

1. greater interference effect measured by angle of movement for observing incongruent movements performed in the mirror view compared to a congruent movements in mirror view
2. sheds light on the pathways that may be engaged by the Action Observation Network when involved in automatic imitation and joint-action
3. the mirror-view preference pathway may be engaged when a specific goal-directed complementary movement is not required

### III. INTRODUCTION

Recent studies have postulated the existence of a direct-matching action observation-action execution mechanism that is implemented via the fronto-parietal Action Observation Network (fp-AON), where observing an action automatically elicits the simulation of motor plans required to perform that action (Jeannerod, 2001; Prinz, 1997; Rizzolatti & Craighero, 2004). Evidence for the presence of such motor resonance comes from studies on automatic imitation, which is the involuntary tendency of people to execute the actions that they observe. Motor interference occurs when the motor system is primed to move in the direction and manner of observed movements (via the mechanism of automatic imitation) but is 'forced' to move in a different fashion (Blakemore & Frith, 2005; Wilson & Knoblich, 2005). Such motor interference can be measured behaviourally via its manifestation as the movement interference effect – observed actions that interfere with simultaneously executed incongruent actions. Movement interference effect has been used to predict the fundamental properties of the Action Observation Network and its role in action understanding.

Research on the fronto-parietal Action Observation Network (fp-AON) suggests that it is: (1) SPECIFIC – the AON is preferentially engaged only when observing actions with biological kinematics (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Decety, & Grèzes, 2006; Gallese, & Goldman, 1998), (2) UNMEDIATED – the motor plans of the observed actions are simulated and 'understood' by the AON via a direct mapping of the visual representations of the observed actions onto the motor representations of the same actions (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996;

Grafton, Arbib, Fadiga, & Rizzolatti, 1996, Kilner et al., 2007), and (3) AUTOMATIC – motor plans of the observed actions are simulated automatically and without any volitional control of the observer as long as the motor plans are already in the observer's motor repertoire (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Gallese, & Goldman, 1998; Kilner, et al., 2003; Molenberghs, Hayward, Mattingley, & Cunnington, 2012).

The present study asked whether the AON is preferentially engaged by a specific viewpoint, and by how “biological” the velocity profile of the movement is.

Participants were shown videos of arm movements with two velocity profiles – natural or constant velocity profile. Human arm movements are typically described as having a bell-shaped 'minimum jerk' trajectory (Flash & Hogan, 1985), where the movement begins slowly, shows smooth acceleration and then slowly decelerates (Rizzolatti, Fogassi, & Gallese, 2001). This is in contrast to the instantaneous acceleration to maximum velocity at the start of the movement, and an instantaneous deceleration to rest at the end of the movement characteristic of a constant velocity movement (Figure 1).

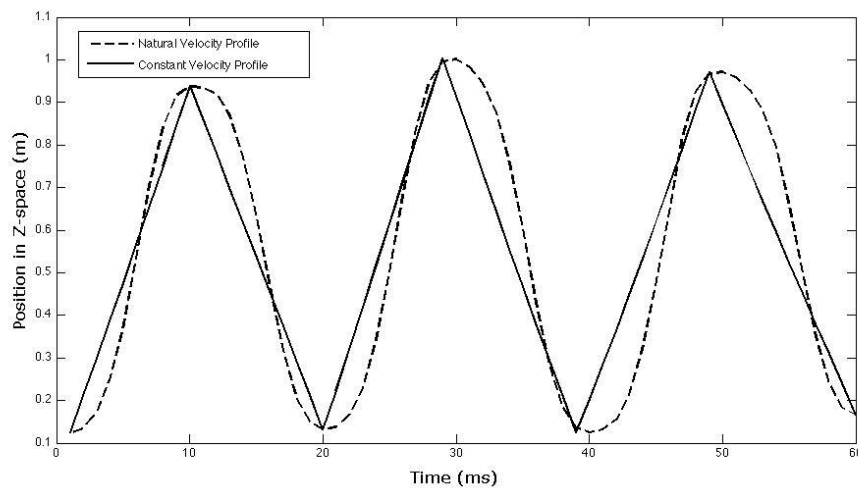


Figure 1. Graphs of movements with Natural Velocity (dashed line) and Constant Velocity (solid line) profiles

The movements were observed from two different viewpoints – mirror and specular. In the 'mirror view', the participants observed movements as if seeing themselves in a mirror making movements with their right hand; in the 'specular view', the participants observed movements as if watching a third-person sitting in front of them making movements with her right arm (Figure 2).



(a)



(b)

Figure 2. (a) Observing video movements in 'mirror view' (b) Observing video movements in 'specular view'

According to theory of motor resonance, there is a direct mapping of visual representation of observed actions onto the motor representation of those actions in the observer's motor system (Grafton, Arbib, Fadiga, & Rizzolatti, 1996). For a right-handed person, the mapping for motor plans of another person making movements with his right hand would be much stronger in the motor repertoire than observing movements made by his left hand. The motor plans for the observed movements are simulated in the 'specular' or 'third-person' view. We predicted that there would be more interference for observing incongruent movements in the specular view than incongruent movements in the mirror view. We also predicted that this effect would be seen only for observing movements with a natural velocity profile because behavioural studies have shown that the fp-AON preferentially responds to observation of biological motion (Kilner et al., 2007). We used angles made by movement trajectories with respect to global horizontal coordinates in the frontal plane as the measure of interference when observing movements incongruent to one's own executed movements.

#### IV. EXPERIMENT 5.1 - EXPERIMENTAL PROCEDURES

##### PARTICIPANTS

Two groups of twelve healthy, right-handed participants in each group took part in the study (mean age = 22; number of males = 6; number of females = 18). Informed written consent was obtained from each subject according to the policies of the Macquarie University Human Research Ethics Committee.

## STIMULI

Participants observed video recordings of the experimenter making either Diagonal to Right or Diagonal to Left movements (see Figure 3). Diagonal to Right movements started at the bottom left corner of the frontal plane (0,0 of the coordinate system) and moved diagonally across to the top right corner of the plane (1,1 of the coordinate system) and returned to the starting point. Diagonal to Left movements started at the bottom right corner of the frontal plane (1,0 of the coordinate system) and moved diagonally across to the top left corner of the plane (0,1 of the coordinate system) and returned to the starting point. Each stroke was approximately 60 cm long. To generate the stimuli, a webcam (Microsoft LifeCam) was used to record movements made by the experimenter with her right arm at 30 Hz. The movement of the hand was simultaneously tracked with an Optotrak Certus Motion Capture System (Northern Digital Inc.) at 200 Hz sampling rate by placing two small markers (infrared light emitting diodes or LEDs) on the index fingertip of her right hand. Programs written in MATLAB (The Mathworks Inc.) were used to determine the frame numbers required to generate videos at 15 Hz with approximately constant velocity (CV). The original videos were resampled to 15 Hz to generate the natural velocity (NV) videos, so that both the CV and NV videos had the same number of frames and sample rate, and the peaks and troughs of the movements coincided (see Figure 1).

For the 'Mirror Movement for Right' experimental group, the experimenter was recorded making Diagonal to Right movement with her right arm, which appeared to the subject as Diagonal to Left movements, known as SPECULAR VIEW. The specular view video was flipped such that the experimenter now appeared to the

subject as making Diagonal to Right movements from the subject's mirror point of view, known as MIRROR VIEW. In this video, the experimenter appeared to make movements with the left arm, just as the subject would appear when making movements with the right arm in front of a mirror (Figure 3. a and b).

