Spatiotemporal Prediction of Observed Action

Contrasts between Different Frames of Reference

Victoria Caroline Brattan

PhD

University of York

Psychology

March 2016

ABSTRACT

Previous research has shown that in both non-human and human primates a network of neural regions exists that is engaged not only when we perform an action but also when we observe that same action being performed. This coupled action-perception system is argued to play a role in several areas of cognitive functioning, with this system being at least partially responsible for the prediction of observed actions. Despite much research surrounding this action-observation system (AON), there continues to be a large debate regarding the principal function of such a system. On the one hand, it is argued that the system allows the prediction and monitoring of one's own actions for fine-grain motor control and kinematic adjustment. On the other hand, researchers argue that the system evolved for the monitoring of others' actions, for social interaction purposes.

Using dynamic transitive actions in the first person perspective (1PP) and third person perspective (3PP), in the series of studies that follow, we aim to determine whether the prediction system functions at an advantage when observing these dynamic images which map closely onto the observation of self-generated as opposed to other-generated actions.

In all, the series of studies primarily highlight the importance of motor experience, enabling us to draw upon our motor repertoire to effectively simulate and accurately predict observed actions. Behavioural and EEG studies using a psychophysics method provide evidence that 1PP actions are advantageous to the prediction system following motor priming, suggesting the underlying neural mechanisms may have predominantly emerged for self-monitoring purposes. However, using a converging method, somewhat opposing results are found, which suggest motor experience can facilitate 3PP actions. When interpreting results to inform theories it is always essential to consider the experimental task employed to interrogate the matter at hand, and determine which underlying mechanisms the method may be drawing upon.

TABLE OF CONTENTS

ABSTRACT ii

TABLE OF CONTENTS iii

LIST OF FIGURES vi

LIST OF TABLES ix

ACKNOWLEDGEMENTS x

AUTHOR’S DECLARATION xi

CHAPTER 1. Introduction and Literature Review 1

  1.1 Shared representations for action and perception 1

  1.2 The emergence and function of shared representations for action execution and observation 8

  1.3 Visual perception as a predictive process 13

  1.4 Timing of action simulation / action prediction. Does prediction of actions involve real-time simulation of action? 17

  1.5 Neural substrates of action prediction/action simulation 21

  1.6 Dissociating systems for observation of self versus other 25

  1.7 Present work 39

CHAPTER 2: Spatiotemporal prediction of observed action with a temporal judgement task 42

  2.1 INTRODUCTION 42

  2.2 EXPERIMENT 1 46

    2.2.1 METHOD 46

    2.2.2. RESULTS & DISCUSSION 51

  2.3 EXPERIMENT 2 56

    2.3.1 METHOD 56

    2.3.2 RESULTS & DISCUSSION 57

  2.3.3 GENERAL DISCUSSION 60

CHAPTER 3: Visual and Motor Priming Effects on Action Prediction 64

  3.1 EXPERIMENT 3: Visual priming of actions in third-person perspective 64

    3.1.1 INTRODUCTION 64

3.1.2 METHOD 65

3.1.3 RESULTS & DISCUSSION 66

3.2 EXPERIMENT 4: Visual and motor priming of actions in first-person perspective 68

3.2.1 INTRODUCTION....................68

3.2.2 METHOD 69

3.2.3 RESULTS & DISCUSSION 70

3.3 EXPERIMENT 5: Motor priming without visual input in first-person perspective 72

3.3.1 INTRODUCTION....................72

3.3.2 METHOD 73

3.3.3 RESULTS & DISCUSSION 74

3.4. CONTRASTING RESULTS ACROSS EXPERIMENTS....................76

3.4.1. The point of subjective equality 76

3.4.2. The slope of the psychometric function 78

3.4.3 Leave-One-Object-Out Analysis....................79

3.5 GENERAL DISCUSSION 79

3.6 CONCLUSION 82

CHAPTER 4: Neural Signals of Prediction Error for First- and Third-Person Observed Actions....................83

4.1 INTRODUCTION....................83

4.2 METHODS....................89

4.3 RESULTS 96

4.4. DISCUSSION 107

4.5 CONCLUSION....................113

CHAPTER 5: Spatiotemporal prediction of actions with a coincidence anticipation task .114

5.1 INTRODUCTION 114

5.2 EXPERIMENT 7 – Without Motor Priming 119

5.2.1 METHODS....................119

5.2.2 RESULTS 123

5.3 EXPERIMENT 8 – With Motor Priming....................125

5.3.1 METHOD 125

5.3.2 RESULTS 126

5.4. GENERAL RESULTS....................127

5.4 DISCUSSION 128

5.5 CONCLUSION 133

CHAPTER 6. Individual differences in action prediction and its relation to time perception and motor control 135

6.1 INTRODUCTION 135

6.2. METHODS 141

6.3. RESULTS 149

6.4. DISCUSSION 155

6.5. CONCLUSION 158

CHAPTER 7. DISCUSSION 160

7.1 RESEARCH AIMS 160

7.2 SUMMARY OF CHAPTERS 161

7.3 IMPLICATIONS 165

7.4 FUTURE RESEARCH 167

7.5 GENERAL CONCLUSIONS 171

APPENDIX A 173

APPENDIX B 174

APPENDIX C 176

APPENDIX D 185

APPENDIX E 189

REFERENCES 193

LIST OF FIGURES

Figure 1.1. Representation of the core and extended AON. 4

Figure 1.2. A Predictive Coding Account of The Mirror Neuron System. 13

Figure 2.1.Static images taken from example video stimuli in the first-person perspective (1PP) and third-person perspective (3PP) conditions. 48

Figure 2.2. Schema of a trial in Experiments 1 and 2. 50

Figure 2.3. Example logistic function fitted to an individual participant's proportion of 'late' responses per temporal offset condition. 53

Figure 2.4. Bar graph depicting the mean point of subjective equality (PSE) for each perspective in Experiment 1. 54

Figure 2.5. Bar graph depicting the mean spread of data for each perspective in Experiment 1. 55

Figure 2.6. Bar graph depicting the mean point of subjective equality (PSE) for each perspective in Experiment 2. 58

Figure 2.7. Bar graph depicting the mean spread of data for each perspective in Experiment 2. 59

Figure 3.1. Bar graph depicting the mean point of subjective equality (PSE) for each perspective in Experiment 3. 67

Figure 3.2. Bar graph depicting the mean point of subjective equality for each perspective in Experiment 4. 71

Figure 3.3. Bar graph depicting the mean point of subjective equality (PSE) for each perspective in Experiment 5. 75

Figure 3.4. Bar graph depicting the mean point of subjective equality (PSE) for each perspective in each experiment. 76

Figure 3.5. Bar graph depicting the mean point of subjective equality (PSE) for each perspective with and without motor priming. 77

Figure 3.6. Bar graph depicting the mean spread of the psychometric functions for each perspective in Experiments 2 to 5. 79

Figure 4.1. Schema of a trial in Experiment 6. 92

Figure 4.2. Mean point of subjective equality for each Action Type and each Perspective in the EEG study. 97

Figure 4.3. Mean amplitude (µV) for non-biological data averaged over electrodes Fz, FCz and Cz in the time-window 100-200 ms following re-onset of action post-occlusion for the two perspectives and three time-offset conditions. 99

Figure 4.4 Grand averaged waveforms for non-biological action at electrode Fz for 1PP actions (A) and 3PP actions (B). 99

Figure 4.5. Grand averaged waveforms for non-biological action at electrode Fz for Early (A), Coherent (B) and Late (C) conditions. 100

Figure 4.6. Mean amplitudes (µV) for biological data averaged over electrodes Fz, FCz and Cz in the time window 100-200 ms following re-onset of action post-occlusion for the two perspectives and three time-offset conditions. 101

Figure 4.7. Grand averaged waveforms for biological action at electrode Fz for 1PP actions (A) and 3PP actions (B). 101

Figure 4.8. Grand averaged waveforms for biological action at electrode Fz for Early (A), Coherent (B) and Late (C) conditions. 102

Figure 4.9. Mean amplitudes (µV) for non-biological data averaged over electrodes Cz, CPz and Pz in the time window 350-450 ms following re-onset of action post-occlusion for the two perspectives and three time-offset conditions. 103

Figure 4.10. Grand averaged waveforms for non-biological action at electrode Pz for 1PP actions (A) and 3PP actions (B). 103

Figure 4.11. Grand averaged waveforms for non-biological action at electrode Pz for Early (A), Coherent (B) and Late (C) conditions. 104

Figure 4.12. Mean amplitudes (µV) for biological data averaged over electrodes Cz, CPz and Pz in the time window 350-450 ms following re-onset of action post-occlusion for the two perspectives and three time-offset conditions. 105

Figure 4.13. Grand averaged waveforms for biological action at electrode Pz for 1PP actions (A) and 3PP actions (B). 106

Figure 4.14. Grand averaged waveforms for biological action at electrode Pz for Early (A), Coherent (B) and Late (C) conditions. 106

Figure 5.1. Schema of a trial in Experiments 7 and 8. 122

Figure 5.2. Bar charts depicting data from (a) Experiment 7 (without motor priming) and (b) Experiment 8 (with motor priming). 125

Figure 6.1. Temporal Bisection task paradigm. 143

Figure 6.2. Schema of a trial in the Variable Foreperiod task. 145

LIST OF TABLES

Table 5.1. Real lift time points (in milliseconds) for each object and each actor gender, determined from the start of the action sequence. 120

Table 6.2. Descriptive statistics (means, minima, maxima, standard errors and variances) for each of the continuous predictor variables. 149

Table 6.3. Results of the multiple linear mixed regression analysis of factors predicting the variance in the coincidence anticipation task, in first and third person perspectives, when participants receive 700 ms of action pre-occlusion. 153

Table 6.4. Results of the multiple linear mixed regression analysis of factors predicting the variance in the coincidence anticipation task, in the first and third person perspectives, when participants receive 1000 ms of action pre-occlusion. 154

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Professor Steven Tipper, for being one of the kindest, most modest and patient supervisors I could have hoped for. Thank you for your continued support, inspiration, guidance and generosity of time.

Thank you to Dr. Daniel Baker for all his statistics knowledge, his Matlab and psychophysics expertise, and particularly for reading several versions of chapters of the thesis and paper drafts. I would also like to give thanks to the members of my Thesis Advisory Panel, Professor Beth Jefferies, and Dr. Silke Göbel. Thank you for your feedback, suggestions and guidance along the way.

I would also like to give sincere thanks to Gareth Prenderghast, Andre Gowse and the YNiC team for their time and effort in improving my coding of experimental presentation in Matlab and Python. Without your support most experiments in the department would never run.

I would especially like to give my most heartfelt gratitude to Andrew Quinn. Thank you for your unwavering support, for being there when I could no longer bear the isolation of research, for your infinite patience, and especially for not letting me give up on myself. Thank you for believing in me when I couldn’t. Thank you Andrew.

To my dearest friends Huarda Valdés Laribi, Liz Kirk and Janine Oostenbroek. Thank you for being there to talk, to celebrate the wins, and to offer bubbly when there was nothing to celebrate. You have been so important to me over these last few years, and I look forward to seeing where we all get to next.

Finally, I would like to thank Mum and Dad. Without your love, care, and support I wouldn’t have done all that I have done with my life, before, during and after the PhD. Thank you for grounding me in the difficult moments and always reminding me of the important things in life – good food, good wine, family, friends, and especially love. No one could have given more than you have.

AUTHOR'S DECLARATION

This thesis comprises the candidate's own original work and has not, whether in the same or different form, been submitted to this or any other university for a degree.

The PhD was funded by a joint studentship awarded by the White Rose Economic and Social Research Council (ESRC) and the University of York Psychology Department.

Studies from empirical chapters 2 and 3 presented in the current thesis have been published in the following peer-reviewed journal:

Brattan, V.C., Baker, D.H. & Tipper, S.P. (2015). Spatiotemporal prediction of observed actions: Contrasts between first- and third-person perspectives after motor priming. *Journal of Experimental Psychology: Human Perception and Performance*. 41(5).

Selected aspects of the research described in this thesis have been presented at the following conferences:

Brattan, V.C., Baker, D.H. & Tipper, S.P. (July 2015). Spatiotemporal prediction of observed actions: Contrasts between first- and third-person perspectives after motor priming. Poster presented at White Rose Doctoral Training Centre Annual Pathways Conference, University of Leeds, UK.

Brattan, V.C., Baker, D.H. & Tipper, S.P. (May 2015). Motor priming improves prediction of first- and third-person perspective actions. Evidence from two spatiotemporal judgments tasks. Poster presented at Concepts, Actions and Objects (CAOS) Conference, University of Trento, Rovereto, Italy.

Brattan, V.C., Baker, D.H. & Tipper, S.P. (May 2014). Visual and motor priming effects on prediction of observed action in the first and third person perspectives. Poster presented at Vision Sciences Society (VSS) 14th Annual Conference, St. Pete Beach, Florida.

CHAPTER 1. Introduction and Literature Review

1.1 Shared representations for action and perception

From the late 1980s it was realised that overt action had an apparently covert counterpart. Any overt action could be represented covertly and have the same characteristics. That is, imagined action was shown to maintain the same temporal characteristics as the same overtly executed action (Decety, Jeannerod, & Prablanc, 1989). For instance, the time to respond whether or not a reach-to-grasp action is plausible is a function of the object-to-be-grasped orientation, and corresponds to the time taken to overtly reach and grasp the object, suggesting a mental representation of arm movement is played out before a response can be given (Frak, Paulignan, & Jeannerod, 2001). It was consequently suggested that mental imagery of action likely involves the same motor regions of the brain that are employed when executing the same action (Jeannerod, 1994, 1997). On a similar line, the observation of action by a third person also constitutes another means by which covert actions are elicited (Jeannerod, 2001). It was thus posited that covert actions (mental imagery or observed actions performed by another) involve the motor system as a means to emulate, simulate, or internally re-enact (Prinz, 2006) action in a manner highly similar to when overtly executing the same action, through 'motor resonance' (Gallese, 2005).

The theory that perception and action are inextricably entwined has generated an extensive body of research, which has strengthened support for the notion that they share common representations - the common coding principle (Prinz, 1997). Studies have demonstrated that we non-consciously and automatically imitate people we interact with (the chameleon effect) (Chartrand & Bargh, 1999; van Baaren, Holland, Kawakami, & van Knippenberg, 2004), and even mimic and synchronise facial expressions (the emotional contagion effect) (Hatfield, Cacioppo, & Rapson, 1994). Furthermore, research demonstrates that one's own actions are modulated by the perception of others' actions (Brass, Bekkering, Wohlschläger, & Prinz, 2000; Brass, Zysset, & von Cramon, 2001; Bach, Peatfield & Tipper, 2007), and that perception of action can be influenced by our own actions (Tipper & Bach, 2008). Perception and action, therefore, would apparently be tightly coupled. Whether this can be evidenced neurally has been a major topic in cognitive neuroscience for more than a decade.

1.1.1 The discovery of cells coding both perception and action

Theories and research relating to this simulation theory of action perception exploded following the discovery of 'mirror neurons' in the macaque monkey. In a series of single cell recordings, di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti (1992) found that a set of neurons within area F5 (ventral premotor cortex) of the macaque monkey were responsive when the macaque being recorded executed a reach-and-grasp action as well as when it observed a similar action being performed by a conspecific or experimenter. The 'mirror' properties of neurons in area F5 have been reaffirmed by subsequent studies (Caggiano et al., 2011; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Kraskov, Dancause, Quallo, Shepherd, & Lemon, 2009; Rizzolatti, Fogassi, & Gallese, 2001; Umiltà et al., 2001). It was further observed that F5 neurons coded not for individual movements (i.e. individual muscle group contractions), but rather specific motor acts; that is, they code for action sequences with specific short-term goals, such as grasping, holding and tearing (Rizzolatti et al. 1981; Rizzolatti et al. 1988; Okano & Tanji, 1987). Visuo-motor properties of neurons were also later discovered within area PF (inferior parietal lobule) of the macaque (Fogassi et al., 2005; Gallese et al., 2002;).[1] The discovery appeared to provide a neural mechanism matching perception and action and marked a ground-breaking point in research for

---

[1] It is, however, worth noting that both regions also contain neurons with motor-only and visual-only properties (Gallese et al., 1996, 2002).

several areas of psychology and cognitive neuroscience, including motor cognition, social cognition, empathy, imitation, and indeed perception in general.

1.1.2 Evidence for shared representations for action and perception in humans

1.1.2.1 fMRI

Given the invasive nature of single cell recordings, research in humans has had to turn to alternative methods to explore the potential existence of a human mirror neuron system. Several studies have employed blood oxygenation level dependent (BOLD) functional magnetic resonance imaging (fMRI). In fMRI research, an increase in BOLD response in a particular neural region is interpreted as that region being active and involved in the task at hand. FMRI studies have followed the logic that an increase in activation in motor planning regions during the mere observation of action demonstrates the presence of mirror neurons in a region. Several studies have demonstrated just this and concluded that the findings provide evidence of a human mirror neuron system by observing such activation in frontal and parietal regions homologous to the macaque F5 and PF (Buccino et al., 2001; Buccino et al., 2004; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Gazzola & Keysers, 2009; Grèzes, Armony, Rowe, & Passingham, 2003; Iacoboni & Dapretto, 2006; Iacoboni et al., 2005; Molnar-Szakacs, Kaplan, Greenfield, & Iacoboni, 2006).

However, many researchers would argue that it is important that activation be recorded for both execution and observation of action; that is, a crossmodal response across the visual and motor modalities is necessary to demonstrate the presence of mirror neurons in a region. A smaller number of studies have demonstrated this (Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008; Kilner, Neal, Weiskopf, Friston, & Frith, 2009; Oosterhof, Tipper, & Downing, 2012).

Homologous to the monkey brain, three regions in the human brain have been proposed to represent both execution and observation of action, described as the human mirror neuron system (hMNS) or action-observation network (AON): the ventral premotor cortex (PMv) together with the posterior inferior frontal gyrus (IFGp)/; the inferior parietal lobule (IPL); and the superior temporal sulcus (STS) (Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010), (despite neurons in STS of the macaque not being considered mirror neurons as they did not fire when the monkeys performed actions without visual feedback (Rizzolatti et al., 1988)). Several other studies suggest that additional areas outside of the three typical AON regions also play a part in action-observation representation, constituting an extended AON. The core and extended AON are depicted in Figure 1.

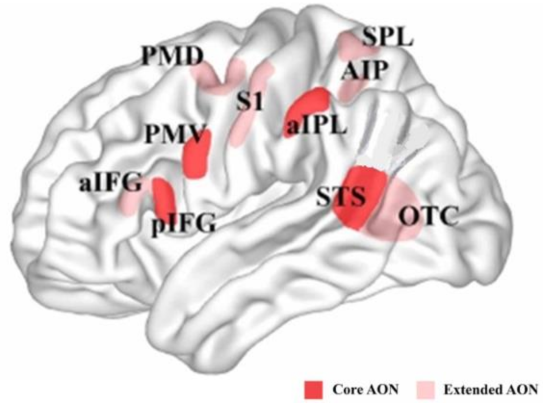

Figure 1.1. Representation of the core and extended AON. In red, the core AON is presented comprising: the ventral premotor cortex (PMV)/posterior inferior frontal gyrus (pIFG), the anterior inferior parietal lobule (aIPL) and the superior temporal sulcus (STS). In pink, the extended AON is presented comprising: the anterior inferior frontal gyrus (aIFG), the dorsal premotor cortex (PMD), the superior parietal lobule (SPL), the anterior intraparietal sulcus (AIP), the somatosensory cortex (S1) and the occipito-temporal cortex (OTC), also including STS. Adapted from Turella, Wurm, Tucciarelli, Lingnau (2013).

1.1.2.2 MEP/TMS Studies

TMS is a technique involving the electrical stimulation of the nervous system. When TMS is applied to the motor cortex, at appropriate stimulation intensity, motor-evoked potentials (MEPs) can be recorded from corresponding muscles in the extremities. The amplitude of these potentials is modulated by the behavioural or experimental context. Fadiga, Fogassi, Pavesi, & Rizzolatti (1995) stimulated the motor cortex of participants with TMS and recorded motor evoked potential (MEP) patterns from hand muscles whilst participants i) observed an experimenter grasp commonly used objects, ii) looked at the same static objects for three seconds, iii) observed an experimenter trace shapes in the air with his arm, and iv) detected the dimming of a light stimulus on a computer screen (to rule out interpretations in terms of attention effects). MEPs significantly increased during the observation of movements (conditions i and iii). These patterns were very similar to muscle contraction patterns when participants executed the same movements themselves. Authors ruled out the possibility of a preparatory response for an impending action by the two conditions which did not represent action (ii and iv). Observation of an object, even if it can be considered the possible target for a movement, did not elicit an effect that was comparable to that elicited during movement. From the study, authors concluded that there is an action-observation matching system, similar to the one found in primate studies (di Pellegrino et al., 1992).

Gangitano, Mottaghy, & Pascual-Leone (2001) expanded on the Fadiga et al. (1995) study by exploring the temporal dynamics of cortico-spinal excitability during observation of reach-to-grasp movements. They demonstrated that the action-observation mirror system compares the observed action with the internal representation in terms of temporal coding. Similar to Fadiga et al. (1995), they found that MEPs were modulated by the observation of grasping movements, but furthermore, found that MEP patterns were modulated by the different phases of the grasping action; MEP amplitude increased with increasing finger aperture, and became smaller during the closure phase. In the macaque, distinct populations of neurons have been shown to have different peaks of activity in response to the phase of movement (Rizzolatti et al., 1988). Gangitano and colleagues demonstrated a similar effect in humans in the absence of movement. The authors thus suggested that the AON/hMNS has detailed (timing) properties.

1.1.2.3 Electroencephalography and magnetoencephalography studies

The electrophysiological and magnetophysiological response associated with the human action-observation network is the suppression of the alpha/mu and beta rhythms. Electrophysiological oscillations in the 8-12/13Hz frequency range over the sensorimotor cortex (*mu*), and in the 15-30Hz (*beta*) range, are at their highest amplitude during rest. Cortical oscillatory power decreases during execution of an action. The attenuation of oscillatory amplitude has generally been associated with desynchronisation of the underlying neural populations, which may reflect an increase in neural activity or increased load on the cells (Pfurtscheller, 1997). Several studies have demonstrated, however, that mu and beta suppression occurs not only during action performance but also during observation of action (Babiloni et al., 2002, 2009; Cochin, Barthelemy, Lejeune, Roux, & Martineau, 1998; Cochin, Barthelemy, & Roux, 1999; Frenkel-Toledo, Bentin, Perry, Liebermann, & Soroker, 2013; Marshall, Young, & Meltzoff, 2011; Muthukumaraswamy, Johnson, & McNair, 2004; Perry & Bentin, 2009; Pineda, 2005; Southgate, Johnson, Osborne, & Csibra, 2009). Thus, mu and beta wave power suppression is argued to be the electrophysiological response associated with human mirror neuron system activity.

To illustrate, Cochin et al. (1999) recorded EEG activity in seven frequency bands over 14 electrode sites whilst participants were at rest, whilst observing an experimenter perform index finger and thumb pincer movements and whilst performing the same movements themselves. Compared to rest, participants showed a decrease in spectral power for the observation and execution condition within the 7.5-10.5Hz range in nine of the fourteen sites, demonstrating low alpha band suppression across posterior frontal and motor regions. Cochin and colleagues posited that this was demonstration that both observation and execution of an action recruit the same neural regions.

Similar results have been observed throughout the EEG literature. EEG mu wave attenuation has been found in adults when observing single-limb hand and foot actions (Pfurtscheller et al., 1997); during aimless finger movements (Babiloni et al., 2002; Cochin et al., 1999); when observing skilled/expert complex movements (Babiloni et al., 2009, 2010); during object-oriented actions (Muthukumaraswamy et al., 2004; Muthukumaraswamy & Johnson, 2004); during non-transitive actions (Babiloni et al., 2002; Cochin et al., 1999; Muthukumaraswamy et al., 2004); and when imagining an action (Pfurtscheller, Brunner, Schlögl, & Lopes da Silva, 2006). Spectral power suppression has also been observed in young infants observing goal-directed acts (Marshall et al., 2011; Southgate et al., 2009).

Although very few studies have examined action observation-action execution matching systems with magnetoencephalography (MEG), very similar results to those obtained with EEG have been replicated with this technique (Hari et al., 1998; Kilner, Marchant, & Frith, 2006; Kilner, 2009; Nishitani & Hari, 2000). In addition, however, MEG has enabled source localisation of the cortical oscillatory activity, therefore providing rich temporal detail of the sequencing of activation of the cortical areas of the AON. To examine the temporal dynamics of cortical activation of motor regions during action observation and perception, Nishitani and Hari (2000) recorded cortical activity with MEG whilst participants executed a reach-to-grasp action on a manipulandum, imitated an experimenter, or purely observed an experimenter perform the grasp action. They found that for each of the conditions, posterior IFG/ ventral premotor cortex was active 100-200ms prior to precentral motor cortex activity. From the results, Nishitani and Hari (2000) claimed that the posterior IFG is an orchestrator for the action observation network.

The notion of a human MNS/AON has not been without criticism (Hickok, 2009; 2014; Jacob & Jeannerod, 2005; Mahon & Caramazza, 2005). In particular, it has been highlighted that whilst single cell recordings have enabled key properties of individual neurons to be characterised, caution should be taken in extrapolating such properties to the human brain to make inferences about system level processes. Non-invasive techniques such as fMRI and M/EEG examine the summative or averaged activity of groups of hundreds and even thousands of neurons. Within a population of cells there will be groups of neurons that code visual-only properties, motor-only properties, and a proportion that code for both (Gallese et al., 1996, 2002; Caggiano et al., 2011). Any activity recorded for both execution and observation of action in humans may be due to groups of neurons coding different features but found within the same region.

Nevertheless, it is clear from several lines of research with differing techniques that motor planning and motor control regions of the human brain are recruited during the observation of action without overt motor output. This may indicate that we in some way experience motor resonance with the actor being observed, internally simulating the actions unfolding before us.

1.2 The emergence and function of shared representations for action execution and observation

1.2.1 A system evolved for social adaptation

Evidently, there is a substantial amount of research demonstrating the existence of shared neural representations for action execution and action observation. The function of such a system, however, has been greatly debated and no definitive conclusion has been drawn at present. Two opposing views have dominated the literature over the last decade, with one in particular gaining great favour. In this view, the shared representations for action execution and observation are underpinned by the neural AON, which according to many, has evolved as a consequence of increasing social communication and social dependency and the requirement to understand the behaviour and intentions of conspecifics. The evolvement of such a common-coding system is argued to have brought about the adaptive advantages of gaining insight into the internal states of others (Hurley, 2008; Rizzolatti & Craighero, 2004; Iacoboni & Dapretto, 2006, Ramachandran, 2000); to facilitate empathy with others (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Avenanti, Bueti, Galati, & Aglioti, 2005; Wicker et al., 2003; Leslie, Johnson-Frey, & Grafton, 2004); to detect deception (Sebanz & Shiffrar, 2009); as well as to predict the actions of others (Blakemore & Frith, 2005), or their goals and intentions (Gallese & Goldman, 1998; Iacoboni et al., 2005) for increased chances of survival (for instance, for a timely flight response), as well as to coordinate our own actions with others (Gergely & Csibra, 2008; Miall, 2003).

1.2.2 A system developed through experience

In challenge to this approach, some authors have disputed the notion of such shared representations having evolved explicitly for social understanding. Instead, they contend that this function has developed through means of Hebbian learning (Hebb, 1949), with mirror neurons coding for both action execution and observation as a consequence of visual action input largely co-occurring with motor output (Keysers & Perrett, 2004). On a similar line, some authors suggest the shared circuits have developed by means of associative learning (Cook, Press, Dickinson, & Heyes, 2010; Heyes, 2001; Heyes, 2010), with the subtle difference that not only contiguity but also contingency is explicitly specified as necessary for mirror neuron formation.

1.2.3 A self- or other- oriented system

Other than the two theories differing with regards to how they suggest such a common-coding system (MNS / AON) could emerge, there is another key distinction between them: The first theory claims the system has an inherently social function, enabling us to effectively interact with others. The latter theory posits that the social advantages of shared representation have in fact emerged as an epiphenomenon of processes evolved for the control and monitoring of one’s own behaviour (Brass & Heyes, 2005; Miall & Wolpert, 1996; Wolpert & Flanagan, 2001). One argues that the principal function is social or other-oriented (e.g. Iacoboni et al., 2005; Oberman & Ramachandran, 2008; Schütz-Bosbach, Mancini, Aglioti, & Haggard, 2006), whilst the second argues for a function that has a ‘self’ focus, potentially facilitating fine-grain visuomotor control (Brass & Heyes, 2005; Wolpert & Flanagan, 2001).

1.2.4 Internal models of action

At the heart of this second hypothesis are forward (predictive) models of motor control. It is claimed that the motor system uses two forms of internal model (Miall, 2003; Wolpert & Ghahramani, 2000): Inverse models project a relationship between intended goals and the motor commands necessary to meet those goals. It transforms representations of location of object and limb location into a motor command to be able to reach for the object. In contrast, forward models project a relationship between the motor command and the estimated (predicted) consequences of an action in terms of sensory feedback and environmental consequence (object is lifted). First posited by Helmholtz (1867) and Sperry (1950), and developed over recent years by researchers in relation to action observation, the notion of forward models of motor control argues that our central nervous system (CNS) utilises a copy of the motor command acting on our muscles – an *efference copy* – to predict the consequences of our motor commands. That is, the CNS predicts how our body will move as a response to a motor command, or how our bodies and environment will interact. To do so, an internal forward model is developed that simulates both our motor behaviour and the environmental dynamics (such as tool dynamics), generating predictions of the relationship between our actions and their consequences. These internal forward models are said not to be fixed, but are learned or trained through experience, with the internal forward model being updated based on *prediction errors* – the discrepancy between the expected outcome and the actual consequence experienced (Wolpert & Flanagan, 2001).

1.2.5 Uses of motor prediction

This prediction error is essential in visuomotor and sensorimotor control. If a cup is not lifted from a table as expected, it may suggest the cup is heavier than expected. In response we react by tightening our grip and engaging our muscles more (Wolpert and Flanagan, 2001). Motor prediction can have several uses in sensorimotor control (Miall & Wolpert, 1996; Wolpert & Flanagan, 2001). For instance, state estimation can be derived. When making a movement we experience sensory signals as a consequence of our actions (reafferent signals). These can be used in estimating our position and velocity with regards to the environment. However, these reafferent signals experience delays as a consequence of neural conduction, receptor transduction and central processing, and can also be distorted by noise (Graf et al., 2007; Miall, 2003; Wolpert & Flanagan, 2001). Utilising predictions based on efference copies of motor commands can overcome these issues related to processing sensory signals. Motor prediction can also be used for sensory confirmation and cancellation, whereby sensory effects and changes resulting from our movements are attenuated to enhance more relevant sensory information. In addition, this same mechanism can alert us as to whether an experienced movement was internally or externally generated, by retrieving information about whether the predicted and actual feedback are congruent or incongruent.

This motor prediction system appears essentially to be one evolved for or developed for fine grain visuomotor and sensorimotor control of one’s own actions. Some authors have suggested that these forward (predictive) models may also be used in prediction of other’s actions (Blakemore & Frith, 2005; Grush, 2004; Prinz, 2006; Wolpert & Flanagan, 2001). However, any social advantages derived from the system may have occurred as a by-product of the system monitoring one’s own actions.

1.2.6 The Mirror Neuron System in a predictive coding framework

Kilner, Friston, & Frith (2007) have proposed an account of the workings of the MNS under the framework of forward / generative models, and in doing so suggest that this may contribute to intention understanding in others.

In line with Hamilton & Grafton (2007), they propose that actions can be described at four levels: (1) the intention level, which refers to the long-term goal of an action; (2) the goal level that describes short-term goals necessary to achieve the long-term intention; (3) the kinematic level that describes the shape of the hand and the movement of the arm in space and time; and (4) the muscle level refers to the pattern of muscle activity required to execute the action. In the predictive coding account of the MNS, each level of the hierarchy of actions is proposed to employ a generative model to predict representations in the level below, e.g. to produce a sensory representation at the kinematic level of an action given the information at the goals or intentions level. The prediction is conveyed to the lower level and compared to the representation/input received and a prediction error is produced, which in turn is conveyed back to the higher level and the representation of sensory causes adjusted, in turn modifying the prediction (Kilner et al., 2007).

For action observation the essence of this approach is that, given a prior expectation about the goal of the person we are observing, we can predict their motor commands. Given their motor commands we can predict the kinematics, based on our own action system and experience. The comparison of the predicted kinematics with the observed kinematics generates a prediction error. The inverse of this, the recognition model, allows the inference of the cause or goal of the action given the visual input.

The prediction and error signals are said to be conveyed via reciprocal patterns of connectivity which have been shown between premotor areas and inferior parietal lobule (Iacoboni et al., 2005; Rushworth, Behrens, & Johansen-Berg, 2006). Their predictive coding account of the MNS is based on minimizing prediction error through these reciprocal interactions. The MNS as a predictive coding framework is depicted in Figure 1.2.

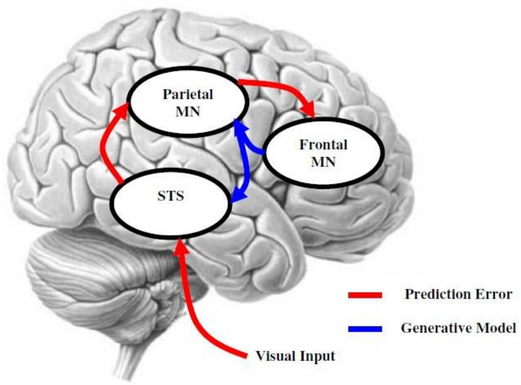

Figure 1.2. A Predictive Coding Account of The Mirror Neuron System. Adapted from Kilner et al. (2007).

It seems therefore that there are arguments for the same motor prediction system or the hMNS/AON to be used for the monitoring of one's own actions, but also for the monitoring of others' actions. Whichever function the system developed or evolved for, there is a large body of research suggesting we do anticipate and predict human as well as non-human dynamics in our environment, and that we possibly draw upon the motor system as a means to do so.

1.3 Visual perception as a predictive process

Predicting the dynamics of our environment is essential for us to respond with an appropriate movement within an appropriate time. For instance, in sport we see predictive estimations being performed regularly, as players make judgements about necessary movements and strength of motion to aim to return a serve in tennis, or prevent a goal in football. Action perception thus involves the complex integration of visual information about exogenous dynamics (objects, tools, the environment), including the velocity of movement, direction of movement, the object's material or weight to estimate impact consequences (you might not instigate a rapid duck for cover when a paper aeroplane flies towards you, as you would a flying golf ball), together with information about the dynamics of our endogenous system (our kinematic capabilities).

Similarly, the ability to anticipate, or predict, others people's actions may be crucial to allow us to engage in collaborative and cooperative activities. Coordinated activities with others, such as moving furniture together, rely to some extent on an expectation of how the other person is likely to pick up their end of the table, and their restricted movement or kinematics given the weight of the object. Likewise, the ability to generate predictions about others' actions is crucial to enable us to expedite our own response to them – for our actions to coincide, cooperate, or compete.

As such, visual perception is argued to be a predictive activity (Graf et al., 2007; Prinz, 2006; Wilson & Knoblich, 2005), and there is much evidence to date to suggest that motion perception is indeed so. Visual prediction has been demonstrated in behavioural and neuroimaging studies through various paradigms, as the following sections highlight.

Behavioural data

The occurrence of *representational momentum* is a task phenomenon that is postulated to demonstrate perceptual prediction activity. Representational momentum is the phenomenon whereby video images depicting motion, or static images implying motion, are perceived as being further forward in their trajectory than is presented; that is, the trajectory of the movement is extrapolated forwards in time and/or space. The paradigm generally employed involves presentation of images of an object or person in motion (induction phase), followed by a brief retention period, followed by a final (probe) image. Participants are required to judge whether the probe image depicts the object/person at the same or different location as the final inducing image. Observers are more likely to respond 'same' when the probe is further forward in the direction of movement. Representational momentum has been demonstrated for static images inferring motion, such as a rocket launching, and a person jumping from a wall (Bertamini, 1993; Freyd, 1983; Reed & Vinson, 1996); for movements in different directions (Hubbard & Bharucha, 1988); for images of non-biological motion (Freyd & Finke, 1984), for video images of full body biological motion in point light actors (PLA) (Jarraya, Amorim, & Bardy, 2005), and for motion in complex scenes (Thornton & Hayes, 2004). Researchers have suggested that the representational momentum phenomenon reflects the anticipated direction of movement, rather than the perceived actual movement (Hubbard & Bharucha, 1988), and as such reflects predictive processes in perception. Indeed, this is supported by studies demonstrating that increasing the uncertainty about object behaviour can reduce and even eliminate the representational momentum effect (Kerzel, 2002). This in turn suggests that experience of an object's behaviour and a level of certainty about the behaviour is necessary.

This trajectory extrapolation effect has also been reported in priming studies. For instance, Verfaillie & Daems (2002) presented participants with a priming phase in which they observed pairs of animated characters performing an action and were asked to judge if they were the same or different actions. In the experimental phase, static images of postures were presented that depicted poses that participants (i) would have seen in the priming phase if an animation had continued longer, (ii) would have seen in the priming phase had the action sequence started earlier, or (iii) was not related to an action in the priming phase. Participants had to determine whether the static test posture was a possible/impossible pose. Facilitatory priming effects were only observable for test postures which had been primed with an action that would have resulted in the test pose had the animation continued longer. Such trajectory extrapolation effects have been supported by other priming studies involving point-light actors (Verfaillie, 1993), rotating two and three-dimensional objects (Kourtzi & Shiffrar, 1997, 1999) and rotating human body movement, but not for actions violating normal human bodily movement (Kourtzi & Shiffrar, 1999).

On similar lines, the flash-lag effect (Nijhawan, 1994), whereby unpredictable effects, such as a brief flash, are generally perceived as trailing behind predictable or continuous events, and likewise, the Fröhlich effect (Fröhlich, 1923; Müsseler & Aschersleben, 1998), whereby the *onset* of rapid moving objects is perceived further forward in the object's course, have both been reported as evidence of the predictive quality of human visual motor perception (Nijhawan, 1994; Fröhlich, 1923; Müsseler & Aschersleben, 1998; Thornton & Hubbard, 2002).

Eye movement data

Studies examining eye-gaze and saccadic movement have also provided support for the predictive property of action perception. In visually-guided action, proactive eye gaze is essential for coordination, planning and control of movement (Johansson, Westling, Bäckström, & Flanagan, 2001; Land & Furneaux, 1997) (Land & Furneaux, 1997; Johansson, Westling, Bäckström, & Flanagan, 2001). It has been hypothesised that if action perception of others involves direct matching of motor representations, the eye gaze produced when observing someone perform an action should equate to the pattern produced when executing an action oneself. Flanagan & Johansson (2003) found that this was indeed the case; when observing another person perform a block stacking task, eye gaze was very similar to the eye gaze-hand coordination produced when performing the same task themselves, and importantly, it maintained a predictive rather than reactive pattern. This was also found for both predictable and unpredictable actions (when the target block of choice was not known in advance) (Rotman, Troje, Johansson, & Flanagan, 2006). Predictive eye gaze movements have also been observed during the pursuit of targets that are transiently occluded, with eye movements demonstrating anticipatory saccades to the target reappearance position (Bennett & Barnes, 2003, 2004; Madelain & Krauzlis, 2003; Orban de Xivry, Bennett, Lefèvre, & Barnes, 2006), and have also been observed in 12 month old infants for goal oriented actions (Falck-Ytter, Gredebäck, & von Hofsten, 2006). The studies suggest that when observing someone perform an action, eye motor programmes are produced that are directed by motor representations for action execution, in that they are proactive and predictive, not reactive, which would suggest that, even when observing another, we use eye gaze in a manner appropriate for motor planning and control.

The occlusion paradigm

The occlusion paradigm is another method that has been widely used of late to explore simulation and prediction of action. Generally, these studies involve the presentation of the beginning of an action sequence, which is then occluded from view by the presentation of a blank screen or occluding object, followed by a static test posture which depicts a position in the sequence that is earlier or later than (or in some studies coherent with) the true action posture had the action continued during the occlusion. Participants are required to respond as to whether they believe the test posture is a depiction of an earlier or later action position in the sequence compared to what would be expected. Findings from some such studies suggest that motion perception and simulation processes are highly accurate and run in real time with the actual action being observed (Graf et al., 2007; Parkinson, Springer, & Prinz, 2011). Other studies, however, have demonstrated a lag error in simulation, suggesting simulation processes run with a constant time delay when observing action (Prinz & Rapinett, 2008; Sparenberg, Springer, & Prinz, 2012). Occlusion studies would thus imply either that anticipatory mechanisms of future action are very precise, or that we do not anticipate forthcoming action. Either way, there is a lack of converging evidence from occlusion paradigms that action perception involves the extrapolation of the moving target forwards in its trajectory. However, the varying findings may be due to issues with the stimuli used as shall be discussed in the subsequent section, and which this thesis in part intends to address.

1.4 Timing of action simulation / action prediction. Does prediction of actions involve real-time simulation of action?

Researchers utilising the occlusion paradigm have been interested in examining whether action perception involves pure trajectory extrapolation of visual/perceptual representations, or an internal simulation of the perceived motor movements through recruitment of motor representations developed from one's motor experience. Other researchers have used the occlusion paradigm to examine the detail of the spatial and/or temporal aspects of human motion perception. The majority of these studies have employed point-light actors (PLAs) whereby motion is depicted by moving dots on a high contrast background, which represent the position of the head and major joints of the body (Johansson, 1973). Graf et al. (2007) used PLAs in an occlusion paradigm to *implicitly* examine timing of action simulation to avoid effects induced by task instruction. Human PLAs conducting various whole-body actions were used as stimuli[2]. The test posture was rotated in depth/space and participants had to respond whether the posture was a continuation of the action in the same or different orientation (at any point in time). Error rates and reaction times (RTs) increased with increasing distance between occluder duration and rotation distance and performance was better overall when the test posture depicted a position that was temporally coherent with the occlusion duration. From this finding, Graf et al. (2007) concluded that action simulation and prediction processes are remarkably accurate in terms of timing and suggested the results provide evidence for ‘real-time’ action simulation.

Another implicit examination of timing of action simulation using an occlusion paradigm was employed by Parkinson, Springer, & Prinz (2011). In their study, PLAs were observed briefly before being occluded and subsequently re-presented embedded in “TV snow” noise. Test motion post-occlusion was also manipulated whereby it was temporally coherent or incoherent with the motion if it had continued during occlusion. The dependent measure was the ability to detect PLA reappearance in various levels of noise. When the re-appearance of the action was coherent with the occlusion period (i.e., the action was where it would have been if it had continued), detection was better than when it mismatched. This again supports the notion that simulation processes operate in real time, and in so being, facilitate perceptual processes by providing current state information (current expectations) about action percepts that are visually degraded or occluded.

---

[2] Nine actions were used: Lifting an object from the floor, pushing something away, knee-bends, waving both arms, standing up from a chair, embracing someone, putting on boots, bowling, throwing a ball overhead with both arms.

These two studies primarily wished to test the real-time simulation hypothesis. However, they were not concerned with the timing detail to determine exactly how accurate simulation mechanisms are. Both Graf et al. (2007) and Parkinson et al., (2011) used a minimum temporal offset between occluder time and post-occlusion test posture of ±300ms. These conditions would not have sufficient temporal resolution to determine the fine grain temporal detail of simulation, or to determine whether simulation mechanisms run with a small temporal gain (suggesting an anticipatory/forward prediction process in accordance with representational momentum studies), or indeed a lag, with regard to the real observed action.

Sparenberg, Springer, & Prinz (2012) conducted three experiments to examine exactly this. As in previous experiments, they used the occlusion paradigm first created by Graf et al. (2007) and PLAs to depict actions[3]. However, they employed psychophysical measures to interrogate the temporal detail of action prediction/simulation mechanisms, and *explicitly* asked participants to judge the temporal coherence of the motion posture post-occlusion with the expected posture, given the occluder duration. Participants were required to state whether the test posture depicted a point in motion that was too early or too late. The important difference in this study was that they temporally manipulated the test posture post-occlusion to create thirteen temporal offset conditions, with just 33ms difference between them. Such conditions provided much higher temporal resolution than the Graf et al. (2007) or Parkinson et al., (2011) studies, allowing them to directly examine the time course and accuracy of action simulation.

Sparenberg and colleagues found a negative point of subjective equality (PSE) for both experiments 1 (300ms occluder) and 2 (500ms occluder) of -23ms and -26ms respectively, which differed significantly from zero. From this, the authors could conclude that action simulation takes more time than the real action itself. With no significant difference between the temporal errors for the two experiments with different occluder durations, the authors further concluded

---

[3] Five action sequences were used: lifting something from the floor, leapfrogging, pushing something away, waving with both hands, bowling.

that this was evidence for an initial time delay that remains constant (a stable intercept effect) during action simulation, possibly due to switching between perception and simulation processes. However, despite such a finding intuitively suggesting that action perception does not involve a predictive process, they did not rule this out. Instead, the authors offered an explanation in terms of anticipation of progress of action occurring as people skip the unimportant elements of an action, and focus on main parts of an action (i.e. the goal). The authors suggest that in their study, participants are required to simulate the full action in detail (including unimportant elements), which may have led to a temporal cost in action simulation.

Although Sparenberg and colleagues provided a means by which to examine the temporal detail of action simulation and potential prediction mechanisms, their findings and conclusions appear somewhat contradictory. This said, their conclusions do not detract from the clear observation that action simulation took longer than the real observed actions, which is an opposite result from that found in a variety of studies examining action prediction. That is, their findings do not correspond with studies suggesting perception is a predictive process, whereby we anticipate behaviour ahead of its occurrence (e.g. Freyd, 1983; Jarraya et al., 2005; Thornton & Hayes, 2004).

However, these somewhat confusing and contradictory results may be due to reasons pertaining to the choice of stimuli used. Firstly, previous studies concentrated on whole-body complex actions, combining transitive and non-transitive actions without a context. Given that many single cell and neuroimaging studies would indicate that the MNS/AON is particularly activated for goal-directed/object-oriented actions(for monkey mirror neuron firing: Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Iacoboni et al., 2005; Umiltà et al., 2001; for human AON activation: Rizzolatti et al., 1996; Johnson-Frey et al., 2003; Shmuelof and Zohary, 2005), it would be advantageous to examine the temporal accuracy of prediction related specifically to transitive actions. Sparenberg et al. (2012) and other studies may have been flawed by a lack of goal/intention in their stimuli, which cannot in these cases be evoked to simulate the action (Gallese & Goldman, 1998; Jeannerod, 2001). Secondly, previous studies have used action stimuli with varying degrees of familiarity to participants. Activities such as throwing a basketball or leapfrogging, as used in these previous studies, may arguably be recently *un*familiar to participants. The stimuli in the Sparenberg et al. (2012) and Graf et al. (2007) studies therefore do not differentiate between actions for which participants can and cannot easily draw upon their own motor repertoire to enable simulation/prediction mechanisms. Thirdly, researchers have observed that showing less information post-occlusion degrades performance in occlusion tasks (Parkinson, Springer, & Prinz, 2012). As each of the occlusion studies described present a simple static image post-occlusion on which to base a decision, it might be argued that performance accuracy is not as would be expected if action were allowed to continue until its completion.

It is on the foundation of these first occlusion studies from Prinz's lab that the experiments of Chapters 2 and 3 of this thesis are based. The present research in part aims to address these and other issues relating to the described occlusion studies in order to examine temporal features of action simulation and prediction.

1.5 Neural substrates of action prediction/action simulation

Several studies demonstrate at a neural level that action perception has predictive properties, and that the motor system may be involved in this predictive mechanism. Evidence for the predictive properties of action perception comes from a particularly interesting single cell study in macaques that provided evidence that there is a subset of 'mirror neurons' that respond selectively to transitive actions even when the final part of the action is hidden from view (Umiltà et al., 2001). Whilst observing an experimenter reach and grasp an object, these neurons within F5 continue to fire and increase their discharge once the experimenter's hand disappears behind an occluder, reaching their peak discharge intensity at the point when the object would be grasped, even though this was not visible. The study provided evidence at the single cell level that predictive or anticipatory mechanisms were operating during observation of goal-directed actions.

As the human homologue of area F5 in monkey, the human premotor cortex has been theorised to play a role in the simulation and prediction of observed actions. As such, the role of the premotor cortex in prediction has been the subject of much research over recent years. Neuroimaging research in human participants has provided consistent support for the involvement of the premotor cortex in action prediction. In an EEG study, Kilner, Vargas, Duval, Blakemore, & Sirigu (2004) also observed neuronal activity prior to the start of an action being observed. They found that the readiness potential, an electrophysiological marker of motor preparation, was present also when observing someone else's hand reach and grasp an object. Moreover, when the onset time of the action was predictable, the readiness potential amplitude increased prior to the observed action onset. The authors postulate from this that the readiness potential is not simply a marker of motor preparation, but one of motor prediction, with the excitation of the motor system prior to observed movement potentially serving to facilitate our own timely response to others.

Prediction or anticipation of forthcoming observed movement has also been demonstrated with fMRI. Stadler et al., (2011) aimed to determine the role of the premotor cortex with regards to its potential predictive function compared to the representation of action in general (ie. holding a mental representation of an action in mind). They employed an occlusion paradigm with four conditions: a 'prediction' condition, in which participants indicated whether the action continued with coherent timing following the occlusion period; a 'freezing' condition involved a static matching task, whereby participants held in mind the final image pre-occlusion and indicated whether the video post-occlusion continued from the same point in time. These two conditions were contrasted against two other conditions using the same stimuli: a 'detection' condition, in which participants indicated whether the action without occlusion was smooth or disrupted; and a ‘counting’ condition, in which participants counted the number of occlusions per video clip disregarding the action. The right pre-SMA was active for conditions relating to maintenance of an internal reference (both prediction and static matching, compared to detection and counting). Activation specific to the prediction condition (contrasted against the static matching condition) was found in the left dorsal premotor cortex (PMd) and left pre-SMA. This prediction condition required a dynamic transformation of the stimuli over time - a simulation process - compared to the mental maintenance of an action representation, as in the ‘freezing’ condition. The authors thus concluded that PMd and pre-SMA activation is specific to simulation and prediction processes. This was supported by a subsequent study (Stadler et al., 2012) involving repetitive TMS to the left PMd and to the vertex during observation of action that was transiently occluded. Applying TMS at the start of the occlusion period produced more prediction errors (increased error rates) than TMS over the vertex, with time-coherent trials being incorrectly judged as incoherent.

Other studies have similarly found premotor cortex involvement in prediction processes when observing others’ actions, but implicate the more ventral PMv/IFG pars opercularis rather than the dorsal region. Ramnani & Miall (2004) examined BOLD activation that was time-locked to the instructional cue in a visuomotor stimulus-response (finger movement) association task, thus examining anticipation of action. This was conducted for the participant’s own action execution preparation, as well as a third person’s (a real person known to the participant) action. PMd activation was observed for the first person condition, but not for third person action anticipation. Instead, areas associated with attribution of mental states to others were activated, including the paracingulate cortex and superior temporal sulcus, as well as the PMv (identified as Broca’s area in the study). Whilst the activation of motor areas for third person action prediction provides support for the simulation theory of action observation/prediction, authors suggest that the fact that separate sub-systems of the premotor cortex are activated for the different conditions suggests that simulation theory alone is insufficient to explain prediction of others’ actions; we may also use mental imagery of others' actions and the simulation of our own actions to aid the prediction process. In this study, however, no observed actions of a third person were visible. The participant was required to imagine a third person in another room responding to the cues. Therefore, the PMv activation may be more attributable to the additional mentalising required for the task, rather than action prediction for others per se. This said, ventral premotor cortex/IFG pars opercularis activation has been associated with action prediction and simulation studies relating to the anticipation of handwriting movements in a PET study (Chaminade, Meary, Orliaguet, & Decety, 2001).

The premotor cortex has consistently been associated with prediction tasks in general, even for abstract stimuli that cannot be mapped onto the human body. For instance, ventrolateral premotor cortex activity has been observed for prediction of geometrical figure size (Schubotz & von Cramon, 2002) and geometrical figure event sequencing (Schubotz & von Cramon, 2004) in serial prediction tasks, for auditory rhythm prediction (Schubotz, von Cramon, & Lohmann, 2003) and pitch prediction (Schubotz & von Cramon, 2002), and has been associated with prediction of event dynamics in general (Schubotz, 2007). Thus premotor areas would appear to be involved in predictive tasks in general, not solely action perception. It is suggested that the type of event (biological/non-biological, hand/finger/limb, visual/auditory) is mapped somatotopically along the ventral-dorsal axis of the premotor cortex (Buccino et al., 2001; Schubotz & von Cramon, 2002, 2004; Stadler et al., 2011), thus explaining differences in the literature with regards to dorsal and ventral premotor cortex activation for action prediction. However, it is further argued that the prediction of any sequentially organised information is enough to elicit premotor cortex activity, with abstract information type being mapped along the PMC in a somatotopic manner, represented by codes of their 'distal' features (Schubotz & von Cramon, 2004; Schubotz, 2007; Hommel et al., 2002).

Despite the literature suggesting the involvement of distinct ventral or dorsal areas of the premotor cortex in action prediction, further studies have been able to converge the opposing findings. As such, research provides consistent support for the involvement of the premotor cortex in action prediction, with the precise location along the premotor cortex likely relating to the body part involved in the action perceived. The PMv/PMd may therefore have a specific predictive function within the context of the action observation network. However, what is yet unclear is the role of the premotor cortex in anticipatory / predictive action perception of self-generated as opposed to other-generated actions, or indeed whether the same subsection of the premotor cortex is recruited during the prediction of these two types of action. Given the debate surrounding the etiology of the putative action-observation network (whether it evolved for social purposes or for monitoring of one’s own actions), it would seem that a crucial line of investigation would be to examine shared representations and the role of the premotor cortex in relation to the prediction of self-generated and other-generated actions.

1.6 Dissociating systems for observation of self versus other

Very few studies have attempted to disassociate systems potentially serving a self-oriented function, as opposed to a social other-oriented function. Several neuroimaging studies have, however, provided evidence for different neural correlates of self-related and other-related representations, which would suggest differing mechanisms underpinning them.

1.6.1 Neural correlates of self and other

Neuroimaging studies employing fMRI have examined judgements of action attribution; i.e., how we distinguish actions generated by ourselves and those of other people. The ‘sense of agency’ - experiencing oneself as the cause of an action - is intricately related to self-ownership (Gallagher, 2000), which is itself related to coherent postural representation of visual input with the internal body schema (Costantini & Haggard, 2007). Studies have demonstrated the involvement of the anterior insula in perceiving movement as self-generated (Farrer & Frith, 2002), imagining oneself perform an action compared to imagining someone else perform the action (Ruby & Decety, 2001), and hearing one's own voice compared to that of another (McGuire, Silbersweig, & Frith, 1996). Attributing another person to the cause of an action, however, involved greater activation in the right inferior parietal cortex (Farrer & Frith, 2002; Spence et al., 1997). Similarly, greater activation in the inferior parietal lobule (IPL) was reported when imagining someone else perform an action, compared to imagining oneself (Ruby & Decety, 2001), and when hearing the voice of another person compared to one's own (McGuire et al., 1996). Farrer and colleagues (2003) found that activity in both the IPL and insula was modulated by the degree of discrepancy between the movement executed by the participant and the visual feedback received on screen, with less discrepancy associated with more activation in the insula and reduced activity in the IPL, and more discrepancy having the opposite pattern of covariance. The degree of involvement of these two areas would therefore appear to be associated with the extent to which a person attributes an action to themselves or another (Farrer et al., 2003).

Several neuroimaging studies have also demonstrated that there are distinct neural representations for viewing action in different perspectives, which are arguably involved in distinguishing self from other (Chan, Peelen, & Downing, 2004; David et al., 2006; Ehrsson, Spence, & Passingham, 2004; Jarraya et al., 2005; Saxe, Jamal, & Powell, 2006). The medial prefrontal cortex (MPFC) has been widely associated with a sense of self (David et al., 2006; Gusnard, Akbudak, Shulman, & Raichle, 2001). Similarly, the first person perspective has been associated with increased activity in somatosensory areas, unlike the third person allocentric perspective (Jackson, Meltzoff, & Decety, 2006; Ruby & Decety, 2001; Saxe et al., 2006).

In summary, somatosensory areas, MPFC, insula and other limbic areas have robustly been reported to relate to sense of agency and self-representation. In contrast, the inferior parietal cortex, and in particular the IPL, has frequently been associated with representation of 'other'.

Several studies have therefore highlighted potential dissociable correlates, pathways and possible mechanisms underlying perception and interpretation of one's own and others' actions.

1.6.2 The importance of perspective

Several studies have demonstrated that human action stimuli in an egocentric perspective can create an affinity with the limb being observed or greater correspondence between the limb observed and one's sense of self. Botvinick and Cohen (1998) were the first to describe the 'rubber hand illusion' (RHI), whereby synchronous stroking of a seen artificial rubber hand and the participant's own occluded hand shifts the perceived position of their own hand toward that of the rubber hand. Whilst the visual-tactile integration is powerful in eliciting the RHI, it necessitates the posture of the rubber hand to equate that of the participant's; the perceptual drift only occurs when the rubber hand is in the egocentric perspective (Costantini & Haggard, 2007; Ehrsson et al., 2004; Pavani, Spence, & Driver, 2000; Tsakiris & Haggard, 2005). The egocentric representation is crucial in matching the rubber hand to the participant's internal body representation, or body schema, which creates a sense of body ownership with the false hand. The egocentric postural coherence of the false hand allows it to be assimilated with, rather than discriminated from the self (Costantini & Haggard, 2007). The rubber hand illusion and neuroimaging studies thus highlight the importance of perspective in associating action with self and dissociating action from other agents. The manipulation of perspective may therefore be a useful tool to examine the function and the shared representations of perception and action.

Despite the extensive neuroimaging data suggesting different neural representations for self- versus other- actions, many of the studies discussed in section 1.3 have examined action observation, action simulation and/or prediction utilising presentation of stimuli that can only be interpreted as others performing an action. They use visual stimuli of actions performed with the actor facing towards the observer or sidelong in a *wide shot*, or simple limb movements in a *cut-in* shot again from a side angle. Such presentation fails to disentangle differing mechanisms that may underpin action observation and related cognitive processes for different perspectives, which have been associated with self or other to differing degrees (Oberman & Ramachandran, 2008; Chan et al., 2004; Ehrsson et al., 2004; Jarraya et al., 2005; Saxe et al., 2006). If conclusions about the function of shared representations are to be drawn with regards to predictive mechanisms for self or for social purposes, it is essential to attempt to disentangle actions and facilitatory mechanisms relating to self and other. Many of the studies discussed in section 1.3 are ambiguous with respect to these potentially differing processes.

One method to attempt to disentangle processes related to self and others in action interpretation and prediction tasks is to utilise stimuli presented in the first person (egocentric) and third person (allocentric) perspectives. This logic was postulated by Oberman and Ramachandran (2008), who suggest any shared representation would have emerged from associations built on visual feedback. The assumption is that egocentric presented stimuli closely resemble the actual visual feedback of performing an action oneself, whereas allocentric stimuli capture the visual input of observing someone else. As mentioned previously, neuroimaging studies have demonstrated distinct neural representations for viewing actions in different perspectives, and are involved in distinguishing self versus other agents of the action (e.g. David et al., 2006; Ehrsson et al., 2004). If a mechanism has emerged for the monitoring of one’s own actions, the prediction of consequences of action would be most effectively achieved in the first person perspective. If the mechanism has emerged for social reasons, action observation would be most efficient in the third-person perspective.

1.6.3 The effect of perspective in cognitive tasks

Visual stimuli presented in egocentric and allocentric perspectives have therefore been used in an attempt to disambiguate between self- and other-related processes. Stimuli in an egocentric perspective are thus photographed or filmed from the perspective of an observer looking at their own body, whilst allocentric images are created from a body perspective that is inaccessible to the observer and thus only attributable to looking at someone else's body. The sections that follow outline some of the behavioural, MEP, fMRI and EEG/MEG studies that have explicitly examined effects of perspective on cognitive tasks and neural activity.

Behavioural data

Conson, Aromino and Trojano (2010) examined whether handedness and visual perspective can modulate a person's ability to discriminate between self and other. Participants were explicitly asked to recognise hands presented in ego- and allocentric views as belonging to themselves or to another person. Results demonstrated that participants were faster to recognise their own hand in the egocentric perspective, and faster to recognise others' hands in the allocentric perspective. In addition, in the egocentric perspective, participants were significantly faster at recognising their self dominant hand compared to non-dominant hand. There was no difference between recognising the right or left hand of others' in the egocentric view. In contrast, in the allocentric perspective, participants were significantly faster at recognising others' hands that were non-dominant to their own (in right handers, recognising other's left hand; in left handers, recognising other's right hand), with no difference between self left or right hand in this perspective.

The findings suggest two things: One, that body specific information (perspective and handedness) is important in sense of ownership and self-other discrimination; and two, that peri-dominant hand space is the preferred reference frame to distinguish other from self (Conson et al., 2010). Leading on from this, we might also suggest, in experimental studies examining action observation mechanisms, that mirror-matched (specular) limb actions in the allocentric perspective would be preferable over the use of anatomy-matched actions, as the latter would have an additional processing disadvantage. Further studies have demonstrated that specular correspondence also applies to action observation and action imagery (Alaerts, Heremans, Swinnen, & Wenderoth, 2009; Conson, Mazzarella, & Trojano, 2009).

Examining perspective in isolation and its influence on representation of action, Anquetil and Jeannerod (2007) found no difference in action representation performance corresponding to first- and third-person perspective action observation. Their behavioural study involved participants mentally imagining grasping actions either from a self-generated (egocentric) perspective or other-generated (allocentric) perspective, as if observing someone else facing them perform the same actions. Utilising a mental chronometry method, they found that the time to complete actions was highly similar when imagined in the 1PP compared to 3PP. Furthermore, the time-to-complete-action difference between the easy-grasp (natural hand orientation) and hard-grasp (unnatural hand orientation) conditions was very similar between the two perspective conditions. Authors concluded from the study that the results demonstrate shared representations for self- and other-generated actions.

However, there is a flaw in the Anquetil and Jeannerod (2007) study. For the allocentric perspective condition, participants were simultaneously presented with images whilst instructed to imagine the action. The static image comprised the right hand of the ‘other’ being used to grasp an object, i.e. an anatomical limb match. However, as discussed, several findings (Alaerts et al., 2009; Conson et al., 2010, 2009) would suggest that this type of limb match would be harder to simulate and therefore disadvantageous. If a mirror-matched limb were used for imagining the allocentric condition, timing differences between conditions may be found, and in turn suggest different representations for ego- and allocentric actions.

Findings and conclusions from the Anquetil and Jeannerod (2007) study have been further challenged by other studies. Studies have highlighted the importance of perspective in integration of visuotactile stimuli in somatosensory tasks. Hoover and Harris (2012) found that participants’ sensitivity to detect temporal asynchrony between proprioceptive and visual information was greatest when the visual feedback of finger movements were presented in an egocentric perspective compared to an allocentric perspective, regardless of whether they were mirror-reversed or inverted (Hoover & Harris, 2012). Furthermore, effects of distractor lights in discriminating location of vibrotactile stimulators on the participant's hand were increased when the seen rubber hand 'holding' the distractors was aligned with the participant's own hand (i.e. in an egocentric perspective) (Pavani et al., 2000), thus suggesting advantageous processing in sensory integration for first-person perspective visual displays.

Bach, Fenton-Adams, Tipper (2014) similarly examined visuotactile integration. Developing on a study by Morrison, Tipper, Fenton-Adams, & Bach (2013), they examined participants' detection of tactile stimulation when observing reach-to-grasp and reach-retraction actions towards painful and non-painful objects, in the ego- and allocentric perspectives. It was assumed that sensory expectation of pain would be achieved through prediction by integrating action information (whether the hand touched the object) with the internal model of the object (whether the object was painful). The authors found an interesting three-way interaction, whereby, in the first person perspective (1PP), participants were quickest to detect tactile stimulation to their index finger when observing grasping actions of painful objects. In contrast, in the third person perspective (3PP) only the main effects of object type and action were found, but no evidence that the two are combined to predict the sensory consequence of action. The authors posit that the first-person perspective has privileged access to mechanisms that predict sensory consequences of action and, in turn, conclude that the findings challenge theories of action-observation common coding systems evolving for the understanding of others' actions.

Whilst these studies have examined integration of visuotactile information as a means to examine prediction mechanisms relating to sensory consequences of action, other authors have used purely visual information to explore action consequences. Kelly and Wheaton (2013), for instance, examined the effects of perspective and handedness of the participant as well as the actor observed on determining an action goal (screwing or unscrewing a screw from a panel). In this sense, they examined 'action prediction' by exploring whether the ability for motor resonance/simulation to occur is impacted on in a limb specific way. Left- and right-handed participants were given training in the use of three types of screwdriver before completing an experimental task in which static images of an actor were presented in an egocentric or allocentric perspective, using their right or left hand. Participants had to determine whether the direction of an arrow on the image indicated that the actor was screwing or unscrewing a screw with the tool. Images in the egocentric perspective generated higher accuracy and faster latencies compared to allocentric images. There was no effect of handedness of participant or observed limb of actor performing the action. The results are in line with previous research indicating that action outcomes are best facilitated in an internal (egocentric) perspective, irrespective of hand used, in line with previous studies (Bach et al, 2014; Conson et al., 2010; Hoover & Harris, 2012; Lindgren, 2012; Oosterhof et al., 2012).

An advantage in cognitive task performance for stimuli presented in the 1PP compared to 3PP has also been observed in memory related tasks. Participant's recall accuracy and memory for tasks and task elements have been found to be significantly superior for simulations in the 1PP compared to 3PP (Lindgren, 2012). Similarly, efficient episodic memory encoding and recollection has been found to be dependent on a first person perspective of the spatial relation between the body and the world (Bergouignan, Nyberg, & Ehrsson, 2014).

If we are to follow the premise offered by Oberman and Ramachandran (2008), several of these studies suggest that common coding mechanisms for action execution and observation may have evolved not for social understanding purposes, but rather for the purpose of monitoring one's own actions, and for fine grain visuomotor control. However, despite these studies suggesting privileged cognitive performance for actions and events experienced in the first-person reference frame, evidence from studies recording MEPs has been mixed.

TMS-MEP data

Schütz-Bosbach, Mancini, Aglioti, & Haggard (2006) measured action facilitation effects using TMS when watching an action attributed to another or attributed to oneself. They were able to manipulate the attribution of action of another's hand to themselves or to another using the established rubber hand illusion (Botvinick & Cohen, 1998). This was done by the other's hand being held in front of the participant's body in a 1PP view, whilst their own hand was hidden from view. The stroking of the other's hand was congruent or incongruent with the stroking of the participant's own hand. The authors measured motor facilitation effects while observing random abductor actions of the experimenter's index finger, by recording motor evoked potentials (MEPs) elicited from the participant's right first-dorsal interosseus (FDI) muscle following TMS to primary motor cortex. The authors found no main effect of the rubber hand illusion/ownership (ie. self-synchronous/other-asynchronous stroking) or of the observed action (experimenter action/no action) on cortical excitability. However, there was an interaction between the two, with observed action in the other-asynchronous condition facilitating MEPs of the observer. The self-synchronous condition did not facilitate MEPs compared to baseline (observation of static hand), rather it suppressed MEPs.

The authors claim that the findings suggest that neural mechanisms map the actions of others to corresponding actions on one's own body but, importantly, they argue that the mechanisms do not simply represent the 'other' as a derivative of, or equal to, the self. They argue that theories of shared representation require a common, agent-neutral, representation for one's own actions and for the actions of others. However, Schütz-Bosbach and colleagues found an agent-specific representation in the primary motor cortex, and thus suggest the motor system differentiates between self and other, rather than equating them. Moreover, the authors conclude from the finding that the neural mechanisms underlying action observation are intrinsically social.

Nevertheless, it is key to note that in the Schütz-Bosbach et al. (2006) study, the condition in which action was attributed to an 'other' (asynchronous stroking) rather than self-attributed was seen from the egocentric perspective, that is, with the experimenter's hand held in front of the observer's body. Whilst the authors claim this is a positive advantage to this study as visual input is kept constant across conditions, one might argue that observing another person's arm in front of oneself at such an angle is highly irregular and unlikely. The increased MEP amplitude reported for the 'other'/asynchronous condition may potentially be due to a conflict between the visual and sensory feedback experienced.

Despite evidence to suggest a shared representation system may have developed for the explicit purpose of social understanding, many other studies have found contradictory results to those found by Schütz-Bosbach and colleagues (2006). Maeda, Kleiner-Fisman, & Pascual-Leone (2002) also explored whether hand orientation in an observed action affects the amount of cortico-spinal excitability by measuring MEPs. Overall, MEP facilitation was greatest when participants observed actions in the egocentric perspective compared to the allocentric perspective. The facilitation was specific to the muscle involved in the action being observed, i.e., MEP facilitation was selective to the FDI muscle of the participant when viewing index finger ab-/adduction movement, and selective to the APB muscle when viewing thumb ab-/adduction actions. Furthermore, the authors demonstrated that MEP facilitation depended on the orientation of the actions observed. Both APB and FDI muscle facilitation were greatest during observation of movements in the egocentric (movement away from observer) compared to the allocentric (movement toward the observer) perspective.

Facilitation of MEP size was greater during observation of natural (Away/Egocentric) hand orientations than unnatural (Toward/Allocentric) hand orientations (rotated not mirrored configuration). Under the framework of the mirror system or action observation system having emerged for social benefits (Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010), it would be predicted that observation of actions with a ‘toward orientation’ would result in larger MEPs. However, this was not the case in the Maeda et al., (2002) study, and is in accordance with later studies (Bach et al., 2014; Kelly & Wheaton, 2013; Oosterhof et al., 2012). This said, the allocentric condition in the Maeda et al. (2002) study utilised stimuli of finger actions in a rotated (anatomical match) configuration. This ‘other’ condition could therefore induce a disadvantaged simulation process for this condition (e.g. Conson et al., 2010, 2009). Ideally, a study would compare the egocentric perspective to allocentric perspectives in both the rotated (anatomical match) and flipped (mirror/specular match) configurations.

This is exactly what the study conducted by Alaerts et al. (2009) explored. They investigated the effects of posture, perspective and body side on MEP amplitudes induced during action observation. Participants observed simple wrist extension movements with the left and right hands in both ego- and allocentric perspectives, and with posture congruent (palm down) or incongruent (palm up) with the observer. In accordance with the Maeda et al. (2002) findings, overall facilitation of MEP amplitude size was greatest in the egocentric compared to allocentric perspective. However, this was only the case for right hand movements. For left hand movements, the allocentric condition elicited the greatest motor facilitation of the extensor muscle. The findings thus provide MEP-TMS support for a mirror-match preference over an anatomical-match when observing actions in a third person perspective, as well as support for imitation studies demonstrating a specular preference when imitating (Bekkering, Wohlschläger, & Gattis, 2000). However, the study did not compare MEP amplitude difference magnitudes from baseline across these two conditions to determine whether one perspective (egocentric or allocentric mirror-match) preferentially facilitates motor excitability. In this regard, the findings are ambiguous with respect to whether a shared representation system has a self or other oriented function.

Single cell data

Despite several years of convincing data from single cell recordings in macaques demonstrating the existence of mirror neurons, very few studies have examined whether these mirror neurons continue to have mirror neuron properties when actions are observed from different perspectives. Caggiano et al., (2011) investigated the role of perspective on firing rates of motor neurons in F5 of the macaque whilst they observed actions from 0, 90°, or 180° perspectives. With specific reference to perspective, the researchers found that different neurons showed different tuning profiles across the different perspectives. Slightly more neurons responded specifically to actions observed from a first-person (0°) perspective (n = 27) than a third-person (90° and 180°) perspective (n =15 and n = 18, respectively). Their results demonstrated there are dissociable neural populations for actions observed from first- and third-person perspectives, with a potential bias for stronger coding of actions from a first-person perspective. The study thus tentatively suggests that mirror neurons have a bias for coding egocentric actions, and provides single cell evidence that neural regions involved in action observation may have an egocentric (self-monitoring) function, rather than a social function.

fMRI data

When considering fMRI studies, Oosterhof et al., (2012) have highlighted that the majority of studies that have attempted to examine shared representations for both executed and observed action failed to find evidence for cross-modal action coding (i.e., similar coding across the visual and motor domains) in ventral pre-motor cortex (PMv). Furthermore, importantly, the only study (Kilner, Neal, Weiskopf, Friston, & Frith, 2009) that reported full cross-modal coding in PMv employed stimuli in the first-person perspective only, where actions were seen as if performed by the participant. The Kilner et al. (2009) study therefore did not test a fundamental aspect of the MNS/AON - the ability to generalise one’s own motor information to actions of others observed from the third-person perspective.

Oosterhof and colleagues (2012) attempted to fill this gap in the literature. Using multivoxel pattern analysis (MVPA), where a classifier trained on action can recognize specific actions that are observed, and vice versa, the authors found action-specific cross-modal visual–motor representations in ventral premotor cortex (PMv) for the first-person but not for the third-person perspective. In contrast, more posterior areas in the parietal and occipitotemporal cortex did show cross-modal coding irrespective of perspective. The findings point to a stronger role for these latter regions, relative to PMv, in supporting the understanding of others' actions. These properties are consistent with the results of Caggiano et al., (2011) with regards to observed actions being coded differently for first- versus third-person perspectives, with the former potentially being coded more strongly in PMv (and it's macaque homologue F5).

EEG and MEG data

In EEG and MEG studies, very few studies indeed have explored action observation with regard to perspective of the observer. In fact, only two studies have been found to date that do this. Frenkel-Toledo, Bentin, Perry, Liebermann, & Soroker (2013) examined EEG oscillation suppression during manual action execution as well as action observation from egocentric (facing away, seeing the actor from behind) and allocentric (facing towards the participant) perspectives, with suppression determined relative to a non-biological movement (viewing a rolling ball).

With regards to effect of perspective in the observed action conditions, authors reported that suppression tended to be greatest in the allocentric rather than egocentric condition. However, it is important to highlight that their egocentric condition was not the typical view that would be seen if the observer were making the action. Instead, a third person perspective is used again, with the actor's back to the observer. This is an important distinction. Reduced suppression of EEG power in this condition compared to the allocentric (actor facing the observing) may be due to an interpretation of the visual input of the egocentric condition as being less socially relevant for the observer compared to the allocentric condition. Similar results have been found in MEG studies (Kilner et al., 2006).

Kilner et al. (2006) had previously similarly investigated the effect of perspective on alpha suppression, utilising MEG. They solely examined action observation, and did so in a manner similar to Frenkel-Toledo et al. (2013) in that participants watched videos of actors that were either facing towards the observer (allocentric) or facing way with their back to the observer (egocentric). Actors made simple arm movements, raising their left/right arm to touch/not touch their ear. Alpha suppression in the full (7-12Hz) range was investigated, compared with averaged amplitude of alpha power across conditions as baseline. Authors reported significant alpha modulation at parietal sensors driven by the hand observed moving (left/right) when the actor was facing towards the observer, whilst no suppression was observed in the facing away condition. The authors suggest that these differing patterns may reflect a process modulated by social relevance of the person observed. A person with their back to us has greatly reduced social salience. Kilner and colleagues speculate that the attenuation of alpha oscillations may be modulated by view selective visual input from the STS. They suggest that signals about actions from other people are filtered, allowing only actions of the most socially relevant persons to pass into the 'mirror system' (Kilner et al., 2006).

The perspective or orientation of an observed action has been associated with self- and other-related action, with 1PP actions generally being more easily mapped onto one’s own self representations and related to self-generated action as opposed to other-generated action. The effect of perspective during action observation on behaviour in cognitive tasks and on neural activity appears to be a salient one, with evidence to suggest that 1PP observed actions have a processing advantage. This advantage is supported by single cell recordings demonstrating that more neurons in area F5 code for 1PP actions than 3PP, and fMRI showing that the human homologue of this area, PMv, demonstrates crossmodal visuo-motor coding only for 1PP actions.

Together with the M/EEG studies demonstrating how neural activity is modulated by social salience, which can relate to perspective, it is clear that perspective is an important feature when examining action observation. Given the role of the premotor cortex in relation to action prediction, future lines of research worth pursuing would be to examine the effect of perspective on prediction accuracy for observed actions to determine whether a 1PP advantage exists for timing of prediction accuracy, as the single cell and fMRI studies to date would imply.

1.7 Present work

The present thesis aims to examine prediction accuracy for actions observed in different frames of reference. More specifically, the thesis examines simulation dynamics and spatiotemporal prediction of observed transitive actions. Developing on previous work conducted by Prinz's lab (e.g. Sparenberg et al., 2012), the studies presented employ actions in the first- and third-person perspectives, corresponding to self and other actions. In determining which frame of reference is advantageous for least prediction error, the thesis has the ultimate aim of determining whether the prediction system, and its underlying mechanisms, may essentially be a self-serving system or have a fundamentally social-oriented function.

Each of the studies presented utilise dynamic action stimuli recorded in the first-person (egocentric) and third person (allocentric) perspectives, i.e. actions involving limb movements away from the observer and towards the observer respectively. Unlike the Frenkel-Toledo (2013) and Kilner (2003) studies, the egocentric perspective or first-person perspective (1PP) conditions depict images of actions from an angle that most accurately correspond to what would be seen if the observer had made the action. Whereas, in the allocentric, or third-person perspective (3PP), the actions can only be interpreted as someone else having performed the action.

A summary of the aims of the empirical chapters that follow are outlined below.

Chapter 2: The first empirical chapter of the thesis is a proof of concept chapter to examine the usefulness of an occlusion paradigm and the psychophysics method to examine the spatiotemporal dynamics of action prediction with the type of stimuli intended to be used throughout the rest of the thesis; that is, using simple hand-on-tool transitive action sequences, presented in first person (1PP) and third-person perspective (3PP) frames of reference. Two behavioural studies are described, the second replicating the first, that shed light on the dynamics of simulation and prediction accuracy for such actions in the two perspectives.

Chapter 3: This chapter describes three studies that employ the same methods outlined in the previous chapter to examine the effects of priming the actions to be observed with real world experience. That is, three distinct groups of participants receive real world visual experience of the actions in the 3PP, or motor and visual experience in the 1PP, or motor priming alone without visual input. We discuss the effects of these different experiences on prediction of action sequences in the two frames of reference.

Chapter 4: This chapter describes an EEG study that examines event related potentials (ERPs) that have been associated with expectancy violation to examine neural markers of prediction error. The study employs a similar paradigm to that employed in the prior two chapters, with participants receiving motor priming with visual input prior to engaging in the experiment, and examines these potential neural markers of prediction error at the re-onset of the action post-occlusion. Mean amplitudes of ERPs are examined for actions in the two perspectives for the biological (transitive) action sequences, as well as for non-biological actions (a rolling ball), employed as a control for lower versus upper visual field effects.

Chapter 5. This chapter again employs a behavioural paradigm to examine action prediction in first-and third-person perspectives. However, the two studies presented in this chapter utilise an alternative method to that employed in earlier chapters. Here, a coincidence anticipation task is used that requires the participant to provide a motor response to coincide with the expected moment in time of an action state. Two studies are presented; one without any motor priming of the actions, and the second with motor priming of the actions without visual input, thus allowing a comparison of results with those elicited from earlier experiments using the temporal judgement psychophysics method. The results are discussed in relation to different mechanisms that converging methods of enquiry may draw upon.

Chapter 6. This final empirical chapter in essence is a pilot experiment, providing an initial exploratory study of individual differences in action prediction performance of the coincidence anticipation task. The chapter extends on Chapter 5 in that it examines the results of the two previous experiments in relation to other cognitive and neurophysiological measures from the same participants of time perception, motor control as well as autistic like traits. Using a multiple linear mixed regression model, the chapter determines whether individual differences can be accounted for by the motor experience received or by any of these additional factors.

CHAPTER 2: Spatiotemporal prediction of observed action with a temporal judgement task

2.1 INTRODUCTION

Anticipation of events in our environment is essential for us to respond with an appropriate movement within an adequate time period. For instance, stepping into an elevator or stepping onto a moving escalator require prediction of the upcoming dynamics of the doors or the stairs to estimate the most appropriate time to step forward. In sport, we see this predictive estimation being performed regularly, as players make judgements about the motions necessary to return a serve in tennis, or prevent a goal in football. Likewise, the ability to generate predictions about other people's actions is crucial to enable us to expedite our own response to them – for our actions to coincide, cooperate, or compete.

However, generating a reactive response in a dynamically changing environment poses many problems. It takes more than 100ms for our movements to be updated as a result of somatosensory feedback (Flanders & Cordo, 1989) and approximately 150-200ms based on visual feedback (Miall, Weir, Wolpert, & Stein, 1993; Saunders & Knill, 2003). Yet we are able to generate responsive movements with great temporal and spatial precision. An explanation for this ability is that our nervous system anticipates the future state of our environment or of other people, thus enabling us to prepare a motor response in a timely manner. It is postulated that we are able to do so based on internal forward (predictive) models developed through our visual and motor experiences, which are updated based on prediction errors, i.e. the discrepancy between the expected outcome and the actual consequence experienced (Wolpert & Flanagan, 2001). Such predictive models allow the nervous system to compensate for the delays in sensory feedback due to neural conduction, receptor transduction, central processing, and noise distortion(Graf et al., 2007; Miall, 2003; Wolpert & Flanagan, 2001), and thus facilitate fine grained visuo-motor control. Such models draw on memory of experience, with accurate estimation (least prediction error) occurring when the motion is predictable and familiar.

As such, visual perception is arguably a predictive activity (Graf et al., 2007; Prinz, 2006; Wilson & Knoblich, 2005) and research to date suggests that motion perception is indeed so. For instance, *Representational momentum*, the phenomenon whereby static images depicting or implying motion are perceived as being further forward in their trajectory than is presented, has been demonstrated in a range of conditions from static images inferring motion (Bertamini, 1993; Freyd, 1983; Reed & Vinson, 1996) to video images of full body biological motion in point light actors (Jarraya et al., 2005). Researchers have suggested that the representational momentum phenomenon reflects the anticipated direction of movement, rather than the perceived actual movement (Hubbard & Bharucha, 1988), and as such reflects predictive processes in perception.

Similarly, in other trajectory extrapolation studies, priming effects have been observable when test postures are primed with an action that would have resulted in the test pose had the priming action sequence continued further. Such trajectory extrapolation effects have been reported in priming studies involving animated characters (Verfaillie & Daems, 2002), point-light actors (Verfaillie, 1993) and rotating human body movement, but not for actions violating normal human bodily movement (Zoe Kourtzi & Shiffrar, 1999).

Furthermore, oculomotor studies demonstrate that when observing someone perform an action, eye motor programmes are produced that are directed by motor representations for action execution, they being predictive, not reactive, which would suggest we use eye gaze in a manner appropriate for motor planning and control (Falck-Ytter et al., 2006; Flanagan & Johansson, 2003).

Such a prediction system is said to be underpinned by activity within the action-observation network (AON), a network of brain regions that become active not only when we perform an action ourselves but also when we observe an action being performed by another (Rizzolatti &

Craighero, 2004; Rizzolatti & Sinigaglia, 2010). It is suggested that these shared neural representations employ our own motor system when simply observing an action, allowing us to internally emulate or simulate that action (Vittorio Gallese, 2005; Grush, 2004; Jeannerod, 2001). Several authors claim that this shared representation system evolved in primates as a means to facilitate social interaction (Rizzolatti & Arbib, 1998; Rizzolatti & Craighero, 2004) – the 'adaptation hypothesis' - allowing us to embody others' expressions and actions, and aiding prediction of other people by drawing on our own motor repertoire (Blakemore & Frith, 2005; Vittorio Gallese & Goldman, 1998; Iacoboni et al., 2005).

A somewhat different perspective postulates that the AON functions not as a consequence of evolution for perception and prediction of others. Instead, it suggests execution-observation common coding has resulted through Hebbian or associative learning, as a consequence of visual input largely co-occurring with motor output (Cook et al., 2010; Heyes, 2001; Heyes, 2010) – the 'associative hypothesis'. Advocates of this theory suggest that the system's principal function is not social, in that it does not have the specific purpose of facilitating action interpretation in others. Rather, the system may have a self-related purpose, to facilitate visuo-motor control.

The etiology and function of the AON are thus debated. Despite this, few studies have attempted to disassociate systems potentially serving a self-oriented predictive function, as opposed to a social, other-oriented function. That is, many studies that have examined action observation and/or prediction have used stimuli that can only be interpreted as others performing an action. Such presentation fails to disentangle differing mechanisms that may underpin action observation and prediction for actions from different perspectives, which have been associated with self or other (Chan et al., 2004; Ehrsson et al., 2004; Jarraya et al., 2005; Oberman & Ramachandran, 2008; Saxe et al., 2006). If conclusions about the function of shared representations are to be drawn with regards to predictive mechanisms for self or for social purposes, it is essential to attempt to disentangle actions and facilitatory mechanisms relating to self and other.