For the 'Mirror Movement for Left' experimental group, the experimenter was recorded making Diagonal to Left movement with her right arm, which appeared to the subject as Diagonal to Right movements. The specular view video was flipped such that the experimenter now appeared to the subject as making Diagonal to Left movements from the subject's mirror view (Figure 3. c and d).

All the videos were resized to fit the screen size of 1360 X 768 pixels.

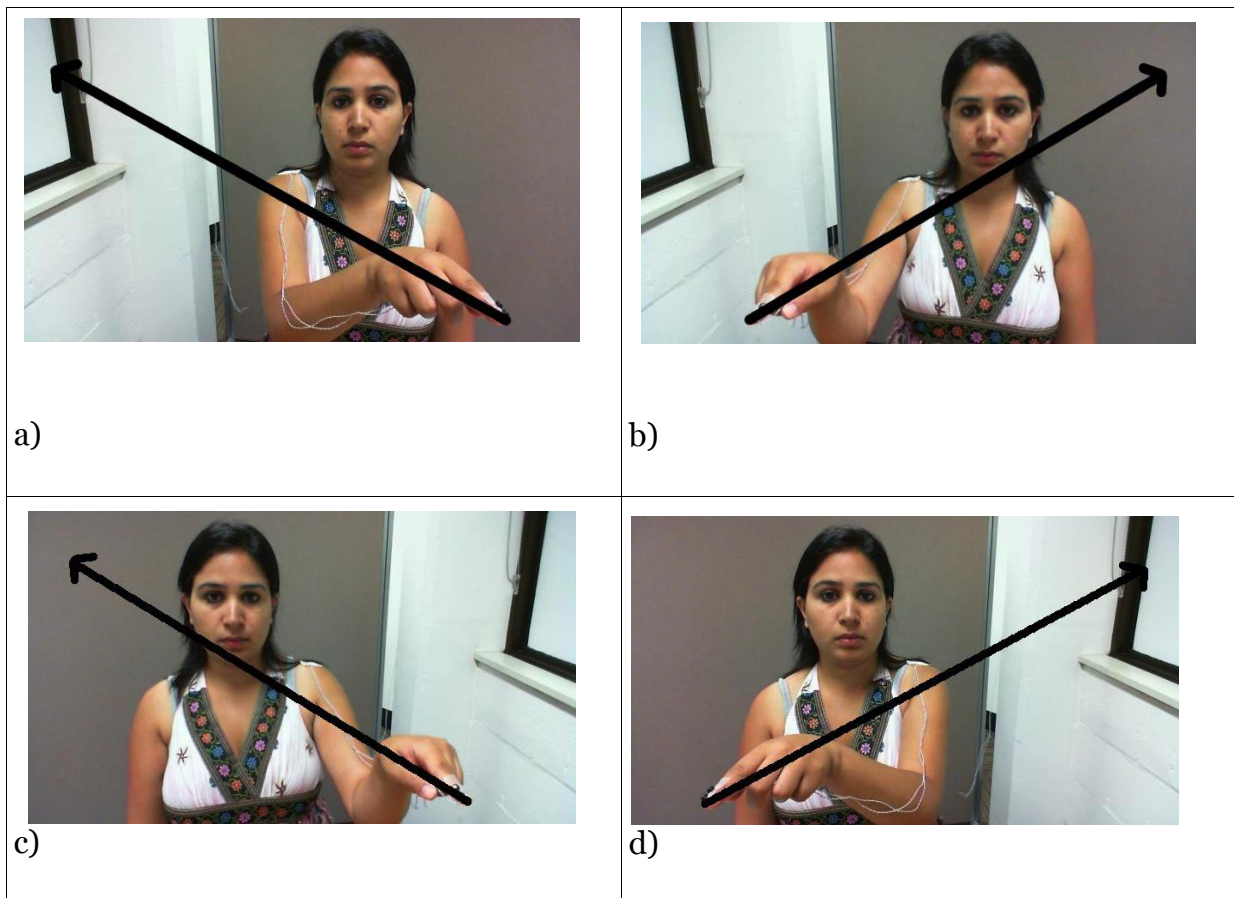




Figure 3. Images of (a) specular view Diagonal to Left movement (1,0) to (0,1) (b) specular view Diagonal to Right movement (0,0) to (1,1) (c) mirror view diagonal to left movement (1,0) to (0,1) and (d) mirror view diagonal to right movement (0,0) to (1,1).

### EXPERIMENTAL DESIGN

Participants sat in a quiet, dark room at a table with a LCD touchscreen (70 X 39 cm, 1360 X 768 pixels, 60 Hz) placed approximately 70 cm in front of them. Hand movements were recorded using the same setup as described in the 'Stimuli' section.

One group of participants (N=12) watched the arm in a specular view in the video making diagonal arm movements in the left frontal plane and the arm in a mirror view (as in looking at oneself in the mirror) in the video making diagonal arm movements in the right frontal plane. A second group of Participants (N=12) watched the arms making opposite movements - the arm in a specular view making diagonal arm movements in the right frontal plane and the arm in a mirror view making diagonal arm movements in the left frontal plane.

Each trial started with the participants tapping on the right foot pedal placed under the table at a position convenient to each subject. A central fixation dot appeared on the screen after the participants tapped the pedal, followed by a beep after 1 second.

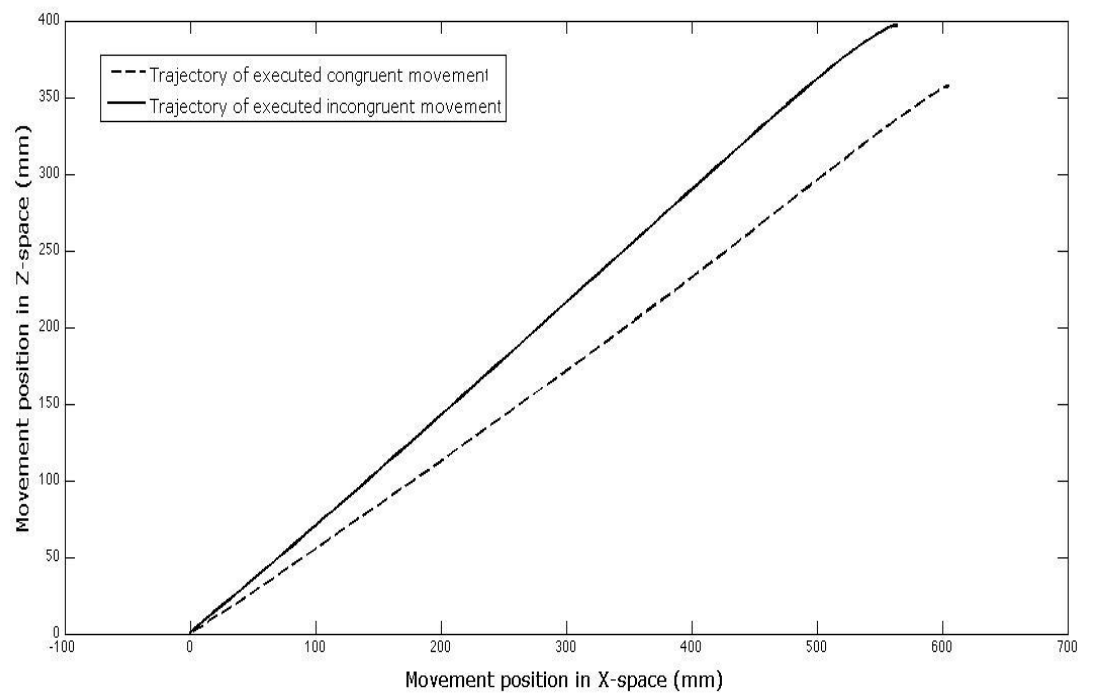
The participants were instructed to place their fingertips about 15 cm away from the left bottom or right bottom of the screen over the table surface for the start point. The stimulus appeared on the screen 1 second after the beep. The participants performed three full movement cycles per trial while simultaneously observing the stimulus on the screen. One full movement cycle comprised an upward movement to the top corner of the screen and one downward movement to the starting position at the bottom corner of the screen. Instructions for the movement to be executed appeared on the screen at the beginning of each block, and the participants executed only one kind of movement in each block – either Diagonal to Right or Diagonal to Left. The movements alternated between blocks.

There were eight blocks per session – four blocks for Diagonal to Right movement and four blocks for Diagonal to Left movement. The participants were not given specific instructions to move synchronously, but they did synchronise their movements with the observed movements by the time they performed a few trials in the first block. The executed movements were either congruent or incongruent with the observed movements. In the congruent condition the participants observed and executed movements in the same direction (e.g. both observed and executed movements were either Diagonal to Left or Diagonal to Right.), while in the incongruent condition, the observed and executed movements were in different directions (e.g. observed movement was Diagonal to Right and executed movement was Diagonal to Left and vice versa.) The following conditions were presented with four repetitions each per block in a randomised order: Observed View (Mirror View versus Specular View) X Movement Congruency (Congruent versus Incongruent) X Velocity Profile (Natural Velocity versus Constant Velocity).

## DATA ANALYSIS

Programs written in MATLAB were used to analyse the data. The first two blocks of the experiment were discarded during the analysis for each subject as they were considered practice blocks. The first upward and the last downward movement of each trial were discarded in order to account for errors in initiation and termination of movements, such that the analysis comprised of two movement cycles (i.e. two upward and two downward movements), and the movement data was segmented into these four parts based on peaks in the velocity profile. Trials with more than 5% of the data missing due to occlusion of both the markers on the fingertip were also excluded. Missing data points were interpolated using spline interpolation for the rest of the trials. The angle of the movement in the frontal plane was calculated as the angle between the position at each time point (relative to the start point) and a vector pointing towards the right. The angle was used as the measure of interference. All movement trajectory angles were shifted to the positive first quadrant such that they were all within the range 0 degrees to 90 degrees. This facilitated averaging and comparing of angles made by upward and downward movements in both the left and right diagonal directions (see Figure 4). Angles were averaged across segmented movements and then across trials for each condition. With this formulation, the greater the interference from observing incongruent movements, the greater the angle of the executed movement, as would be the case if the movement trajectory was shifted to the direction of the observed movement.

a)



b)

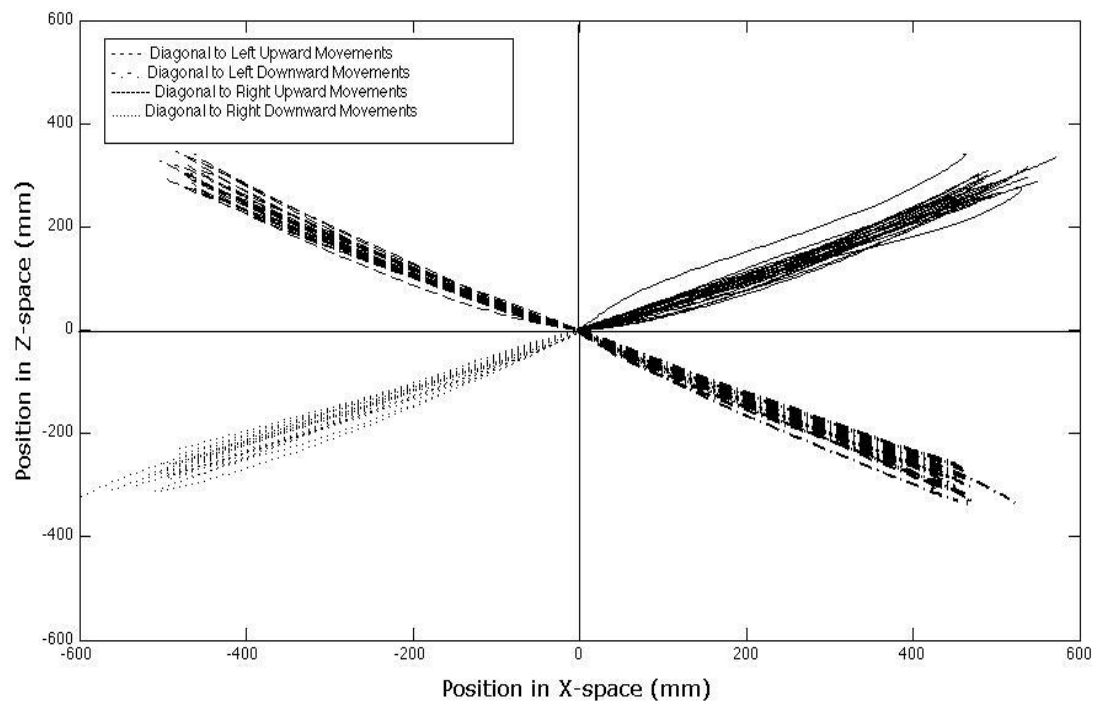


Figure 4. Trajectories of Diagonal to Right and Diagonal to Left movements segmented and angles of congruent and incongruent movements compared with each other.

a) Segmented trajectories of Diagonal to Right and Diagonal to Left movements. The four trajectories analysed per trial were segmented into upward and downward movements. The trajectories are plotted in X-Z space (X being the left-right position and Z being the height (up-down position) of each movement).; b) Trajectory of executed movement shifted when executing a congruent and an incongruent movement. Trajectories of congruent movements (dashed line) and incongruent movements (solid line) were shifted so that they started at the same point (0,0) for Diagonal to Right movements as in the figure below.

## STATISTICS

2X2X2 repeated measures ANOVA was performed using SPSS. The three factors analysed were Movement Congruency (Congruent versus Incongruent), Observed View (Mirror View versus Specular View), and Velocity Profile (Natural Velocity versus Constant Velocity).

## RESULTS

The angle of movement was significantly greater when observing incongruent movements (mean =  $34.28^{\circ}$ ) compared to congruent movements (mean  $33.64^{\circ}$ ). This is supported by a main effect of Movement Congruency ( $F(1,11) = 28.937$ ,  $p < 0.001$ ). There was a significant interaction between Movement Congruency and Observed View,  $F(1,11) = 4.803$ ,  $p = 0.050$  (Figure 5.). No other main effects or interactions were significant.