One method to attempt to differentiate self and other related processes is to utilise stimuli presented in the first person perspective (1PP, egocentric) and third person perspective (3PP, allocentric), as postulated by Oberman and Ramachandran (2008). If a mechanism has emerged for the monitoring of one's own actions, predicting the consequences of an action would be most effectively achieved (that is, have the least prediction error) in the 1PP. In sharp contrast, if the mechanism has emerged for the social reason of understanding someone else's actions, action prediction would be most effective in the 3PP (Bach et al., 2014; Oberman & Ramachandran, 2008).

Whilst previous work has largely examined the prediction of consequences of observed actions (e.g. Aglioti, Cesari, Romani, & Urgesi, 2008; Urgesi, Savonitto, Fabbro, & Aglioti, 2012), few studies have explored the temporal dimension of action prediction. Examining temporal aspects of action observation allows us to determine whether the motion perception system is temporally predictive, potentially enabling us to respond to our environment in a timely manner. The current study examines the ability to determine future action states, and specifically the temporal acuity of prediction, via a spatio-temporal judgement task. The technique is adapted from an action occlusion paradigm (Parkinson et al., 2011, 2012; Prinz & Rapinett, 2008; Sparenberg et al., 2012), which has previously been used to explore temporal prediction of actions using pointlight images. However, some of these studies have combined transitive object-directed and intransitive non-object related, and familiar and unfamiliar actions, and have found inconsistent results, not always in accordance with the notion that perception is predictive (cf. Sparenberg et al., 2012). However, given that many single cell and neuroimaging studies would indicate that the MNS/AON is particularly activated for goal-directed/object-oriented actions (for monkey mirror neuron firing: Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Umiltà et al., 2001; for human AON activation: Iacoboni et al., 2005; Johnson-Frey et al., 2003; Shmuelof & Zohary, 2006) it would be beneficial to examine the temporal accuracy of prediction related specifically to transitive actions. Here high quality video images of simple everyday object-related actions are presented, such as picking up a wine glass, to examine temporal prediction of action. In particular, the study examines temporal prediction of actions presented in the 1PP and 3PP. In accordance with the proposal that the AON emerged as a consequence of visual input co-occurring with motor output, but which has enabled us to extrapolate predictive processes to observation of others, it is hypothesised that predictive acuity will be at its best during the observation of 1PP actions. Such a result might suggest that the AON is a system that principally feeds into motor control processes, as opposed to a system evolved for the interpretation of others' actions or social interaction.

In Experiments 1 and 2, potential differences in a spatio-temporal judgement task are examined when observing actions in first-person and third-person perspectives. Experiment 2 forms a replication of the first experiment with a different sample to validate the paradigm and the stimuli used.

2.2 EXPERIMENT 1

2.2.1 METHOD

2.2.1.1 Participants

Thirty-one participants (14 male) were recruited through the University of York, Department of Psychology participant pool. Prior to testing it was decided to exclude participants if their point of subjective equality (PSE) value (determined from the fitted psychometric function) was beyond the stimulus range presented in the experiment (between -200 and 200ms) indicating their sensitivity (or detection threshold) was too low for the present study to determine it accurately. This criterion rejected seven participants; data from the remaining twenty-four participants (nine male) were analysed. Included participants were between 19 and 38 years of age (M=26.5,

SD=4.8) and had normal or corrected-to-normal vision. They received a small payment or course credit in compensation for their time. Procedures were approved by the Department of Psychology Ethics Committee at The University of York.

2.2.1.2 Materials

Stimuli were recorded using a Panasonic full HD 1920x1080p (50p) Camcorder, mounted on a tripod. Action sequences were recorded from a bird's eye perspective, looking down onto a table covered with a black cloth. Each action sequence recorded comprised a transitive action involving an actor's forearm and hand reaching towards an object on a table, grasping it, lifting it and removing it from the table in the direction of the actor. Action sequences were recorded with five different objects: a mug, a wine glass, a hammer, a pair of scissors and a jug of water. Each action was performed by a male and by a female actor using their right hand, producing ten template sequences in the first person perspective; that is, the hand appearing from the inferior edge of the screen.

Recordings were edited using Sony Vegas Pro v10, which was used to trim the recordings so that each action sequence began with 300ms prior to the action beginning (i.e. prior to the hand appearing and moving towards the object) and 300ms post-completion of the action. Actions were rendered at 60Hz. Full action sequences (without occlusion) had a duration of 2383ms minimum and 3567ms maximum (M =2754.9ms).

From these template sequences in the 1PP, 3PP action sequences were created by flipping the image about the horizontal axis (see Figure 1). 3PP actions were therefore a mirror-match, rather than an anatomical-match, of the 1PP actions. This manipulation was based on studies demonstrating that we imitate mirror-matched actions better than anatomically matched actions (Chiavarino, Apperly, & Humphreys, 2007) and that whilst perspective and handedness are important in sense of ownership, peri-dominant-hand space is the preferred reference frame to distinguish other from self (Conson, Aromino, & Trojano, 2010; Conson, Alaerts, Heremans, Swinnen, & Wenderoth, 2009; Mazzarella, & Trojano, 2009). Therefore, in experimental studies examining action observation mechanisms, mirror-matched limb actions in the allocentric perspective (3PP) would be preferable over the use of anatomically-matched actions, which would have an additional processing disadvantage[4].

Presentation of visual stimuli and response recording was programmed using Python v2.7 (www.python.org) and Pygame modules (www.pygame.org). Visual stimuli were presented on a 1280x1024 monitor, with 1024x576 image dimensions on a black surround, at a viewing distance of 64cm, subtending a visual angle of 28x15 degrees, at a 60Hz screen refresh rate.

An occlusion image was created using a grey-scale average of a frame from a video prior to the start of the action (eg. a cup on the table top without the hand in shot was averaged to grey-scale).

Figure 2.1.Static images taken from example video stimuli in the first-person perspective (1PP) and third-person perspective (3PP) conditions. 3PP action sequences were created from the 1PP video sequences by flipping the images about the horizontal axis.

---

[4] Bach, Fenton-Adams, & Tipper (2014) investigated observation of anatomical- and mirror-matched action observation and found no evidence for differences between these 3PP conditions.

2.2.1.3 Design and Procedure

Experimental trials began with 1000ms of an action sequence video. The action video was then replaced by the grey-scale occlusion image, presented for a fixed duration of 500ms. The occluder was then followed by the continuation of the action video until the end of the sequence. The point from which the action sequence continued post-occlusion was manipulated in 13 time steps, with the time between the last frame pre-occlusion and the first frame post-occlusion ranging from 300ms to 700ms in steps of 33ms (2 frames). This produced 13 offset periods between -200 and 200ms. Thus, an offset period of zero corresponded to a coherent trial, whereby the post-occlusion - pre-occlusion frame difference temporally corresponded exactly to the duration of the occlusion (500ms).

Participants were instructed to imagine the continuation of the action during the occlusion period. Once the action continued after occlusion, participants were requested to respond with a key press to indicate whether the point from which the action continued was temporally earlier or later than the actual action would be expected to be given the occlusion period and their expectation. Participants were asked to respond whilst the action was still continuing and before completion of the sequence when the screen went to black. Task responses were given with the right hand. A self-paced inter-trial interval was employed, requiring the participant to press the spacebar to progress to the next trial. Figure 2 depicts an experimental trial.

An ‘earlier’ trial refers to a negative temporal offset (<0); that is, the time between the last frame pre-occlusion and the first frame post-occlusion is less than the occlusion period (<500ms). A ‘later’ trial refers to a positive temporal offset (>0); the time between the last frame pre-occlusion and the first frame post-occlusion is greater than the occlusion period (<500ms).

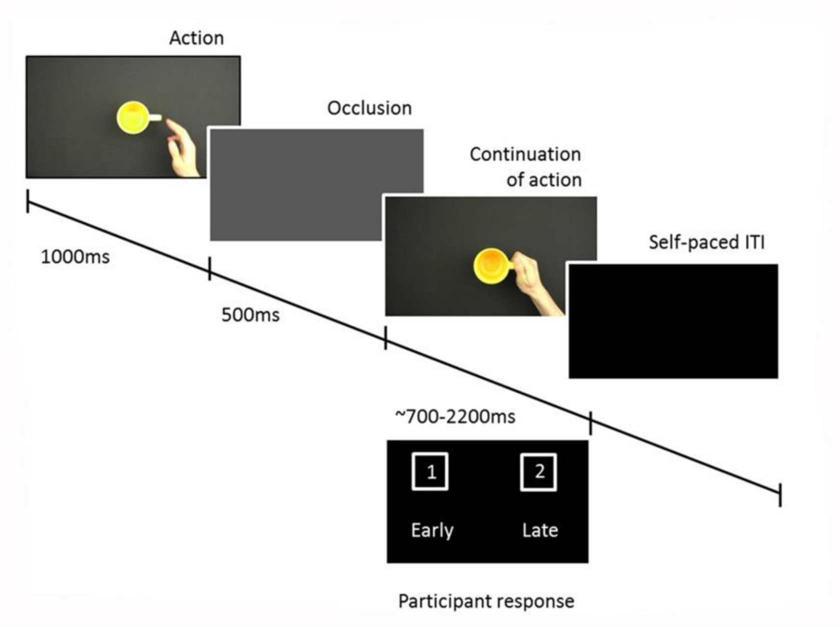

Figure 2.2. Schema of a trial in Experiments 1 and 2. Each trial began with 1000ms of the start of an action sequence, followed by an occlusion screen for a fixed duration of 500ms. The continuation of the action then followed until its completion, with the re-start being incoherent-early, incoherent-late, or coherent with the length of the occluder. Participants had to respond during the continuation of the action as to whether they thought the action re-started from a point that was too early or too late.

The experiment began with a *familiarisation phase*, and then a *practice phase,* before proceeding to the main *experimental phase*. In the familiarisation phase, participants viewed each template video (i.e. without occlusion) twice (once in each perspective), and were asked to simply observe. Twenty practice trials (10 in each perspective) were then presented, allowing participants to adjust their judgement and response speed. Trials presented in this practice phase were the temporal offset extremes (offsets of -200ms and 200ms) for each object in each perspective (gender of the hand was randomised). ‘Correct/Incorrect’ feedback was provided to participants at the end of each practice trial.

The main experimental phase consisted of 390 trials in each of the 1PP and 3PP conditions (780 trials in total) (5 actions x 13 offset periods x 6 repetitions), divided into ten equal blocks. The 1PP and 3PP conditions were presented in alternate blocks which were counterbalanced between participants. Trials that were not responded to within the given response time were repeated once at the end of the block. Each block began with 10 familiarisation trials in the perspective (1PP/3PP) corresponding to that block. Each block ended with a ‘Break’ screen allowing participants to rest their eyes and to proceed to the next block when ready to do so.

The temporal offset was varied using the method-of-constant-stimuli. In this method, stimuli levels (in this case, the temporal offsets) are not related from one trial to the next, but are presented randomly. This prevents participants from being able to predict the level of the next stimulus, and as such reduces habituation and expectation.

Trials were presented in a pseudo-random order, ensuring that the same object or temporal offset was never presented three times consecutively. From the proportion of ‘late’ responses per stimulus offset condition, logistic psychometric functions were fitted to each individual’s data to estimate their point of subjective equality (PSE) and spread of their data.

2.2.2. RESULTS & DISCUSSION

Due to a technical error, the temporal shifting of the action post-occlusion resulted in shifts of one frame difference from those intended. The resulting temporal shifts relative to the occlusion duration were as follows: -216, -183, -149, -116, -83, -49, -16, 16, 49, 83, 116, 149, 183 ms. This unintended manipulation however does not preclude the assessment of the temporal acuity of action prediction, as the same sample resolution is obtained used for the fitting of psychometric functions to individuals' data. The manipulation was rectified for all subsequent experiments.

Data were collapsed across object and actor gender and analysed in terms of temporal offset (test motion) and perspective. Temporal offsets were determined relative to the occluder duration. Firstly, participants’ proportion of ‘late’ responses across the 13 temporal offset conditions were analysed in a one-way ANOVA. Data for both the 1PP and 3PP conditions showed a statistically significant effect of temporal offset (F (12,276) = 73.78, $p<.001$, η^2_p =.76 for the 1PP; F(12,276) = 64.12, $p<.001$, η^2_p =.74 for the 3PP). Importantly, the linear trend was significant for both 1PP and 3PP conditions (F(1,23)=228.62, $p<.001$, η^2_p =.91; F(1,23)=162.30, $p<.001$, η^2_p =.88 respectively). This indicates that participants could perform the task, as data show a significant linear increase in the proportion of late responses with increasing temporal offset.

For each individual participant's data, a logistic function was fitted to the proportion of 'late' responses for each temporal offset condition by minimising the mean squared error of the fit. The number of free parameters was determined per individual by nested modelled F-tests as some participants had a high lapse rate. This lapse rate refers to an error rate for stimuli conditions that are close to the extremes, with the error made likely due to a brief lapse in attention or other event, such as sneezing, that leads the participant to miss the presentation of the stimulus.

This determined the main parameters of interest: the point of subjective equality (PSE) as well as the spread of the data. See Figure 2.3 for an example of an individual fitted psychometric function.

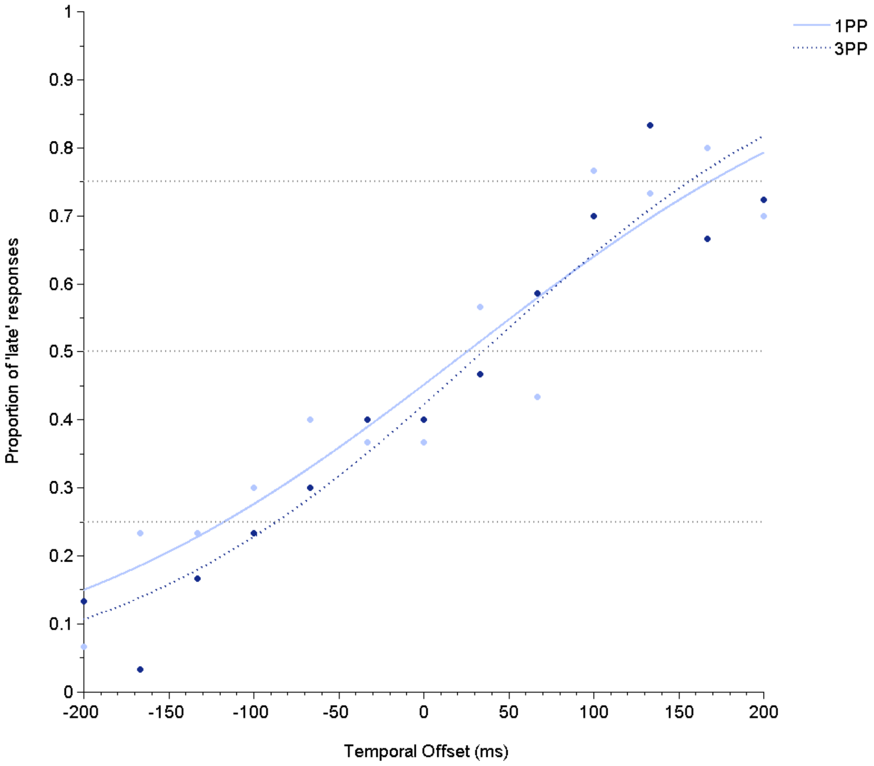

Figure 2.3. Example logistic function fitted to an individual participant's proportion of 'late' responses per temporal offset condition. The solid line depicts the function for first person perspective actions (1PP) and the dashed line for third person perspective actions (3PP).

The PSE determines the temporal offset that would elicit an ‘early’ / ‘late’ response probability of .5, and is a determinant of the individual's subjective experience of a ‘real-time’, or temporally coherent, outcome. A negative PSE value thus indicates that a condition in which less video had been removed than the occluder time was perceived as being coherent with the occluder, and would in turn indicate that mental simulation was progressing slower than the real action itself. A positive PSE indicates that a ‘later’ condition was perceived as being coherent with the occluder, and that the mental simulation was progressing faster than the real action.

An average PSE was determined across participants for each perspective. For the 1PP condition, an average PSE of 22.40ms (SE=8.19) was observed, which was marginally significantly different from zero (t(23) = 1.84; p = .079). For the 3PP condition, an average PSE of 24.79ms (SE=8.19) was observed, which was also marginally significantly from zero (t(23) = 1.93; p = .066). That is, there were trends in the data for simulations to run faster than reality. A repeated measures t-test demonstrated that there was no significant difference between the PSEs for the two perspective conditions (t(23) = -0.2067; p = .838) . Figure 4 depicts the mean PSEs for the two perspective conditions and their standard errors adjusted for the repeated measures design according to O'Brien & Cousineau (2014).

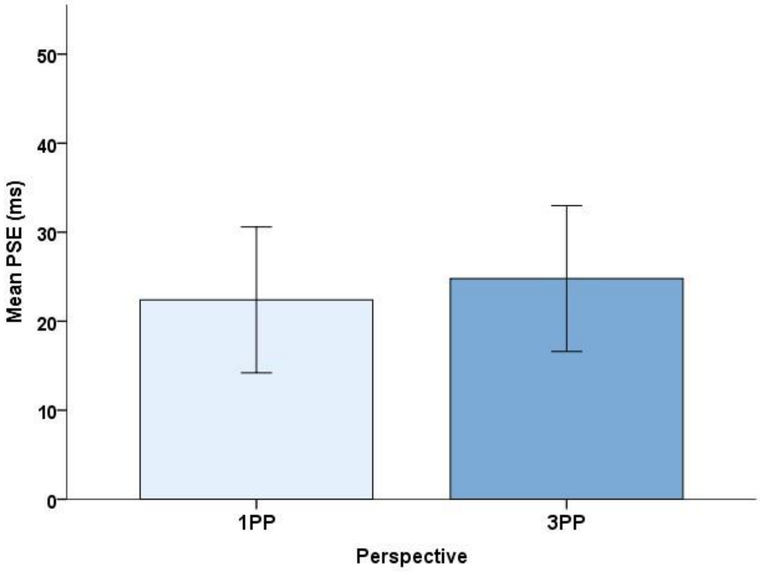

Figure 2.4. Bar graph depicting the mean point of subjective equality (PSE) for each perspective in Experiment 1. Light blue bars show the mean PSE for first person perspective (IPP) actions, dark blue bars show the mean PSE for third person perspective (3PP) actions. Error bars depict ±1 standard error.

An average spread of the data was determined across participants for each perspective. The spread of the data is an additional measure that can be used to determine the performance on a particular psychophysics task. The spread is a determinant of an individual's ability, or sensitivity, to detect a change, or in this case detect a temporal shift in the action sequence. The spread has an inverse relation to the slope (gradient) of the psychometric function. As such, a small spread indicates good performance in detecting a spatio-temporal shift and a large spread indicates poorer sensitivity. For the 1PP condition, an average spread of 219.18 (SE=15.32) was observed. For the 3PP condition, an average spread of 245.85 (SE=15.32) was observed. A repeated measures t-test demonstrated that there was no significant difference in the spread of the two perspective conditions (t(23) = -1.23; p = .231). Figure 5 depicts the mean spread for the two perspective conditions and their standard errors adjusted for repeated measures according to Cousineau and O'Brien (2014).

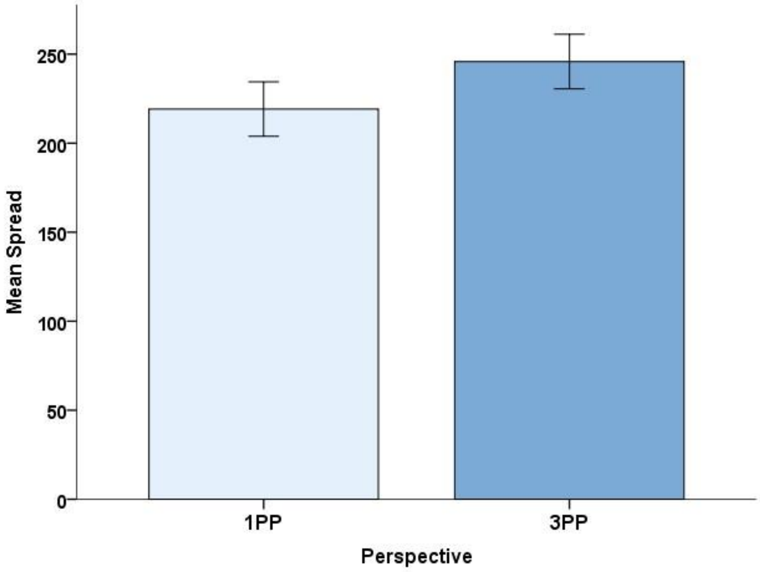

Figure 2.5. Bar graph depicting the mean spread of data for each perspective in Experiment 1. Light blue bars show the mean PSE for first person perspective (IPP) actions, dark blue bars show the mean PSE for third person perspective (3PP) actions. Error bars depict ±1 standard error.

Before discussing the results of Experiment 1 in detail, given that this is the first experiment to use such stimuli in an occlusion task to probe prediction, a second experiment was conducted to determine whether the same results could be replicated with a different participant group, as well as to remove the technical flaw identified in Experiment 1. The details of this replication are provided in Experiment 2.

2.3 EXPERIMENT 2

2.3.1 METHOD

2.3.1.1 Participants

Thirty-two participants (13 male) were recruited through the University of York, Department of Psychology participant pool. Participants were excluded if their point of subjective equality (PSE) value was beyond the stimulus range presented in the experiment (between -200 and 200ms) indicating their sensitivity was too low for the present study to determine it accurately. This criterion rejected 8 participants; data from the remaining twenty-four participants (nine male) were analysed. Included participants were between 18 and 28 years of age (M=20.5, SD=2.2) and had normal or corrected-to-normal vision. They received a small payment or course credit in compensation for their time. Procedures were approved by the Department of Psychology Ethics Committee at The University of York.

2.3.1.2 Materials, Design and Procedure

The same materials and stimuli were used for this second experiment as in Experiment 1. This experiment also followed the same design and procedure as in Experiment 1 (section 2.2.1.3), with the only change being the adjustment of the temporal offset to adjust for the technical issue of Experiment 1. That is, the temporal offset conditions were as intended with 13 temporal offsets in steps of ~33ms (2 frames) up to a maximal offset of +/- 200ms. Temporal shifts relative to the occlusion duration were therefore as follows: -200, -167, -133, -100, -67, -33, 0, 33, 67, 100, 133, 167, 200ms.

2.3.2 RESULTS & DISCUSSION

Data were collapsed across object and actor gender and analysed in terms of temporal offset (test motion) and perspective. Temporal offsets were determined relative to the occluder duration. Firstly, participants' proportion of 'late' responses across the 13 temporal offset conditions were analysed in a one-way ANOVA. Data for both the 1PP and 3PP conditions showed a statistically significant effect of temporal offset (F (12,276) = 66.67, p<.001,η^2_p =.74 for the 1PP; F(12,276) = 85.83, p<.001, η^2_p =.79 for the 3PP). Importantly, the linear trend was significant for both 1PP and 3PP conditions (F(1,23)=225.33, p<.001, η^2_p =.91; F(1,23)=316.81, p<.001, η^2_p =.93 respectively). This indicates that participants could perform the task, as data show a significant linear increase in the proportion of late responses with increasing temporal offset.

As in Experiment 1, for each individual participant's data, a logistic function was fitted to the proportion of 'late' responses for each temporal offset condition by minimising the mean squared error of the fit. The number of free parameters was determined per individual by nested modelled F-tests as some participants had a high lapse rate. This determined the two main parameters of interest: the point of subjective equality (PSE) and the spread of the data.

An average PSE was determined across participants for each perspective. For the 1PP condition, an average PSE of 19.29ms (SE=7.14) was observed, which was not significantly different from zero (t(23) = 1.29; p = .208). For the 3PP condition, an average PSE of 37.29ms (SE=7.14) was observed, which differed significantly from zero (t(23) = 2.56; p = .018). A repeated measures t-test demonstrated that there was no significant difference between the PSEs for the two perspective conditions (t(23) = -1.78; p = .088). Figure 6 shows the mean PSEs for each perspective.

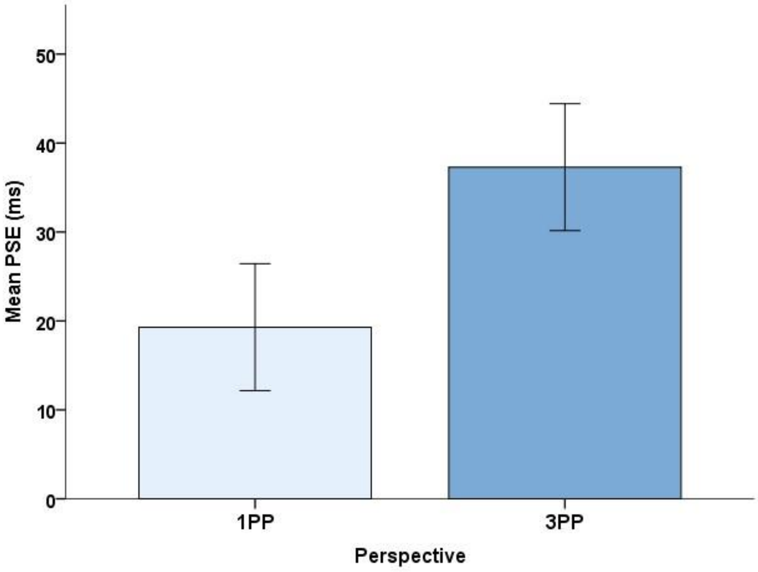

Figure 2.6. Bar graph depicting the mean point of subjective equality (PSE) for each perspective in Experiment 2. Light blue bars show mean PSEs for first person perspective (IPP) actions, dark blue bars show the mean PSE for third person perspective (3PP) actions. Error bars depict ±1 standard error.

The average spread of the data was determined across participants for each perspective. For the 1PP condition, an average spread of 206.35 (SE=11.57) was observed. For the 3PP condition, an average spread of 202.27 (SE=11.57) was observed. A repeated measures t-test demonstrated that there was no significant difference in the spread of the two perspective conditions (t(23) = 0.25; p = .806). Figure 7 shows the mean spread of the data for each perspective.

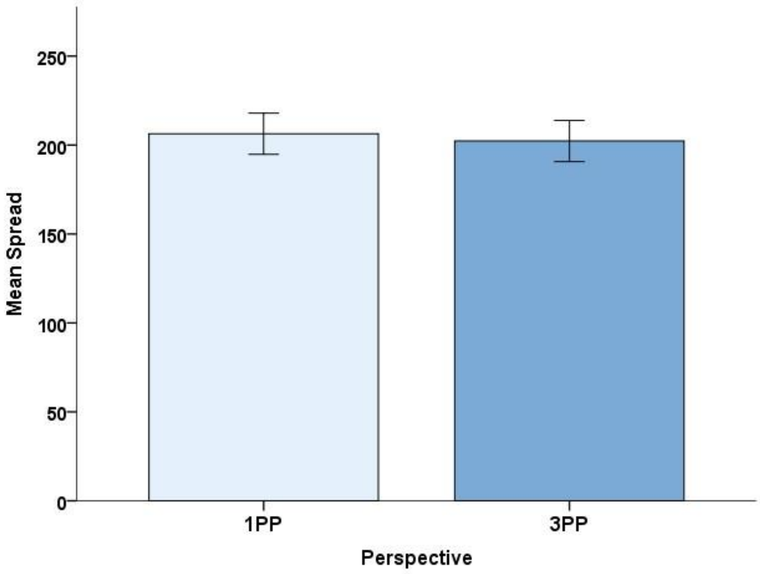

Figure 2.7. Bar graph depicting the mean spread of data for each perspective in Experiment 2. Light blue bars show mean spread for first person perspective (IPP) actions, dark blue bars show the mean spread for third person perspective (3PP) actions. Error bars depict ±1 standard error.

2.3.2.1 Leave-One-Object-Out (LOOO) Analysis

In order to verify that there was not one particular stimulus object potentially influencing the data over the others, an additional analysis was conducted whereby psychometric functions were fitted to each individual participants' proportion of 'late' responses, iteratively removing data corresponding to each of the five stimulus object type in turn. From data aggregated over Experiments 1 and 2, the average PSE and spread across participants were determined for each of these five analyses. Variability in the stimuli was desirable in order for results to be generalisable to other brief transitive actions, and not specific to a particular type of grasp. The objects used therefore elicited reach and grasp kinematics with varying degrees of complexity, requiring power grasp or precision grip movements. These differences in the fine kinematics of the reach and grasp actions naturally resulted in differences in the PSE elicited by each object. The results of the ANOVA examining the PSE across object type and perspective, combining data from both Experiments 1 and 2 are presented in Appendix A.

2.3.3 GENERAL DISCUSSION

The purpose of the Leave-One-Object-Out analysis was to justify the use of these particular five objects/actions in the further study of the temporal prediction of action. Variance in kinematics and complexity of kinematics was required in order for results to be generalisable to other transitive action types, and we see that this variance can have an effect on prediction error. The variance in the kinematics of action required to grasp and lift each object elicited differing PSEs and data spread across action type. The reduction in prediction error with the removal of the jug or the scissors suggests that these actions may produce more uncertainty and therefore more anticipation (prediction error) potentially due to the more complex fine motor control required in the case of the scissors, or due to a heavier weight in the case of the jug, which would not be easily estimable. The variance in the individual object actions was sufficient to have a potential effect on the PSE across perspective conditions, however, the lack of an object x perspective interaction indicates that the prediction error is similar for both first person and third person perspectives and consistent across transitive action type. This LOOO analysis therefore provides confirmatory evidence of the 1PP-3PP action prediction consistency across transitive actions, and validates the use of these objects in the further study of temporal action prediction in subsequent chapters.

Before interpreting the data further it is worth discussing the PSE value that would constitute optimal performance; that is, whether a PSE close to zero or a significantly positive PSE is optimal for engagement with the environment and/or motor control. It is important that we are able to anticipate an action outcome and that our internal simulation of that action continue such that predictions of future states can guide action. However, it is critical for visuomotor performance that this prediction be as accurate as possible, whereby the forward model and reality match. Representational momentum studies demonstrate that there is an automatic simulation process of future states. However, such tasks require participants to recall from memory the last stimulus seen and in doing so participants make errors in reporting stimuli in loci they would have moved to. In sharp contrast, the current paradigm presents stimuli that have continued along their action trajectory and the task is to identify their accurate action state. In this situation, performance closer to zero is closer to reality (that is, there is less prediction error between the simulated action and the real action dynamics). Hence, subsequent motor processes directed towards the stimulus would be more accurate. We therefore posit that a PSE closer to zero is indicative of optimal performance.

Given the above premise, there are two aspects of the data to be discussed. First, action simulation processes appear to be somewhat more rapid than the actual observed action dynamics. This is an interesting contrast to previous similar studies that have shown that action simulation processes run significantly more slowly than the actual action (e.g., Prinz & Rapinett, 2008; Sparenberg et al., 2012). At this stage it is uncertain why this contrast has emerged, but it is worth noting a number of interesting methodological differences that might mediate the difference in results. Firstly, previous studies have focussed on whole-body complex actions, combining transitive and intransitive actions. Given that many single cell and neuroimaging studies would indicate that the MNS/AON is particularly activated for goal-directed/object-oriented actions (e.g. Gallese et al., 1996; Rizzolatti et al., 1996) it may be the case that lack of goal/intention in intransitive conditions influences the simulation processes on which temporal judgements are made (Gallese & Goldman, 1998; Jeannerod, 2001). Secondly, previous studies have used action stimuli with varying degrees of familiarity to participants. Activities such as throwing a basketball or leapfrogging, as used in these previous studies, may arguably be recently *un*familiar to participants. The stimuli in the Sparenberg et al. (2012) study therefore do not differentiate between actions for which participants can and cannot easily draw upon their own motor repertoire to enable simulation/prediction mechanisms. Thirdly, the use of point light actions (Graf et al., 2007; Parkinson et al., 2011, 2012; Sparenberg et al., 2012) may also influence the nature of timing judgements. Finally, researchers have observed that showing less information post-occlusion degrades performance in occlusion tasks (Parkinson et al., 2012). As each of the occlusion studies described present a simple static image post-occlusion on which to base a decision, it might be argued that performance accuracy is not as would be expected if actions were allowed to continue until their completion, as in these present studies.

As noted, the stimuli contrast on all these dimensions. They are all highly familiar and simple transitive reach-to-grasp actions, which are presented in high quality full colour videos, and the display for judgement is a continuation of the action rather than a static image. Which of these stimulus properties mediates the change in temporal judgement decisions is not clear at this time. Certainly, however, the stimulus properties that shift temporal simulations from slower to faster than the actual observed action dynamics are certainly worthy of further study.

The central focus of these first studies was to examine contrasts between 1PP and 3PP views of action. In accordance with the logic proposed by Oberman & Ramachandran (2008), an account arguing that simulation of observed actions evolved as a process to facilitate the understanding of other people might predict better spatio-temporal judgements when viewing 3PP actions. In contrast, an account arguing that simulation processes emerged to predict one's own action states might predict more accurate performance when viewing 1PP actions. The results of these first studies are equivocal. The spread of the data, used as a measure of how well participants can perform the task was equal across action perspective, demonstrating participants performed the spatio-temporal judgement task with equal ability across the action perspectives. Examining the PSE, based on these first studies, at most it would appear that the prediction system is not viewpoint dependent, and that there is an anticipation bias whereby we simulate actions faster than real world dynamics and thus overestimate the action state in spatio-temporal terms.

Although there is a trend for the 1PP viewing condition to be somewhat more accurate than 3PP, this is not significant in this study. The lack of consistent contrast between 1PP and 3PP has certainly been observed in other situations, for example, in behavioural studies (Bach et al., 2014) and fMRI studies, where common neural population codes for producing and observing action are observed in parietal cortex in both 1PP and 3PP views (e.g. Oosterhof, Tipper, & Downing, 2012). However, in both of these studies other situations did detect contrasts between 1PP and 3PP. For example, when more complex aspects of action had to be integrated, Bach et al., (2014) observed faster responses when observing 1PP than 3PP actions, and in fMRI ventral premotor cortex encoded joint production and perception of actions only in the 1PP (Oosterhof et al, 2012).

Therefore, in the experiments that follow in Chapter 3, other experimental situations are examined that might reveal contrasts in temporal prediction between 1PP and 3PP observed actions, as well as those which might improve prediction performance. In the following chapter, the first experiment aims to facilitate the processing of 3PP actions via a visual priming manipulation. The following two experiments determine whether prediction can be facilitated via two motor priming manipulations.

CHAPTER 3: Visual and Motor Priming Effects on Action Prediction

3.1 EXPERIMENT 3: Visual priming of actions in third-person perspective

3.1.1 INTRODUCTION

Many of the occlusion studies discussed in Chapter 2 found that prediction performance was significantly impaired when the whole body actions were inverted (Graf et al., 2007; Parkinson et al., 2011; Sparenberg et al., 2012). Under the assumption that humans have no visual experience of inverted movements and cannot draw upon their motor repertoire to simulate such actions (Loula, Prasad, Harber, & Shiffrar, 2005), the authors of these studies concluded that simulation of biological motion requires more than trajectory extrapolation alone. Researchers have postulated that such simulation likely requires first-hand experience, either visual or motoric, of the actions. Several studies have examined how visual experience may be sufficient to influence how we perceive or predict actions. A body of research has demonstrated how individuals can acquire motor skills or modify behaviour based on outcomes through observational learning (Buchanan & Wright, 2011; Carroll & Bandura, 1982; Chamley, 2003). Furthermore, perceptual experience alone has been found to influence how we perceive other's actions. For instance, Cross, Stadler, Parkinson, Schütz-Bosbach, & Prinz, (2011) found that temporal prediction of actions improved consistently after observational training of gymnastic moves. In neuroimaging, Higuchi, Holle, Roberts, Eickhoff, & Vogt, (2012) demonstrated that activation intensities in prefrontal areas of the AON during observational practice of guitar chord playing predicted the behavioural effects on chord playing. These studies suggest the emergence of motor resonance processes through observational experience alone.

Other studies, however, have determined the importance of motor experience in the simulation of action, demonstrating that action simulation mechanisms are enhanced by the capability of performing an observed action (e.g. Aglioti, Cesari, Romani, & Urgesi, 2008; Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Urgesi, Savonitto, Fabbro, & Aglioti, 2012). These studies are expanded on in Section 3.2 of this chapter. This said, there remains little research examining the extent to which motor experience compared to visual experience impacts action observation, given that it is difficult to tease apart experience in these two forms (visual input generally accompanies one's own motor output). Only a limited number of studies have examined the two in comparison (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Urgesi et al., 2012)

Experiments 3 to 5 in this chapter intend to bring together research from the areas of action prediction, and motor and visual experience effects on action perception, with the aim to assess how visual and motor experience may each contribute to action prediction mechanisms. The research additionally intends to assess whether experience in either modality improves prediction performance preferentially or selectively for actions that map most closely onto self-generated actions (first person perspective) or other-generated (third person perspective) actions.

In the first of the experiments that follow, we determine whether real-world visual priming can facilitate prediction of 3PP actions.

3.1.2 METHOD

3.1.2.1 Participants

Thirty-three participants (nine male) were recruited through the University of York, Department of Psychology participant pool. As in Experiments 1 and 2, participants were excluded if their point of subjective equality (PSE) value was beyond the stimulus range presented in the experiment. Nine participants were excluded on this basis and subsequent analyses were conducted on the remaining 24 participants (eight male). All were aged between 18 and 33 years of age (M=22.3,

SD=3.7) and had normal or corrected-to-normal vision. They received a small payment or course credit in compensation for their time. Procedures were approved by the Department of Psychology Ethics Committee at The University of York.

3.1.2.2 Materials & Procedure

The same stimuli and paradigm were used as in Experiments 1 and 2. In Experiment 3, after the familiarisation phase and before the practice phase of the main computer based task, participants observed the experimenter perform the transitive actions on the same objects from across the table using their left hand (thus replicating the image of the action flipped about the horizontal axis as in the 3PP condition). Each transitive action was performed 4 times on each object. The same main experimental computer task as in Experiments 1 and 2 was then performed by participants.

3.1.3 RESULTS & DISCUSSION

As in Experiments 1 and 2, all participants produced monotonically increasing proportions of 'late' responses with increasing temporal offset for both the 1PP (F(1,23)= 232.09, p<.001, η^2_p =.91) conditions and 3PP (F(1,23)= 234.76, p<.001, η^2_p =.91) conditions, indicating that they could perform the task well.

From the logistic functions fitted to each individual participant's data, an average PSE was determined across participants for each perspective. For the 1PP condition, an average PSE of 23.55ms (SE=6.20) was observed, which was not significantly different than zero (t(23) = 1.76; p = .091). For the 3PP condition, an average PSE of 29.43ms (SE=6.20) was observed, which differed significantly from zero (t (23) = 2.24; p = .035). However, a repeated measures t-test demonstrated that there was no significant difference between the PSEs for the two perspective conditions (t(23) = -.67; p = .509) (see Figure 3.1). A combined analysis of Experiments 2 (without visual priming) and 3 (with visual priming) also failed to detect any differences between the baseline Experiment 2 and the visual 3PP action priming condition of Experiment 3 on the PSE for 1PP actions (t(23) = -.24; p = .81) or 3PP actions (t(23) = .39; p = .70).

For the 1PP condition, an average spread of 217.79 (SE=12.80) was observed. For the 3PP condition, an average spread of 211.14 (SE=12.80) was observed. A repeated measures t-test demonstrated that there was no significant difference in the spread of the two perspective conditions (t(23) = .37; p = .717).

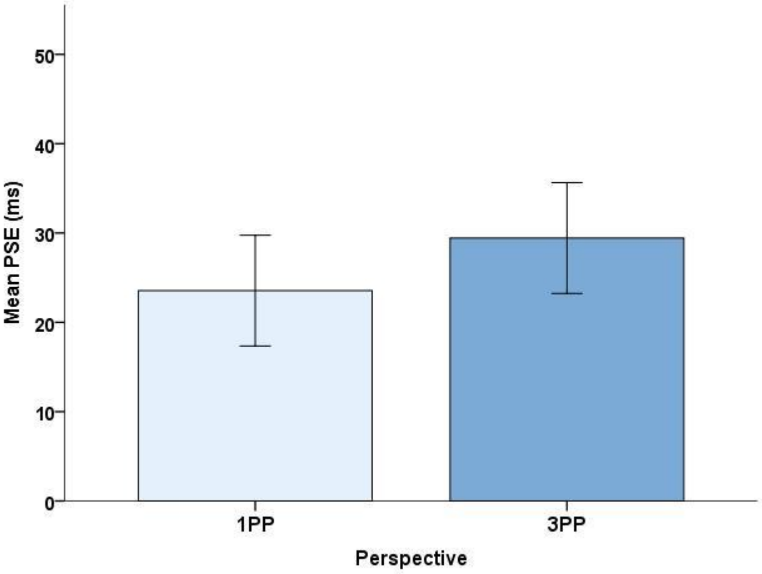

Figure 3.1. Bar graph depicting the mean point of subjective equality (PSE) for each perspective in Experiment 3. Light blue bars show the mean PSE for first person perspective (IPP) actions, dark blue bars show the mean PSE for third person perspective (3PP) actions. Error bars depict ±1 standard error.

The results of this experiment are therefore very clear. Although participants received real world visual experience of another person reaching out and grasping the objects in the same manner as subsequent 3PP visual displays, there was no effect on spatio-temporal judgements. As noted, it was ensured that the viewed priming actions were a close match to the 3PP actions in the computer task, and hence it was predicted 3PP performance would improve. The results are unable to provide support for an account claiming the simulation process is primarily involved in the prediction of another person's actions.

However, a counter argument may be that our priming events were limited, certainly much reduced compared with prior studies (e.g., Cross et al., 2011). Nevertheless, in these latter studies, participants were learning much more complex and unfamiliar actions such as gymnastic movements. For typical participants there would be no prior motor representations of these complex and difficult actions. In contrast, we would argue that the very simple everyday reach-to-grasp actions in our study would benefit from a few exposures, if visual exposure is effective in temporal judgement tasks. The following two experiments manipulate motor experience with a similar level of four exposures to each stimulus. As will be seen, with this similar level of exposure, contrasts between 1PP and 3PP now emerge. Hence the studies to be reported suggest large amounts of exposure are not necessary when everyday actions are simple and very familiar, and furthermore, motor representations are more influential than prior visual exposure on temporal judgements of viewed actions.

3.2 EXPERIMENT 4: Visual and motor priming of actions in first-person perspective

3.2.1 INTRODUCTION

The importance of prior motor experience in the simulation of action has previously been demonstrated. For example, Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, (2005) conducted fMRI in expert ballet dancers, expert capoeira dancers and inexpert controls whilst they watched ballet or capoeira dance sequences. Greater activation was observed in areas of the AON when participants watched dance in their expertise. In a later study, Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, (2006) utilised the fact that male and female ballet dancers have different motoric dance experiences but have equal levels of visual familiarity of ballet moves.