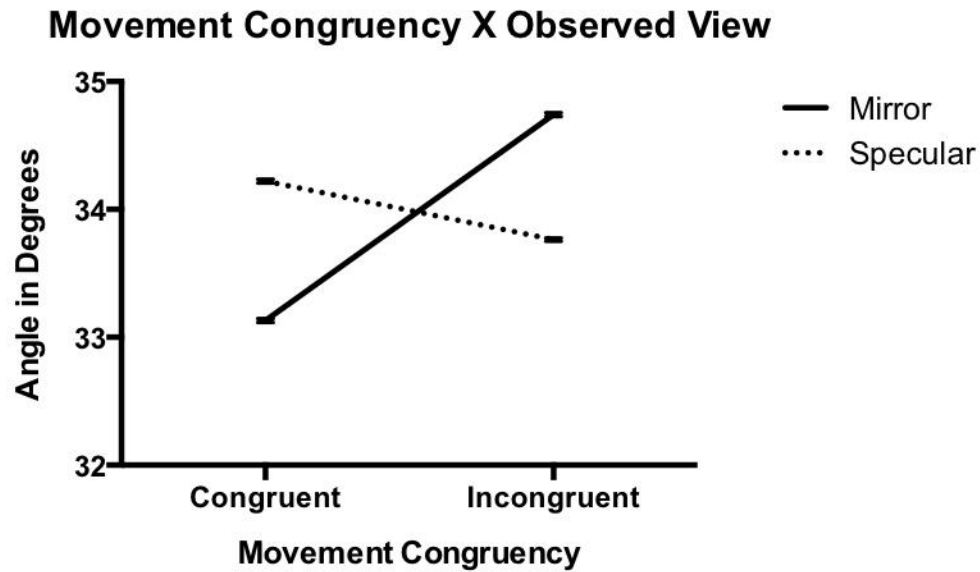


Figure 5. The mean angle of executed movements for observing movements in ‘mirror’ or ‘specular’ view that are either congruent or incongruent with the executed movements

In order to clarify this two-way interaction, we performed post-hoc paired t-tests to examine the source of the interaction between Movement Congruency and Observed View. The angle for observing incongruent movements in mirror view (mean =  $34.74^{\circ}$ ) was significantly greater than the angle for observing congruent movements in mirror view (mean =  $33.13^{\circ}$ );  $t(11) = -3.067$ ,  $p = 0.011$ . However, there was no significant difference in the angle for observing incongruent movements in specular view (mean =  $33.764^{\circ}$ ) compared to the angle for observing congruent movements in specular view (mean =  $34.222^{\circ}$ );  $t(11) = 1.015$ ,  $p = .316$ .

## V. DISCUSSION

The present results show that observing incongruent movements of a model has a measurable interference effect on simultaneously executed movements. However, the significant interaction between Movement Congruency and Observed View came as a surprise. We hypothesised that, in accordance with the classical model of the AON, there should be greater interference when observing incongruent movements made by an arm in specular view than in mirror view. The classical model predicts that the motor plans of the observed action are simulated in the brain of the observer as if the observer himself was performing the action. This model is supported by the evidence that the AON is more active for observing complementary actions rather than mirror-imitative actions (Abend, Bizzi, & Morasso, 1982). As all the participants were right handed, we predicted that there would be greater interference for observing incongruent in the specular view rather than in mirror view. On the contrary, the results showed that incongruent movements in the mirror view interfered more with executed movements than congruent movements in the mirror view.

Consistent with the results in Chapters 02, 03 and 04, there was no detectable effect of velocity profile of observed movements on executed movements in either the congruent or incongruent conditions in both the mirror and specular views. A possible explanation as to why we did not see any effect of velocity profile in the experiment could be the relatively low frame rate for the video used (15 frames per second). It is known that we “fill in” between frames if we do not observe them, and it is plausible that we fill in the frames according to typical laws of human

movement. It is possible that at higher frame rate, we would see a bigger difference for observing videos of movements.

Interestingly, the result that incongruent movements in the mirror view interfered more with executed movements than congruent movements in the mirror view is supported by the findings of many imitation studies (Avikainen et al., 2003; Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007). Studies on imitation in children show that they prefer to imitate the movements made by arms in mirror view condition. For example, if the experimenter raised her left arm while being seated in front of the child, the child would raise her right arm (Avikainen et al., 2003; Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007; Bekkering, Wohlschläger, & Gattis 2000). Studies show that adults also prefer to imitate in a similar fashion (Bekkering, Wohlschläger, & Gattis 2000; Chiavarino, Apperly, & Humphreys 2007). Therefore, our results are consistent with many results of studies on imitation.

However, there are other experiments which show that the AON is preferentially engaged for observing complementary movements (Jiménez et al., 2012; Williams, & Gribble 2012; Mazzarella et al., 2012; Bortoletto, Mattingley, & Cunnington, 2013). Because of these contrasting results, we propose that there might be two motor resonance pathways – i) mirror-imitation pathway, and ii) the more complementary-action pathway. The AON might engage the mirror-imitation pathway when a specific goal-directed complementary movement is not required, e.g., when making arm movements like in our study or when raising or waving an arm. The AON might



engage the complementary-action pathway in joint-action or observational learning situations. A study showed that right-handed participants learned movements better by watching right-handed models, irrespective of as the observational viewpoint (first-person or third person), and left-handed participants learned better by watching left-handed models irrespective of the viewpoint (Wakita, & Hiraishi 2011). These findings suggest that the Action Observation Network is a complex interacting system that is sensitive to the context of the observed movements, action goals and intentions, and the environment. By 'action goals' we mean the desired state that can be attained by a particular action (for example, moving arm from one point to the other diagonally in a specified manner as in this experiment) (Rohbanfard, & Proteau, 2011). Defined like this, “goals” are simply end-points of an action or movement rather than any abstract goals set in the future.

The results of our study show that 'motor resonance' is more than simple direct visual mapping that is not influenced by action context. Our results are consistent with the hypothesis that the AON is sensitive to context, visual cues as well as high-level abstractions in terms of what constitutes a goal and understanding (Rohbanfard, & Proteau, 2011). The various contexts and cues that influence the AON and the effect of selective attention on the need to be explored in detail while keeping in mind the highly variable and abstract nature of a “goal”.

# CHAPTER 06: GENERAL DISCUSSION

## CHAPTER 06: GENERAL DISCUSSION

Human beings are moving, agile creatures. We move and we are constantly on the move. We not only communicate with speech (which is a motor act) but also with gestures, actions, and body language, not to mention with facial expressions. We are social creatures who need to act and understand and respond to others' actions. The question of how we manage the complex feat of understanding the actions of others has long been investigated by philosophers and scientists alike. There has been an rapid increase in research on action and action understanding in recent years. The broad questions that guided my doctoral research are - How do we understand the goals of other people's actions and then infer the intentions behind those actions such that we can plan our own action responses? How can we study the behavioural manifestations of the processes involved in action understanding?

Towards such broad comprehension of action understanding, the specific aims of my thesis were four-fold:

1. To review the recent research on the Action Observation System in order to isolate the proposed fundamental properties of the Action Observation System.
2. To test the validity of the underlying assumptions by designing experiments that employ the movement interference effect paradigm.
3. To discuss the fundamental properties of the Action Observation System based on the results of my experiments and compare them to evidence from research literature, and find out which theory or theories are best supported by the evidence.

## I. A SUMMARY OF THE RESULTS OF EXPERIMENTS

### EXPERIMENT 3.1

Experiment 3.1 attempted to replicate the results of Kilner et al. (2007). In the Kilner et al. (2007) study, interference effects due to observing movement incongruent with the executed movements were found only when the executing movements were in the vertical direction. I was cautious about accepting their conclusions about the Action Observation System, since all they all were based on analysing the results for vertical direction executed movements alone. The researchers did not offer a good theoretical reason explaining why they saw effects in one plane but not the other, even though they acknowledged this observation. Therefore I wanted to re-examine the primary hypothesis of Kilner et al., (2007) by replicating their study. I had hypothesised that there would be greater interference to executed movements during observation of incongruent movements than during observation of congruent movements. I had also predicted that such interference would be seen for observing a human (video) make incongruent movements with a natural velocity profile, but not for observing dot movement.

Using a careful experimental design, I failed to replicate the findings of Kilner et al. (2007). I did not find any significant interference effects of observing either a human movement or a dot movement, regardless of whether the movement kinematics matched that of biological motion or not. Although we must be very careful when interpreting null results (it is possible that the large 4-way omnibus ANOVA could not detect the subtle differences in movement interference because of a lack of power), nevertheless, the findings of Kilner et al. (2007) need to be treated cautiously. The ambiguity in the effect of movement direction was not explained in

their study. In fact, splitting the analysis based on movement direction simply because it was main effect does not explain anything about movement interference effects, and by extension, about the Action Observation System. I therefore found that the movement interference effect paradigm needed modification.

#### EXPERIMENT 4.1

In this experiment, I presented dot and video stimuli similar to those presented in Experiment 3.1, but using diagonal movements. The ‘Dot’ stimuli and ‘Video (human)’ stimuli were presented within a single experimental run and determined if angle made by movements was a more sensitive measure than variance in movements. Diagonal movements were used instead of horizontal and vertical movements since diagonal movements are biomechanically more similar to each other than horizontal and vertical movements are. Also, Kilner et al. (2003, 2007) found contradictory results when they used horizontal and vertical movements in their study. Further, I did not find any effects of movement interference in Experiment 3.1, where I used horizontal and vertical movements. Therefore, the main aim of Experiment 4.1 was to develop a measure of interference more sensitive than variance by using movements that are less variant than horizontal and vertical movements.

The results of Experiment 4.1 showed a significantly greater interference when observing incongruent diagonal movements on executed movements than when observing congruent diagonal movements. Therefore, angle of the movements when observing stimuli in different conditions can be used as a measure of movement

interference. The pattern, however, was not entirely clear. In particular, the difference in movement interference due to observed effector (human/video vs dot) and the kinematics it entails (natural vs constant velocity profile) may have been masked by carry-over effects of observing the “Video” and ‘Dot’ in a randomised manner. For example, during the “Dot” condition, participants may actually be imagining the movements. I next examined the effect of observed stimuli on movement interference by splitting the “Dot” and “Video” effectors between two groups of participants.

#### EXPERIMENT 4.2

As videos are visually more detailed and interesting than a dot moving on the screen, the significant results in the previous experiment may reflect a carry-over of the videos on the dot conditions. This carry-over effect may mask differences in effects due to observed effector and movement kinematics on movement interference. Experiment 4.1 already showed that angle of executed movements was an effective measure of movement interference. Using the same variable to measure interference, I separated the observed effector between two groups, such that one group saw only the “Dot” movements and the other group saw only the “Video” movements. I had predicted that there would be interference on observing incongruent movements relative to congruent movements, demonstrated by greater variability in angle of executed movement trajectory. I had also predicted that there would be an effect of observing a human and that there may not be an effect of observing a dot.

In support of my hypothesis, I found no interference effects for observing “Dot” movements suggesting that participants in Experiment 4.1 were indeed imagining the video (human) movements, thereby screening the actual influence the observed effector had on movement interference. Consistent with the results of Experiment 4.1, for the group that observed only the “Video (human) effector, there was greater variability in angle for observing incongruent movements compared to congruent movements. There was also a greater variability in angle for executing Diagonal to Left movements than for Diagonal to Right movements. Executing Diagonal to Left movement may have generated greater angle than executing Diagonal to Right movements because of the inherent difficulty is flexing the wrist and rotating the arm to generate Diagonal to Left movements. The results demonstrate that observing incongruent movements interferes with simultaneously executed movements presumably due to motor interference generated by the automatic imitative tendency to copy the observed movements.

When creating the stimuli, the experimenter was recorded making Diagonal to Right movement with the right arm, which appeared to the participant as Diagonal to Left movements from the participant's point of view, known as the SPECULAR VIEW. The specular view video was flipped such that the experimenter now appeared to the participants as making Diagonal to Right movements from the participant's mirror point of view (as in looking at oneself in the mirror), known as the MIRROR VIEW. Therefore upon examining the actual video stimuli, I noticed that participants always observed Diagonal to Right movements mirror view and Diagonal to Left in specular view. It is possible that this viewpoint biased the results of the experiments such that

Movement Direction emerges as a significant factor. I addressed the issue of observational viewpoint on motor interference in the next experiment.

### EXPERIMENT 5.1

In this experiment participants observed diagonal movements (as in Experiments 4.1 and 4.2) from two different viewpoints – mirror and specular. In the 'mirror view', the participants observed movements as if seeing themselves in a mirror making movements with their right hand; in the 'specular view', the participants observed movements as if watching a third-person sitting in front of them making movements with her right arm. According to theory of motor resonance (Grafton, Arbib, Fadiga, & Rizzolatti, 1996) for a right-handed person, the mapping for motor plans for the observed movements that are simulated in the 'specular' or 'third-person' view would be much stronger in the motor repertoire than observing movements made by his left hand. Therefore, I predicted that there would be more interference for observing incongruent movements in the specular view than incongruent movements in the mirror view. I also predicted that this effect would be seen only for observing movements with a natural velocity profile because behavioural studies have shown that the AOS preferentially responds to observation of biological motion (Kilner et al., 2007). As in Experiments 4.1 and 4.2, I used angles made by movement trajectories with respect to global horizontal coordinates in the frontal plane as the measure of interference when observing movements incongruent to one's own executed movements.



The results showed that observing incongruent movements of a model exerted significantly greater interference on simultaneously executed movements than congruent movements. Contrary to my prediction that there should be greater interference when observing incongruent movements made by an arm in specular view than in mirror view, the results showed that incongruent movements in the mirror view interfered more with executed movements than congruent movements in the mirror view. No such difference was found for observing movements in the specular view. The specular view did not exert any differential effect on movement congruency. Studies on imitation (Avikainen et al., 2003; Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007) support the result of Experiment 5.1. These studies show that adults (Bekkering, Wohlschläger, & Gattis 2000; Chiavarino, Apperly, & Humphreys 2007) and children (Avikainen et al., 2003; Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007; Bekkering, Wohlschläger, & Gattis 2000) prefer to imitate the movements made by arms in mirror view condition.