The male and female ballet dancers observed gender-specific ballet moves whilst being scanned in fMRI. They found increased activity in the AON when participants observed action within their motor repertoire compared to the actions they frequently observed but of which they had no physical experience. The authors concluded that the AON responds with motor experience over and above visual experience and that this system integrates observed actions with movements in one's own motor repertoire (see also, Cross, Hamilton, & Grafton, 2006; Knoblich & Flach, 2001 for similar observations). Hence these studies demonstrate that action simulation mechanisms are enhanced by the capability of performing an observed action, and that we integrate information from motor experience with current visual input, which can facilitate predictive mechanisms to determine action outcomes.

Therefore, in the current study we provided motor experience prior to the spatio-temporal judgement task. That is, participants reached to grasp and pick up each of the 5 objects in the study 4 times. We predicted two possible outcomes. First, that there might be a general improvement in temporal judgement accuracy for all forms of viewed action after motor priming. That is, both 1PP and 3PP spatio-temporal judgements are more accurate. However, second, because the motor priming is by necessity an egocentric 1PP activity, temporal judgements of 1PP actions may differ from those of 3PP actions.

3.2.2 METHOD

3.2.2.1 Participants

Thirty-two participants (12 male) were recruited through the University of York, Department of Psychology participant pool. As in Experiment 1 and 2, participants were excluded if their point of subjective equality (PSE) value was beyond the stimulus range presented in the experiment. Eight participants were excluded on this basis and subsequent analyses were conducted on the remaining 24 participants (11 male). All were aged between 18 and 31 years of age (M=22.5,

SD=3.4) and had normal or corrected-to-normal vision. They received a small payment or course credit in compensation for their time. Procedures were approved by the Department of Psychology Ethics Committee at The University of York.

3.2.2.2 Materials & Procedure

The same stimuli and paradigm were used as in Experiments 1 and 2. In Experiment 3, however, after the familiarisation phase and before the practice phase, participants performed the transitive actions themselves, with eyes open. Participants were asked to observe the experimenter place the object on a table covered with a black cloth, on a marker set at 34cm from the participant's edge of the table. Participants were asked to begin each action with their hands off the table, and then reach towards, grasp and remove each object from the table as if they were about to use the object and in a manner that replicated as precisely as possible the action just observed (eg. grasp the wine glass by placing the fingers on the stem of the glass to lift the object), such that participants received motor experience that was specific to the actions they would judge. On completion of each action (when the object was removed from the table completely towards the participant), the experimenter took the object from the participant and placed it back on the marker ready for the next action. Each action was performed with the participant's right hand, four times on each of the five objects. The same main experimental computer task as in Experiment 1 was then performed by participants.

3.2.3 RESULTS & DISCUSSION

As in the previous experiments, all participants produced monotonically increasing proportions of 'late' responses with increasing stimulus interval offsets for both the 1PP ($F(1,23)=274.17$, $p<.001$, $\eta^2_p = .92$), and 3PP conditions ($F(1,23)= 198.34$, $p<.001$, $\eta^2_p = .90$), demonstrating that participants could perform the task well.

From the logistic functions fitted to each individual participant's data, an average PSE was determined across participants for each perspective. For the 1PP condition, an average PSE of -3.26ms (SE=6.88) was observed, which did not differ significantly from zero (t(23) = -.27; p = .79). For the 3PP condition, an average PSE of 26.84ms (SE=6.88) was observed, which was marginally greater than zero, but did not reach significance (t(23) = 1.81; p = .083). A repeated measures t-test demonstrated that there was a significant difference between the PSEs for the two perspective conditions (t(23) = -3.09; p = .005, *d* = .63). See Figure 3.2.

For the 1PP condition, an average spread of 215.88 (SE=13.40) was observed. For the 3PP condition, an average spread of 247.86 (SE=13.40) was observed. A repeated measures t-test demonstrated that there was no significant difference in the spread of the two perspective conditions (t(23) = -1.69; p = .105).

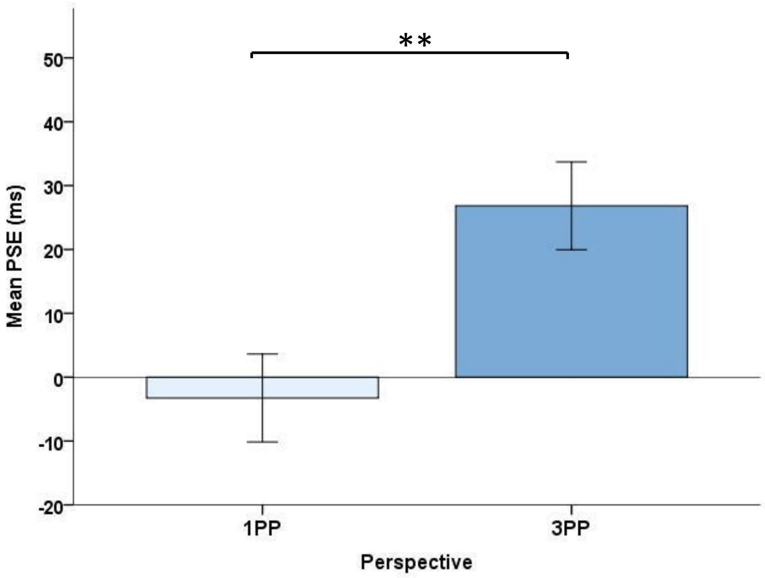

Figure 3.2. Bar graph depicting the mean point of subjective equality for each perspective in Experiment 4. Light blue bars show the mean PSE for first person perspective (IPP) actions, dark blue bars show the mean PSE for third person perspective (3PP) actions. Error bars depict ±1 standard error. * = .005.

This is the first of this series of studies to detect a significant contrast between 1PP and 3PP viewed action when judging temporal aspects of action. It appears that prior motor experience is important for facilitating performance when viewing 1PP actions. This contrasts with the findings of Experiment 3 where prior visual experience of 3PP actions had no significant effect on performance. The results of Experiments 3 and 4 are in line with previous observations concerning the role of vision and motor experience on action simulation processes. For example, Aglioti, Cesari, Romani, & Urgesi, (2008) and Urgesi, Savonitto, Fabbro, & Aglioti, (2012) examined action anticipation in basketball and volleyball players respectively and compared this with supporters who had similar visual experience. Only those with prior motor representations could accurately judge the future states of throws and serves based on viewed players' body kinematics. Furthermore, participants given physical practice training improved their abilities to predict actions by reading body kinematics. Those assigned to observational training alone improved only in understanding the ball trajectory (Urgesi et al., 2012). Our findings are aligned with this prior work showing motor experience is also required to temporally predict bodily actions. However, our results go further by demonstrating that motor experience can selectively facilitate temporal judgements of actions viewed from a first person perspective.

3.3 EXPERIMENT 5: Motor priming without visual input in first-person perspective

3.3.1 INTRODUCTION

A further issue concerns whether the effects produced in Experiment 4 are purely due to action priming. Note that when practising the reach and grasp actions participants were able to observe their actions, as would be expected in such a naturalistic situation. Therefore, it is unclear whether the difference between 1PP and 3PP detected in Experiment 4 is due to motor priming or whether it is caused by a combination of motor priming and concomitant visual input from the 1PP.

Experiment 5 therefore adopts an approach similar to that of Casile and Giese, (2005). They assessed the visual recognition of gait before and after non-visual motor training, in which participants were blindfolded whilst learning a novel upper-body coordinated movement. The study showed a selective improvement in recognition of subsequently observed actions that were physically trained compared to novel actions, despite participants having no visual input during the training phase. The Casile and Giese (2005) study therefore demonstrated that motor experience, without visual experience, has a direct influence on action recognition. We now examine whether pure motor experience, when participants are unable to observe their own action, also has a facilitation effect when making temporal judgements and whether this is selective for 1PP actions.

3.3.2 METHOD

3.3.2.1 Participants

Thirty-six participants (16 male) were recruited through the University of York, Department of Psychology participant pool. As in all other experiments, participants were excluded if their point of subjective equality (PSE) value was beyond the stimulus range presented in the experiment. Twelve participants were excluded on this basis and subsequent analyses were conducted on the remaining 24 participants (12 male). All were aged between 18 and 29 years of age (M=22.9, SD=3.5) and had normal or corrected-to-normal vision. They received a small payment or course credit in compensation for their time. Procedures were approved by the Department of Psychology Ethics Committee at The University of York.

3.3.2.2 Materials & Procedure

The same stimuli and paradigm were used as in Experiments 1 and 2 in Chapter 2 and Experiments 3 and 4 in the current chapter. In Experiment 5, after the familiarisation phase and before the practice phase, participants performed the transitive actions themselves. Participants were instructed to reach and grasp each object as in Experiment 3, such that they received motor experience specific to the actions to be judged, but *with eyes closed*. On completion of each action (when the object was removed from the table completely towards the participant), they were instructed to open their eyes once the object had been placed in its usual location by the experimenter. Participants were then able to look at the object until they were ready to grasp it, at which point they closed their eyes and completed the reach-to-grasp action. These self-paced actions were performed with the participant's right hand, four times on each of the five objects. The same main experimental computer task, with temporal offsets as in Experiment 2 was then performed by participants.

3.3.3 RESULTS & DISCUSSION

As in all previous experiments, all included participants produced monotonically increasing proportions of 'late' responses for increasing temporal offsets; i.e. the linear trend was significant for 1PP actions (F(1,23)= 68.65, p<.001, η^2_p =.75), and 3PP actions (F(1,23)= 61.73, p<.001, η^2_p =.73), indicating they could perform the task well in both perspective conditions.

From the logistic functions fitted to each individual participant's data, an average PSE was determined across participants for each perspective. For the 1PP condition, an average PSE of -14.01ms (SE=8.85) was observed, which did not differ significantly from zero (t(23) = -.86; p = .397). For the 3PP condition, an average PSE of 18.46ms (SE=8.85) was observed, which also did not differ significantly from zero (t(23) = 1.55; p = .134). Importantly, a repeated measures t-test demonstrated that there was a significant difference between the PSEs for the two perspective conditions (t(23) = -2.59; p = .016, *d*= .53). See Figure 3.3.

In terms of the spread of the data in Experiment 5, for the 1PP condition, an average spread of 239.30 (SE=18.85) was observed. For the 3PP condition, an average spread of 216.62 (SE=18.85) was observed. A repeated measures t-test demonstrated that there was no significant difference in the spread of the two perspective conditions (t(23) = .85; p = .403).

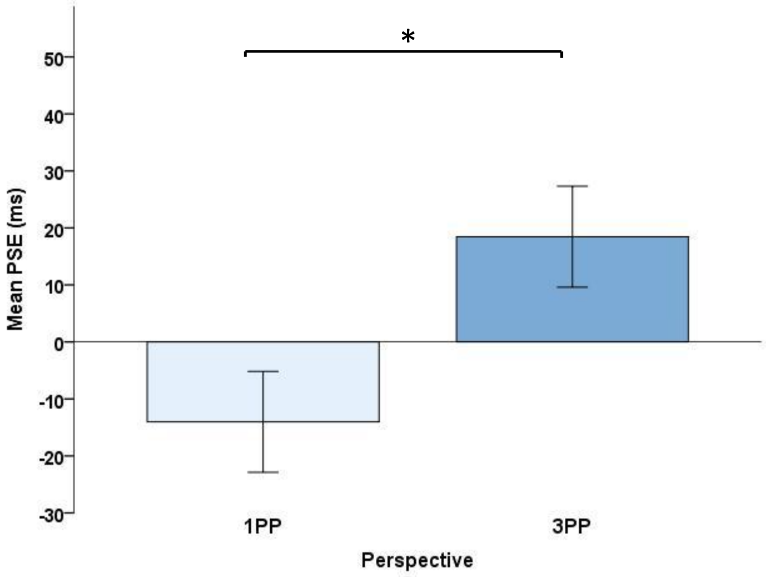

Figure 3.3. Bar graph depicting the mean point of subjective equality (PSE) for each perspective in Experiment 5. Light blue bars show the mean PSE for first person perspective (IPP) actions, dark blue bars show the mean PSE for third person perspective (3PP) actions. Error bars depict ±1 standard error. * < .05.

Experiment 5 examined the effect of motor priming when there was no concurrent visual input. It has essentially confirmed the findings of Experiment 4. Indeed, a 2 (perspective) x 2 (experiment) ANOVA contrasting Experiments 4 and 5 showed a highly significant main effect of viewpoint (F(1,46) = 15.57, p <.001, η_p^2=.25), but no main effect of experiment (F(1,46) =.28, p= .60), nor an interaction (F(1,46) = .02, p=.88). Thus, when participants have some motor experience of the actions to be subsequently judged there is a significant contrast between 1PP and 3PP viewed actions. That is, 3PP actions are simulated at a faster rate than 1PP actions and the latter tend to be somewhat more accurate.

3.4. CONTRASTING RESULTS ACROSS EXPERIMENTS

3.4.1. The point of subjective equality

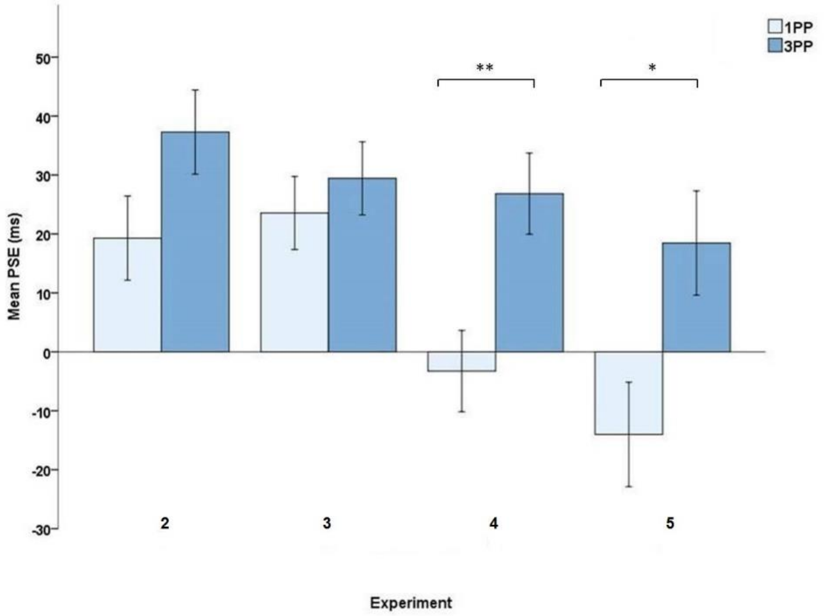

Figure 3.4. Bar graph depicting the mean point of subjective equality (PSE) for each perspective in each experiment. Light blue bars show mean PSEs for first-person perspective (1PP) actions, dark blue bars show mean PSEs for third-person perspective (3PP) actions. Error bars depict ±1 standard error. * < .05. ** = .005.

Figure 3.4 summarises the overall data pattern in terms of point of subjective experience (PSE) in the spatio-temporal judgement tasks across Experiments 2 to 5. We have noted, in line with previous research, the critical importance of motor experience in the simulation of actions. To further extract the pattern of performance across experiments we performed a combined analysis. This examined the effects of perspective (1PP vs 3PP) and the effects of motor priming (no motor priming vs motor priming). The latter involved the combination of Experiments 2 and 3 in the no motor priming condition and Experiments 4 and 5 in the motor priming condition. This 2 (perspective) x 2 (yes/no motor priming) ANOVA demonstrated no significant effect of motor priming. However, of central importance, there was a significant effect of perspective (F(1,94) = 17.61, p = .001, η_p^2=.16). That is, in all studies the spatio-temporal prediction performance in the 1PP condition tended to be more accurate than the 3PP condition, with the latter 3PP revealing simulation processes tending to be faster than the observed actions. However, this main effect of perspective was modulated by a marginally significant interaction between perspective and yes/no motor priming (F(1,94) = 3.53, p= .06, η_p^2=.04. Planned comparisons revealed that the 3PP judgements were not significantly influenced by whether participants experienced motor priming prior to the task (t(94) = .79, p=.43). However, in sharp contrast, there was a significant change in the accuracy of the 1PP temporal judgements, with significantly slower motor simulations after motor priming (t(94)=2.13, p=.034, *d*= .44). Figure 3.5 depicts these differences in the temporal prediction of action in 1PP and 3PP with and without motor priming.

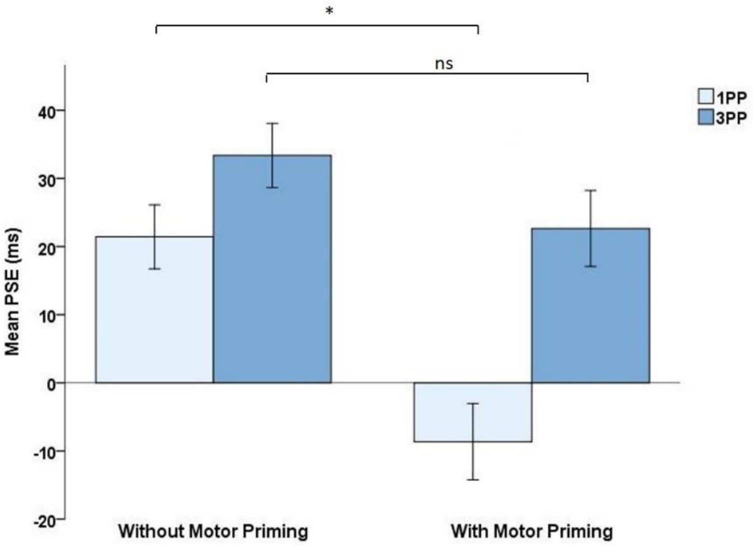

Figure 3.5. Bar graph depicting the mean point of subjective equality (PSE) for each perspective with and without motor priming. Light blue bars show mean PSEs for first-person perspective (1PP) actions, dark blue bars show mean PSEs for third-person perspective (3PP) actions. Error bars depict ±1 standard error. * < .05.

3.4.2. The slope of the psychometric function

In Experiments 1 and 2 in Chapter 2, the slope of the psychometric function averaged over participants did not significantly differ between first-person and third-person action perspectives. The same was demonstrated in Experiments 3 to 5. This was the case despite the motor priming with visual input (Experiment 4) or without visual input (Experiment 5), which did have the effect of differentiating the PSE between perspectives. As the slope of the psychometric function is generally used as a measure of sensitivity, it would indicate that participants' sensitivity did not change over experiments; that is, participants' sensitivity did not improve following motor priming. This would at first appear contradictory to the results demonstrated by the point of subjective equality. However, these apparently contradictory results simply indicate that despite a lack of change in sensitivity to the stimuli, participants do experience a change in perception. Specifically, the PSE is a measure of accuracy, related to the measure of central tendency, and provides a measure of constant error (in this case prediction error). On the other hand, the spread or slope of the psychometric function provides a measure of precision, more related to the standard deviation of the data and the variable error. The two are independent of one another. As such, this series of experiments has shown that participants are high in accuracy following motor priming, but participants' judgements are low in precision over the 5 experiments. Variable error does not vary appreciably with motor experience or changes in perception. Figure 3.6 summarises the overall data pattern in terms of slope of the psychometric functions in the spatio-temporal judgement tasks across Experiments 2 to 5.

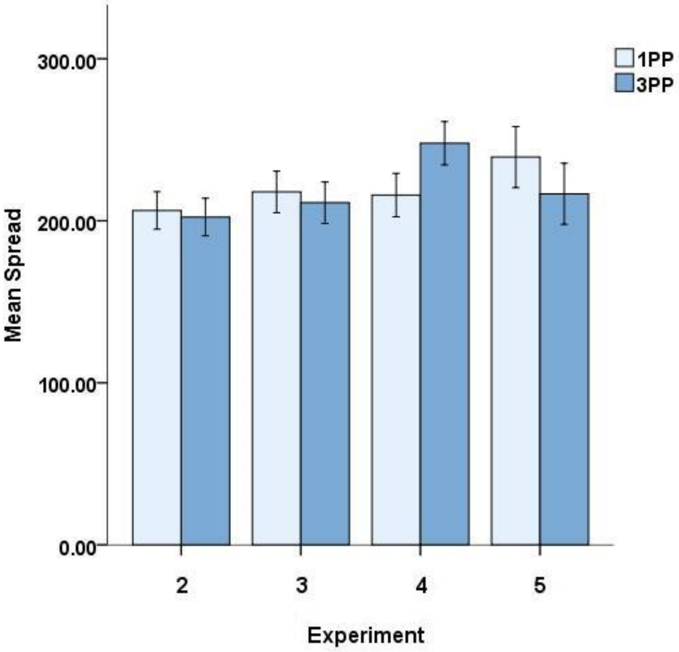

Figure 3.6. Bar graph depicting the mean spread of the psychometric functions for each perspective in Experiments 2 to 5. Light blue bars show the mean PSE for first person perspective (IPP) actions, dark blue bars show the mean PSE for third person perspective (3PP) actions. Error bars depict ±1 standard error.

3.4.3 Leave-One-Object-Out Analysis

To examine the individual effects of visual priming, visual and motor, and motor priming only on action prediction for each of the five objects used in each experiment, a leave-one-object-out (LOOO) analysis was performed on the data, as described in section 2.3.2.1 of Chapter 2. This aimed to determine whether the same pattern of results arises for each object type across experiments. The statistical analyses of the LOOO analyses are provided in Appendix B, and demonstrate that the same pattern in contrast in PSE between 1PP and 3PP observed action sequences was similar across transitive action type.

3.5 GENERAL DISCUSSION

There are a number of conclusions that can be drawn concerning the function and mechanisms of the action simulation processes, although our conclusions concerning the aetiology of the action observation network remain limited. The adaptation theory of the AON suggests that we recruit motor regions to create motor simulations of observed actions as a means to anticipate and interpret the actions of other people. That is, the account suggests the AON is a mechanism underlying action prediction that has evolved to facilitate social interaction (Rizzolatti & Arbib, 1998; Rizzolatti & Craighero, 2004). By this account we reasoned that when viewing 3PP actions that more closely match what would be perceived when observing another person, action timing judgements might be more accurate than when viewing 1PP actions. In all experiments we have found no evidence for this pattern. Indeed, even when 3PP actions were visually primed with real world reach and grasp actions that equated to the actions subsequently observed, 3PP actions gained no advantage (Experiment 3). In contrast, 1PP action timing judgments tended to be more accurate.

Although 3PP action prediction remained less accurate we do not rule out a role of the AON in the prediction of other people's actions. Indeed the forward prediction error observed for 3PP actions, indicating the simulation is further along the motion path, would enable compensation for any unpredictability in the actions of other people. In essence, as when intercepting a moving object over which we have no control, the motor system has to predict future states to place effectors appropriately for the objects arrival; then similarly, as we never have control over the final properties of another person's actions, forward prediction error would enable adjustments to be made. Thus, for an unfamiliar agent or action it would be more advantageous to slightly over anticipate, and we note the forward errors are small (< 40ms) enabling efficient interpersonal interactions.

However, it is worth noting that the observation that simulation processes for 3PP actions appeared to be somewhat faster than the actual observed action contrasted with previous similar studies (Sparenberg et al., 2012). That is, in the Sparenberg et al. (2012) study, motor simulation appeared to be slower than the actual actions. They additionally manipulated the occlusion duration and found the same negative bias (slower simulation than real action) for the different occluder durations, suggesting a stable time error. As a means to reconcile their findings with previous studies that suggest perception is predictive, the authors suggested this error may be due to a switching cost from a perception to a simulation mechanism. However, we suggest that it is worth considering the role of stimulus type, whether point light images, transitive vs intransitive, whole body vs single hand grasps, familiar vs unfamiliar, and whether the stimulus to be judged is static or a continuation of the action. As we have revealed with contrasts in viewpoint (1PP vs 3PP), further study of stimulus type may provide new insights into when and why action simulation processes are faster or slower than reality, and in turn when perception is necessarily predictive.

In contrast to the 3PP data, 1PP action prediction tended to be more accurate (closer to zero) in all conditions. Following the logic of Oberman & Ramachandran, (2008) and that the 1PP more closely matches the visual input when performing an action oneself, the results support the notion that action observation systems emerged to guide one’s own actions. At the least, the results would suggest that the system is less attuned to serving a social function as it is to providing an accurate state estimation for 1PP actions.

Of note, and in support of the idea that the system emerged for self action prediction, is that the contrast between 1PP and 3PP was most evident after motor priming, where participants received brief experience of grasping and lifting the objects in a manner similar to what would subsequently be observed (Experiments 4 & 5). It is striking that only minimal motor priming (4 reaches to each object) was sufficient to improve timing judgements. Our findings are in line with the literature clearly showing that it is prior motor experience/skill that influences motor simulation processes (e.g., Calvo-Merino et al., 2005) and that action prediction based on body kinematics is improved following motor practice (Urgesi et al., 2012). In particular, motor priming without any visual input (Experiment 5) is able to facilitate 1PP action judgements, and this result supports that of Casile & Giese (2005). The lack of contrast between Experiment 4, in which there was both visual and motor priming, and Experiment 5 in which there was only motor priming, might suggest that our effects were purely motor and vision played little role. However, we are cautious concerning this conclusion, as the condition examining purely visual observation of 1PP action without motor output was not possible in our current design. Thus it may yet be demonstrated that visual and physical experience may provide complementary and mutually reinforcing benefits to action prediction.

3.6 CONCLUSION

In sum, this series of experiments has demonstrated more than one property of the AON. The experiments examined the ability to make spatio-temporal judgements about future states of observed action. The ability to develop internal forward models of action and run an action simulation process is important to enable accurate visuomotor processes. It appears we have an anticipatory bias when observing actions of which we have little or no first-hand experience, but which reduces as we gain physical experience of these actions. Moreover, prediction differences can be observed between viewing action that closely matches our visual experience when performing an action (1PP) and that experienced when observing another person (3PP). The data confirm that motor priming has a selective effect on spatio-temporal prediction of 1PP rather than 3PP actions. This effect of motor priming, firstly, supports the theory that internal forward models of action and simulation processes draw upon one’s own motor representations, and secondly, supports the notion that the major role of such action simulation and prediction processes, and their underlying mechanisms (the AON), is to facilitate one’s own actions. This said, such action simulations can be extended to enable similar computations when observing another person’s actions, although they retain greater prediction error which may arguably have the social benefit of dealing with uncertainty and unpredictability of others.

CHAPTER 4: Neural Signals of Prediction Error for First- and Third-Person Observed Actions

4.1 INTRODUCTION

There has been an extensive amount of research examining the human neural network that underpins the observation of action, largely driven by evidence that the same network underpins action execution. This network is also thought to underpin action prediction mechanisms, which have been investigated more recently. Despite sustained interest in action observation and prediction processes and mechanisms, there remain several unexplored questions. One such question relates to the influence of visual perspective on neural activity during action prediction processing. Whilst behavioural studies indicate clear differences in performance for actions observed in different perspectives, to date little research has examined the effects of viewpoint during observation and prediction on neural activity.

In the previous chapter, we determined that only following motor experience (but not visual experience alone), spatiotemporal prediction of observed actions improves for transitive actions observed in a first-person perspective, but that this effect is not generalised to third-person perspective actions. The present study aims to determine whether such differences can be observed neurally, by examining evoked potentials in EEG using a similar paradigm as outlined in the previous two chapters.

4.1.1 Effects of visual perspective in behavioural studies

The effect of visual perspective during action observation on cognitive processes appears to be a salient one. Studies have demonstrated that actions presented in the first person perspective appear to have a processing advantage in visuotactile integration (Bach et al., 2014; Hoover &

Harris, 2012; Pavani et al., 2000); in action direction determination (Kelly & Wheaton, 2013); and participants' recall of task elements is superior when experienced in an egocentric perspective (Bergouignan et al., 2014; Lindgren, 2012).

The evidence suggests that 1PP observed actions have a processing advantage. This advantage is supported by single cell recordings demonstrating that within the macaque mirror neuron system more neurons in area F5 code for IPP than 3PP actions (Caggiano et al., 2011), which may tentatively be interpreted as mirror neurons having a bias for coding egocentric actions. FMRI has further demonstrated that the human homologue of this area, PMv, demonstrates crossmodal visuo-motor coding only for 1PP actions (Oosterhof et al., 2012).

4.1.2 Action Prediction and Visual Perspective

Studies have demonstrated that motor priming, or physical experience of actions, provides an advantage when predicting the consequences of observed actions (Aglioti et al., 2008; Cross et al., 2009; Urgesi et al., 2012), when recognising observed actions (Casile & Giese, 2006), as well as when predicting the spatiotemporal dynamics of observed actions, as demonstrated in the previous chapter. Developing on previous action prediction literature that demonstrated that we more accurately predict actions in the spatiotemporal domain when those actions fall within our own motor experience (Sparenberg et al., 2012), the studies presented over the previous two chapters provided the novel manipulation of presenting actions from different perspectives. These perspectives either mapped onto the visual input received when performing an action oneself, or were actions that could only be interpreted as another individual performing the action. The series of studies determined that only following motor experience, spatiotemporal prediction of observed actions improves for transitive actions observed in a first-person perspective, but that this effect is not generalised to third-person perspective actions. Such a result could suggest that action prediction mechanisms may not have evolved for the prediction and in turn interpretation of others' actions, as mirror neuron theory would posit (Rizzolatti &

Craighero, 2004), but have a much more self-relevant purpose, potentially in terms of motor control and kinematic adjustment. This said, a spatiotemporal anticipation bias was observed for third-person perspective actions, which persisted even following motor experience of the actions to be observed. We offered the interpretation that this may be a consequence of the system compensating for the added uncertainty of interacting with unfamiliar others or actions.

Our results may thus support the notion that prediction mechanisms for motor control may also serve the higher level cognitive function of social prediction, as has previously been postulated (Press, Heyes, & Kilner, 2011; Wolpert & Flanagan, 2001). However, whilst the predictive coding account of the AON (Kilner et al., 2007) (please see section 1.2.6 of Chapter 1) is based on minimizing prediction error, we suggest that if this same system is employed to predict and interact with others, then the forward or generative model may need to take into account the additional uncertainty of observing unfamiliar others, an uncertainty allowance, that is summed to our prediction based on our motor experience. This may have the ultimate consequence of the prediction error signal being reduced when observing others (which may lead to the anticipation bias we have observed in our previous behavioural studies). This current study aims to test just this, by examining the event related potentials (ERPs) associated in previous literature with expectancy violation following spatiotemporal incoherency compared to coherency in 1PP and 3PP observed actions.

4.1.3 EEG - Event Related Potential components in prediction

4.1.3.1 The observer Error Related Negativity - oERN

In terms of ERP components of interest associated with action monitoring and prediction violation, there are two potential candidates to examine: the observer Error Related Negativity (oERN) and the P300. Within the action monitoring literature, previous research has demonstrated a negative going deflection in EEG data at frontocentral sites following one’s own erroneous motor response, termed an error-related negativity (ERN), shown to peak approximately 100-200 ms following one’s own erroneous responses (Falkenstein et al., 1990; Gehring, Goss, Coles, Meyer, & Emanuel, 1993). More recently, a similar ERP component has been identified for observed action that is modulated by an observed actor’s response appropriateness. This observer Error Related Negativity (oERN) has been identified for observed erroneous responses in Go/No-Go tasks as well as Flanker tasks and has been shown to peak somewhat later than the ERN for one’s own errors (Koban, Pourtois, Vocat, & Vuilleumier, 2010; Bates, Patel, & Liddle, 2005; Miltner, Brauer, Hecht, Trippe, & Coles, 2004; van Schie, Mars, Coles, & Bekkering, 2004). Experimental design of these studies meant that it remained unknown whether the oERN reflected observed erroneous compared to accurate responses, or an observed violation of expected response. More recent work by Kobza & Bellebaum (2013), using a study design allowing prediction error of both correct and incorrect observed actor responses, demonstrated the oERN component reflects an action prediction error.

Source localisation analyses in previous studies of the oERN have found that the component’s topography and sources resemble that of the ERN, with medial prefrontal cortex (MPFC) and the anterior cingulate cortex (ACC) determined as the sources of the ERN (Dehaene, Posner & Tucker, 2004; Bellebaum & Daum, 2008; Gehring & Willoughby, 2002; Gentsch, Ullsperger, & Ullsperger, 2009; Holroyd et al., 2004; Miltner et al., 2004) and oERN components (Koban et al., 2012; Koban et al., 2010; Kobza & Bellebaum, 2013). The MPFC and ACC’s disinhibition to response error has been related to involvement in action monitoring to allow modification of performance, particularly in goal-directed actions (Holroyd & Coles, 2002). Kobza and Bellebaum’s (2013) work would suggest that the MPFC/ACC’s involvement in performance monitoring depends less on accuracy of actions, but on predictions and their violations.

Whilst previous studies have used typical Go/No-Go and Flanker paradigms, in this present study, we aim to examine whether the same oERN component can be identified in relation to predicted action violation when the observed action is unpredicted (incoherent) in terms of spatiotemporal dynamics of action. As in previous studies described in Chapters 2 and 3, participants observe transitive actions performed on tools after having actively performed those same actions prior to observation. Participants view the actions from 1PP and 3PP viewpoints. During the dynamic video sequences, the action is occluded from view for a period, after which the action continues again in a manner coherent with the occlusion duration, or from a point in time that is earlier than would be expected, or later than would be expected, given the occlusion duration and their expectation based on their own motor experience of the action.

We would hypothesise that the oERN would be evident for conditions in which the dynamics of the action continue from a point that is earlier or later than expected compared to when the action continues coherently after the occlusion period. In addition, we would predict that the oERN would be greater for first-person perspective actions compared to third-person perspective actions, if 1PP actions are more salient for the prediction system, and if the system predominantly subserves one's own action monitoring for kinematic adjustment.

4.1.3.2 The P300

The second ERP component of interest is the P300. This component is defined as a positive deflection of the event related potential that begins approximately 300 ms following stimulus onset or response onset. The component has been largely investigated with oddball paradigms, which involve detection of infrequent 'target' stimuli in a succession of frequent 'non-target' or standard stimuli. The P300 component is reliably elicited when a target stimulus as opposed to a non-target, is detected, irrespective of stimulus modality. The amplitude of the P300 is larger for unexpected than for expected outcomes (Linden, 2005), and typically increases in magnitude from the frontal (Fz) to parietal (Pz) electrode sites (Johnson, 1993). The P300 is believed to be a neural index of the mechanisms involved in updating internal representations of the environment to make an appropriate response (Polich, 2007).

Although innumerable studies have examined the P300 with the oddball paradigm, and associated it with detection of infrequent target stimuli, or unusual stimuli (Escera, Alho, Schröger, & Winkler, 2000), several authors have linked the P300 to the wider phenomenon of deviance detection, whereby the stimulus experienced deviates from a specific predicted outcome (Knolle, Schröger, & Kotz, 2013) . In our present study, we provide motor priming of the actions-to-be-observed, which may generate specific predictions about the spatiotemporal dynamics of the action. In such a case, any observed perturbations in these dynamics should be salient and elicit a prediction error. Here we examine whether such a prediction error can be observed as a P300 ERP component following spatiotemporal incoherence following the occlusion of the action.

In terms of perspective, there are two possibilities with regards to the P300. As in the Knolle et al. (2013) study, it is possible that the 1PP observed actions will generate greater P300 ERPs compared to 3PP observed actions if the 1PP can be thought of as more salient than the 3PP actions. However, as Knolle and colleagues also suggest (Knolle et al., 2013), the P300 ERPs may reflect the difficulty of computing prediction error. In this case we would expect predictions to be more specific for 1PP actions, whereas some prediction uncertainty would remain for actions observed in a third person perspective, requiring greater processing effort. Therefore if the processing of prediction errors is more efficient in detecting visual error in the 1PP, it will produce a reduced signal in this perspective compared to the 3PP that requires greater processing power. In such a case, a greater P300 response to spatiotemporally incoherent visual stimuli would be observed for the 3PP observed actions.

4.2 METHODS

4.2.1 Participants

Twenty-four participants (nine male) were recruited through the University of York, Department of Psychology participant pool. Participants were aged between 18 and 39 years (M=22.17, SD=5.24) and had normal or corrected-to-normal vision. They received a small payment or course credit in compensation for their time. Procedures were approved by the Department of Psychology Ethics Committee at The University of York.

4.2.2 Materials

For the biological actions, the same stimuli were used as outlined in Experiments 1 to 5 (please see Chapter 2, section 2.2.1.2). Here we note differences from previous stimulus presentation, the main one being the inclusion of a new non-biological (rolling ball) condition to control for low-level visual properties of the scene, such as upper and lower visual field presentation, but without human action properties. Each 1PP non-biological action sequence recorded comprised a small ball (2cm diameter) rolling towards an object at the centre of a table from a starting point at the inferior edge of the table, hitting the object, bouncing off the object and rolling back in the opposite direction. This rolling ball action was designed to match as much as possible the human reach-to-grasp actions. As for the biological action, sequences were recorded with five different objects: a mug, a wine glass, a hammer, a pair of scissors and a jug of water. From these non-biological template sequences in the 1PP, 3PP non-biological sequences were created by flipping the image about the horizontal axis.

Stimuli were recorded using a Panasonic full HD 1920x1080p (50p) Camcorder, mounted on a tripod. Action sequences were recorded from a bird's eye perspective, looking down onto a table covered with a black cloth. Recordings were edited using Sony Vegas Pro v10, which was used to trim the recordings so that each action sequence began with 300ms prior to the action beginning (i.e. prior to the ball or hand appearing and moving towards the object) and 300ms post-completion of the events. The software was also used to adjust the playback rate so that the length of each ball action sequence equated to the average length of the biological action with the same object over the male and female actor sequences. Actions were rendered at 60Hz.

4.2.3 Procedure

The experiment began with a *familiarisation phase*, followed by motor priming, and then a *practice phase,* before proceeding to the main *experimental phase*. In the familiarisation phase, participants viewed each template video (i.e. without occlusion) twice (once in each perspective), and were asked to simply observe. Practice trials were then presented, allowing participants to adjust their judgement. Trials presented in this practice phase were the temporally incoherent (Early / Late) conditions for each object in each perspective (gender of the hand was randomised for the biological actions), for each action type. 'Correct/Incorrect' verbal feedback was provided to participants at the end of each practice trial.

In the current experiment, after the familiarisation phase and before the practice phase, participants performed the transitive actions themselves, with eyes open. This procedure followed that employed in Experiment 4 of Chapter 3 (please see section 3.2.2.2 for details). Each action was performed four times on each of the five objects.

Experimental trials began with a fixation cross for 1000 ms. Following this, 1000 ms of the beginning of an action sequence was displayed. The action video was then replaced by the grey-scale occlusion image, presented for a fixed duration of 500ms. The occluder was then followed by the continuation of the action video until the end of the sequence. The point from which the action sequence continued post-occlusion was manipulated, so that the sequence continued either coherently with the occlusion duration, whereby 500ms were removed from the video sequence (the *Correct* condition); or with a temporal offset of ±300ms. The *Early* condition had 300ms less than the occlusion period removed from the video, whereas the *Late* condition showed the continuation of the video with 300ms more than the occlusion period removed from the video, such that the continuation of the action appeared to jump backwards (Early) or forwards (Late) compared to where the action would continue from if it were coherent with the occlusion duration.

Note that this is a significant reduction in the range of errors trials, where in previous studies there were 13 temporal offset conditions ranging from -200 to 200ms. This simplified design was felt to be more suited to the ERP method in order to reduce the duration of the experiment. This change probably results in less behavioural sensitivity to the error detection task, as noted in the Results section.

Participants were instructed to imagine the continuation of the action during the occlusion period. Once the action continued after occlusion, participants were requested to give a verbal response to indicate whether the point from which the action continued was temporally earlier or later than the actual action would be expected to be, given the occlusion period and the participant’s expectation. Participants were asked to provide their response on seeing a question mark presented for 2 seconds at the end of the action sequence.

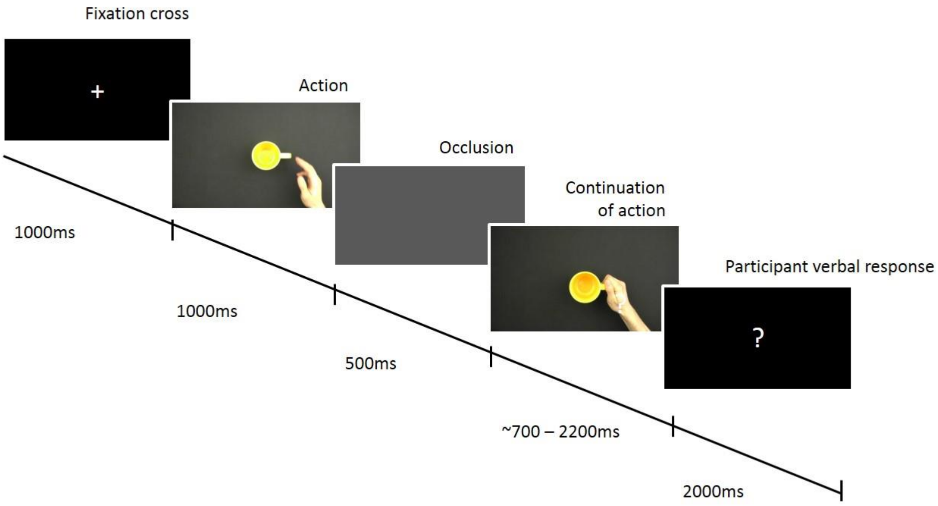

Figure 4.1. Schema of a trial in Experiment 6. Each trial began with a fixation cross for 1000 ms, which was immediately followed by 1000ms of the start of an action sequence. An occlusion screen was then displayed for a fixed duration of 500ms. The continuation of the action then followed until its completion, with the re-start being incoherent-early, incoherent-late, or coherent with the length of the occluder. At the end of the action sequence a question mark was presented for 2000 ms, during which time participants provided a verbal response as to whether they thought the action re-started from a point that was too early or too late.

The biological actions consisted of 300 trials in total; 150 trials in each of the 1PP and 3PP conditions, and 50 trials in each of the Early, Coherent and Late conditions per perspective. The 300 trials were divided into ten equal blocks (30 trials in each block). At the end of each biological action block, a non-biological (ball) action block was presented. Non-biological actions consisted of 150 trials in total; 75 in each of the 1PP and 3PP conditions, 25 in each of the Early, Coherent and Late conditions. These were also divided into ten equal blocks (15 trials in each block). A Non-Bio action block immediately succeeded a Bio Action block, and the 1PP and 3PP conditions were presented in alternate blocks (i.e. Bio 1PP, Non-bio 1PP, Bio 3PP, Non-bio 3PP etc.), which were counterbalanced between participants. Each Bio/Non-bio block began with 10 familiarisation trials in the perspective (1PP/3PP) corresponding to that block, which involved presenting the action sequence from beginning to end without an occlusion. At the end of the Non-Biological action block, a ‘Break’ screen was displayed, allowing participants to rest their eyes and to proceed to the next block when ready to do so.