## II. MAIN CONCLUSIONS OF THE EXPERIMENTS

In conclusion, the results of Experiments 4.1, 4.2 and 5.1 show that:

1. the angles made by movement trajectories with respect to global horizontal coordinates in the frontal plane were an effective new measure of movement interference;
2. observing incongruent movements of a model exerted significantly greater interference on simultaneously executed movements than congruent movements;

3. there was greater variability in angle for observing incongruent movements compared to congruent movements only the for “Video (human)” effector, with no movement interference effects for observing a “Dot” effector once carry-over effects were removed;
4. we prefer to imitate the movements made by arms in mirror view condition as demonstrated by the greater angle for observing incongruent movements than congruent movements in the mirror condition but not in the specular condition; and
5. the role of movement kinematics has a complex relationship on specific movement interference effects such as that employed in the experiments of Kilner et al. (2007) and in the experiments in this thesis.

### III. AN EXAMINATION OF THE PROPOSED PROPERTIES OF THE ACTION OBSERVATION SYSTEM

In Chapter 02 of this thesis, I suggested that the current literature claims that the Action Observation System is:

- i) AUTOMATIC - motor plans of the observed actions are simulated automatically at the same time of action observation and without any volitional control of the observer as long as the motor plans are already in the observer's motor repertoire,
- ii) UNMEDIATED - motor plans of the observed actions are simulated automatically at the same time of action observation and without any cognitive effort required from the observer, and

- iii) SPECIFIC – as only biological motor plans can exist in the motor repertoire, there can be representation of only the actions with biological kinematics.

In this section, I will examine each of these properties based on the results of my experiments and highlight the different arguments about them.

#### ACTION OBSERVATION SYSTEM AS AUTOMATIC AND UNMEDIATED

Studies on automatic imitation point out to the ‘automatic’ nature of the Action Observation System. The automatic imitation effects have been found when participants have been instructed not to respond to the stimuli (task-irrelevant) that generate the effects (Stuermer et al., 2000; Heyes et al., 2005), when they are not needed by the participants to attend to the positions where the task-irrelevant stimuli appear (Leighton & Heyes, 2010; Brass et al., 2000), and their response to the task-irrelevant stimuli interferes with the actual performance (Bertenthal et al., 2006; Brass et al., 2000; Gillmeister et al., 2008; Stuermer et al., 2000; Heyes et al., 2005; Leighton & Heyes, 2010).

The results of Experiments 4.1, 4.2 and 5.1 support the proposal that the Action Observation System functions in an automatic manner. In Experiments 4.1, 4.2 and 5.1 involving a sensitive measure (angle) and matched diagonal movements, observing incongruent movements of a model exerted interference on simultaneously executed movements, suggesting that the motor plans of the observed incongruent movements are automatically simulated, presumably in the Action Observation System of the observer. The simulation of motor plans is likely

the cause of the automatic imitative tendencies and the movement interference effects observed in Experiments 4.1, 4.2, and 5.1.

The results of Experiment 4.2 show that there were no movement interference effects for observing only the “Dot” movements whereas observing incongruent “Video (human)” movements interfered with executed actions when compared with observing congruent movements. One possible reason why there was no interference for observing “Dot” stimuli, was that the participants had no visual movements to guide their own movements – there was no hand movement they could trace. This suggests that it might be important for the Action Observation System to observe actions made by a hand in order for motor resonance to occur. Anything moving on the screen with biological kinematics may not be sufficient to elicit a response from the AOS. The results support the hypothesis that the Action Observation System is sensitive, and mediated by, the “form” of observed movements (Longo & Bertenthal, 2009).

Other studies have also shown that the Action Observation System may be sensitive to observing hand movements over abstract movements like those of a dot on a screen (Peery & Bentin, 2009; Longo & Bertenthal, 2009; Kilner et al. 2003; Tai et al. 2004; Press et al. 2007). Mu-rhythms provide interesting support for this hypothesis. Mu-rhythms are EEG oscillations that are desynchronised by covert motor activity, and repeat at a frequency of 8-13 Hz. They are most pronounced when the body is physically at rest. Peery and Bentin, (2009) hypothesised that if action execution and action observation share a neural circuit via the Action Observation

System, mu-rhythm desynchronisation must be found for both executing and observing actions. They recorded mu-rhythms as participants observed either right or a left hand that reached and grasped objects. They also recorded the mu-rhythm as the participants observed images of still objects, static grasping images, or a ball moving a screen. They found greater mu-suppression in the contralateral hemisphere than in the ipsilateral hemisphere with respect to the hand that reached and grasped objects. Greater mu-suppression was found for observing novel movements in comparison with repetitive movements, (i.e., 'observing novel movements (e.g., objects grasped in different ways each time) in comparison with repetitive movements (e.g., objects grasped in the same way each time). Mu-suppression was found for observing static images of a grasping action, suggesting that the Action Observation System might be involved in extracting motion information from images of implied motion. No mu-suppression was recorded for observing a ball move on the screen and for still objects. These results are consistent with the results of Experiment 4.2, where no interference effects were found for observing a dot movement. These results support the hypothesis that action observation and action execution share a neural circuit. They also suggest that there might indeed be a "human-bias" intrinsic to the Action Observation System as predicted by Press et al. (2007) as no mu-suppression was found when observing a ball on the screen.

Consistent with the findings of Peery and Bentin (2009), Ogoshi et al. (2013) also examined mu-suppression and found that there was lowest mu-suppression for observing bouncing balls in comparison with greater mu-suppression for imagining the action of a moving hand. In the baseline condition, participants observed a video of visual white noise. In the second video, participants observed bouncing (Ball

condition). In the third video, participants observed a moving hand (Observation condition). In the fourth video, participants not only observed the moving hand as in the third video, but also imagined performing the same movement (Imagination condition). There was greatest mu-suppression for the 'Imagination' condition and the lowest mu-suppression for observing bouncing balls. Mu-suppression for the 'Observation' condition was slightly larger than that of the Ball condition. The results not only show that the Action Observation System might be engaged for action observation, but also for imagining actions.

It is interesting to note that while Peery, and Bentin, (2009) found no mu-suppression for a single ball moving on the screen such as in Experiments 4.1 and 4.2, Ogoshi et al. (2013) found mu-suppression for observing bouncing balls was almost as strong as for observing a hand move on the screen. It may be possible that there was a strong carry-over effect in Ogoshi et al. (2013) as they had a condition in which the same participants not only watched video clips of hand movements but also imagined them. The action representation may be reinforced for these participants, which shows itself as a carry-over effect in the little mu-suppression found for observing bouncing balls in the Ogoshi et al. (2013) study. On the other hand, in the experiment of Peery and Bentin (2009), participants observed only one video clip along with a static image and a moving ball. It is possible that reinforcement of action representation is lower in such an experimental design. These contrasting findings suggest that rather than an all or none representation of action, there may be a gradation to action representation that is strengthened with sensorimotor associations via prior experience and practice (Catmur, and Heyes, 2013).

The Action Observation System is not only influenced by the observed effector but also by observational viewpoint. The results of Experiment 5.1 show that the observational viewpoint has a bearing on movement interference effects such that there is interference to executing movements when observing incongruent movements relative to congruent movements in mirror view. It is possible that the observational viewpoint is linked to the task-demands of the experiment. In Experiment 5.1 the participants were not instructed to imitate, but task-irrelevant cues (incongruent movements in either the mirror view) interfered with their action execution. Therefore, the interference effects seen in Experiment 5.1 could also be used to support the case for automatic imitation.