4.2.4 EEG Recording

EEG data were recorded continuously from 64 Ag-AgCl electrodes, according to the International 10-20 system, using a Waveguard cap (ANTNeuro, The Netherlands) with active shielding and ANT-Neuro amplifier. In addition, data were also recorded from the left and right mastoids. The ground was located at site AFz. Electrode site impedances were kept below 10 KΩ. Data were sampled at a rate of 1000Hz and the data online referenced to the common average. To control for eye movements, bipolar vertical and horizontal electro-oculograms (VEOG/HEOGs) recorded blinks and saccades. Data were acquired using ASA (AntNeuro, The Netherlands) software.

4.2.4.1 Triggers

Event markers were coded within the experimental paradigm script in Python v.2.7 (www.python.org) and sent to the system amplifier. These event markers were located at three specific time points of interest: 1) the start of the action sequence, 2) the start of the occlusion period, and 3) the end of the occlusion period/start of the re-onset of the action post-occlusion.

4.2.5 ERP Preprocessing and Analysis

Preprocessing and analysis of the EEG data were conducted offline using Brain Vision Analyzer (BVA) software version 2.0 (Brain Products, Munich, Germany). The continuous data were high-pass filtered using an IIR filter (phase shift-free Butterworth filter) with a 0.1 Hz cut-off and low-pass filtered using a 30Hz cut-off with 24dB/Octave. Noisy or flat channels were identified visually and removed, or interpolated by spherical splines (Perrin, Pernier, Bertrand, & Echallier, 1989) if necessary. This topographic interpolation allows defective channels to be replaced by obtaining virtual EEG channel values based on real values, interpolating scalp potentials.

4.2.5.1 Epoch formation

Filtered data were then epoched into the conditions of interest using a time window of 800ms. For the ERP analysis, which focusses on the period post-occlusion to detect prediction error, data were epoched into a time window of -200ms to 600ms relative to the end of the occlusion period/re-onset of the post-occlusion action (the third trigger). Data were epoched according to Perspective (1PP/3PP), Offset (Early, Correct, Late), and Action Type (Biological Action/Non-Biological (Ball) action).

4.2.5.2 Artifact Rejection

Artifact rejection was performed in two steps. Firstly, muscle artifacts and significant eye movements were identified using semi-automatic artefact rejection, with a ± 75 μV/ms voltage step threshold, visually inspected and epochs containing artifacts rejected. Secondly, an ocular correction was performed using the Gratton and Coles (Gratton, Coles & Donchin, 1983) method without raw average subtraction to reduce or eliminate the effects of eye movements on the EEG.

For the biological action trials (300 in total, 50 per condition), the number of artifact-free trials analysed per participant ranged from 146 to 300 (M = 254.5, SD = 48.34). The number of trials included in the analysis did not differ across the 6 biological action conditions (F(5,115) = 1.61, p = .16). For the non-biological action trials (150 in total, 25 in each condition), the number of artifact-free trials analysed per participant ranged from 67 to 150 (M = 126.17, SD =23.72). The number of trials included in the analysis did not differ across the 6 non-biological (ball) action conditions (F(5,115) = 1.17, p = .33).

Averaged waveforms per condition were generated for each individual, to produce evoked potentials time-locked to the re-onset of action post-occlusion. Mean amplitudes in microvolts (μV) were calculated for the time-windows relating to the two ERP components of interest. Mean amplitude was defined as the difference between the mean baseline voltage in the time-window -

200 to 0 ms pre-stimulus onset and the mean amplitude in the time window 100-200ms post-occlusion (to assess the oERN), and the mean amplitude in time window 350-450 ms post-occlusion (to assess the P300).

Grand-averaged waveforms were generated across participants for each condition for visual inspection and to produce grand averaged evoked response plots.

4.3 RESULTS

4.3.1 Behavioural Data

Statistical analyses revealing Mauchley's test of sphericity was significant were Greenhouse-Geisser corrected. Participants produced monotonically increasing proportions of 'late' responses with increasing temporal offset for all action types and perspectives: 1PP Non-bio F(1.5,34.57)= 339.94, p<.001, η^2_p =.94); 1PP Bio F(2,46) = 268.31, p < .001, η^2_p = .92; 3PP Non-Bio F(1.2,27.56)= 394.03, p< .001, = η^2_p =.95; 3PP Bio F(1.4, 33.18) = 358.49, p< .001, η^2_p = .94. As in Chapters 2 and 3, logistic functions were fitted to each individual participant's proportion of 'late' responses for each of the Time Offset conditions, and an average point of subjective equality (PSE) was determined across participants for each perspective in each action type.

A 2 (perspective) x 2 (action type) repeated measures ANOVA demonstrated no significant effect of action perspective on prediction error (F(1,23) = 0.07, p = .80), indicating that the prediction error was similar for 1PP actions (M = 64.67, SE = 5.80) and 3PP actions (M = 67.47, SE = 5.28) . However, there was a significant main effect of action type on prediction error, F(1,23) = 5.46, p = .03, η^2_p = .19, with non-biological (ball) actions eliciting least prediction error (M = 57.58, SE = 5.27) compared to the biological actions (M = 74.56, SE = 5.54). There was no significant interaction effect between the viewing perspective and the action type on prediction error (F(1,23) = .19, p = .67). This indicates that the effect of action type was not modulated by the viewing perspective, or that the pattern of results in terms of perspective was similar for both the biological and the non-biological actions. Figure 4.2 depicts the mean prediction error for the two action types in the two perspectives.

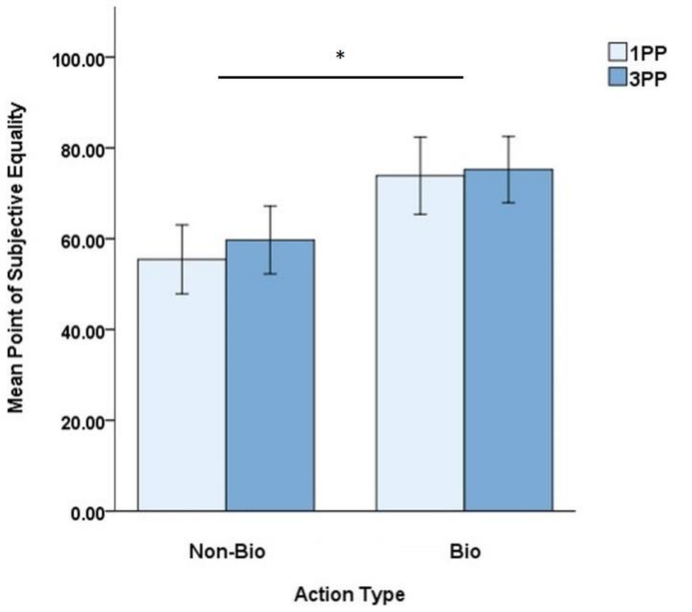

Figure 4.2. Mean point of subjective equality for each Action Type and each Perspective in the EEG study. Light blue bars depict 1PP action, dark blue bars show 3PP actions. * p < .05.

4.3.2 Electrophysiological Results

The amplitude of the oERN and P300 components were defined according to prior literature to determine unbiased a priori electrode sites for inspection, and following visual inspection of the grand-averaged waveforms to determine the time windows of interest. Previous ERP studies have shown that the oERN/ERN component is best recorded at frontocentral electrode positions (Falkenstein, Hoormann, Christ, & Hohnsbein, 2000; Holroyd & Coles, 2002; Nieuwenhuis et al., 2001, Koban et al., 2010). The P300 component has been reported as best recorded at more parietal midline sites Cz, CPz and Pz (Johnson, 1993: Polich, 2003).

Mean amplitudes (in microvolts) per individual per condition were calculated, defined as the mean voltage relative to baseline between 100 and 200 ms at electrodes Fz, FCz, and Cz for the oERN. For the P300, the mean voltage relative to baseline from 350 to 450 ms after re-onset of action post-occlusions was calculated at electrodes Cz, CPz and Pz.

4.3.2.1. EEG - Observer Error Related Negativity (oERN)

4.3.2.1.1. oERN - Non-Biological Action (Ball actions)

A repeated measures ANOVA was performed on the mean amplitude of the ERPs time locked to the re-onset of the action post-occlusion, averaged over electrodes Fz, FCz and Cz, within a time window of 100-200ms. Perspective (1PP, 3PP) and Time Offset (Early, Correct, Late) were set as main factors. The ANOVA importantly demonstrated that there was a non-significant main effect of perspective (F(1,23) = 1.23, p = .279). There was, however, a main effect of Time Offset (F(2,46) = 3.35, p = .044, η^2_p = .13), with Early conditions eliciting a greater negative amplitude (M = -1.79, SE = .14) compared to Coherent conditions (M = -1.44, SE = .11) and a significantly greater amplitude than Late conditions (M = -1.32, SE = .10). The Perspective x Time Offset interaction was non-significant (F(2,46) = .23, p = .80). Figure 4.3 shows the mean amplitude averaged over electrodes Fz, FCz and Cz for the Perspective and Time Offset conditions. Figures 4.4 and 4.5 depict the averaged waveform at electrode Fz, where the largest mean amplitude was recorded between 100-200ms following continuation of the action post-occlusion for the Perspective and Time Offset conditions.

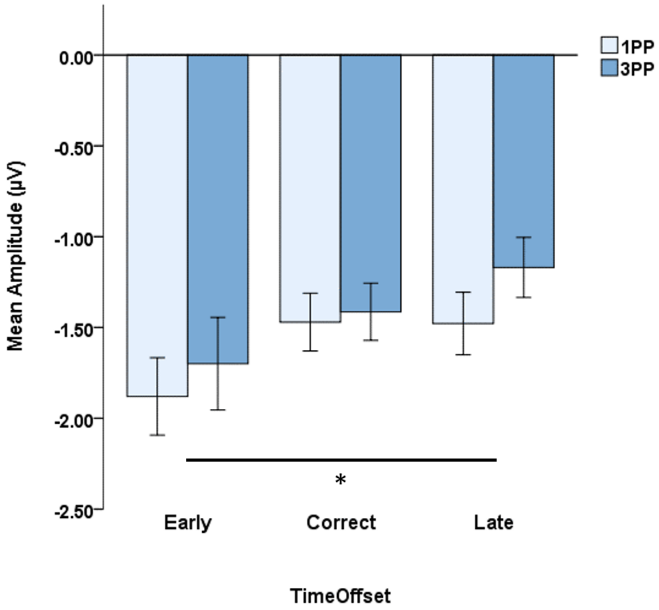

Figure 4.3. Mean amplitude (µV) for non-biological data averaged over electrodes Fz, FCz and Cz in the time-window 100-200 ms following re-onset of action post-occlusion for the two perspectives and three time-offset conditions. Error bars depict ±1 SE of the mean. * p<.05.

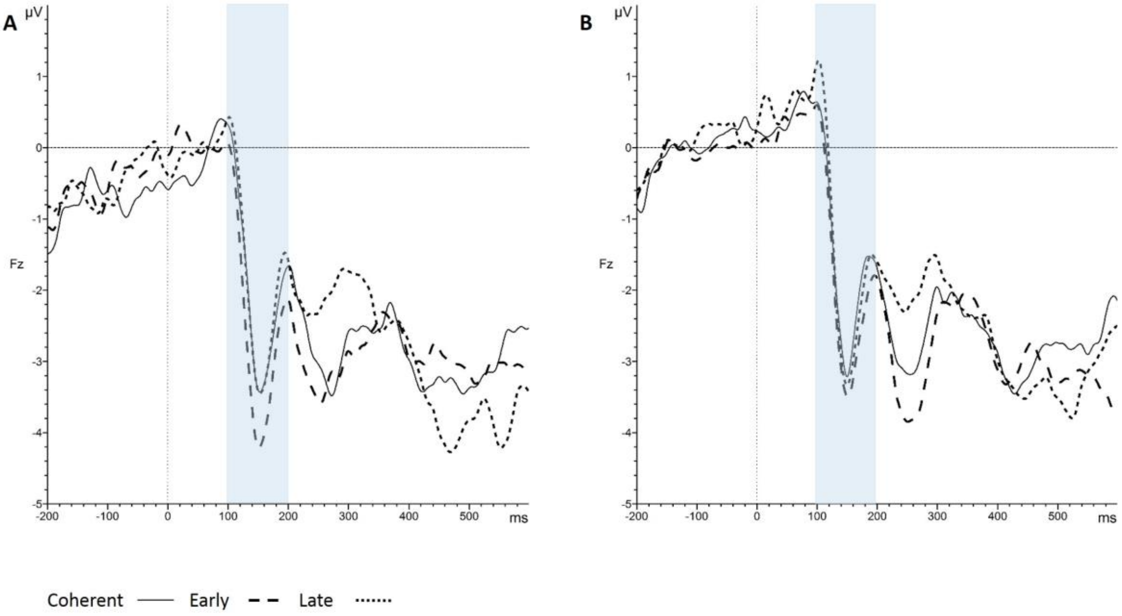

Figure 4.4 Grand averaged waveforms for non-biological action at electrode Fz for 1PP actions (A) and 3PP actions (B). Solid lines depict the Coherent condition, dashed lines the Early condition, and dotted lines the Late condition. Blue shaded area shows the time-window of interest for the oERN component.

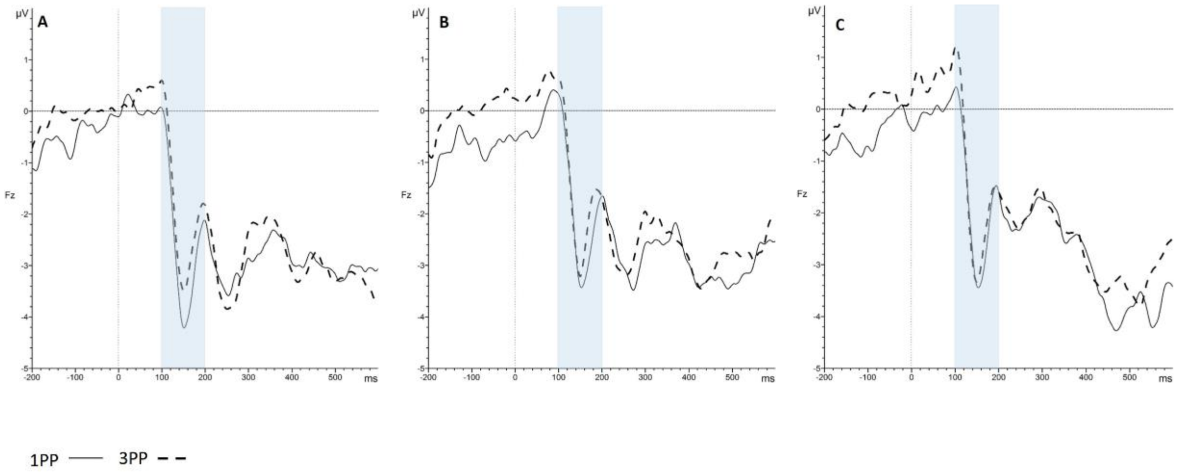

Figure 4.5. Grand averaged waveforms for non-biological action at electrode Fz for Early (A), Coherent (B) and Late (C) conditions. Solid lines represent 1PP actions, dashed lines 3PP actions. Blue shaded area shows the time-window of interest for the oERN component.

4.3.2.1.2. oERN – Biological Actions

A repeated measures ANOVA was performed on the mean amplitude of the ERPs time locked to the re-onset of the action post-occlusion, averaged over electrodes Fz, FCz and Cz, within a time window of 100-200ms. Perspective (1PP, 3PP) and Time Offset (Early, Correct, Late) were set as main factors. Importantly, there was a significant main effect of Perspective (F(1,23)=4.60,p=.043, =.17), with 1PP action eliciting a greater negative deflection overall (M = -1.45, SE = .24) compared to 3PP actions (M = -1.18, SE = .30). There was also a main effect of Time Offset (F(2,46)= 4.16, p=.022, η^2_p = .15), with Coherent conditions generating a greater negative deflection (M = -1.55, SE =.31) compared to both Early (M = -1.12, SE = .26) and Late conditions (M = -1.27, SE = .27). The Perspective x Time Offset interaction was non-significant (F(2,46) = 2.99, p = .06). Figure 4.6 shows the mean amplitude averaged over electrodes Fz, FCz and Cz for the Perspective and Time Offset conditions. Figures 4.7 and 4.8 depict the averaged waveform at electrode Fz, where the largest mean amplitude was recorded between 100-200ms following continuation of the action post-occlusion, for the Perspective and Time Offset conditions.

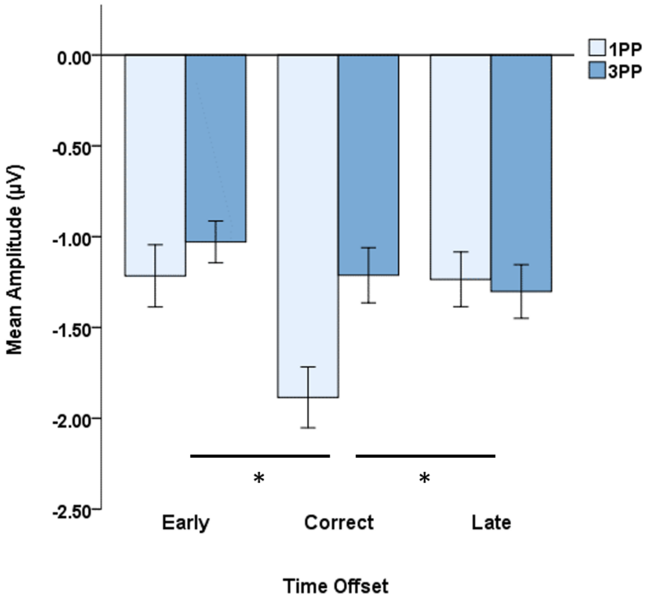

Figure 4.6. Mean amplitudes (µV) for biological data averaged over electrodes Fz, FCz and Cz in the time window 100-200 ms following re-onset of action post-occlusion for the two perspectives and three time-offset conditions. Error bars depict ±1 SE of the mean. * p<.05.

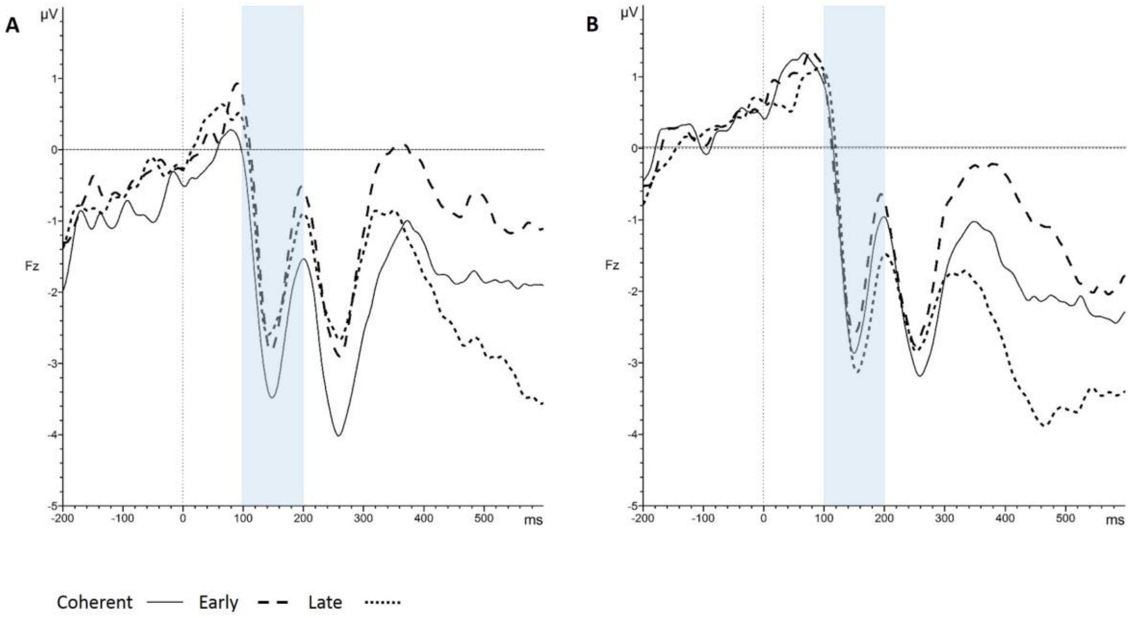

Figure 4.7. Grand averaged waveforms for biological action at electrode Fz for 1PP actions (A) and 3PP actions (B). Solid lines depict the Coherent condition, dashed lines the Early condition, and dotted lines the Late condition. Blue shaded area shows the time-window of interest for the oERN component.

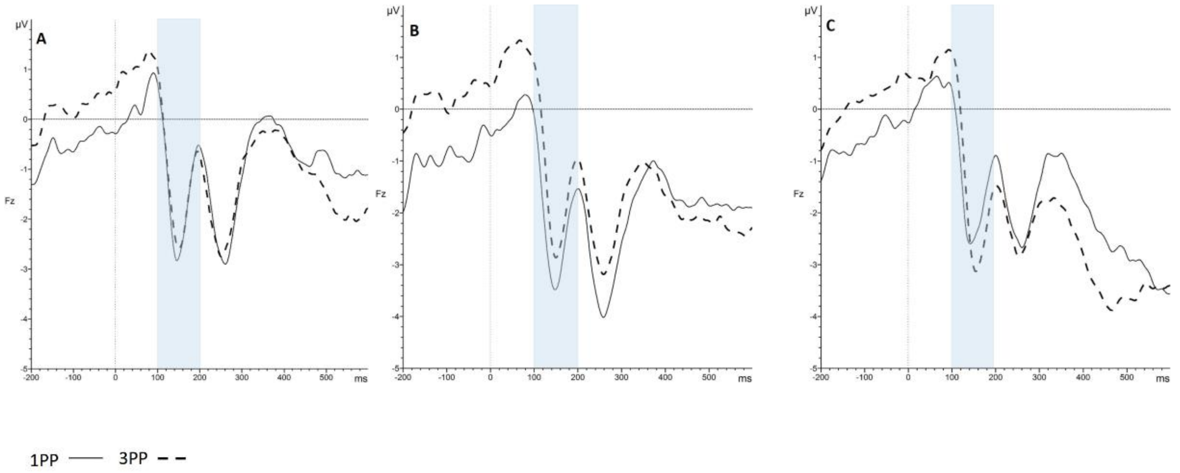

Figure 4.8. Grand averaged waveforms for biological action at electrode Fz for Early (A), Coherent (B) and Late (C) conditions. Solid lines represent 1PP actions, dashed lines 3PP actions. Blue shaded area shows the time-window of interest for the oERN component.

4.3.2.2. EEG - P300

4.3.2.2.1. P300 - Non-Biological (Ball) action

A repeated measures ANOVA was performed on the mean amplitude of the ERPs time locked to the re-onset of the action post-occlusion, averaged over electrodes Cz, CPz and Pz, within a time window of 350-450ms. Perspective (1PP vs 3PP) and Time Offset (Early, Correct, Late) were set as main factors. Importantly, there was a non-significant effect of Perspective (1PP M = 1.37, SE = .12; 3PP M = 1.39, SE = .12; F(1,23) = .008, p = .928). A significant main effect of Time Offset was observed (F(2,46) = 10.309, p < .001, η^2_p = .31), with both Early (M = 1.43, SE =.17) and Late conditions (M = 1.91, SE = .16) generating significantly greater mean amplitudes compared to the Coherent condition (M = .81, SE = .13) (Early – Coherent p=.01; Late – Coherent p < .001). The Perspective x Time Offset interaction was non-significant (F(2,46) = 1.85, p = .17). Figure 4.9 shows the mean amplitude averaged over electrodes Cz, CPz and Pz for the Perspective and Time Offset conditions. Figures 4.10 and 4.11 depict the averaged waveform at electrode Pz, where the largest mean amplitude was recorded between 350-450ms following continuation of the action post-occlusion, for the Perspective and Time Offset conditions.

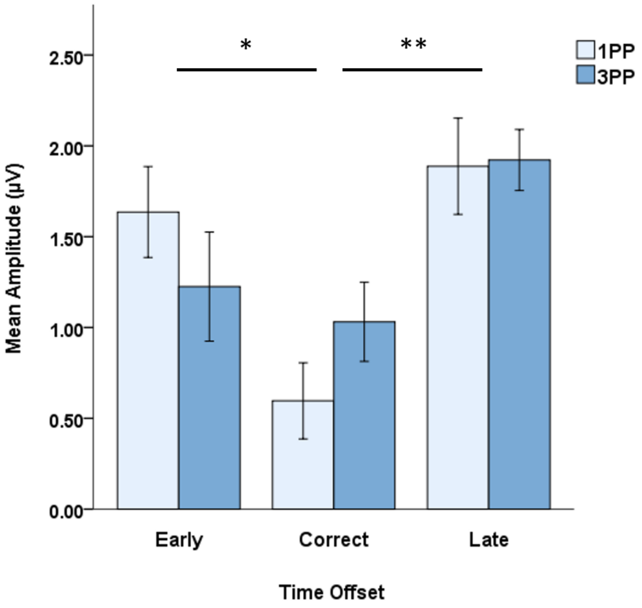

Figure 4.9. Mean amplitudes (µV) for non-biological data averaged over electrodes Cz, CPz and Pz in the time window 350-450 ms following re-onset of action post-occlusion for the two perspectives and three time-offset conditions. Error bars depict ±1 SE of the mean. * p =.01. ** p = .001.

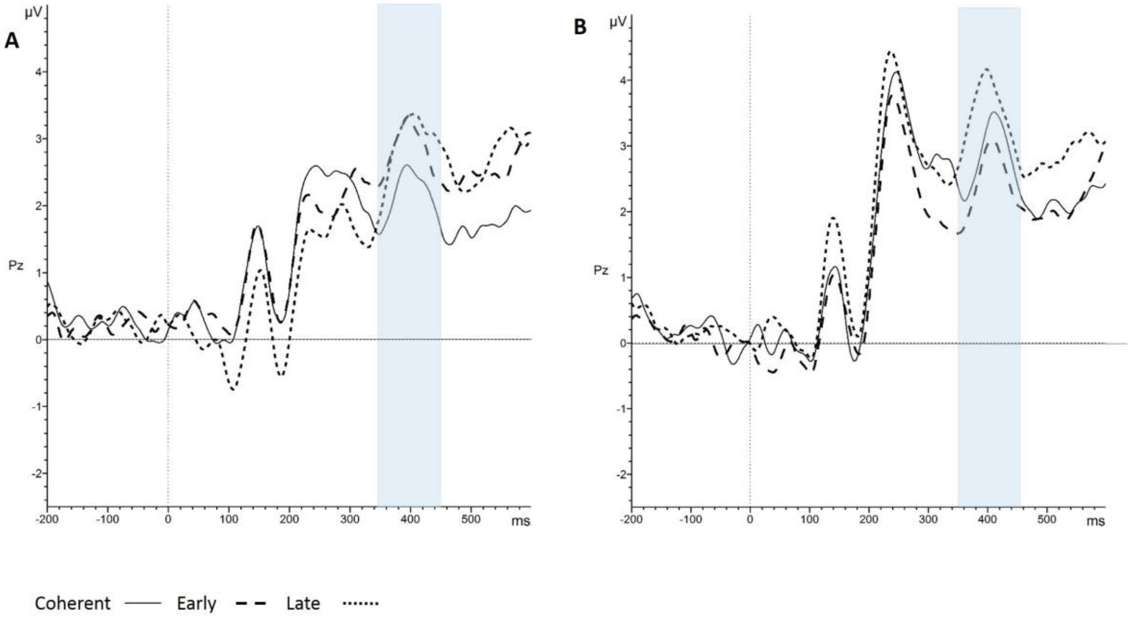

Figure 4.10. Grand averaged waveforms for non-biological action at electrode Pz for 1PP actions (A) and 3PP actions (B). Solid lines depict the Coherent condition, dashed lines the Early condition, and dotted lines the Late condition. Blue shaded area shows the time-window of interest for the P300 component.

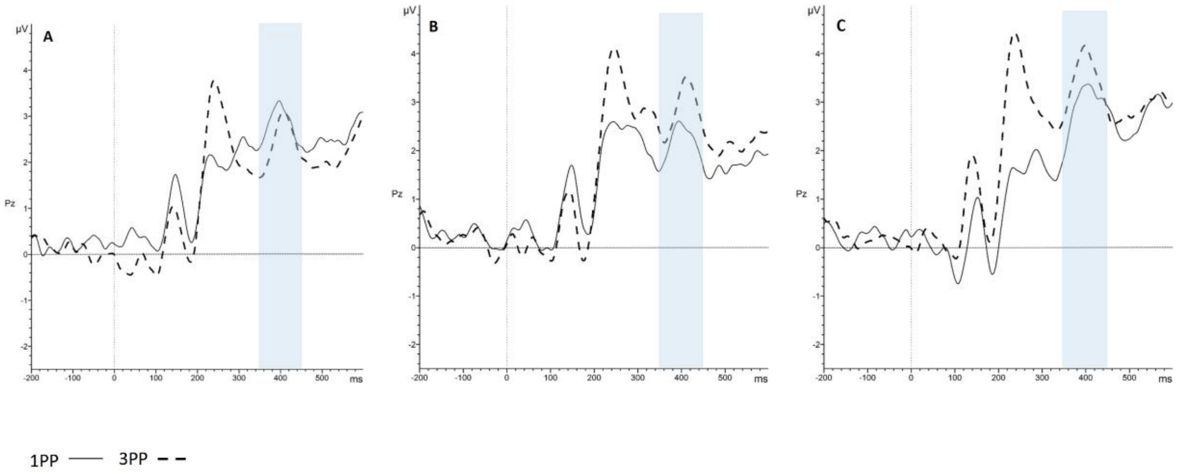

Figure 4.11. Grand averaged waveforms for non-biological action at electrode Pz for Early (A), Coherent (B) and Late (C) conditions. Solid lines represent 1PP actions, dashed lines 3PP actions. Blue shaded area shows the time-window of interest for the P300 component.

4.3.2.2.2. P300 – Biological Action

A repeated measures ANOVA was performed on the mean amplitude of the ERPs time locked to the re-onset of the action post-occlusion, averaged over electrodes Cz, CPz and Pz, within a time window of 350-450ms. Perspective (1PP vs 3PP) and Time Offset (Early, Correct, Late) were set as main factors. The ANOVA demonstrated a significant main effect of Perspective ($F(1,23) = 9.41$, $p=.005$, $\eta^2_p = .29$), with 3PP actions generating a greater P300 mean amplitude ($M = 1.73$, $SE = .09$) than 1PP actions ($M = 1.22$, $SE= .09$). A significant main effect of Time Offset ($F(2,46) =18.89$, $p<.001$, $\eta^2_p = .45$) was also observed. Contrasts revealed significantly greater P300 mean amplitudes for the Early ($M = 1.64$, $SE = .13$) compared to the Coherent condition ($M = .84$, $SE = .09$), and for the Late ($M = 1.94$, $SE = .13$) compared to Coherent condition (both $ps < .001$), and no significant difference between the Early and Late conditions. A significant Perspective x Time Offset interaction was also observed ($F(2,46) = 5.64$, $p = .006$, $\eta^2_p = .20$). Figure 4.12 shows the mean amplitude averaged over electrodes Cz, CPz and Pz for the Perspective and Time Offset conditions. Figures 4.13 and 4.14 depict the averaged waveform at electrode Pz, where the largest mean amplitude was recorded between 350-450ms following continuation of the action post-occlusion, for the Perspective and Time Offset conditions.

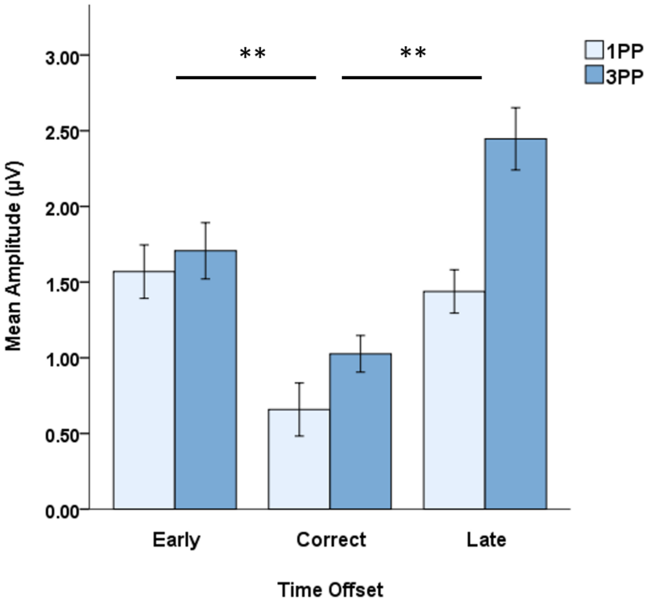

Figure 4.12. Mean amplitudes (µV) for biological data averaged over electrodes Cz, CPz and Pz in the time window 350-450 ms following re-onset of action post-occlusion for the two perspectives and three time-offset conditions. Error bars depict ±1 SE of the mean. ** p < .001.

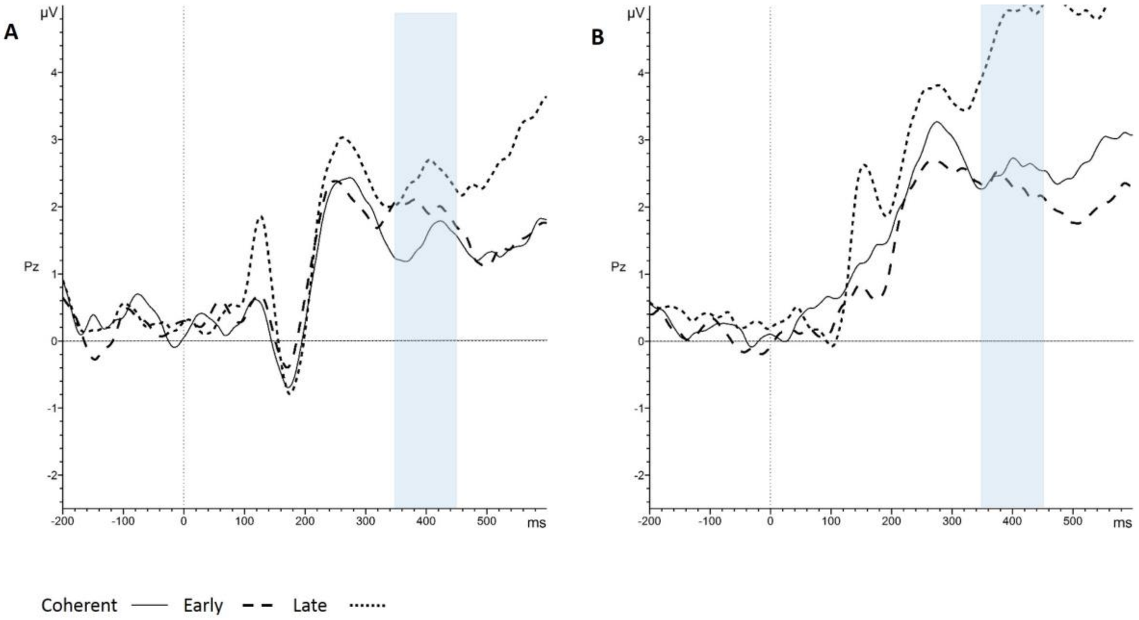

Figure 4.13. Grand averaged waveforms for biological action at electrode Pz for 1PP actions (A) and 3PP actions (B). Solid lines depict the Coherent condition, dashed lines the Early condition, and dotted lines the Late condition. Blue shaded area shows the time-window of interest for the P300 component.

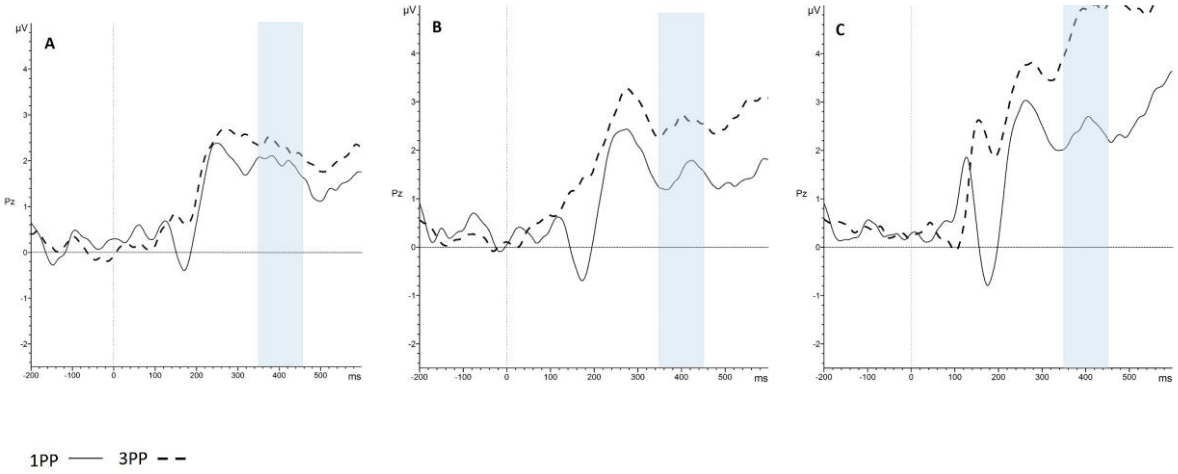

Figure 4.14. Grand averaged waveforms for biological action at electrode Pz for Early (A), Coherent (B) and Late (C) conditions. Solid lines represent 1PP actions, dashed lines 3PP actions. Blue shaded area shows the time-window of interest for the P300 component.

4.4. DISCUSSION

4.4.1. Behavioural Data

The results from the behavioural data of the biological actions were unexpected as they do not replicate the findings from the previous behavioural study that examined action prediction following motor priming with eyes open (Experiment 4, Chapter 3). There are two principal differences in results compared to Experiment 4: The motor priming (with concomitant visual input) in Experiment 4 demonstrated a significant difference in action prediction between the two frames of reference, with prediction being much closer to accuracy for 1PP actions, compared to prediction of 3PP actions, whereas in this present study we find no difference in prediction accuracy for 1PP and 3PP biological action following the same type of motor priming with eyes open. Furthermore, action prediction accuracy is much worse for both 1PP and 3PP actions in this current study (Experiment 6) compared to Experiment 4 (~70ms difference for 1PP, and ~50ms for 3PP actions). There are a couple of differences between Experiment 4 and this present experiment which may contribute to these observed differences in results:

Firstly, in the current study, only three temporal offset conditions were used, with intervals of 300ms (-300ms, 0ms, +300ms). In sharp contrast, previous experiments involved 13 temporal offsets with intervals of just 33ms (intervals of almost ten times smaller) in order to sample finely over the psychometric function. Two temporal offsets (three temporal conditions in all) were used in this current experiment in order to keep the experiment duration to a minimum whilst also interrogating prediction of non-biological action. However, a reduced resolution along the psychometric curve would mean we can be less precise about the extent of the prediction error in this experiment. Thus, the elevated prediction error observed in this study compared to Experiment 4 may not be due to poorer performance on the part of this group of participants, but more related to the reduced sensitivity of the experimental design to examine the behavioural data.

Secondly, this present study included additional conditions of non-biological ball actions in both perspectives. The non-biological actions observed alternately between transitive action blocks may have facilitated prediction mechanisms for biological action in the 3PP, or hindered prediction mechanisms for 1PP actions, and thus contribute to the lack of difference in prediction performance for these biological actions. That is, including new conditions in a within-participants design can produce interactions between conditions, changing previous observations (see influential companion effects, Poulton, 1982).

4.4.2. Electrophysiological Results

4.4.2.1 Non-biological (ball) data

With regards to the non-biological (ball rolling) actions, we observe that in contrast to the biological actions, there were no differences between perspective conditions in mean amplitude of components at either the 100-200 ms or 350-450 ms time windows. This is likely due to such an action not being mapped onto one's own body movement schema. When processing the observation of non-biological action, the viewpoint may be less relevant, as the action is always being generated by an external entity; the action, whether it start from the inferior or the superior edge of the table, will be processed in much the same manner. The kinematics of such action cannot be emulated through the same processes as observing human biological action as we have no motor experience of moving in the manner of a rolling ball. As such, any deviation from the expected spatiotemporal dynamics of the action may be processed equally for actions originating from upper and lower regions of the screen.

If we are unable to draw upon our own motor experience for simulation of non-biological action, this could raise the question as to why we see in the behavioural data increased prediction accuracy for the non-biological compared to biological actions. However, it is important to note that the kinematics of non-biological action are much simpler than biological action. The trajectory of non-biological action is generally linear and speed remains constant, whereas biological action is more varied, with the kinematics of the action changing and slowing as a hand approaches closer to a target object, and the grasp varying with the target object shape, weight and complexity of fine-grain motor adjustments required to lift the object.

Importantly, the non-biological action results support an interpretation of the biological action in terms of the visual mapping of self- (1PP) and other-generated (3PP) action, rather than any differences observed being as a consequence of upper and lower visual field processing.

4.4.2.2 Biological data

4.4.2.2.1 Observer Error Related Negativity (oERN)

The results from the oERN ERP analysis indicate that a greater negative deflection was observed for 1PP actions compared to 3PP actions at re-onset of the action post-occlusion, as might have been predicted. However, surprisingly, the oERN analysis demonstrated that, unlike the predicted effect of the Early and Late conditions generating larger negative deflections than the Correct condition, whereby the action follows the occlusion in a spatiotemporally coherent manner, instead we observe a greater negative deflection for the Coherent trials compared to the Early and Late conditions. The non-significant perspective x time offset interaction indicated that this pattern was maintained for both the 1PP and 3PP actions. This was an unpredicted result as the oERN literature would suggest that a deviance from an expected outcome would elicit a greater negative-going deflection compared to an expected outcome (Koban et al., 2010, Koban et al., 2012; Kobza et al., 2013). We observe in this instance a reversal of such findings, whereby the coherent condition trials generate a larger error signal than the incoherent conditions.

To interpret this finding we have to consider the paradigm used and the participants' task. Following the same paradigm as in the previous behavioural studies, using psychophysics, participants were required to provide an 'Early'/'Late' response to every trial, including trials that were spatiotemporally coherent. The greater amplitude observed for coherent trials compared to incoherent trials may therefore indicate a response conflict between that which participants observe to be correct/as expected, and simultaneously being required to provide an inconsistent response with their observation (which would equate to an erroneous response). The visual input for the coherent trials is incompatible with the task requirement. The greater negative deflection may therefore be more associated with a response conflict. Although the response has not yet been provided at this point in time, participants may unconsciously already have experienced a response conflict in preparation for providing their vocal response. The latency of the observed component also resembles the latency of the ERN, shown to peak between 100-200 ms (Gehring et al., 1993), more than the oERN which generally has a slightly delayed latency. We would like to posit that the greater negative deflection for Coherent compared to Incoherent conditions may thus indicate a response conflict associated with the preparation of an inconsistent/erroneous response compared to what is observed and what the participant wishes to respond.

Examining the main effect of perspective in light of the above, the results are as would be predicted if 1PP actions are more salient than 3PP actions, and furthermore are in line with previous studies that have demonstrated greater deflections for self-generated deviants as opposed to externally-generated deviants (Knolle et al., 2013) and greater N100 suppression effect for self- compared to externally-generated/unpredictable sounds (Knolle, Schröger, Baess, & Kotz, 2012).

Although the 1PP actions visually presented to participants are not self-generated, the visual input of 1PP action maps closely onto what would be perceived when performing an action - it has higher visuospatial congruence between a viewer’s own action and the observed sequence. As such, we would postulate that the neural signals of prediction and expectancy violation are not only observable with the typical Flanker or Go/No-Go tasks, but are also evident in this novel paradigm. That is, EEG has identified some of the neural systems that mediate the processes of spatiotemporal prediction of observed action. More importantly, the data show that the error signal is more prominent when viewing 1PP than 3PP actions, supporting our notion that these mechanisms are important for action monitoring for self-related actions (in order to make necessary adjustments in time and space), more than for the monitoring of others' actions.

4.4.2.2.2. P300

The results of the P300 ERP analysis on the biological action data revealed a greater positive deflection for Early and Late time offset conditions compared to the Coherent condition. That is to say, when the action post occlusion continued from a point that was spatiotemporally inconsistent with the real action dynamics, a greater P300 ERP response was recorded compared to when the action continued from a spatiotemporally coherent point in time. This result was as predicted. A large body of research examining effects on the P300 have used established paradigms, such as the Flanker task or a Go/No-Go task, and have interpreted the P300 in terms of the ERP being a neural signature of deviance detection, elicited by rare or unusual stimuli (Escera et al., 2000). More recently, studies have demonstrated that the P300 may be responsive to prediction error (Knolle et al., 2012). These studies are, however, limited in their interpretation by the paradigm that they employ. By using a paradigm not used previously to examine the P300, we again find that the P300 would appear to be responsive to prediction error. Previous literature associates the P300 to memory processes, enabling the access to representations held in short term memory to make comparisons between the deviant stimulus observed and the standard stimulus. We may interpret our present results in the same way, as participants make comparisons between the visual stimulus observed and their internal representation of action dynamics, with this representation potentially being drawn from the recent motor experience of the very actions being observed.

In terms of the central issue of perspective, we find that the greater P300 amplitude is elicited for third-person perspective observed actions compared to first-person perspective actions. Two opposing accounts of what mechanisms the P300 reflected were discussed previously. The first account assumed that if the neural system underpinning action prediction is more attuned to processing 1PP actions, as behavioural studies in previous chapters indicate, then greater P300 amplitude would be observed for temporally incoherent conditions in the 1PP compared to the 3PP. A greater prediction error signal would be observed as the 1PP actions would be more salient. This hypothesis was made following the logic of previous literature (e.g. Baess, Jacobsen, & Schröger, 2008; Knolle et al., 2013). However, the second account proposed that the P300 amplitude can reflect the difficulty of a computation. It is largely assumed that the amount of effort, and in turn neural resources, allocated to a task is determined by the difficulty or task load (Gopher & Navon, 1980; Kahneman, 1973). As task difficulty determines the extent of resource allocation it leads to higher physiological costs. In fMRI research, the hemodynamic response measured (the blood oxygenated level dependent (BOLD) response) reflects energy use by neurons and therefore a reduced BOLD signal may reflect increased processing efficiency (Huettel, Song, McCarthy, 2009). In line with this, we would predict that the processing of fine-grained temporal properties of an action would be harder for 3PP than 1PP, and hence P300 would be greater for the former than the latter. This is the result that has been observed in the current study. The results may suggest that the task related to 3PP actions makes greater demands on the processing system.

This result and interpretation does contrast with the earlier oERN response observed at 100-200 ms where we observe a greater negative deflection for first compared to third-person perspective actions. We would suggest that the neuronal processing within these different time-windows varies in terms of the level of conscious processing of the stimuli. That is, early ERP components are considered exogenous components, varying with the physical properties of stimuli and reflect automatic processing; whereas later ERP components (such as the P300) are endogenous components, reflecting more conscious higher level cognitive processing of the stimuli (Brandeis & Lehmann, 1986; Portella et al., 2014). As such the perspective of the observed action may be processed in discreet ways within the two time-windows of interest in the current study. In this study, the earlier component may reflect pre-awareness detection of a conflict, whereas the P300 may relate to the processing and comparison of the observed stimuli with internal representations of expected action dynamics, which may account for the greater oERN amplitude for 1PP compared to 3PP actions, but a greater P300 amplitude for 3PP compared to 1PP actions, as more processing resources are required for 3PP in the case of the later P300 time-window.

4.5 CONCLUSION

In this EEG study, evoked potentials were examined following the re-onset of action dynamics post occlusion that were temporally coherent or incoherent with the occlusion period. Biological transitive actions and non-biological (ball rolling) actions were presented in the first-person and third-person perspectives. The results of the non-biological data, employed as a control condition, allow the biological action data to be interpreted in terms of visual mapping of self- vs other-generated actions, rather than differences being due to lower vs upper visual field processing. The study demonstrated greater amplitudes in the 100-200ms time window post-occlusion for 1PP compared to 3PP actions when there was a conflict between that observed and the response requirement. This may suggest that 1PP actions, or self-generated actions, are more salient for the action monitoring system. Further support for this suggestion is provided by the later ERP component, the P300, the amplitude of which was greater for incoherent conditions compared to the temporally coherent condition. Although in this instance the P300 amplitude was reduced for 1PP compared to 3PP actions, there is evidence to suggest that this may reflect a processing advantage in the higher cognitive process of comparing visual inputs to an internal representation. The observed results may support the notion that the mechanisms underlying action monitoring and prediction are more attuned to self-related actions than for the prediction of others.

CHAPTER 5: Spatiotemporal prediction of actions with a coincidence anticipation task

5.1 INTRODUCTION

In the behavioural studies set out in Chapters 2 and 3, spatiotemporal prediction of action was interrogated with psychophysics methods. In the current chapter we again wish to interrogate spatiotemporal prediction processes, but via the use of an alternative paradigm. The chapter aims to determine whether the results of the previous behavioural studies are replicated under different task requirements of the participants, using response time as the principal measure. More specifically, the chapter aims to i) examine spatiotemporal prediction of actions presented in first- and third-person perspectives with the use of a coincidence anticipation (response time) task; ii) examine the effect of motor priming on action prediction in relation to response time.

Previous studies discussed in this thesis so far have examined action prediction with a spatiotemporal judgement task. This involved participants making a perceptual judgement of whether an observed action state was spatiotemporally too early or too late in its transition following occlusion compared to an expectation. Such a task may be considered an abstract manner of interrogating prediction mechanisms in that in order to make a judgement, a comparison must be made between the perceived action and the participant's internal action schema. Additionally, the action post-occlusion is spatiotemporally manipulated to be coherent or incoherent with the length of the occlusion. Such action dynamics, in the incoherent conditions, are highly unlikely to occur in the real world, and participants' task of making abstracted judgements would not be required in a real-life context. It may be argued, therefore, that the results of the previous studies may be a consequence of the experimental lab manipulation, which in turn lack real world ecological validity (Neisser, 1976).

In fact, if we consider the actions which would necessitate the use of anticipation or prediction mechanisms in a real world context, interceptive actions such as those performed in sporting activities, and coincidence timing as we see in cooperative interactions, are some of the tasks that would draw on these mechanisms, each of which involves a simultaneous corresponding motor act during perceptual processing of dynamic information. If dorsal perceptual systems are, as has been argued (Milner & Goodale, 1995; Goodale & Haffenden, 1998), primarily for action purposes, then ideally to interrogate action prediction we would use a paradigm that allows participants to act in response to the action being observed, as would be the case in a natural context. In support of this, studies have demonstrated that the timing precision observed in sporting experts' interceptive abilities is apparent only through perception and movement control linkages (Farrow & Abernethy, 2003).

An alternative method therefore would be to aim to more directly tap into the mechanisms and motor codes employed to perform an action when observing it. An alternative paradigm to the judgement task of previous chapters may thus entail the participant performing a similar lift action to the lift movement observed when the object is lifted from the table. Thus, with a change in task, participants task performance more readily draws upon the movement kinematics (to some degree) required to perform the action being observed.

The large majority of studies examining temporal aspects of action prediction to date have used similar paradigms to those used in our previous studies; that is, using a judgement task with participants determining whether the action was a coherent continuation of the action sequence or not post-occlusion, or whether the action was too late/too early in two-alternative forced choice tasks (Graf et al., 2007; Parkinson et al., 2011; Prinz & Rapinett, 2008; Sparenberg et al., 2012). Among the action prediction literature, a limited number of studies utilise response time or a motor act as a measure of prediction accuracy (Bootsma, 1989; Cross, Stadler, Parkinson, Schütz-Bosbach, & Prinz, 2011b).

Despite few studies using reaction time to examine action prediction, there may be good reason to examine spatiotemporal prediction with different task requirements, particularly with regards to lab only based manipulations. In essence, a perceptual judgement task removes the perception and action coupling that is inherent within natural anticipation performance in situ. Starkes et al., (1995) aimed to determine the effects of expertise on action prediction in a more natural context as opposed to a lab-based testing environment. They examined prediction of the landing location of volleyball serves, with players' vision of different time points of the serve being occluded with liquid crystal occluding glasses (Milgram, 1987)[5]. This natural setting study replicated lab-based experiments that had used film sequences (Wright et al., 1990). Both studies demonstrated that experts had superior spatial prediction ability than novices. However, in the Starkes et al. (1995) study, participants made their predictions from a static position, providing a verbal response, and thus despite the natural setting, the study did not require the more ecologically valid response of providing the motor act required to return the serve. A later study, with squash players (Abernethy, Gill, Parks, & Packer, 2001), aimed to do just this, maintaining the perception-action coupling as much as possible. Abernethy (2001) requested players to continue playing their shot despite visual occlusion. This natural setting study also replicated the lab-based experiments demonstrating that superior expertise produced superior prediction abilities.

Yet, these studies did not directly compare prediction between coupled and uncoupled perception-action responses. Thus, in a subsequent study, Farrow and Abernethy (2003) demonstrated that different perceptual processes may be engaged during anticipation tasks that depend on factors including the expertise of the observer and, importantly for the purposes of this chapter, the degree of perception-action coupling inherent in the task requirements. The

---

[5] Crystal occluding glasses allow vision to be occluded for transient periods of time, with onset/offset of occlusion controlled by the experimenter with remote activation.

authors directly interrogated the effects of making judgements (providing a verbal response) in contrast to providing a motor response. Similar to the Starkes et al (1995) and Abernethy (2001) studies, participants wore crystal occluding glasses in a natural setting of a tennis game. Participants were expert or novice tennis players, who had vision occluded during different stages of the opponent's tennis serve (pre-contact vs post-contact occlusion). Additionally, there were two response conditions; an uncoupled perception-action response whereby participants had to remain static and provide a verbal response as to whether the service return needed a forehand or backhand swing (which indicated the direction they would move), and a coupled perception-action response that required participants to move as if to return the service. The study demonstrated a significant interaction between the response mode (coupled/uncoupled perception-action response) and the skill level of participants. Expertise effects on prediction accuracy were clear under the coupled condition, but not the uncoupled condition.

The Farrow and Abernethy (2003) study would suggest that following motor priming, prediction accuracy would be better in a task requiring a motor act in response to an observed action, compared to a more abstracted judgement response on the coherency of the action continuation. Although we do not compare the two types of study directly, we aimed to determine whether the results of the perceptual judgement task of Chapters 2 and 3 would be replicated with a different task demand, specifically a coincidence anticipation task. This task requires participants to provide a motor response that involves releasing a finger from a response key at the time point when an object is considered to be lifted from a table, although this exact moment is occluded from view. This type of task in effect allows a coupled perception-observation response from which to obtain the main measure of spatiotemporal prediction.

In our previous studies, we found that following motor experience of the action to be observed, action prediction improved only for first person perspective actions. However, the Farrow and Abernethy (2003) study might suggest that this may be a result of the task requirement, and that if a task employed a perception-action coupled response, then perhaps prediction accuracy would improve also for third-person perspective actions. This is based on the fact that coupled perception-action tasks draw upon the same mechanisms (i.e. simultaneous perception processes and motor control responses) that are necessary in action prediction tasks in a natural context, which in general require a motor response to be made as a consequence of an action on the part of another individual, as we see in interceptive actions or coinciding actions when cooperating with others. Thus, in accordance with our previous studies, it was hypothesised that spatiotemporal action prediction would improve following direct motor experience of the transitive actions to be observed compared to prediction without such experience. However, in this study, in line with the conclusions following the Farrow and Abernethy study (2003), it was hypothesised that such motor experience may also improve prediction of actions in the third-person perspective as well as the first-person perspective.

In addition, in the current study, we also introduce a variable action duration pre-occlusion, providing participants with a jittered length of time during which the action sequence is visible before the onset of occlusion. A previous study by Parkinson et al. (2012) explored the effect of different durations of action visually available before occlusion onset and found that the more information, the more accurate participants' prediction performance. However, in contrast to the Parkinson and colleagues (2012) study, which used a psychophysics paradigm much like that employed in the studies presented in the previous chapters, the current study has implications for the length of time available to simulate the action during the occlusion period before the object is lifted from the table. In the current study, a longer period of action sequence visually available pre-occlusion equates to less time during the occlusion before participants are required to provide a response (coinciding with the lift time of the object from the table). As such, we might suggest that, with the use of the current coincidence anticipation task design, the shorter period participants have pre-occlusion to watch the unfolding action provides more time during occlusion to engage a switch from perceptual to simulation processes (as Sparenberg and colleagues (2012) argue) and prepare a response. We might thus hypothesise that in the current study, prediction performance would be more accurate in general for the shorter pre-occlusion action duration trials. On a more exploratory line, the chapter in turn will examine how the effects of perspective and motor priming interact with the time to simulate occluded action.

5.2 EXPERIMENT 7 – Without Motor Priming

5.2.1 METHODS

5.2.1.1 Participants

Twenty-four participants (7 male) were recruited through the University of York, Department of Psychology participant pool. Participants were aged between 19 and 28 years (M=20.63, SD=1.71) and had normal or corrected-to-normal vision. They received a small payment or course credit in compensation for their time. Procedures were approved by the Department of Psychology Ethics Committee at The University of York.

5.2.1.2 Materials

Materials and stimuli were comprised of the same video sequences used for the behavioural experiments described in Chapters 2 and 3 (Experiments 1 to 5; please see Section 2.2.1.2 of Chapter 2). As a brief reminder, ten video sequences in the first person perspective were created of transitive actions involving an actor’s hand reaching towards an object on a table, grasping it, lifting it and removing it from the table in the direction of the actor. As before, transitive actions were performed on five objects: a mug, a wine glass, a hammer, a pair of scissors and a jug of water by two actors of different genders. Third person perspective sequences were created by flipping the images about the horizontal axis.

Presentation of visual stimuli and response recording was programmed using Python v2.7 (www.python.org) and Pygame modules (www.pygame.org). Visual stimuli were presented on a 1280x1024 monitor, with 1024x576 image dimensions on a black surround, at a viewing distance of 64cm, subtending a visual angle of 28x15 degrees, at a 60Hz screen refresh rate.

5.2.1.3 Design and Procedure

The practice and main experimental task, to be described below, was to lift the finger from a key at the point in time when it was judged an object was lifted from the table. However, a *familiarisation phase* and a *lift demo phase* of the experiment were undertaken before the main experimental trials began. In the familiarisation phase, participants viewed each template video twice (once in each perspective; 20 video sequences in total), and were asked to simply observe. Twenty lift demo trials were then presented (5 objects x 2 actor genders x 2 perspectives) to ensure that participants were fully aware of what was meant by the objects' 'lift time point'. The lift demo trials involved the presentation of the template sequences again, during which the image was paused at the point in time that the object was lifted from the table. The image paused for a duration of two seconds before continuing until completion. Table 5.1. shows the real lift times (in milliseconds) for the five objects for the two actor genders.

Table 5.1. Real lift time points (in milliseconds) for each object and each actor gender, determined from the start of the action sequence.

Lift time point in milliseconds

Actor gender	**Object**					
	Cup	**Glass**	**Hammer**	**Scissors**	**Jug**	**Mean**
Male	1467	1317	1083	1467	1650	**1396.8**
Female	1483	1517	1250	1383	2083	**1543.2**
Mean	**1475**	**1417**	**1166.5**	**1425**	**1866.5**	**1470**

In the following *practice* and main *experimental phases*, trials began with a fixation cross presented until participants started the experimental trial sequence by pressing and releasing the space bar. Participants were instructed to use their left hand to press the space bar. This presented a smaller fixation cross, which remained on screen until the participant pressed and held down the 'enter' key with their right index finger. Pressing and holding the enter key initiated the start of a transitive action sequence, which unfolded for a jittered duration of 700ms or 1000m. The action video was then replaced by the grey-scale occlusion image. Participants were instructed to imagine the continuation of the action during the occlusion, and to provide a response by raising their finger from the enter key at the moment in time they believed the object to be lifted from the table (though this was not visible). This occlusion image remained on the screen until the participant made a key release response or until the end of the length of the full action sequence.

If a participant failed to respond during the length of an action sequence, and before the screen went to a fixation cross, the trial was repeated once at the end of the block. A self-paced inter-trial interval was employed, requiring the participant to press the spacebar on seeing the fixation cross to progress to the next trial. Figure 5.1 depicts an experimental trial.

In the practice phase, twenty practice trials were presented (5 objects x 2 actor genders x 2 perspectives) to allow participants to adjust their judgement and response speed. In the practice phase, on participants' raising their finger from the response key, the occlusion screen was replaced by the continuation of the action sequence from the time point the participant's finger was lifted, in a manner as if the action had continued normally behind the occlusion; i.e. the time between the start of the action sequence and the time point from which it re-started post-occlusion equated to the time elapsed between the participant pressing and releasing the response key. Participants thus received visual feedback, with the image jumping forwards or backwards from where they would expect it to be if they were too early or too late with their response, respectively. On completion of the action sequence, participants also received written feedback, indicating that they were either ‘too early’ or ‘too late’ with their response, or ‘correct’. Participants had to be within 17ms of accuracy to receive ‘correct’ feedback.

The main experimental phase consisted of 100 trials in each of the 1PP and 3PP conditions, divided into ten equal blocks (200 trials in total; 5 actions x 2 actor genders x 2 repetitions in each block). The 1PP and 3PP conditions were presented in alternate blocks, counterbalanced across participants. Each block began with 10 familiarisation trials in the perspective (1PP/3PP) corresponding to that block. Each block ended with a ‘Break’ screen allowing participants to rest their eyes and to proceed to the next block when ready to do so. In the experimental phase, participants did not receive visual or written feedback on their response time. Instead, when participants released their finger from the response key, a black screen with a fixation cross was presented. Participants had to press the spacebar with their left hand to progress to the next trial.

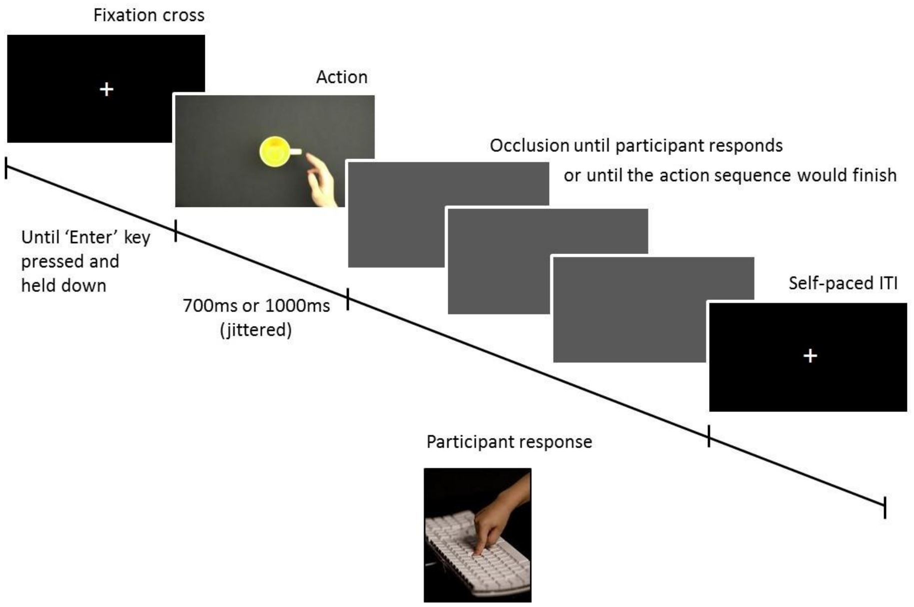

Figure 5.1. Schema of a trial in Experiments 7 and 8. Each trial began with a fixation cross presented until the participant pressed and held down the ‘enter’ key. This started an action sequence that was presented for a jittered duration of either 700 ms or 1000 ms. An occlusion screen was then presented. Participants had to respond during the occlusion of the action by

raising their finger from the response key at the point in time they thought the object was lifted from the table. ITI= Inter-trial interval.

5.2.2 RESULTS

For each participant, a response time (RT) in milliseconds was determined from participants' release of the response key in relation to the onset of the action sequence. From the RT, a prediction error (in milliseconds) was calculated by subtracting the time point at which the object was actually lifted from the table from participants' RT. Negative values would thus indicate RTs of shorter latency than the real lift time point, and positive values indicate RTs of longer latency than the real lift time point. For the purposes of this main analysis, average RTs and prediction errors were calculated over participants, collapsing across actor gender and object, and analysed in terms of perspective, experiment and pre-occlusion action length.

It is well know that there is generally a lag between providing a response and the operating system receiving the input from the response device. This device latency varies with both the model of the response device, in this case a DELL USB keyboard, and the operating system. Response device latency tests conducted by Psychology Software Tools, Inc. (www.pstnet.com) have demonstrated that for the keyboard and operating system used in this study, response device latency is on average 13.98 ms (SD = .74). As such, for this study, participants' RTs were adjusted accordingly by 14 ms.

In addition, it is worth noting that Parkinson et al. (2012) demonstrated that the amount of information provided prior to occlusion can also affect accuracy of action prediction in occlusion tasks. Bearing this in mind, and that in this particular experiment we jittered the duration of pre-occlusion action available to observers, the analysis additionally includes the pre-occlusion action duration to examine whether this influenced spatiotemporal prediction accuracy in this coincidence anticipation task.

A repeated measures 2 x 2 ANOVA was conducted on the data from Experiment 7, with both perspective (1PP vs 3PP) and pre-occlusion jitter length (700 vs 1000 ms) as within-participants variables. The ANOVA revealed a non-significant main effect of perspective (1PP M = 60.95 ms (SE = 6.80); 3PP M = 62.43 ms (SE = 6.80); F(1,23) = .02, p = .90). However, a significant main effect of jitter was revealed (F(1,23) = 27.29, p <.001, η^2_p = .54), with 1000 ms of action pre-occlusion (less time between occlusion onset and object lift point) (M = 103.95; SE = 8.79) eliciting more prediction error than 700 ms of action pre-occlusion (more time between occlusion onset and object lift point) (M = 19.43; SE = 8.79). There was a marginally significant perspective x jitter interaction (F(1,23) = 3.79, p = .06).

In Experiment 7, the results depict positive prediction errors for the two perspective conditions. The positive errors indicate that participants' responses were on average of longer latency than the actual point of lift of the objects from the table. Such delayed responses suggest that participants were simulating the actions at a rate that was slower than the real dynamics of the unfolding action. To visually depict the findings of the experiments in terms of action simulation, a figure reversing the sign of prediction error values in presented in Figure 5.2a. This figure more clearly represents the findings in terms of speed of action simulation in relation to the action dynamics. Figure 5.2a shows the prediction errors observed for the two perspective conditions for both jitter durations in Experiment 7 (without motor priming).

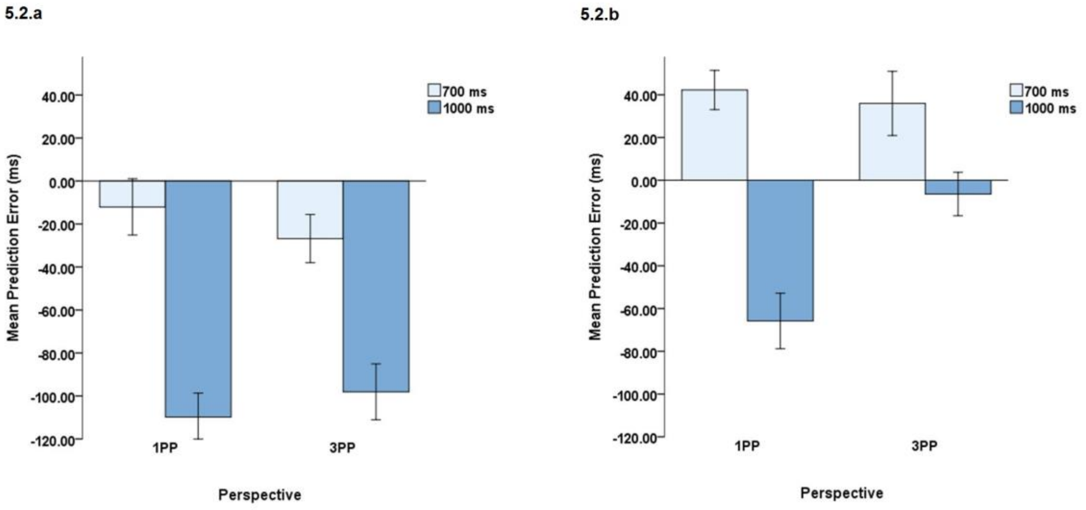

Figure 5.2. Bar charts depicting data from (a) Experiment 7 (without motor priming) and (b) Experiment 8 (with motor priming). Plots show mean prediction error (in milliseconds) for action observed in each perspective, with sign values reversed to depict internal simulation of action relative to the real action dynamics. Negative values depict slower simulation than the real action dynamics. Light blue bars show prediction error following 700 ms of action sequence pre-occlusion, dark blue bars show prediction error following 1000ms of action sequence pre-occlusion. Error bars depict ±1 standard error of the mean.

5.3 EXPERIMENT 8 – With Motor Priming

5.3.1 METHOD

5.3.1.1 Participants

Twenty-four participants (9 male) were recruited through the University of York, Department of Psychology participant pool. Participants were aged between 18 and 26 years (M=20.25, SD=2.45) and had normal or corrected-to-normal vision. They received a small payment or course credit in compensation for their time. Procedures were approved by the Department of Psychology Ethics Committee at The University of York.

5.3.1.2 Materials, Design and Procedure

The same stimuli and paradigm were used as in Experiment 7 (Sections 5.2.1.2. and 5.2.1.3). In Experiment 8, however, after the familiarisation phase and before the lift demo and practice phases, participants performed the transitive actions themselves, with eyes closed, as outlined in Experiment 5 (Chapter 3, Section 3.3.2.2). As a reminder, participants were asked to observe the experimenter place the object on a table covered with a black cloth, on a marker set at 34cm from the participant's edge of the table. Participants were asked to reach towards, grasp and remove each object from the table as if they were about to use the object. Each action was performed with the participant's right hand, four times on each of the five objects. For greater detail, please see Section 3.3.2.2. The same main experimental computer task as in Experiment 7 was then performed by participants.

5.3.2 RESULTS

A repeated measures 2 x 2 ANOVA was conducted on the data from Experiment 8, with both perspective (1PP vs 3PP) and pre-occlusion jitter length (700 vs 1000 ms) as within-participants variables. The ANOVA revealed a significant main effect of perspective (1PP M = 11.79 (SE = 7.05), 3PP M = -14.77 (SE = 7.05); F(1,23) = 5.97, p = .02, η^2_p = .21). A significant main effect of jitter was also revealed (F(1,23) = 20.29, p <.001, η^2_p = .47) (1000 ms of action pre-occlusion M = 36.13, SE = 9.44; 700 ms of action pre-occlusion M = -39.10 (SE = 9.44)). There was a also a significant perspective x jitter interaction (F(1,23) = 28.06, p = <.001, η^2_p= .55). Figure 5.2b shows the prediction errors observed for the two perspective conditions and two jitter durations following the motor practice received in Experiment 8. As previously, prediction error values in the figure have their sign reversed to more adequately depict the speed of internal simulation of the action compared to the real action dynamics, with negative values showing slower simulation compared to the real action.

5.4. GENERAL RESULTS

The main aim of these two experiments was to i) determine action prediction accuracy for the two perspectives of action with this task, and ii) determine whether there is an effect of motor experience on action prediction accuracy in this task. In order to examine both these aspects, driven mainly to examine the difference in results between Experiments 7 and 8, the data from the two experiments were entered into a single analysis.

A mixed ANOVA was conducted with pre-occlusion (jitter) duration (700ms vs 1000ms) and perspective (1PP vs 3PP) as within-participant factors, and experiment (no motor priming vs motor priming) as the between-participant factor. The 2 x 2 x 2 ANOVA revealed a non-significant main effect of perspective (M 1PP = 36.37 (SE = 4.59), M 3PP = 23.83 (SE = 4.59); F(1,46) = 2.48, p = .122) and a non-significant main effect of experiment (M Exp 7 = 61.69 (SE = 38.94), M Exp 8 = -1.49 (SE = 38.94); F(1,46) = 1.32, p = .257). However, as observed in previous studies, a marginally significant perspective x experiment interaction was revealed (F(1, 46) = 3.1, p = .085, η^2_p = .06). A main effect of pre-occlusion action duration was revealed (F(1,46) = 47.19, p <.001, η^2_p = .51), with the pre-occlusion action length of 700ms eliciting least prediction error (M = -9.84, SE =6.71) compared to the 1000ms action duration prior to occlusion (M = 70.04, SE = 6.71). There was a non-significant jitter x experiment interaction, though a significant jitter x perspective interaction was revealed (F(1,46) = 25.06, p < .001, η^2_p = .35). A significant three-way interaction of jitter x perspective x motor priming was also demonstrated (F(1,46) = 4.52, p = .039, η^2_p = .09). Figure 5.2.a and 5.2.b show the mean prediction error in milliseconds for Experiments 7 and 8 respectively, for the two perspective conditions and the two jittered pre-occlusion action durations.

Planned comparisons revealed that the 1PP action prediction was not significantly influenced by whether participants experienced motor priming prior to the task (700 ms pre-occlusion: t(23) = .91, p=.37; 1000 ms pre-occlusions: t(23) = .94, p=.36). Also, 3PP action prediction was not influenced by motor priming when there was more time between occlusion onset and lift-point (700 ms pre occlusion) (t(23) = 1.05, p = .31), and that only 3PP action prediction improved when there was limited time between occlusion onset and lift-point (1000 ms pre-occlusion) following motor priming (t(23) = 2.15, p = .043).

5.4 DISCUSSION

This chapter aimed to examine action prediction through the use of an alternative paradigm to that used so far in the thesis. Whilst other chapters have used psychophysics and a two-alternative forced choice spatiotemporal judgement task, this chapter employs a coincidence detection task, requiring participants to provide a motor response that coincides with the point in time an object is lifted from a table whilst occluded from view. The principle measure of prediction accuracy or prediction error is therefore no longer the point of subjective equality (PSE), but the response time of participants. We principally aimed to determine whether the results from Experiments 2 and 5, of Chapters 2 and 3 respectively, would be replicated with this alternative paradigm, and again i) examine spatiotemporal prediction of actions presented from two different frames of reference, and ii) examine how motor experience of the actions influences action prediction in the two perspectives.

The first thing to note from Experiment 7 is that participants' prediction error values for both the 1PP and 3PP actions were positive. This indicates that participants released their finger from the response key, to indicate the lift point of an object, somewhat after the actual lift time-point of the action. This was particularly the case when participants had less time between occlusion onset and time-of-lift to simulate the action (the 1000 ms pre-occlusion condition). This suggests that participants' internal representation of the action unfolded slower than the real action; in other words, that their simulation of the action dynamics was slower than the real action dynamics. This result is in contrast to the results observed in Experiments 1 and 2 of Chapter 2 which suggested participants were generally simulating the action faster than the real action dynamics and in turn predicting the action states ahead of time, which falls in line with many representational momentum studies (e.g. Jarraya, Amorim, & Bardy, 2005). Here, we see an opposing result.

Cross et al., (2011) used a similar paradigm to the current study to examine action prediction in an fMRI study. Participants watched gymnasts and wind-up toys moving behind an occluding panel and were required to press a button when they expected the agent to reappear. With this similar paradigm, they also found that participants generally responded later than the actual reappearance of the agent. Our results in this response time study are consistent with those obtained by Cross et al. (2011) in terms of participants' responses being slower than the action dynamics. That is to say, in both our present study and Cross and colleagues (2011) study of action prediction with response time as the principal measure, participants' internal action simulation was slower than the real action's spatiotemporal dynamics and no anticipation bias was observed before motor training.

Similarly, as commented earlier in the thesis, Sparenberg and colleagues (2012), using a two-alternative forced choice task, demonstrated that participants had a negative PSE overall, indicating that simulation of the observed actions took longer than the action itself. Results of action prediction studies have therefore not always been consistent, with some studies demonstrating a positive prediction error, and others demonstrating a negative prediction error. As commented in Chapter 2, the reasons for such inconsistencies may lie in the details of the experimental paradigm used, the actions to be simulated, familiarity of such actions, and the task requirements. In our present study, the same stimuli were used as in our previous set of behavioural experiments, and most elements of the paradigm remained the same with the exception of the participants' response task. It may be the mere act of providing a motor response that has influenced action prediction performance in a contrasting way in this study compared to that previously reported. Although this behavioural result was not expanded upon by Cross and colleagues (2011), we would like to speculate why these differences may have occurred.

Let us consider the task of trying to hit an approaching ball. The information required to complete the task includes the visual aspects of the time-to-arrival of the ball at a specific point in space, as well as the motoric information relating to the individual’s capacity to act, which requires initiating an action response at a specific time before arrival of the ball. Although in this study we do not ask participants to provide a motor response of this kind, we try to emulate it with the coincidence anticipation task, requiring a coinciding motor response at the time-of-lift. In this coincidence anticipation task, participants must take into account the time required to initiate an action to provide their response, as well as assess the time of lift. We would speculate that in this study perhaps participants are not accounting for the intervening time interval accurately, and thus respond with a longer latency than the actual time-of-lift. This is particularly the case for both action perspectives before any motor training of the action. In our study, the observed result of a longer latency of response compared to the actual object lift-point may be a consequence of unfamiliarity of providing such a response rather than a more natural coinciding action (such as hitting a ball with a bat), and in turn not accounting for the motor intervention time interval. If, according to Gibson (1979), perception is for action, then the more a task requirement is separated from the action actually required (or separated from what the system evolved for), then the more inaccurate the perceptual processes are likely to be (Bootsma, 1989).

An alternative explanation would relate to the type of motor response required. As the action itself does not exactly equate to the action being observed, that is, grasping and lifting the object with a full hand movement, but rather an index finger lift, this motor act may actually interfere with the perception and prediction of the observed action. Several studies have already demonstrated that performing an incoherent action to that being observed negatively affects performance of the observation (Hamilton, Wolpert, & Frith, 2004) and prediction of actions

(Springer et al., 2011). If the motor act required to provide a response mapped more accurately onto the action being observed, perhaps we would have observed an anticipation bias, or faster simulation (faster response times than the lift-point), as we see in our first set of experiments before motor priming.

However, the slower action simulation result observed may be explained in simpler terms, particularly as simulation is much slowed when less time is available to participants between occlusion onset and object lift-point. The main effect of pre-occlusion action duration shows that when more information is provided prior to occlusion, prediction error is greater. In this study two jittered pre-occlusion action durations were provided (700 ms and 1000 ms), with trials providing 700 ms of action prior to occlusion eliciting improved action prediction performance compared to trials with 1000 ms of action prior to occlusion. This is in contrast to results reported by Parkinson et al (2012), who showed that more information prior to occlusion onset generated improved performance. However, their study employed a psychophysics paradigm much like that reported in the first three empirical chapters of this thesis. In contrast, the current study requires participants to provide a motor response during the occlusion period. In this regard, in trials in which more information is provided prior to occlusion onset, less time transpires during the occlusion before the object lift-time-point and before the participant would be expected to provide a response. As such, a longer pre-occlusion action duration equates to a shorter period during which participants can switch from a perceptual processing system to a simulation system in the occlusion phase. This perception-to-simulation switching process was speculated to account for the prediction error in the Sparenberg et al., (2012) study. In the current study, participants would therefore have less time to engage a simulation process and also prepare a motor response to coincide with the actual object lift-time-point. For conditions in which participants have more time to engage simulation processes and prepare a motor response, participants are much more accurate, irrespective of the frame of reference.

More interestingly in relation to the principal aims of this chapter are the results observed in Experiment 8 in which participants perform the actions-to-be-observed before completing the same task as in Experiment 7. This simple and brief motor experience (picking up each object just four times) provides an improvement in action prediction accuracy. However, the three-way interaction between perspective, motor priming and the length of pre-occlusion action available demonstrates that the advantage provided by motor priming appears to be highly selective. We observe that when participants have less time to engage a simulation process system and prepare a motor response, 3PP actions are selectively improved following motor priming.

Although we see a replication of the pattern of findings from Experiments 4 and 5 (Chapter 3) in terms of motor priming improving action prediction as hypothesised, in our first set of studies this effect was selective to 1PP actions. In contrast, in this current study, we observe that 3PP observed actions are improved following motor priming when there is limited time to engage simulation processes.

This result was somewhat unexpected. It was predicted that both 1PP and 3PP actions would see an improvement in spatiotemporal prediction following motor priming, whereas we observe that following motor priming, and with less time to engage a simulation process and/or a motor response, 3PP actions are selectively improved. Our reasoning for our initial hypothesis goes some way to explain the result observed. It was anticipated that the involvement of a motor act as a response would tap into a different processing system. This processing system may be that used in a more natural action anticipation context in a real world environment where we generally need to provide a motor response in relation to an action performed by another, as we see in interceptive actions or in coincidence timing actions required when interacting and cooperating with others. In our previous spatiotemporal judgement tasks of Experiments 1 to 5, visual coherence of the reach-grasp action has to be assessed. In the present button release task, a coupled perception-action coincidence task is required of participants. The type of task requirements in this chapter therefore may tap into processing mechanisms that are more attuned to perception and prediction of others' actions (3PP actions) for the purposes of interaction – whether this be to coincide movements and cooperate, or for interception.

5.5 CONCLUSION

This chapter investigated the spatiotemporal prediction of action with an alternative paradigm to that used previously to determine whether the same effects of motor priming and perspective on action prediction performance could be observed with a coincidence anticipation task as opposed to a spatiotemporal judgement task. With this alternative paradigm, while some results are replicated others are in sharp contrast to those previously reported. Without motor training of the actions to be observed, participants' tended to simulate the actions slower than the real spatiotemporal dynamics of the action when there is limited time to prepare a response, in both first- and third- person perspective actions. However, following motor priming, participants' performance is improved, with 3PP actions becoming preferentially influenced, generating faster response times, or in other terms eliciting faster simulation mechanisms. This said, only when participants have less time to engage a simulation process and engage a motor response during the occlusion phase are 3PP actions selectively improved following motor priming. This selective improvement of 3PP action compared to 1PP actions contrasts sharply with results from experiments in previous chapters demonstrating a selective improvement of 1PP actions following motor priming. The reason for this shift in prediction performance within the two perspectives may largely be due to the task requirement in this study. The fact that participants are required to provide a motor response to coincide with a particular element of the unfolding action is more akin to action prediction tasks that one might encounter in the real world, in that when making predictions about observed actions, an individual likely has to provide a response towards an action initiated by another individual, as when intercepting an action or coinciding movements with another person for cooperation. As such, the coincidence anticipation task, employing a perception-action coupled response, may draw upon one’s motor repertoire and engage underlying prediction mechanisms that are more sensitive to actions observed from a third person perspective.

CHAPTER 6. Individual differences in action prediction and its relation to time perception and motor control

6.1 INTRODUCTION

Previous chapters have examined spatiotemporal prediction accuracy of observed transitive actions, as determined across groups of participants. In this chapter, this spatiotemporal action prediction is examined in relation to cognitive measures of time perception, as well as motor control. Motion processing, and intrinsic to this, spatiotemporal processing of action, are inextricably linked with temporal processing, and temporal processing has its implications for motor control processes. This chapter thus begins to examine interdependencies between measures of these three areas of sensory perception and motor processing. In examining the relations between these, the current chapter explores individual differences in the abilities to accurately process spatiotemporal dynamics of action and how these differences may be explained by variability in processing accuracy of temporal information and/or motor control mechanisms.

The perception of motor sensory stimuli / motion processing

Any perceptual stimulus that is dynamic in nature evolves over both dimensions of space and time. This is the case whether it be in the auditory, somatosensory or visual mode. The sensory stimulus is not purely spatial or temporal in nature, but requires evaluation of patterns of activity in both of these domains. In tight relation to this, action observation and prediction mechanisms, which draw upon motion processing, are reliant to a large extent on temporal perception abilities. To accurately determine where in space an action state should be within its unfolding dynamic trajectory at a given moment, it is essential to simultaneously and adequately process the evolution of time. To internally simulate an action effectively in order to make judgements about where an action state should be in space (as in the paradigm used in the first three empirical chapters of this thesis), or to determine when a transitive action reaches a particular state (as in the previous chapter) thus require analysis of the temporal elements of the percept. In order to gain an understanding of how the brain processes complex dynamic real word events that mediate both our own actions and the understanding of others' actions, we therefore need an understanding of the mechanisms underpinning our ability to process order, intervals and duration of sensory and motor events.

Neuroimaging studies in healthy adults of temporal monitoring, involving time estimation, reproduction and production, have implicated several cortical and subcortical cerebral structures, including the cerebellum (Bueti, Bahrami, & Walsh, 2008; Lewis & Miall, 2003; Lee et al., 2007); prefrontal cortex (Pouthas et al., 2005; Tregellas, Davalos, & Rojas, 2006; Koch et al., 2002); the premotor cortex, supplementary motor area (SMA) and pre-SMA (Ferrandez et al., 2003; Macar, Anton, Bonnet, & Vidal, 2004; Schubotz, Friederici, & von Cramon, 2000; Tregellas et al., 2006); parietal cortex (Bueti et al., 2008), IFG pars opercularis (Schubotz et al., 2000; Tipples, Brattan, & Johnston, 2013) as well as basal ganglia, putamen and caudate nucleus (Pouthas et al., 2005; Rao, Mayer, & Harrington, 2001). Such studies suggest that time perception is attributed to a distributed cortico-subcortical network, which includes contributions of neural activity within sensory and motor areas. As Schubotz et al. (2000) highlight, the neural structures underlying time perception include the same network responsible for motor planning and coordination of movements. Some of the cerebral regions in this temporal processing network, therefore, are also shared with the mirror neuron system and responsible for motor simulation (including the pre-motor cortex, IFG, IPL and STS) (Tipples et al., 2013).