Shmuelof, & Zohary, (2008) looked at what they called “mirror-image representation” of action in the Action Observation System. They called the allocentric view a mirror-image, which is known as SPECULAR view in Experiment 5.1. They found greater activation in the ipsilateral hemisphere for observing movements seen from an allocentric (specular) view. Egocentric view (MIRROR view in my experiments) elicited greater activation in the contralateral hemisphere. There may be evidence for the mirror-like imitation observed in children and adults, where observing movements in a mirror view (even though right hand appears as left hand but on the same side as the right hand) elicits activation in the hemisphere responsible for making movements with the right hand. The findings of this neuroimaging study are consistent with the result of Experiment 5.1 in that observational viewpoint has a differential effect on the Action Observation System, which can be measured behaviourally as the movement interference effect.

In the context of observational learning, several brain imaging studies show the Action Observation System involves the observer in processes similar to those that occur during physical practice (Brown, Wilson, & Gribble, 2009; Buccino et al., 2001; Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009; Fogassi et al., 2005; Frey & Gerry, 2006; Gallese, Fogassi, Fadiga, & Rizzolatti, 2002; Shmuelof & Zohary, 2006).

Rohbanfard & Proteau, (2011) addressed the role of viewpoint in the context of observational learning through a behavioural study. They looked at four sets of participants observing a right- or a left-handed model perform some tasks in either a first-person view or a third-person view. Participants performed a pre-test, learning, and took two retention tests, one after 10 minutes, and the other after 24 hours. Total movement time (TMT) and the time required to complete each segment of the movement (IT for intermediate time) was calculated and compared for all the conditions. The results showed that in the context of learning, handedness was more important than the observational viewpoint - right-handed participants learned better from observing a right-handed model; left-handed participants learned better from observing a left-handed model. In this experiment, however, specular view was compared to a view from behind the model, which cannot qualify as mirror-view. Also, many visual details such as body language and facial expressions are absent when looking at a model in the first-person view (from the back). Perhaps the participants would have learned differently when observing models in mirror or specular view and when the handedness of the model and the participant was matched.

It should follow from the automaticity of the Action Observation System that it is also unmediated or uninfluenced by other cognitive processes related to action



semantics (Gallese et al., 1996; Gallese, & Goldman, 1998; Rizzolatti, Fogassi, & Gallese, 2001; Rizzolatti et al., 1996; Rizzolatti et al., 1999). This particular claim poses no issues if unmediated simply means without the conscious will of the observer or without any cognitive effort on the part of the observer. From the results of Experiments 4.1, 4.2 and 5.1, and the other studies that are summarised in this section, it could be said that the Action Observation System is influenced by visual properties such as imagination of observed movements, observational viewpoint and handedness of the observer and the actor (among many others). The Action Observation System might therefore be unmediated only at the most basic level of automatic imitation.

#### ACTION OBSERVATION SYSTEM AND MOVEMENT KINEMATICS OF BIOLOGICAL AND NON-BIOLOGICAL MOTION

Many researchers propose that the Action Observation System is specifically engaged for observing biological motion (Bouquet et al., 2007; Di Dio et al., 2013; Kilner et al., 2007; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Decety, & Grèzes, 2006; Gallese, & Goldman, 1998; Perani et al., 2001). The argument for this proposal is as follows: motor resonance occurs only for observed movements that are already the observer's motor repertoire (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). As there can be no motor plans for movements other than those with biological kinematics, there can be no motor resonance for observing movements with non-biological kinematics. The movement interference effect experiments by Kilner et al. (2003, 2007) support this hypothesis. Kilner et al. (2003) did not find a movement interference effect for observing incongruent robotic movements compared to the baseline condition where participants executed arm

movements without observing any stimuli. It could be that the robotic movements did not generate any interference effects either because of their movement kinematics or because of non-human form of the robot. Kilner et al. (2007) addressed this issue of form and kinematics by manipulating two effectors, video (human) and a dot, moving with natural and constant velocity profiles. They found movement interference for observing incongruent natural velocity profile movements only in the case of “Video” stimuli, but in the case of “Dot” stimuli they found movement interference for both natural and constant velocity profiles. They interpreted the results stating that there may not be sufficient information in the “Dot” stimuli to activate the regions of the brain that are involved in differentiating between biological and non-biological motion. Their interpretation was furthered when movement interference was found when a robotic arm moved with biological kinematics (Oztop, Chaminade, Franklin, 2004; Franklin, Oztop, Cheng, 2005). In yet another study, movement interference was found for video observation of humanoid robots that moved with biological kinematics (Kupferber A. et al, 2009).

However, the influence of movement kinematics on Action Observation System is far from clear. The results of Experiments 4.1, 4.2 and 5.1 show that observing incongruent movements elicit movement interference irrespective of movement kinematics. Similarly, Shen et al. (2009) investigated movement interference effects between a human and a robot, where participants had to interact with a small child-sized humanoid robot (KASPAR) using arm waving movements. The experimental set-up was intended to be more “playful” than constrained in order to simulate a “real-life” environment better. The experimenters found no movement interference effects whatsoever when adults and children interacted with the humanoid robot. As

in the Kilner et al. (2003) study, they found a main effect of movement direction, where executing horizontal movements had greater mean variance than executing vertical movements. There was no effect of movement congruency and they supposed the lack of this effect due to a more “natural” environment within the experimental set-up. These results suggest that the environment in which human beings interact with both animate beings and inanimate objects such as robots influences action perception.

Consistent with the earlier study (Shen et al., 2009), Press et al., (2005) found that both human and robotic movements could show the effect of automatic imitation, though to different degrees. Participants performed a prespecified movement (e.g. opening their hand) on appearance of a human or robotic hand in pose of a compatible movement (opened) or an incompatible movement (closed). The prespecified action (open or close) was initiated faster when it was prompted by compatible movement stimulus than when it was prompted by the incompatible movement stimulus. However, the human hand showed a stronger automatic imitation effect on performance than the robotic hand. These results suggest that effector shape can override the obviously non-biological kinematics of the robot and allow the Action Observation System to be engaged for both of them.

Press, Gillmeister, and Heyes (2007) used the same paradigm as in Press et al. (2005) to find out if prior sensorimotor experience with robotic movements enhanced the effects of automatic imitation. Participants performed the same tasks as specified in the Press et al. (2005) study and tested on automatic imitation trials,

after which they were given training with opening and closing their hand as they observed a human hand or a robot hand execute compatible movement (opened) or an incompatible movement (closed). When tested for automatic imitation after training, they found that stimulus-compatible training, increased automatic imitation of robotic stimuli (faster response on compatible trials, compared to incompatible trials) and eliminated the human bias observed before the training. These findings suggest that the development of the Action Observation System relies on sensorimotor experience. It is possible that there is a “human bias” only because of our more frequent interactions with other human beings leading to more familiarity with them rather than with robots.

Extending hypothesis that sensorimotor training can affect movement interference (Press et al., 2005), Capa et al. (2010) looked at whether the movement interference effect was sensitive to short-term visuomotor priming. Movement interference was measured in two groups of participants who had observed the same set of incongruent movements. However, one group had received prior visuomotor practice with the incongruent movements and the other group had not. The results showed that there was greater movement interference in the group that had received prior practice compared to the group that did not. They support the hypothesis that even a short-term sensorimotor experience with an action can affect its perception (Marshall et al., 2009; Press et al. 2005; Press, Gillmeister, & Heyes, 2007).