Given such neuroimaging evidence, it is quite plausible to assume that when observing actions and engaging motor simulation processes, we are recruiting not only brain regions associated with the execution of those movements being observed/simulated, but also the temporal patterning of the unfolding action.

Motor production and control

As stated previously, the mirror neuron system is so called as the neural regions that comprise it are activated when producing movement as well as when observing a movement being produced by another. Subcomponents of the mirror neuron system would thus apparently be involved in producing movement, observing and predicting movement, as well as processing of temporal information. In fact, as producing movements involves coordinated changes in muscle activation over time, in the order of tens of milliseconds, motor control and timing are inextricably related (Mauk & Buonomano, 2004).

Considering the evidence that the motor system plays a significant role in action observation, prediction, and potentially intention understanding in others, it is plausible that a dysfunctional motor control/planning system may lead to an ineffective action prediction mechanism. In this study, we therefore assess the fine and gross motor skills of individuals in order to examine the relationship between motor control and performance on the action prediction task previously reported.

Autistic spectrum disorder

In close relation to this, there is growing research interest in the motor skills and deficiencies in individuals with autism spectrum disorder (ASD). Although not formally assessed or considered within the diagnostic criteria for ASD, motor function impairments have been reported to characterise ASD in a large amount of research in both children and adults (eg. Gowen & Miall, 2005; Hallet et al., 1993; Jansiewicz et al., 2006; Rinehart, Bradshaw, Brereton, & Tonge, 2001; Forti et al., 2011).

Typically developing infants engage in co-ordinated vocal and facial interactions with caregivers from an early age. These reciprocal vocalisations, imitations of oro-facial expressions, and following of eye gaze (coordinated on a fine timing scale) form the very beginnings of the natural to-and-fro of conversation that develops over the first few years of life, and the very bases of social reciprocal communication. Some research has demonstrated that motor synchrony in infant-mother dyadic interactions predicts socio-emotional development in typically developing children (Feldman, Greenbaum, Yirmiya, & Mayes, 1996). Furthermore, Yirmiya et al., (2006) found weaker motor synchrony in these dyadic interactions in a high risk ASD group (siblings of children diagnosed with ASD) compared to a low risk group. Moreover, studies have demonstrated impairments in individuals with ASD to anticipate or predict actions and respond appropriately (Brisson, Warreyn, Serres, Foussier, & Adrien-Louis, 2012; Cattaneo et al., 2007; Martineau, Schmitz, Assaiante, Blanc, & Barthélémy, 2004; Schmitz, Martineau, Barthélémy, & Assaiante, 2003). These studies have indicated that individuals with ASD may have an impairment in feed-forward mechanisms making effective anticipation of events difficult, and instead are more reliant on feedback processes, as compared to neurotypicals.

A dysfunction in a common mechanism for motor control and action observation/ prediction may thus be the underlying reason for both these types of impairment observed in ASD, which in turn have consequences for an individual’s capacity for social reciprocal communication (Leary & Hill, 1996). That is, a dysfunctional motor circuitry may lead to impairments seen in ASD (Fabbri-destro, Gizzonio, & Avanzini, 2013).

Given such research, variability in performance in action prediction across individuals in a sample may be related to other cognitive and neurophysiological factors. As such, this chapter examines action prediction in relation to scores on a motor control assessment, measures of time perception, as well as the pre-screening tool used in ASD diagnosis, the Autism Quotient (Baron-Cohen, Wheelwright, Skinner, & Martin, 2001). More specifically, this chapter aims to determine the extent to which performance variance on the spatiotemporal prediction task outlined in the previous chapter can be accounted for uniquely by the motor practice provided prior to the task, or in addition by time perception ability, motor control, as well as levels of autistic traits.

Each participant in the study detailed in the previous chapter also undertook four additional assessments to the coincidence anticipation task. Participants were assessed on an explicit and an implicit time perception task (the temporal bisection task, and variable foreperiod task respectively), a complete motor control assessment of fine and gross motor skills (PANESS, Denckla, 1985), and also completed the pre-screening autism measure, the Autism Quotient (AQ, Baron-Cohen et al., 2001).

Based on the neuroimaging literature that suggests time perception, motor production, observation, and prediction may share common networks (eg. Schubotz et al., 2000), at least in part, and the relatively recent speculations that a dysfunctional motor production system may underlie deficits in ASD (Fabbri-destro et al., 2013), it was hypothesised that measures of time perception performance, basic motor skills and indices of autistic traits would demonstrate interdependencies among each other and with the measures of action prediction. Furthermore, if these variables do share common underlying mechanisms, and all are essential to the coincidence anticipation task employed in this study, we would expect that not only the Experiment Assignment (whether participants received motor priming or not) would contribute to the variance in performance on the action prediction task, but also that these additional variables would contribute significantly to the variance on the action prediction task.

The results of Chapter 5 indicate that the advantage afforded by motor priming appears to be highly selective (with only 3PP observed action being improved following motor priming and when participants have less time to engage a simulation mechanism), and data demonstrate greater variation in performance when participants are presented with 1000 ms pre-occlusion (less time to switch to a simulation mechanism). Therefore, it is expected that Experiment

Assignment would be a significant contributor to variance in performance when participants receive 1000 ms of visual input pre-occlusion, but not when they receive 700 ms of input; that is, Experiment Assignment will be a significant predictor of performance when participants have less time between visual offset and point of lift to switch to a simulation process (1000 pre-occlusion), compared to when they receive more time to switch (700 ms pre-occlusion). As such, a regression analysis was conducted on the coincidence anticipation performance data relating to these two conditions of pre-occlusion duration separately.

6.2. METHODS

6.2.1. Participants

The same participants as those who undertook the action prediction experiment in the previous chapter (in both the with- and without-motor priming conditions) also undertook the experiments and tasks described below (please see sections 5.2.1.1 and 5.3.1.1).

6.2.2 TASKS

All tasks described below were conducted under the same testing conditions as in the action prediction task described in the previous chapter. For both computer based experiments described below (the Temporal Bisection and Variable Foreperiod tasks), presentation of visual stimuli and response recording were programmed in PsychoPy v1.73 (Peirce, 2007, 2008). Visual stimuli were presented on a 1280x1024 CRT monitor, with images presented on a black surround, at a viewing distance of 64cm, subtending a visual angle of 28x15 degrees, at a 60Hz screen refresh rate.

6.2.2.1. Temporal Bisection

2.2.1.1. Materials

The image used for the presentation of the temporal stimuli in the bisection task was a blue colour filled circle, 7.5 cm in diameter, presented in the centre of the monitor. During the pre-training and training phases, visual feedback was given following participants' responses in the form of a green tick or a red cross.

2.2.1.2. Design and Procedure

The paradigm involved three phases: pre-training, training, followed by the main experimental phase. In the pre-training phase, participants were familiarised with two anchor durations of 200 ms and 800 ms, representing 'short' and 'long' durations respectively. To do this, a blue circle was presented on the screen alternately for a ‘short’ then ‘long’ period of time for a total of eight trials. Participants were informed of this sequence and were required to indicate after each trial whether the stimulus appeared for a ‘short’ or ‘long’ duration by pressing the corresponding response key. Following a response, visual feedback was provided in the form of a green tick or a red cross for correct and incorrect responses, respectively. This feedback was presented for two seconds before the next temporal trial was presented. In the following training phase, the blue circle was presented for a further eight trials, with the ‘short’ and ‘long’ durations being presented in a random order. Participants were required to discriminate between the two anchor durations, indicating with a key press whether they believed the blue circle appeared for a ‘short’ or a ‘long’ duration. Participants again received visual feedback following their response on each trial. Training terminated when the participant made no errors in the block of eight training trials.

Following these pre-training and training phases, participants completed the main experimental task. In the experimental phase, in each trial, participants were presented with the blue circle that appeared in the centre of the screen for a duration of time that was either one of the anchor durations, or one of five intermediate durations (i.e. 7 test durations: 200, 300, 400, 500, 600, 700, 800 milliseconds). A black screen was subsequently presented and participants were required to respond with the corresponding key press whether the length for which the blue circle appeared was closer to the ‘short’ or closer to the ‘long’ duration previously learned in the pre-training and training phases. Participants were required to provide a response as soon as possible after the blue circle disappeared and had no more than two seconds in which to respond before the next temporal trial was presented. In the main experimental task, feedback was not provided. The next trial began on providing a key response, with the blue circle appearing 1000 ms into the start of the trial.

The blue circle appeared for these seven time trials in ten consecutive blocks, with each anchor and intermediate duration being presented once per block (70 trials in total). The temporal stimuli were presented in random order within each block. Figure 6.1 depicts a schema of a trial in the Temporal Bisection task.

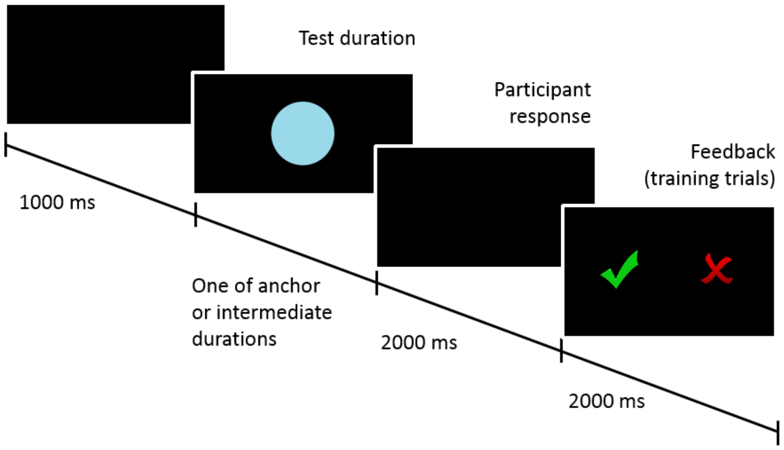

Figure 6.1. Temporal Bisection task paradigm. A blue circle appeared for a duration of time equal to one of the anchor durations (200 or 800 milliseconds), or one of the intermediate durations (300, 400, 500, 600 or 700 milliseconds). Participants had a maximum of two seconds to respond as to whether the blue circle appeared for a period of time closer to the 'short' or 'long' anchor duration learned in the pre-training and training phases. Participants received feedback in the training phase, but did not during the main experimental testing phase. Following a response (or feedback in the training), a blank screen was presented for 1000 ms before the next test duration was presented.

2.2.1.3. Data analysis

The proportion of 'long' responses (pLong), produced at each test duration was calculated for each individual. This was achieved for a given duration, by dividing the number of 'long' responses by the sum of short and long responses. Logistic psychometric functions were fitted to each participants' proportion of 'long' responses for each temporal duration condition by minimising the mean squared error of the fit.

These psychophysical functions allow extrapolation and quantification of indexes of timing sensitivity and ability: The duration that produces 50% pLong responses (when the individual is equally likely to classify the duration presented as 'short' or 'long') is known as the bisection point (BP) or point of subjective equality (PSE). In human timing, the PSE is usually around the arithmetic mean of the two anchor durations (Wearden, 1991).

2.2.2. Variable Foreperiod task

2.2.2.1. Materials

At the beginning of each trial, a 1,500 Hz pure tone auditory stimulus was presented for 50 ms. The visual stimuli consisted of a yellow cross of 5cm squared which served as the cue stimulus. This fixation cross was presented for the duration of the foreperiod length, which was varied. Three foreperiod conditions were used: 800, 1600 and 2400 milliseconds. The imperative (target) stimulus consisted of a downward pointing white arrow (a 1.5 x 1 cm bar attached to an arrowhead with a maximum width of 2 cm). The imperative stimulus replaced the cue/foreperiod stimulus and was presented for 500 ms. Stimuli were presented on a black background.

2.2.2.2. Design and Procedure

This task consisted of two phases, a practice phase and an experimental phase. In the practice phase, participants were presented with each of the three foreperiod durations just once, in a random order. That is, the auditory 1500 Hz pure tone was presented for 50 ms. Simultaneously with the auditory tone, the visual cue stimulus (yellow cross) was presented on the screen for one of the foreperiod durations (800, 1600 or 2400 ms). Immediately following this, the imperative stimulus (the white downward-pointing arrow) was presented for a fixed duration of 500 ms. Participants were required to press the space bar as soon as possible on seeing the imperative stimulus (the white arrow). The time limit for response was 2000 ms after the arrow's onset. The following trial began 1000 ms following the participant's response. These three trials were simply to ensure that the participant could follow the instructions and understood what was required of them.

Following the practice phase, participants undertook the main experimental phase. Each trial in this phase was exactly the same as in the practise phase. Participants received 60 consecutive trials in total, with each of the three foreperiod conditions presented 20 times in a random order. The task was presented as a velocity game, with participants being requested to respond by pressing the space bar as quickly as possible when they saw the white arrow.

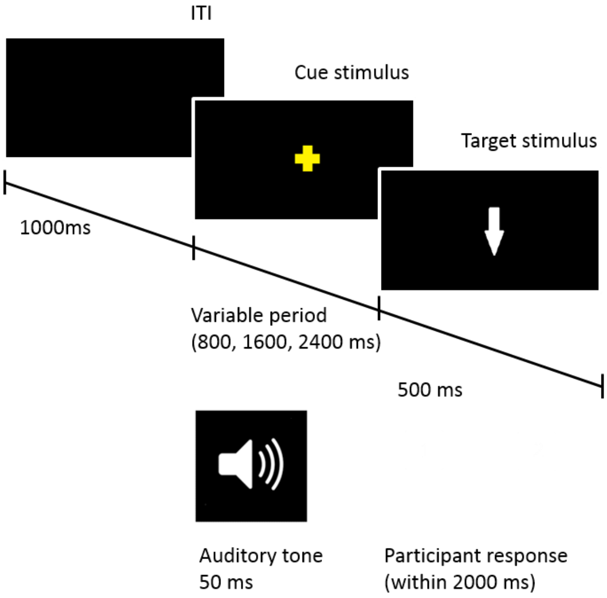

Figure 6.2. Schema of a trial in the Variable Foreperiod task. Participants were presented with an auditory tone for 50ms simultaneously with the visual presentation of a yellow cross. This cue stimulus appeared for one of the temporal conditions (800, 1600, 2400 ms) that represented the variable foreperiod. Following the yellow cross, the target stimulus comprising a white arrow was presented for 500 ms. Participants were required to provide a key response as soon as possible on seeing the target stimulus, and had no more than 2000 ms in which to respond. ITI = Inter-trial interval.

2.2.2.3. Data analysis

Participants' response time (RT) data were analysed, with RT calculated relative to the onset of the imperative stimulus (white arrow presentation). Trials were treated as errors and removed from the RT analysis if a response was made during the foreperiod itself or during the first 100 ms after imperative stimulus onset (premature responses), if the RT was slower than 1500 ms (delayed responses) or no response was provided (null responses).

As time elapses during the foreperiod without the target stimulus being presented, the probability of the target stimulus occurring in the next time interval increases. The cognitive system is believed to utilise this probability to endogenously increase response preparation. As such, mean reaction time decreases as a function of increasing foreperiod length (the variable foreperiod effect; Woodrow, 1914). To examine individual differences in the foreperiod effect, a Pearson's correlation coefficient was calculated per participant to determine the relationship between the foreperiod interval and response time.

2.2.3. The Physical and Neurological Examination for Subtle Signs (PANESS)

Participants were also asked to undertake an assessment of their basic motor functions. The PANESS (Denckla, 1985) allows examination of the complete range of neurological subtle signs of motor function, including both fine and gross motor skills. Although primarily used in previous research to assess children's motor skills, having been standardised to allow for the assessor to account for the chronological age of the participant, in this study the PANESS was employed with the adult participants, with any errors being noted regardless of age.

The PANESS allows for the assessment of several different tasks of motor control. These include stressed gaits, balance, coordination, motor persistence, repetitive timed movements, involuntary movements (such as choreiform and tremors), overflow on the gaits and timed movements, and dysrhythmia.

The PANESS assessment is provided as Appendix C, which details each of the tasks required of the participant. Regarding scoring, for each of the forward, backward and sides-of-feet gait tasks, the examiner scored the number of errors in ten steps, and recorded presence of overflow (i.e. extension of hand at the wrist). For balance tasks, the number of hops (maximum of 50) and seconds standing (maximum of 30 for each foot) was recorded. For the motor persistence task, the time during which the participant maintained eyes closed during stance was recorded (maximum of 20 seconds for each stance). For repetitive timed movements, the time to complete a set number of movements was recorded using a stopwatch, as well as the presence of overflow (proximal, oro-facial, and mirror movements) and dysrhythmia. Abnormal movements (i.e. choreiform movements and tremor) were also recorded throughout.

Errors were recorded for the measures of gait, balance, motor persistence, overflow, and dysrhythmia, and ordinal scores (0, 1, and 2) were given, with higher scores indicating increasing abnormal performance. Ordinal scores were summed across the right and left sides of the body for all measures to create summary scores for the following categories: (1) Gaits – error scores for heel, toe, sides of feet, and tandem gaits; (2) Balance – error scores for one-footed hops and stands; (3) Speed of repetitive timed movements – z-scores were summed; (4) Dysrhythmia – on timed movements; (6) Overflow – on gait and timed movements.

The assessor demonstrated each task to be performed whilst providing verbal instructions from the test description. Higher scores on the PANESS indicate increased errors, dysrhythmia and overflow. The PANESS scoring sheet is provided as Appendix D.

2.2.4. Autism Quotient

The Autism Quotient (Baron-Cohen et al., 2001) is a self-report measure developed for use in the general population to assess autistic traits in individuals with normal IQ (>70). In the study conducted by Baron-Cohen et al. (2001) and in more recent studies, individuals with ASD score significantly higher than members of the general population (Baron-Cohen et al., 2001; Hoekstra, Bartels, Cath, & Boomsma, 2008; Ketelaars et al., 2008). Comprised of 50 questions, it quantitatively assesses characteristics related to the triad of impairments (language and communication, social reciprocal communication, and stereotyped and repetitive behaviours) that form the diagnostic criteria of autism spectrum disorder according to the diagnostic manual DSM-IV (American Psychiatric Association (APA), 2000). Although the more recent DSM-V (APA, 2013) has now updated diagnostic criteria to reduce the three domains to two domains (social communication and interaction, and restricted and repetitive behaviours or interests), there is not as yet an updated version of the Autism Quotient.

There is currently some debate about the subscales inherent within the measure. Research has demonstrated that the AQ assesses five subscales (Baron-Cohen et al., 2001) – Social skills, Communication, Imagination, Attention to Detail and Attention-Switching. However, other research has demonstrated a three-factor structure of the assessment (Social skills, Details/Patterns, Communication/Mind-reading) (Austin, 2005; Hurst, Mitchell, Kimbrel, Kwapil, & Nelson-Gray, 2007) and a four-factor structure (Stewart & Austin, 2009). Nevertheless, it remains the only major screen to examine autistic traits in the general population, and the AQ is currently used as a screening tool for referral to diagnostic services as recommended by the National Institute for Health and Care Excellence (NICE) guidelines (NICE, 2012). The Autism Quotient is provided as Appendix E. A four-point Likert scale was used to score the AQ.

6.3. RESULTS

Multiple linear mixed regression analyses were conducted to determine the amount of variance in performance on the coincidence anticipation task uniquely accounted for by motor practice, time perception, motor skills and autistic traits, in both the 1PP and 3PP conditions. Predictors thus included the categorical variable of Experiment Assignment (no motor priming vs motor priming); and four continuous predictor variables: the Point of Subjective Equality (PSE) on the Temporal Bisection task (explicit time perception measure); the Correlation Coefficient from the Variable Foreperiod task (implicit time perception measure); Physical and Neurological Examination of Subtle Signs (PANESS) score (motor skill assessment); and the Autism Quotient (AQ) (measure of autistic-like traits). Descriptive statistics (means, standard errors (SE), maxima and minima values, and variances) for each of these continuous variables are provided in Table 6.1.

Table 6.1. Descriptive statistics (means, minima, maxima, standard errors and variances) for each of the continuous predictor variables.

Variable	Mean	Minimum	Maximum	Standard Error	Variance
PSE	485.00	348.37	613.73	9.22	4078.31
VF Coefficient	-0.87	-1.00	0.61	0.04	.06
PANESS score	17.96	5	38	1.27	77.11
AQ	106.48	78	152	2.07	206.30

Note: PSE = Point of subjective equality on the Temporal Bisection task; VF = Variable Foreperiod; PANESS = Physical and neurological examination of subtle signs; AQ = Autism quotient.

As the predictor variable determined from the Variable Foreperiod coefficient had close to zero variance in the sample, this predictor violates the assumption of zero-variances. For this reason, this predictor variable was excluded from further analysis in the regression.

Two regression analyses were conducted: One examining the predictor variables in relation to the coincidence anticipation data when participants receive 700 ms of action sequence prior to occlusion (which resulted in more time to switch from perception to simulation during occlusion), for the first and third person perspectives; and a second analysis examining the predictor variables in relation to the coincidence anticipation data when participants receive 1000 ms of action sequence prior to occlusion (less time to switch to a simulation process during occlusion).

A hierarchical regression method was employed, with the categorical variable of Experiment Assignment (motor vs no-motor practice) entered into the model first, PSE on the Temporal Bisection task entered second, and PANESS score and AQ entered third in a forced entry manner. The rationale for this method was that based on the series of studies presented so far in the thesis, whether or not participants received motor practice prior to undertaking the action prediction task was deemed likely to predict performance on the coincidence anticipation task. As such, the categorical variable of Experiment Assignment was entered first. The explicit time perception measure of PSE on the Temporal Bisection task was entered into the model second as it was considered the next most important variable likely to predict performance given the close relationship between the spatiotemporal coincidence detection task and the need to accurately determine the elapse of time. The results of the multiple linear mixed regression analyses are provided in Tables 6.2 (DV = action prediction with 700 ms pre-occlusion), and 6.3 (DV = action prediction with 1000 ms pre-occlusion).

All continuous data entered into the regression models met the assumption of non-zero variances (PSE variance = 4078.31; PANESS variance = 77.11; AQ variance = 206.30, RT 1PP 700 ms pre-occlusion variance = 46107.89; RT 3PP 700 ms pre-occlusion variance = 52750.66; RT 1PP 1000 ms pre-occlusion variance = 27246.02; RT 3PP 1000 ms pre-occlusion variance = 31064.40). Data also met the assumptions of normally distributed errors, homoscedasticity and linearity. Tests confirmed that data met the assumption of collinearity (all predictors' tolerances > 0.1; all predictors' variance inflation factor (VIF) < 10.0). Furthermore, there were no significant correlations among the predictor variables (all $r \leq .11$) indicating there was no multicollinearity.

For the regression analysis of action prediction data with 700 ms pre-occlusion, an analysis of standard residuals was carried out, which showed that the data contained no outliers (1PP: Standard Residual Min = -2.06, Max = 1.68; 3PP Standard Residual Min: -2.27, Max: 1.61). The data also met the assumption of independent errors (1PP: Durbin-Watson = 1.76; 3PP: Durbin-Watson = 1.80). Similarly, for the regression analysis of action prediction data with 1000 ms of visual input pre-occlusion, an analysis of standard residuals was carried out, which also showed that the data contained no outliers (1PP: Standard Residual Min = -2.07, Max = 1.62; 3PP Standard Residual Min: -2.65, Max: 1.67). These data also met the assumption of independent errors (1PP: Durbin-Watson = 1.87; 3PP: Durbin-Watson = 1.83).

The regression analysis of performance data when 700ms of visual input were presented pre-occlusion demonstrates that none of the predictor variables entered into the three models can account for the variance in participant performance on the action prediction (coincidence anticipation) task. Whilst an increase in explained variance occurs from Model 1 (just Experiment Assignment entered as a predictor) to Model 2 (Experiment Assignment and Temporal perception measure entered as predictors), the change in variance explained does not reach significance. This is the case for action prediction performance when actions are presented in both the first and third person perspectives.

In contrast, the regression analysis of performance data when 1000ms of visual input are presented pre-occlusion (less time to switch from perception to simulation processes) demonstrates that, when actions are presented in the third person perspective, only the Experiment Assignment predictor makes a significant contribution to the model, in all three models.

In the 1000 3PP analysis, the experiment assignment accounts for 7% of the variability in performance on the action prediction task. When PSE (time perception sensitivity) is included in the model, this increases to 13%, then 17% of the variance when all four predictors are included in the model. Temporal perception therefore accounts for 6% of the variation, and together motor skill and AQ traits account for 5% of variation. The change in amount of variance that can be explained only approaches significance in the case of Model 1 (when Experiment Assignment is included in the model). When other predictors are included in the model (Models 2 and 3), the change in variance accounted for by the predictors is non-significant.

Table 6.2. Results of the multiple linear mixed regression analysis of factors predicting the variance in the coincidence anticipation task, in first and third person perspectives, when participants receive 700 ms of action pre-occlusion.

First Person Perspective									
	Model 1			Model 2			Model 3		
Variable	B	SE B	β	B	SE B	β	B	SE B	β
Constant	-12.06	43.94		334.25	237.73		99.46	333.61	
Experiment	54.30	62.14	.13	61.53	61.55	.15	66.50	61.75	.16
PSE				-.72	.49	-.22	-.67	.49	-.20
PANESS							4.41	3.56	.18
AQ							1.21	2.17	.08
R^2		.02			.06			.10	
ΔR^2		.02			.05			.04	
F for ΔR^2		.76			2.20			.97	

Third Person Perspective									
	Model 1			Model 2			Model 3		
Variable	B	SE B	β	B	SE B	β	B	SE B	β
Constant	-26.80	46.94		326.65	254.46		65.61	355.91	
Experiment	62.77	66.38	.14	70.15	65.88	.15	75.71	65.88	.17
PSE				-.74	.52	-.21	-.68	.52	-.19
PANESS							5.13	3.80	.20
AQ							1.29	2.32	.08
R^2		.02			.06			.11	
ΔR^2		.02			.04			.05	
F for ΔR^2		.89			2.00			1.12	

Note: PSE = Point of subjective equality on the temporal bisection task; PANESS = Physical and neurological examination for subtle signs score; AQ = Autism Quotient; ΔR^2 = Change in R^2.

Table 6.3. Results of the multiple linear mixed regression analysis of factors predicting the variance in the coincidence anticipation task, in the first and third person perspectives, when participants receive 1000 ms of action pre-occlusion.

First Person Perspective

	Model 1			**Model 2**			**Model 3**		
Variable	B	SE B	β	B	SE B	β	B	SE B	β
Constant	-109.83	33.74		189.37	181.37		30.58	254.37	
Experiment	44.02	47.73	.14	50.28	46.96	.15	53.73	47.09	.16
PSE				-.62	.37	-.24	-.58	.37	-.22
PANESS							3.59	2.72	.19
AQ							.67	1.66	.06
R^2		.02			.08			.12	
ΔR^2		.02			.06			.04	
F for ΔR^2		.85			2.82			1.00	

Third Person Perspective

	Model 1			**Model 2**			**Model 3**		
Variable	B	SE B	β	B	SE B	β	B	SE B	β
Constant	-98.07	35.09		223.11	188.21		-3.24	262.65	
Experiment	91.63	49.62	.26*	98.33	48.73	.28**	103.05	48.62	.30**
PSE				-.67	.39	-.24	-.63	.39	-.23
PANESS							3.67	2.81	.18
AQ							1.31	1.71	.11
R^2		.07			.13			.17	
ΔR^2		.07			.06			.05	
F for ΔR^2		3.41*			3.01			1.22	

Note: PSE = Point of subjective equality on the temporal bisection task; PANESS = Physical and neurological examination for subtle signs score; AQ = Autism Quotient. ΔR^2 = Change in R^2; * p=.07, **p ≤.05.

6.4. DISCUSSION

The present study aimed to determine whether variability in performance across individuals on the coincidence anticipation task could be accounted for solely by the experiment to which participants were assigned; that is, whether they received motor practice of the actions to be observed or not, or whether other factors might also contribute to the individual differences in performance. These other factors included temporal perception ability, motor control and autistic-like traits.

All participants in the study undertook the coincidence anticipation task, as described in Chapter 5. The task elicited a response time (RT) for each participant that provided a measure of participants' action prediction ability. This action prediction ability was determined for two variables: First, participants received 700 or 1000 ms of visual input prior to action occlusion, which resulted in longer (700ms preview) and shorter (1000ms preview) periods during occlusion before response was required. Second, half of all participants in the study received motor priming of the actions to be observed prior to undertaking the computer-based task. Additionally, all participants completed four additional assessments: a temporal bisection task, an explicit measure of time perception ability; a variable foreperiod task, an implicit measure of time perception; the PANESS, an assessment of motor control; and the Autism Quotient, a self-report questionnaire to assess autistic-like traits in an individual.

In order to determine the unique variance that the motor priming contributed to the action prediction performance, multiple linear mixed regression analyses were conducted. This allowed an examination of the degree to which each predictor variable affected the outcome when the effects of all other predictors were held constant. A regression analysis was conducted on performance data for the two pre-occlusion action durations separately.

The results of the regression analysis demonstrated that the Experiment Assignment predicted participants' action prediction performance, but only for performance of 3PP actions when 1000 ms of action was presented pre-occlusion (time between visual offset and point of object lift was less compared to 700 ms of action pre-occlusion). Moreover, this relationship was not moderated by time perception ability, motor skill or autistic traits. Experiment Assignment therefore accounted for considerable variance in participants' action prediction performance after controlling for these additional factors. Experiment Assignment was not a significant predictor in any of the other performance conditions. The three variables of motor control, time perception and autistic traits did not account significantly to the variance in action prediction performance in any of the conditions assessed.

The results thus support the original hypothesis that whether participants receive motor practice or not would significantly contribute to the individual differences in performance when participants observe 3PP actions and receive less time to switch from a perception to a simulation process during occlusion before the point of object lift. Importantly, we observe that this effect is not modulated by individual differences in time perception ability, motor control or autistic like traits. This result therefore re-affirms conclusions drawn in Chapter 5 of the thesis that highlight the importance of experience and motor repertoire in improved accuracy of internal simulation and prediction of the spatiotemporal dynamics of observed actions. In this particular coincidence anticipation task, the effect of motor priming is particularly salient for 3PP actions when individuals have less time to switch to a simulation process from a perceptual process, necessary when no visual input is received in order to estimate the time point of object lift.

Surprisingly, however, action prediction performance in this study was unrelated to time perception, in contrast to the original hypothesis. To perform well on the coincidence anticipation task, it was hypothesised that participants would have to draw upon neural networks of time perception to accurately estimate the elapse of time, which in itself is crucial in order to determine the moment the object is likely to be lifted from the table. However, the regression analysis demonstrated that a non-significant amount of variance in the action prediction performance in both the 1PP and 3PP conditions was explained by participants' time perception performance. The hypothesis was therefore not supported. This was similarly the case regarding motor control ability, assessed using the PANESS, and autistic traits, assessed using the AQ.

Surprisingly still, is that no correlations were observed between time perception, motor control performance and autistic traits in the participant sample in this study. The results of the regression and correlation analysis do not support the original hypothesis that these three predictors would contribute significantly to action prediction performance, and furthermore appear contrary to research and opinion papers drawing close relations between time perception and ASD (Allman, DeLeon, & Wearden, 2011; Allman, 2011), action prediction and motor control (Schubotz, 2007; Schubotz, 2004), action prediction and ASD (Brisson et al., 2012; Cattaneo et al., 2007; Martineau et al., 2004; Schmitz et al., 2003) and the tight coupling between spatiotemporal monitoring of motion processing and time perception. Even more surprising is the result given the evidence from neuroimaging data indicating that these mechanisms are underpinned by largely overlapping neural networks (Schubotz et al., 2000; Tipples et al., 2013).

However, the results of the present study may be due less to a dissociation among these predictor factors, and more a consequence of the limitations of the study. Firstly, the sample size is arguably low for the number of predictor variables examined in this study (Green, 1991; Miles & Shevlin, 2001). Secondly, a small section of the PANESS motor assessment involved converting the times of particular motor movements to z-scores normed on 17 year old's data. This part of the assessment may not therefore be sensitive enough to the variability in timed motor movements of the sample with an average age of 20 years. Nevertheless, this element of the assessment formed only a small part of the overall examination, and aimed mainly to provide preliminary insight into the potential relationship between motor control and action prediction. Thirdly, the sample population was derived from an undergraduate student population from a Russell group University, largely in their late teens-early twenties. The sample would be considered to be in the highest percentile in terms of cognitive and physical abilities, and thus performance on each of the tasks employed would not have the variance which would be observable if sampling from a more varied population. Nevertheless, this study aimed to provide a pilot sample to begin to explore the interdependencies between these predictor variables from a behavioural perspective. With a larger sample size and a more heterogeneous sample population, more representative of the general population, we might observe the behavioural interdependencies increasingly suggested by neuroimaging and behavioural research.

6.5. CONCLUSION

This present study aimed to provide preliminary data to examine individual differences in performance on the coincidence anticipation task in relation to other cognitive and neurophysiological measures of time perception, motor control and autistic traits, and to determine the unique variance accounted for in action prediction performance by motor priming. The multiple regression analyses conducted demonstrated that time perception, motor skill and autistic traits were not significant predictors of performance on the action prediction task. Only the predictor factor of whether participants received motor priming or not prior to undertaking the coincidence anticipation task contributed significantly to individual differences in performance. However, this was only the case when participants observed actions in the third person perspective and received a reduced amount of time during occlusion before accurate response was required (1000ms pre-occlusion vision), that is, when they had less time to begin to internally simulate the action before the point which had to be anticipated (time point of object lift). The results of the study therefore support the results of the previous chapter, and indeed of previous studies throughout the thesis, which demonstrate the importance of motor experience in the ability to effectively simulate and anticipate the spatiotemporal dynamics of action. These final two empirical chapters, however, highlight how the fine details of the task (such as the jittered length of action prior to occlusion) and the frame of reference in which the action is observed are all contributing factors to how effectively an individual is able to anticipate action dynamics and the extent to which motor experience can impact on this ability.

CHAPTER 7. DISCUSSION

7.1 RESEARCH AIMS

The aims of the present thesis were multifold. The broader, overarching, objective of the thesis was to interrogate theories postulating that the existence of a fronto-parietal neural network, evidenced as active in both production and perception of actions, may have evolved for the purposes of intention understanding in other people (e.g. Iacoboni et al., 2005; Rizzolatti & Craighero, 2004). Opposing theories (Miall & Wolpert, 1996; Wolpert & Flanagan, 2001) suggest, however, that this perception-action coupled system facilitates action monitoring of one's own actions, and thus postulate that its main purpose is for fine grain motor control; to allow us to make appropriate timely adjustments to our own motor planning and commands.

In order to interrogate these theories, the present work explored the fine grain spatiotemporal dynamics of internal action simulation, and in turn prediction of transitive action sequences. Importantly a major manipulation in the experiments throughout the thesis was the frame of reference in which the perceived actions were presented; that is, either from a first-person or a third-person perspective. First-person perspective actions closely represent the visual input one would receive if performing an action oneself; whereas the display of third-person perspective actions could only be visually resolved as another person performing the action.

With the use of two types of behavioural paradigm and an electroencephalography study, the thesis aimed to determine whether action prediction performance was more accurate in one of these perspectives over another, under the assumption that if the action-perception coupled system evolved for the purposes of interpretation of others' actions and/or social interaction, performance would be better in the third-person perspective than, or at least equal to, performance when actions are presented in the first-person perspective.

7.2 SUMMARY OF CHAPTERS

Chapter 2

The first empirical chapter of the thesis, Chapter 2, provides a proof of concept of the use of an occlusion paradigm to interrogate action prediction mechanisms in the spatiotemporal domain. The psychophysics method of a two-alternative forced choice design proved useful and effective in determining action simulation and prediction performance in the tens of milliseconds range. The first two studies of the thesis, without any priming in the visual or motor domains, indicate that individuals have a tendency to perceptually anticipate actions ahead of their actual state. The extent of this anticipation seems to be equal for actions in the 1PP and 3PP.

The first two experiments detailed in this chapter replicate findings from alternative methods of examination of action prediction, such as is seen in representational momentum studies (e.g. Thornton & Hayes, 2004). However, our findings are in contrast to some recent research using a similar paradigm (Sparenberg et al., 2012), which showed a simulation lag when observing actions, and suggests that this may be due to a perception-to-simulation switching cost. That is, the delay in switching into simulation mode resulted in the simulation running a little behind reality. This said, these incongruent findings may be the result of fine details of the experimental stimuli employed in the two studies.

Chapter 3

Chapter 3 is an extension of the first empirical chapter in that it employs the same experimental design as in the first empirical chapter, and examines the effects of visual priming, visual and motor priming, and motor priming alone on action simulation processes and prediction performance. The three experiments that comprise the chapter are then examined and discussed in relation to the last study of Chapter 2, used as a baseline experiment, without any priming manipulation. The set of studies suggest we have an anticipatory bias when observing actions of which we have little or no first-hand experience, but which reduces as we gain physical experience of these actions. Interestingly, the priming studies indicate that motor priming has a selective effect on spatiotemporal prediction of 1PP actions, with little to no effect on prediction of 3PP action, at least within the context of the paradigm employed in this set of studies.

The effect of motor priming observed in this set of studies would indicate that the principal role of action simulation and prediction processes, and their underlying neural mechanisms, is to facilitate one’s own actions. However, the observed results do not preclude the possibility of the same mechanisms being used beyond such a process, to facilitate anticipation of others’ actions. It merely suggests that the system may be more finely attuned to one’s own action monitoring. This said, the greater prediction error which continues to be observed for 3PP actions, even following motor priming, may grant important social advantages of dealing with the unpredictability of others.

Chapter 4

This chapter employed EEG to examine neuronal signals, specifically event related potentials, associated with observation and prediction of action in first- and third-person perspectives following motor priming, with the aim to determine whether the same differences observed behaviourally following motor priming were also evident neuronally. In terms of the earlier ERP of the oERN (observed some 100-200ms post occlusion offset) a greater negative deflection was observed when participants were processing 1PP compared to 3PP actions, albeit for trials that were coherent with the occlusion duration. The fact that the greater deflection was for coherent rather than incoherent trials is likely due to the response conflict generated by the paradigm used, as participants are required to provide a response of ‘Early/’Late’ even for the coherent (correct) trials. With such response conflict generating a greater deflection for coherent trials, the fact that 1PP actions elicited a greater deflection than 3PP actions is in line with previous studies (Knolle et al., 2013) that have demonstrated greater deflections for self-generated deviants/mismatches as opposed to externally-generated deviants/mismatches, and importantly is consistent with the earlier behavioural findings of this thesis, suggesting 1PP actions are more salient than 3PP actions for the deviance detection and action prediction mechanism.

With respect to the examination of the later ERP – the P300 (observed some 350-450 ms post occlusion offset), we observed a greater positive deflection for the incoherent trials (Earlier and Later conditions as opposed to the coherent condition), as predicted by deviance detection studies (e.g. Knolle et al., 2013). However, in the case of this ERP, a greater deflection was elicited for the observation of spatiotemporal deviance in actions in 3PP. Considering previous neuroimaging research, this result may be interpreted in terms of the 3PP actions being more computationally difficult for the underpinning mechanism to process, thus leading to greater neuronal excitation for 3PP compared to 1PP when the spatiotemporal dynamics of the simulated action are not as predicted. The contrasting neuronal responses observed with regard to the two perspectives, within the ERPs associated with the two distinct time-windows of interest, are speculatively interpreted in terms of different levels of conscious processing associated with the timecourse of neuronal activity.

Chapter 5

Chapter 5 turns back to behavioural measures of action prediction mechanisms, this time with an alternative paradigm to that used in previous chapters. In this paradigm, participants were required to provide a motor response, whilst the action being observed was occluded, at the point in time the participant thought the object was lifted from the table. Two experiments were presented; one without motor priming, and a second in which participants received motor experience of the actions to be observed prior to undertaking the same task. This allowed a direct comparison with Experiments 2 and 4 of Chapters 2 and 3 respectively. This change in experimental design – a coincidence anticipation task - elicited somewhat differing results from the studies that employed a psychophysics method of interrogation.

In this instance, in general, it would appear that simulation processes are slower than the real action dynamics when participants have little experience of the actions, with participants providing a motor response after the actual time of object lift. This is the case for 1PP and 3PP actions, and also for both jittered pre-occlusion action lengths shown, which was an additional manipulation in this study. When a greater length of action time pre-occlusion was shown, however, prediction performance was much poorer compared to when less action was shown pre-occlusion. In the case of the former, this equates to less time between occlusion onset and object lift point, and thus participants potentially have less time to switch from perception processes to simulation without vision. This potentially leads to greater error in response timing. Moreover, with this paradigm, the most salient difference was observed following motor priming of the action, which led to an improvement in prediction performance as previously seen, but selectively for 3PP actions and when participants had less time between occlusion onset and object lift point.

These two experiments again highlight the importance of motor priming in being able to accurately internally simulate and predict the dynamics of action in the spatiotemporal domain. And yet, what this chapter most clearly indicates is that the task demands can tap into quite different processes. In this case, the coincidence anticipation task, requiring a motor response during non-visual simulation, arguably has a more tightly coupled action-perception nature, and as such taps into mechanisms that are more attuned to 3PP actions. This processing system may be that used in a more natural action anticipation context, where we provide a motor response in relation to an action performed by another person, as we see in interceptive actions or in coincidence timing actions, required when interacting and cooperating with others.

Chapter 6

This final empirical chapter was an initial exploration of individual differences in action prediction performance elicited by the coincidence anticipation task of Chapter 5 in relation to other cognitive and neurophysiological measures of time perception, motor control and autistic traits. The chapter aimed to determine the unique variance in performance accounted for by the effects of motor priming and these additional measures. Somewhat surprisingly, only motor experience of the actions to be observed accounted for a significant amount of variance in participants' performance on the coincidence anticipation task, and this was not modulated by any of the other predictor variables. However, the variance in individual performance was only accounted for in the third person perspective condition when participants had less time between occlusion onset and object lift time; i.e. when they had less time to internally simulate the action before the point which had to be anticipated. For all other conditions, none of the predictor variables accounted for a significant amount of variance in performance across individuals. Whilst the results of this final empirical chapter supported the notion of the importance of motor experience in the ability to effectively simulate and anticipate the spatiotemporal dynamics of action, they equally highlight that other contributing factors are at play in such prediction tasks. These other factors are above and beyond the effects of perspective and any of the other cognitive, motoric or social traits measured as part of this study (given the small to null percentage of variance in performance explained by these factors). As such, the chapter underlines the need for continuing research in the area to further elucidate the contributing processes and mechanisms that facilitate action anticipation systems.