The results of the experiments discussed in this section including Experiments 4.1, 4.2 and 5.1 suggest that the top-down effects of agency beliefs and the “environment”

in which interactions occur play a significant role in eliciting responses from the Action Observation System. While the Action Observation System might simulate the motor plans of observed movements automatically and without the intention of the observer to do so, it is very variable in its engagement by different effectors, their movement kinematics, form, as well as other factors like attention, attribution of agency to the observed movements, etc. Human beings do not act in isolation interact in various social settings. They are also heavily engaged in “virtual” interactions such as imagining various actions and courses of action, mental simulations of social situations when reading, watching shows and movies and even when listening to conversations or the radio. This ability to move across genres and various modes of information and interactions is what sets human being apart from monkeys.

## APPENDIX – ACTION REPRESENTATION IN THE FRONTO-PARIETAL ACTION OBSERVATION NETWORK

At the end of the general discussion, I would like to present a basic overview about what is meant by ‘action representation’ as well as some other related concepts.

Understanding the language used to interpret the results of studies on Action Observation System will aid in clearing many confusions and confounds related to it.

I find the addition of this appendix to be important as the study of the Action Observation System, though pursued with great intensity and in great numbers, is still in its infancy. The concepts related to the Action Observation System are still being developed as is the vocabulary used to describe them.

Action representation is a fundamental component of the process of motor cognition.

How are actions represented in the human brain? In order to answer this question, we need to understand what ‘action’ and ‘representation’ are. In the context of

perception, representation can be defined as the end-point of a perceptual process (Jeannerod, 2006). A perceptual process can refer to vision, audition or actions.

Every perceptual process - visual, auditory, or motor - has its own characteristics. We are concerned here primarily with the representation of motor perceptual processes.

What is an action? While the words “actions” and “movements” have been used interchangeably in the thesis for ease of understanding, there is a difference between them. In the context of the Action Observation System, I consider “action” to be a ‘goal-directed movement’ that is happening in the here and now (Uithol, 2011). This emphasis on the ‘here and now’ is important because of what a ‘goal’ means. While

an action is a concrete movement for which there are exact motor plans, such as the motor plans for a precision grip or a pincer grip, a 'goal' is more abstract in nature. A goal is not visible in the external world. For example, the goal of picking up a pen on the table could be to put the pen in its case, but what is seen is the arm moving towards the pen and picking it up; the final 'goal' is known by the observer only when the movement of putting the pen in its case is seen. Therefore an action goal exists in the future. It corresponds to that state of the external world if and when a particular action is successfully performed (Jeannerod, 2006). Understanding the 'goal' of any action must therefore involve a prediction about the future state of events upon the completion of that action if action understanding is to be useful at all. It would be counterproductive and slow if the brain were to wait for the completion of every action before its goal was discerned. Therefore, action representation must broadly represent future events (Searle, 1983), and being PREDICTIVE in nature, it must precede an action that has not yet been executed. I therefore argue that the Action Observation System might be the neural framework that underlies the representation non-executed actions. A covert representation of the goals of actions always precedes the over execution of the actual actions. This allows for the intricate and highly diverse social interactions, where we adjust our own action based on the actions of those we are engaging with - for example, someone picks up a glass of champagne from a table and moves it to us, we 'know' that he or she is offering the glass to us and we adjust our movements according to whether we want to accept the glass or not.

The idea of 'whether we want to accept the glass or not' brings us to the point of what 'intentions' are. We understand the 'intention' of the person offering us the glass of

champagne because of the possibility of executing the movements required to pick up the glass from the table and move the arm towards us. It is because those movements are executable by ourselves we understand the intention behind them. A ‘motor intention’ is thereby an executable goal-directed movement. An impossible action cannot be a motor intention, such as flying because human beings cannot fly (unless they board a plane or wear a glider over themselves). However, we routinely understand the actions that we cannot ourselves execute, such as when we watch a bee flying to a flower and hovering over it before diving into the flower. The actions of ‘flying’, ‘hovering’ and ‘diving’ are all represented in our brains but we ourselves cannot ‘intend’ to perform all those actions. Therefore, all action representations cannot be intentions (Jeannerod, 2006).

Based on this understanding of these concepts and the language used to describe them, we can say that the AOS at the most basic level is concerned with simulating the observed actions and representing them in the brain, such that they provide an underlying framework for “understanding” non-executed actions. Whereas the simulated motor plans of the goal-directed movements exist in ‘here and now’ the end-goals have to, of necessity, exist in the future. The AOS “understands” the end-goals of actions as far as they go because of their predictive nature that draws on conditioning, learning and internal models. This kind of “action understanding” that is MEDIATED and INFERENTIAL in nature, lies one level above the understanding of non-executed actions or observed actions. It also involves the bringing-in of semantic knowledge, which, according to the classic hypothesis of the AOS, should lie beyond it.



Semantic knowledge about objects provides information about what to do with it (goal-information) and how to use it (grasp-grip information) (van Elk, van Schie, & Bekkering, 2008). This kind of knowledge cannot be passed on via the mechanisms of evolutionary biology, but must be learned by observation and practice. van Elk, van Schie, and Bekkering (2008) looked at how the AOS draws on semantic knowledge for action understanding. In the first experiment, participants were asked to attend to either the goal of the observed action (attend-to-goal condition) or to correctness of the grip (attend-to-grip condition). Participants performed a button-press response as the action being either correct or incorrect. The reaction times showed that they were faster in detecting the correct goals rather than grips. There was also greater interference to detecting the correct goal in the trials where they were asked to attend to the grip. In the second experiment, participants were asked to attend to action-irrelevant cues such as object orientation. In this condition, no interference was found to grip- or goal-related violations, thus ruling out the possibility that interference in the earlier study was due to perceptual differences in the stimuli. These results imply that in cases where “higher-order” action understanding is required, the AOS no longer functions in an unmediated and semantics-free manner.

Majdandzic et al. (2007) looked deeper at the effect of immediate goals (goals of actions in the here and now) versus final goals (end-goals that exist in the future) on the AOS in an fMRI study. In the “Final Goal” condition, there was differential preparatory activity in the left inferior parietal cortex and in the superior frontal gyrus (bilaterally). In the “Immediate Goal” condition, there was differential activity

in occipito-temporal and occipito-parietal cortex, suggesting that actions could be planned, and therefore understood at different levels.

As there are multiple levels of abstraction and hierarchy with respect of actions and action goals, it is problematic to use the term “mirror neurons” when referring to action understanding in the human brain (Uithol, Haselager, & Bekkering, 2008). “Mirror neurons” can refer to the strictly congruent neurons with mirror properties found in area F5 of monkeys, but is not appropriate for use with the human brain. Action understanding in human beings involves many cortical networks that require intense study at every level, and hence, the term “Action Observation System” is a more apt term for humans.

I conclude this appendix and this thesis by observing that actions and their representation in the human brain, possibly via the Action Observation System, is a complex field of study that needs to be tackled from all possible fronts. It is important not only to do experimental work on the Action Observation System, but also to engage in philosophical debates about the epistemology of action and its representation and develop a strong and consistent language to describe and interpret the findings about the Action Observation System.

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