7.3 IMPLICATIONS

The set of studies outlined in this thesis have gone some way to expand on previous literature examining prediction of observed actions. Whilst Graf et al. (2007) and Parkinson et al. (2011) studies suggested our internal simulation of action runs in real time with the real action dynamics, our studies suggest that other factors are at play. Conclusions from these earlier studies were clouded by their use of a mixture of transitive and intransitive, familiar and unfamiliar actions. In this thesis, using stimuli that were more controlled, we can make some firm conclusions regarding the spatiotemporal prediction of simple single limb transitive actions. In particular, the familiarity and/or motor experience of the observed action can determine the speed of the simulation process, as does the frame of reference of the observed action. Employing the same paradigm as these earlier studies we find that we generally have an anticipation bias, simulating action faster than the real action dynamics. However, following motor experience of actions, predictive mechanisms become more accurate.

Pertinent to this thesis are the conclusions drawn regarding the different frames of reference of the observed action. Interestingly, it would appear that this motor experience can impact positively on prediction of observed actions in both first-person and third-person perspectives. However, this is only revealed when interrogating prediction processes via convergent methods of investigation. 1PP actions were seen to be selectively improved when using psychophysics methods of examination, whilst 3PP actions were selectively improved following motor priming when a coincidence anticipation task was used, this latter method likely employing processes similar to those engaged when reacting to external events. The contrasting methods seemingly tap into, or facilitate, differing mechanisms which may underlie observation and prediction of actions performed in different frames of reference.

This leads to two main implications with regards to the literature: Firstly, the perception-action coupled neural system (AON/MNS) may have emerged for both self-generated actions, potentially for fine-grained motor control and adjustment purposes, as well as for other-generated actions, potentially for social interaction purposes. As such, the series of studies supports the notion offered by authors such as Blakemore and Frith (2005) and Wolpert and Flanagan (2001), who suggest the forward modelling of action may be used not only for sensorimotor prediction, but the same computations may also facilitate observation of others to allow us to predict others' reactions and respond in a timely manner to external events.

Secondly, this set of studies highlights how it is essential to use various methods of investigation when interrogating matters of cognitive processes. The stimuli employed as well as the task demands should be considered. Any results obtained and conclusions drawn from them are limited to within the context of the method, until converging methods are employed.

7.4 FUTURE RESEARCH

Whilst this thesis has provided some insight into the cognitive processes underpinning fine-grained spatiotemporal dynamics of simulation and predictive processes, the research has brought to light some limitations of the studies conducted and the ensuing conclusions, and in doing so invites proposals and opportunities for future research.

One of the areas of limitation relates to how familiar objects are associated with multiple actions depending on the actor's goal (Ansuini et al., 2006; Ansuini, Giosa, Turella, Altoè, & Castiello, 2008) and the time course of priming effects for these different action types. Two types of action come to mind: prehensile actions (precision and power grips), used to grasp and move objects; and functional use actions, which are strongly linked to object identity (Buxbaum, Veramonti, & Schwartz, 2000) and are associated with activation of conceptual information (Buxbaum & Saffran, 1998). An object, such as a pair of scissors for example, may thus afford two potential actions: a grip within the handles to cut with the scissors, or a grasp by the blades to move or pass the scissors to someone else. Thus, there are 'conflict' objects that afford more than one type of action, and 'non-conflict' objects which afford the same action in order to grasp-to-move or grasp-to-use.

Neuroimaging studies have demonstrated that grasp-to-move and grasp-to-use actions are associated with different activation patterns (Buxbaum, Kyle, Tang, & Detre, 2006; Creem-Regehr & Lee, 2005; Culham & Valyear, 2006; Johnson-Frey, 2004) and furthermore are disrupted by lesions in different neuroanatomical regions (Buxbaum, Kyle, Grossman, & Coslett, 2007;

Buxbaum, Sirigu, Schwartz, & Klatzky, 2003). As such, two different routes to action have been proposed (Johnson-Frey, 2004; Pisella, Binkofski, Lasek, Toni, & Rossetti, 2006). One is specialised for object acquisition (grasp-to-move) and is a bilateral system localized in part to the superior parietal lobules and intraparietal sulci. This “grasp” system would seem to encode action constraints imposed by the body or environment and may operate independent of long-term conceptual information (Cant, Westwood, Valyear, & Goodale, 2005; Garofeanu, Króliczak, Goodale, & Humphrey, 2004). The other is specialised for grasp-to-use and is a left lateralised system localised to the inferior parietal lobule. This “use” system has been shown to subserve conceptual knowledge about functional actions (Buxbaum & Saffran, 1998).

Whilst priming in the conceptual system has been shown to last weeks (Cave, 1997), priming of grasping actions and other dorso-dorsal stream functions has been shown to last only short periods of time (Jax & Rosenbaum, 2007, 2009). This evidence would thus predict different longevities of the priming effect for grasp versus functional use actions in an action prediction task. More specifically, it would predict that motor priming (with or without visual input) would have a longer lasting beneficial effect on action prediction performance in the grasp-to-use actions compared to the grasp-to-move actions.

By using a similar design to the action prediction occlusion paradigm employed in the first two chapters of this thesis, using dynamic video images of grasp-to-move and grasp-to-use actions in a within-participants design, this hypothesis could be interrogated. Such a study would allow measurement of action prediction performance at different time points post motor priming to examine the decay time of the priming effect on these two action types. If the priming effect has different longevities for the two action types, it would provide evidence in support of the notion that a dorso-dorsal stream does not store information for long periods of time and that it evolved to process information in a dynamically changing environment, processing information online de novo, drawing only on very recent experience.

The study would tease apart prediction mechanisms related to different types of action, which are said to employ different neural pathways. More specifically, the study would primarily (i) determine whether motor priming of actions (whereby the participants perform the actions to be observed) facilitates both action types; (ii) determine whether the beneficial motor priming effect on action prediction has different longevities for different types of action, and in turn (iii) determine whether prediction mechanisms that draw on motor experience have access to a generative model (feedback connections) via the two neural pathways corresponding to the two types of action. This would have consequences for the predictive coding account of action prediction and theories of the mirror neuron system.

A second limitation of the current work relates to the direction of hand and object trajectory in the video stimuli used. Considering specifically the conclusions drawn from the first two empirical chapters, it may be suggested that the results observed are partly due to the fact that the stimuli involve the object being removed towards the actor. In the 1PP, this may be observed as the object being moved closer towards the observer; that is, into the observer's peripersonal space, whereas in the 3PP the object is removed from the table in a direction further away from the observer. This ushers the question as to whether the 3PP stimuli may be interpreted as less socially relevant to the observer than the 1PP actions, which in turn may lead to reduced prediction performance in the spatiotemporal judgement task.

Kilner et al. (2006) and Frenkel-Toledo et al., (2013) investigated the effect of perspective on alpha suppression (used as an indicator of action simulation), utilising MEG and EEG respectively. In both studies, participants watched videos of actors that were either facing towards the observer (allocentric) or facing away with their back to the observer (egocentric), performing simple arm movements. In both studies alpha suppression was found to be greatest in the allocentric condition compared to the egocentric condition. However, in both the Frenkel-Toledo et al. (2013) and Kilner et al. (2006) studies, the 'egocentric' condition was not the typical view that would be seen if the observer were making the action. Instead, an alternative third-person perspective is employed again, with the actor's back to the observer. This is an important distinction. These differing patterns may reflect a process modulated by social relevance of the person observed. A person with their back to us has greatly reduced social salience. In a similar vein, one might argue that transitive actions that involve the object being removed from the peripersonal space of the observer have less social relevance than those that involve an object being placed closer towards the observer. In fact, Griffiths and Tipper (2009) showed that action simulation, where reach path was primed by observing another person's reach around an obstacle, was only activated when the observed stimuli and actions were in the observer's peripersonal space. In turn, this may lead to reduced prediction performance for those 3PP actions, as the action is no longer of significance to us as the action would not require a response from us.

A potential study would involve presenting stimuli whereby the transitive actions involve actors grasping the objects to pass them across the table, as opposed to removing them in the direction of the actor. This would mean that in the 1PP, the object is passed further away from the observer, and in the 3PP the object is moved into the peripersonal space of the observer. The study would have two potential hypotheses: Firstly, the results from the first set of studies may be replicated whereby the prediction is superior in the 1PP, which would support the notion that predictive mechanisms first and foremost serve a self-oriented purpose of facilitating motor control. However, an alternative hypothesis would be that this study would elicit contrary results to the first set of studies, with prediction being superior in the 3PP following motor priming, or at least on par with 1PP actions. This result would support a notion that prediction mechanisms are used also for prediction of others' action, but specifically when the actions are of social significance to us and potentially require a response from us.

7.5 GENERAL CONCLUSIONS

The principal aim of the present thesis was to interrogate theories relating to the principal function of the neural mechanisms underpinning action observation, simulation and prediction. Whilst some theorists have postulated that the action-perception coupled neural system (the AON/MNS) evolved for the purposes of monitoring others' actions for social interaction (e.g. Blakemore & Frith, 2005; Gallese & Goldman, 1998; Iacoboni et al., 2005), others posit that the system emerged to facilitate the monitoring of one's own actions for fine-grain motor control and adjustment (Miall & Wolpert, 1996). In a series of studies designed to examine the spatiotemporal prediction of action, with actions presented from different frames of reference, this thesis has demonstrated that we have a general tendency to anticipate action dynamics ahead of the actual action trajectory when we have little-to-no experience of that action. Having first-hand motor experience of observed actions enables us to make our predictions more precise, but only for observed action in the first person perspective. This would suggest that when all other sensory input is held constant (i.e. no proprioception), our motor experience facilitates the updating of forward models of action and our predictions, but potentially only for self-generated actions, and therefore suggests that the system predominantly facilitates the monitoring of one's own actions, for appropriate readjustment of kinematics for action completion. An EEG study of the event related potentials relating to expectancy violation also indicates the saliency of first-person perspective actions over third-person perspective actions.

Nevertheless, with the use of an alternative paradigm, a coincidence anticipation task, to interrogate spatiotemporal prediction of action, third-person perspective action prediction is facilitated following motor priming. The differing task demands required in this paradigm appear to draw on different mechanisms and may be more evocative of processes employed when intercepting actions or coinciding movements with others, which may thus explain the facilitation of third-person perceptive actions over first-person perspective actions. A preliminary exploratory study demonstrates that it is predominantly motor experience that accounts for individual differences in performance, and that factors including time perception, motor control and autistic traits do not account for any variance in performance on the spatiotemporal prediction task, although a future study with a more varied sample population may yield different results. This set of studies overall highlights how the mechanisms underpinning action simulation and prediction may effectively be employed in the forward modelling and prediction of not only one's own actions but also those of others, potentially to facilitate cooperative behaviours, and that one must consider the experimental design and stimuli employed, as well as task demands when interpreting results as such factors may have a significant impact on the results obtained and conclusions drawn.

APPENDIX A

Chapter 2

Leave-One-Object-Out (LOOO) Analysis

A 5 (object) x 2 (perspective) ANOVA combining data from both Experiments 1 and 2 demonstrated a main effect of object on the PSE (F(3.34,156.85) = 72.63; p<.001, η^2_p = .61, Greenhouse-Geisser corrected). There was no main effect of perspective (F(1,47)=2.23; p=.14). Importantly, there was no object x perspective interaction (F(4,188) = 1.08; p=.37) indicating that the pattern of similarity in the PSE for 1PP and 3PP observed action was similar across transitive action type.

This same pattern of results was observed for the spread of the data: Combining data across Experiments 1 and 2, the 5 (object) x 2 (perspective) ANOVA demonstrated a main effect of object on the spread of the data (F(2.23, 104.93) = 10.92; p<.001, η^2_p = .19, Greenhouse-Geisser corrected). There was no main effect of perspective (F(1,47)=.05; p=.83), and again importantly there was no object x perspective interaction (F(2.46,115.53) = .73; p=.57, Greenhouse-Geisser corrected) indicating that the pattern of similarity in the spread for 1PP and 3PP observed action was similar across transitive action type.

APPENDIX B

Chapter 3

Leave-One-Object-Out (LOOO) Analysis

Experiment 3 – Visual Priming in 3PP

A 5 (object) x 2 (perspective) ANOVA of Experiment 3 demonstrated a main effect of object on the PSE (F(2.31, 53,61) = 14.47; p<.001, η^2_p = .37, Greenhouse-Geisser corrected). There was no main effect of perspective (F(1,23)= .89; p=.36), and no object x perspective interaction (F(4,92) = 1.74; p=.15) indicating that the pattern of similarity in the PSE for 1PP and 3PP observed action was similar across transitive action type.

Experiment 4 – Visual and Motor Priming in 1PP

A 5 (object) x 2 (perspective) ANOVA of Experiment 4 demonstrated a main effect of object on the PSE (F(2.54, 58.41) = 39.15; p<.001, η^2_p = .63, Greenhouse-Geisser corrected). There was a main effect of perspective (F(1,23)= 7.57; p=.01). Importantly, there was no object x perspective interaction (F(2.71,62.34) = .30; p=.88, Greenhouse-Geisser corrected) indicating that the pattern of contrast in PSE for 1PP and 3PP observed action was similar across transitive action type. That is, for each object presented in the experiment, the PSE was smaller for 1PP action compared to 3PP actions.

Experiment 5 – Motor Priming (no visual input) in 1PP

A 5 (object) x 2 (perspective) ANOVA of Experiment 5 demonstrated a main effect of object on the PSE (F(2.45, 56.40) = 12.92; p<.001, η^2_p = .36, Greenhouse-Geisser corrected). There was a main effect of perspective (F(1,23)= 6.22; p=.02). Importantly, there was no object x perspective interaction (F(2.16, 49.72) = .43; p=.79) indicating that the pattern of contrast in PSE between 1PP and 3PP observed action was similar across transitive action type. Thus, the same pattern of results was observed in this current experiment as in Experiment 4. That is, for each object presented in the experiment, the PSE was smaller for 1PP action compared to 3PP actions.

APPENDIX C

Physical and Neurological Examination for Subtle Signs

NAME:______________________________________ **ID:** ______________________

BIRTHDATE: ______/______/______ **DATE EXAM:** ______/______/______

PRESENT AGE:___________ **EXAMINER:**______________

GENDER: ________________

LATERAL PREFERENCE PATTERN Circle “**R**” or “**L**” after each item

Note: Use a piece of paper with a small hole in it and hand to child. It is important to have child use both hands to hold the object.

"Make believe that this is a camera and you’re looking at me to take my picture.”

1. **EYE**:	Look through hole in paper	**L**	**R**	Code EYE R L

“Now I'm going to ask you to 'make believe' a lot of actions. OK?”

Note: Done with child standing

“Show me how you…”

2. **FOOT**:	Kick ball	**L**	**R**	Code FOOT
	Stamp out fire	**L**	**R**	R L Mixed

Note: Done with child sitting

“Show me how you…”

3. **HAND**:	Comb hair	**L**	**R**	Code HAND
	Brush teeth	**L**	**R**	
	Cut with scissors	**L**	**R**	R _______
	Throw ball	**L**	**R**	
	Hit ball with bat	**L**	**R**	L _______
	Hit ball with racket	**L**	**R**	
	Hammer	**L**	**R**	*Mixed _______
	Use Screwdriver	**L**	**R**	
	Saw	**L**	**R**	*if 3 or more items are performed with nondominant hand, code as “mixed” and use L-handed norms
	Flip Coin	**L**	**R**	
	(Open Door with key)	**L**	**R**	

*If child commits BPO error, prompt saying “Now show me what it would look like if you were holding the ___.”

Observations (e.g., body part as object errors):

GROSS MOTOR – GAITS

Errors for gait items include falling, incorrect foot placement, or discontinuing task early. Wiggling, squirming, awkward body use, tics, posturing (e.g., clinched fist, cortical thumb), pronation of palm inward, etc., should be noted qualitatively in the observations section, but do not constitute errors. Also look for asymmetries in movements of arms and legs during normal, unstressed walking. Hands should not be in pockets, and cuffs should be rolled up if necessary so child's hands are visible. If child puts hands in pockets or on hips, say "*Hands at your side*" For all Gaits except backward gaits, the child should walk towards the examiner. The examiner should remain close enough to protect the child from falling.

Tell the child at the beginning of each Gaits item, "*Begin with your arms relaxed by your side*."

1. **GAIT - On Heels (10 steps)**

"First, walk on your heels toward me, like this."

[Demonstrate: Walk while up on the heels of the feet; arms hanging naturally. Examiner should stand several feet in front of the child to allow enough room to walk 10 steps towards the examiner.]

		R	**L**
Errors:	0	0	0
	1 – 2	1	1
	3 or > 3	2	2
Tried but failed (couldn't do)		CD	CD
Child refused. Didn't test		CR	CR
No data (did not examine, etc.)		ND	ND

Hand overflow/postures present? 0 R L B
(If NO, circle 0, if YES, circle R, L, or Both)

Observations (specify R/L)____
(e.g., awkward body use, tics, posturing, asymmetrical or reduced arm swing, odd hand postures, etc.)

2. **GAIT - On Toes (10 steps)**

"Go back to where you started and walk toward me again, this time on your toes."

[Demonstrate: Walk with arms at side, walking on balls of feet. Do NOT describe as walking on tippy toes. If child tries to get up on toes like ballet "en pointe" demonstrate moderate position for toe-walk and explain, *"Not tippy-toes, medium toes."*]

		R	**L**
Errors:	0	0	0
	1 – 2	1	1
	3 or > 3	2	2
Tried but failed (couldn't do)		CD	CD
Child refused. Didn't test		CR	CR
No data (did not examine, etc.)		ND	ND

Hand overflow/postures present? 0 R L B
(If NO, circle 0, if YES, circle R, L, or Both)

Observations (specify R/L)____
(e.g., awkward body use, tics, posturing, asymmetrical or reduced arm swing, odd hand postures, etc.)

3. **GAIT - On Sides of Feet (10 steps)**

Administer and score for all ages; however, when transferring scores to the coding sheet, pay particular attention to age (errors are not considered abnormal if child is < 9 years old).

"Now walk on the sides of your feet, like you are at the beach, and you're trying to protect the bottom of your feet from the hot sand." [Demonstrate: Arms at your side, walk on outer border of feet, showing eversion position. If necessary, elaborate, "Walk on the tough outer part of your feet, like this.]

		R	**L**
Errors:	0	0	0
	1 – 2	1	1
	3 or > 3	2	2
Tried but failed (couldn't do)		CD	CD
Child refused. Didn't test		CR	CR
No data (did not examine, etc.)		ND	ND

Hand overflow/postures present? 0 R L B
(If NO, circle 0, if YES, circle R, L, or Both)

Observations (specify R/L)____
(e.g., awkward body use, tics, posturing, asymmetrical or reduced arm swing, odd hand postures, etc.)

4. **TANDEM GAIT (heel to toe) Forward (10 steps)**

"Now I want you to walk like a tightrope walker. Be sure you put your heel right up against your toe and go as far as you can like that. Don't leave any space in between your feet and don't step on your foot."
[Demonstrate heel-toe walking and remain at the end so child walks toward you]

Errors:	0	0
	1 – 2	1
	3 or > 3	2
Tried but failed (couldn't do)		CD
Child refused. Didn't test		CR
No data (did not examine, etc.)		ND

Observations (specify R/L)____
(e.g., asymmetrical or reduced arm swing, odd hand postures)

5. **TANDEM GAIT (heel to toe) Backward (10 steps)**

Administer and score for all ages; however, when transferring scores to the coding sheet, pay attention to age, as errors are only abnormal for children **10 and older**.

"Now do the same thing backwards, with one foot behind the other, touching heel to toe. Again, don't leave any space between your feet and don't step on your heels."
[Demonstrate. If necessary, elaborate, *"I want you to really go backwards, so you can't see."*

Errors:	0	0
	1 – 2	1
	3 or > 3	2
Tried but failed (couldn't do)		CD
Child refused. Didn't test		CR
No data (did not examine, etc.)		ND

Observations (specify R/L)____
(e.g., awkward body use, tics, posturing, asymmetrical or reduced arm swing, odd hand postures, etc.)

6. TANDEM – Stand Heel to Toe. Eyes Closed. – 20”

Administer and score for all ages; however, when transferring scores to the coding sheet, pay particular attention to age, as errors are only abnormal for children ages **10 and older**.

“Now I want you to put one foot in front of the other, just as you did when you were walking before. This time, though, I want you to close your eyes and stay that way as long as you can, or until I tell you to relax.”
[Demonstrate how to stand on narrow tandem base. Time with stopwatch for the duration of success or up to 20 sec.]

*If the child does not meet 20”, record time here: _________

20	seconds	0
19 – 10	seconds	1
< 10	seconds	2
Tried but failed (couldn't do)		CD
Child refused. Didn’t test		CR
No data (did not examine, etc.)		ND

FL Tendency to fall?	**Y**	**N**
BL Arm(s) out to help balance?	**Y**	**N**
IP Impersistence (opens eyes)?	**Y**	**N**

Observations (specify R/L)____
(e.g., awkward body use, tics, posturing, odd hand postures, etc.)

7. STAND Feet Close, Eyes Closed, Arms & Fingers Outstretched – 20"

“Now I want you to stand like Frankenstein. Put your feet next to each other, close side-by-side, and raise your arms level with shoulders like this. Now, spread all your fingers apart, close your eyes, and stay as still as you can like this for as long as you can or until I say relax.”
[Demonstrate stance, arms up and straight out at shoulder level, fingers abducted, eyes closed. Time with stopwatch for the duration of success or up to 20 sec. Watch for involuntary movements.]

*If the child does not meet 20”, record time here: _________

20	seconds	0
19 – 10	seconds	1
< 10	seconds	2
Tried but failed (couldn't do)		CD
Child refused. Didn’t test		CR
No data (did not examine, etc.)		ND

FL Tendency to fall?	**Y**	**N**	
BL Arm(s) out to help balance?	**Y**	**N**	
IP Impersistence (opens eyes/drops arms)?	**Y**	**N**	
CF Choreiform (Abnormal arm/finger movements)?	**Y**	**N**	**(R L B)**

Observations (specify R/L)____
(e.g., awkward body use, tics, posturing, odd hand postures, etc.)

8. **FINGER-TO-NOSE** (Testing coordination in 4 quadrants in space)

Note: This is done with child standing.

"Now I am going to test your aim. Choose one pointer finger and put it on the tip of your nose." [Examiner holds own pointer finger directly in front of child's nose and far enough out that the child needs to extend his/her arm fully without leaning forward to reach examiner's finger] *"Now, I want you to aim for the very tip of my finger and then go home to your nose. Go ahead and do it."* [Wait for child to perform action] "*Good. Now, I am going to move my finger, and I want you to look for the very tip of my finger and aim for it, and then go home to your nose."* [Examiner moves finger to four points of an imaginary square, i.e. up and right, down and right, up and left, and down and left of the middle point]. If necessary, reiterate, *"Aim for the very tip of my finger."* After completing one hand, say *"Now we're going to do it with the other pointer finger."*

	R	**L**
Normal	0	0
Mild dysmetria, minor limb tremor[a]	1	1
Intention tremor[b], past-pointing	2	2
Tried but failed (couldn't do)	CD	CD
Child refused. Didn't test	CR	CR
No data (did not examine, etc.)	ND	ND

Note: [a] Score 1 point if child does not reach the tip of the finger.
[b] An Intention tremor is characterized by horizontal movement (e.g., at a right angle to the target) and tends to become larger as approaches target.

Observations (specify R/L)____
(e.g., awkward body use, tics, posturing, odd hand postures, etc.)

9. **STICK Out Tongue for 20", Eyes Closed**

"Now, relax a minute. Keep your arms relaxed, stand in a comfortable way, but when I say go, close your eyes, open your mouth, and gently stick out your tongue. Keep your tongue as still and steady as you can for as long as you can or until I say relax."
[Demonstrate relaxed but eyes-closed stance, tongue gently protruded and kept steady]

Note: Child should not clamp tongue with teeth or lips, or protrude tongue so forcefully that it causes discomfort or gagging. If necessary, elaborate, *"No, you just have to show me enough so that I can see it."*

Observe sustained and/or involuntary darting tongue movements (e.g., tongue moves in and out of mouth, or side to side). A natural curl to the tongue is not considered a choreiform movement.

*If the child does not meet 20", record time here: _________

20	seconds	0
19 – 10	seconds	1
< 10	seconds	2
Tried but failed (couldn't do)		CD
Child refused. Didn't test		CR
No data (did not examine, etc.)		ND

AM Choreiform ("reptile") tongue (writhing or darting tongue movements)? **Y** **N**
IP Impersistence (opens eyes or closes mouth)? **Y** **N**

Observations (specify R/L)____
(e.g., any nonspecific tremor, awkward body use, tics, posturing, odd hand postures, etc.)

10. STAND on One Foot for 30” (eyes open)

“Now I want you to stand on one leg for as long as you can. I'll tell you when to relax.”
[Demonstrate balance by standing on one leg with arms relaxed at side and one leg lifted off floor, bent back at knee. Correct any exaggerated or "ballet" postures of raised leg attempted by examinee and re-demonstrate. If child attempts to hold their foot up or use another compensation strategy, allow the activity, but repeat the task again, stating, *“This time try it without holding your foot,”* and score best attempt.]

Note: Allow to choose which leg to stand on first, and record choice.

*If the child does not meet 30”, record time here: R ____ L _____

Circle foot used first R L

		R	L
30	seconds	0	0
29 – 20	seconds	1	1
< 20	seconds	2	2
Tried but failed (couldn't do)		CD	CD
Child refused. Didn’t test		CR	CR
No data (did not examine, etc.)		ND	ND

Observations (specify R/L)____

11. HOP on one foot

Allow child to hop as many times as they can, up to 50 hops. Note, however, that only 25 successful hops are required to receive maximum credit at age 7 or 8.

“Next, I want you to hop on one foot. Make sure to hop in the same spot, not moving across the room, but more like a 'Jack-in-the-Box.' Choose whichever foot you like to hop first; then we'll do the other. Keep hopping till 1 stop counting”
[Demonstrate hopping in place and gently correct if hopping is of progressive moving type. Allow child to choose which foot to hop on first]

“Ready? Now! "
[Count in a “whispery voice” for duration of success or up to 50 hops, providing encouragement if needed]

Repeat for second foot, allowing child to rest first if necessary:
"Now do the same hopping on the other foot. Ready? Now!”

*If the child does not make 25/50 hops, record number of hops here: R_____ L ______

Circle foot used first R L

		R	L
≤ 8 yrs (25 hops)	≥ 9 yrs (50 hops)	0	0
24 – 12	49 – 25	1	1
< 12	< 25	2	2
Tried but failed (couldn't do)		CD	CD
Child refused. Didn’t test		CR	CR
No data (did not examine, etc.)		ND	ND

Observations (specify R/L)____

(e.g., dysrhythmia)

RAPID/SEQUENTIAL MOVEMENTS

Position child on chair directly across from examiner. Say, *"Sit up straight in chair, feet flat on floor and hands on lap with palms facing down."*

"Now we are going to see how fast you can move your feet, hands, fingers and tongue - all your fast muscles. Each time we do a movement, you can choose which side to do first. Watch me first and I'll show you how to do each one."

[Demonstrate each item. Keep shoes on unless either examiner or examinee has on high heels or platform soles, in which case remove shoes. Be sure the height of the chair allows the child's feet to rest flat on the floor.]

For timed items,

- ∗ Each movement should start in the same position: *Sitting up straight in chair, feet flat on floor and hands on lap with palms face down.*
- ∗ **Circle** the first side chosen for each item.
- ∗ Record time in seconds to two decimal points for milliseconds.
- ∗ **ALLOW PATIENT TO GET INTO SET BEFORE BEGINNING TO TIME**. Qualitative observations are made throughout, but SCORE TIME only after they have gotten into set.
- ∗ Number of taps, pats, or sets to be timed is indicated in **parentheses** next to each item.
- ∗ Code extraneous **overflow** and **dysrhythmic movements** (0 if absent, 1 if present).
- ∗ Code the following in the time slot if
  - Child tried but failed or couldn't do – code as CD
  - Child refused – code as CR
  - Item was not examined – code as ND

Proximal Overflow: Errors on the same side involving larger muscle groups, even if a different limb (e.g., mimicking foot movement with hand). Finger flapping on Finger Sequence is coded as a Proximal Overflow

Mirror movement: Errors on the same limb on the opposite side. Coded even if only observed at the beginning of the task and then disappears. Code even if observed during practice.

Sequencing errors on Finger Sequence are coded as a Dysrhythmia

If Child CAN'T DO the movement (CD), also score "1" for Dysrhythmia for each side unable to be completed.

Position subject on chair directly across from examiner. Say, *“Sit up straight in chair, feet flat on floor and hands on lap with palms facing down.”*		OVERFLOW			DYS-RHYTHMIC/ SEQUENCING ERROR
“I’m going to ask you to do some movements as fast as you can but you also need to do them as well as you can.”	Time ******* *Record to 2 decimals*	PROXIMAL (CEPHAL)	ORO-FACIAL	MIRROR	
Foot tap *(20 taps)* *“First, choose one foot and tap it like this, like you are impatiently waiting for someone, on the floor. Keep the heel of your foot on the floor and tap the front of the foot fast, like this. Ready? Now!"* [Complete one trial of first foot] *"Now the same with the other foot. Ready? Now!”* [Repeat for second side.]	L:____ R:____	0 1 0 1	0 1 0 1	0 1 0 1	0 1 0 1
Foot heel-toe tap *(10 sets)* *“Now, rock one foot back and forth, heel-toe, heel-toe, as fast as you can, like this. Ready? Now!”* [Repeat for second side.]	L:____ R:____	0 1 0 1	0 1 0 1	0 1 0 1	0 1 0 1
Hand pat *(20 pats)* *“Now we are up to the hands. Choose one hand and pat it on your lap, like this, as fast as you can. Keep your arm steady and just use your wrist. Ready? Now!"* (Demonstrate rapid patting. Correct, if slaps hard, to gentle fast pats.)	L:____ R:____	0 1 0 1	0 1 0 1	0 1 0 1	0 1 0 1
Hand pronate/supinate *(10 sets)* *“The next thing we do with the hands is patting, like this, back and palm, flip-flop, flip-flop, as fast as you can. Keep your arm close against your side. Choose one hand and- Ready? Now!”* [Demonstrate hand pronation and supination alternating pats on lap.] Note: Correct “rolling” on the elbow or arm by saying, *“It’s a real ‘pat,’ pat the palm, pat the back, pat the palm, pat the back…”*	L:____ R:____	0 1 0 1	0 1 0 1	0 1 0 1 ***OK < 9yo, but circle anyway***	0 1 0 1
Finger tap *(20 taps)* *"Were up to the fingers. I want you to tap the thumb and index finger together as fast as you can. Ready? Now!”* [Demonstrate thumb/index finger rapid tapping.]	L:____ R:____	0 1 0 1	0 1 0 1	0 1 0 1	0 1 0 1

Appose finger succession *(5 sets)* *"Now this is the hardest one we do. Watch me; tap each finger against the thumb in order, then do them again, like this. Do not go backwards, always this way - pointer, middle, ring, pinkie, 1, 2, 3, 4. Try it."* [If necessary, can make the sound of different tones as fingers hit thumb] *O. K. Now try it on the other hand. Good. Now get ready to choose one hand and do these taps in order as fast as you can. Ready? Now!"* [If necessary, cue to keep thumb still and move fingers down to thumb rather than vice versa. Count 20 taps, even if sequencing is wrong but each finger should tap the thumb, not roll across the thumb]	L:____ R:____	0 1 0 1	0 1 0 1	0 1 0 1 ***OK < 13yo, but circle anyway***	0 1 0 1
Tongue side to side *(10 sets)* *"Now we need to do tongue-wiggling. Move your tongue side-to-side like a dog wagging its tail. Like this…touch each corner of your lips, then the other, back and forth as fast as you can. Ready?"* [Demonstrate tongue going laterally, from one angle of lips to other. Correct if does in/out rotatory movement and re-demonstrate.]	______	0 1 (Jaw Synkinesis = Shifting of lower jaw back and forth)			0 1

APPENDIX D

PANESS Scoring Sheet

Name/Subject #: DoE: Age:
Gender: DoB:

Lateral Preference: EYE: R L FOOT: R L Mixed HAND: R L *Mixed

---

- Code PANESS scores below. Note that some movements are coded differently depending upon age.
- If "CD" is circled on the PANESS, code as a "2" if movement is expected to be WNL for age group.
- Tandems, Stand, and Tongue have unilateral scores only.

GAITS	**R**	**L**		
1. Heels	0 1 2	0 1 2		
2. Toes	0 1 2	0 1 2		
3. Sides (Code errors only if age ≥9 yo; if age ≤ 8, code as 0 regardless of errors)	0 1 2	0 1 2		
4. Forward Tandem	0 1 2			
5. Backward Tandem (Code errors only if age ≥10 yo; if age ≤ 9, code as 0 regardless of errors)	0 1 2			
STATIONS	**R**	**L**		
6. Tandem (Code errors only if age ≥10 yo)	0 1 2			
7. Stand with Two Feet	0 1 2		**Right Axial**	=
________ (R side #1-3, 10, 11)			(Range 0-10)	
10. Stand on one foot	0 1 2	0 1 2	**Left Axial**	=
________ (L side #1-3, 10, 11)			(Range 0-10)	
11. Hop (Unilateral)	0 1 2	0 1 2	**Total Axial**	=
________ (R + L + 4,5, 6, 7)			(Range 0-28)	

OVERFLOW GAITS	**R**	**L**		
1. Heels	0 1	0 1	***Right Overflow**	=
________ (Code errors only if age ≥6 yo)			(Range 0-3)	
2. Toes	0 1	0 1	***Left Overflow**	=
________ (Code errors only if age ≥6 yo)			(Range 0-3)	
3. Sides	0 1	0 1	***Total Overflow**	=
________ (Code errors only if age ≥9 yo)			(Range 0-6)	

INVOLUNTARY MOVEMENTS	**R**	**L**
7. Choreiform (Abnormal arm/finger movements)	0 1	0 1
8. Tremor (Finger to nose)	0 1 2	0 1 2
9. Choreiform (Reptile tongue)	0 1	

MISC. OBSERVATIONS	R		L		
Posture Hemiparetic	0	1	0	1	**Miscellaneous and Involuntary Totals**
Posture Dystonic	0	1	0	1	**Right** = _______ (R Invol. 7 + R Invol. 8 + R Misc.) (Range 0-7)
Nystagmus	0	1	0	1	**Left** = _______ (L Invol. 7 + L Invol. 8 + L Misc.) (Range 0-7)
Strabismus	0	1	0	1	**Total** = _______ (R Misc. & Invol. + L Misc.& Invol + Invol. 9) (Range 0-15)

Right Misc. _______ (Range 0-7) **Left Misc.** _______ (Range 0-7)

Total Gaits and Stations = ___________________ (Total Axial + *Total Overflow + Total Miscellaneous & Involuntary)
(0-49) (0-28) (0-6) (0-15)

PANESS Timed Movements

OVERFLOW – TIMED MOVEMENTS	R			PANESS Score	L			PANESS Score
Foot Tap (FT)	0	1	2	_________	0	1	2	
Heel/toe tap (HT)	0	1	2	_________	0	1	2	
Hand Pat (HP)	0	1	2	_________	0	1	2	
Hand Pronate/Supinate (HPS) (For Mirror, Code errors only if age ≥9 yo)	0	1	2	*_________	0	1	2	*_____
Finger Tap (FR)	0	1	2	_________	0	1	2	
Finger Apposition (FS) (For Mirror, Code errors only if age ≥13 yo)	0	1	2	*_________	0	1	2	*_____

***Timed Right Overflow** _________ (Range 0-12) ***Timed Left Overflow** ____ (Range 0-12)

Under **R** and **L**, transfer scores directly from PANESS. Code as a

Score of 0 if no overflow is present regardless of age appropriateness.
Score of 1 if only Proximal **or** Oro-Facial **or** Mirror are present *or* if both Proximal ***AND*** Oro-facial
Score of 2 if Both Proximal ***AND*** Mirror *or* if both Oro-facial ***AND*** Mirror *or* Proximal ***AND*** Oro-facial ***AND*** Mirror

Under **PANESS Score**, directly transfer scores from answers recorded under Right and Left, except when asterisk is present. If *, copy the score to the **PANESS Score** only if score is abnormal for age; otherwise, if age appropriate, change score to 0 in this column.

Tongue (jaw synkinesis) 0 1

***Total Timed Overflow** __________ (Sum R Overflow + L Overflow + Tongue)
(Range 0-25)

DYSRHYTHMIA – TIMED MOVEMENTS	**R**		**L**	
Foot Tap (FT)	0	1	0	1
Heel/toe tap (HT)	0	1	0	1
Hand Pat (HP)	0	1	0	1
Hand Pronate/Supinate (HPS)	0	1	0	1
Finger Tap (FR)	0	1	0	1
Finger Apposition (FS)	0	1	0	1

Right Dysrhythmia ___________ (Range 0-6) **Left Dysrhythmia** ___________ (Range 0-6)

Tongue	0	1		

Total Dysrhythmia __________ (Sum R Dysrhythmia + L Dysrhythmia + Tongue)
(Range 0-13)

MISC. TIMED OBSERVATIONS	**R**		**L**	
Choreoathetoid (Extended arm/elbow turned outward)	0	1	0	1
Hemiparetic (Flexed elbow)	0	1	0	1
Other (_____________________)	0	1	0	1

Right Timed Misc. ___________ (Range 0-3) **Left Timed Misc.** ___________ (Range 0-3)

Total Timed Misc. ____________
(Range 0-6)

TIMED MOVEMENTS (SFA Scores)

	Right			Left		
	Seconds	z-Score	SFA Score	Seconds	Z-Score	SFA Score
FT	________	________	0 1 2	________	________	0 1 2
HT	________	________	0 1 2	________	________	0 1 2
HP	________	________	0 1 2	________	________	0 1 2
HPS	________	________	0 1 2	________	________	0 1 2
FR	________	________	0 1 2	________	________	0 1 2
FS	________	________	0 1 2	________	________	0 1 2

Right SFA______________________ **Left SFA** _______
(Range 0-12) (Range 0-12)

Under **Seconds,** copy times in seconds to decimal points for each Right and Left sided movement.
Under **z-Score**, calculate z-values using Mean and Standard Deviation from the PANESS Timed Motor Movements Norms.
Normative data are stratified by child's **age**, **gender**, and **handedness**.
Use right-handed norms for left-handed children 11 years or older.
Calculate reverse scored z-values [(Normative score - Child's Score) / Standard Deviation (SD)] so that positive scores indicate better performance.
To determine **SFA score**:
If **z-score** is greater than -1 SD below the mean (i.e., Child is WNL or Child is more than 1 SD *above* the mean, thus faster), SFA = 0
If **z-score** is between -1 SD and -2 SD below the mean, SFA = 1
If **z-score** is less than -2 SD below the mean (i.e., indicating very poor performance), SFA = 2

Tongue ________ 0 2
(jaw synkinesis)

Circle 0 or 2 for the tongue. If the child is:
For children age 5-9, the mean is **< 6** seconds: **For children Age 10 and above**, the mean is <3 seconds:
If Time is ≤ 6 seconds, score as 0. If time > 6 seconds, score as 2. If Time is ≤ 3 seconds, score as 0. If time > 3 seconds, score as 2.

***Total SFA** __________ (Sum R SFA + L SFA + Tongue SFA)
(Range 0-26)

TOTALS

Total Right Overflow ___________ (*Right Overflow [pg 1] + *Timed Right Overflow [pg 2])
(Range 0-15) (Range 0-3) (Range 0-12)

Total Left Overflow ___________ (*Left Overflow [pg 1] + *Timed Left Overflow [pg 2])
(Range 0-15) (Range 0-3) (Range 0-12)

Total Overflow ___________ (*Total Overflow [pg 1] + * Total Timed Overflow [pg 2])
(Range 0-31) (Range 0-6) (Range 0-25)

Total Gaits & Stations ___________ (Total Axial [pg 1] + *Total Overflow [pg 1] + Total Miscellaneous & Involuntary [pg 1])
(Range 0-49) (0-28) (0-6) (0-15)

Total Timed ___________ (Total Timed Overflow [pg 2] + Total Dysrhythmia [pg 2] + Total Timed Misc. [pg 2] + Total SFA [pg 3])
(Range 0-70) (Range 0-25) (Range 0-13) (Range 0-15) (Range 0-26)

Total PANESS ___________ (Total Gaits and Stations + Total Timed)
(Range 0-119) (Range 0-49) (Range 0-70)

* Indicate totals in which only abnormal scores for age group are included.

APPENDIX E

The Adult Autism Spectrum Quotient (AQ)

Ages 16+

SPECIMEN, FOR RESEARCH USE ONLY.

For full details, please see:

S. Baron-Cohen, S. Wheelwright, R. Skinner, J. Martin and E. Clubley, (2001)
The Autism Spectrum Quotient (AQ) : Evidence from Asperger Syndrome/High Functioning Autism, Males and Females, Scientists and Mathematicians
Journal of Autism and Developmental Disorders 31:5-17

Name:.. Sex:...

Date of birth:.................................. Today's Date................................

How to fill out the questionnaire

Below are a list of statements. Please read each statement very carefully and rate how strongly you agree or disagree with it by circling your answer.

DO NOT MISS ANY STATEMENT OUT.

Examples

E1. I am willing to take risks.	definitely agree	slightly agree	[✓ slightly disagree]	definitely disagree
E2. I like playing board games.	definitely agree	[✓ slightly agree]	slightly disagree	definitely disagree
E3. I find learning to play musical instruments easy.	definitely agree	slightly agree	slightly disagree	[✓ definitely disagree]
E4. I am fascinated by other cultures.	[✓ definitely agree]	slightly agree	slightly disagree	definitely disagree

1. I prefer to do things with others rather than on my own.	definitely agree	slightly agree	slightly disagree	definitely disagree
2. I prefer to do things the same way over and over again.	definitely agree	slightly agree	slightly disagree	definitely disagree
3. If I try to imagine something, I find it very easy to create a picture in my mind.	definitely agree	slightly agree	slightly disagree	definitely disagree
4. I frequently get so strongly absorbed in one thing that I lose sight of other things.	definitely agree	slightly agree	slightly disagree	definitely disagree
5. I often notice small sounds when others do not.	definitely agree	slightly agree	slightly disagree	definitely disagree
6. I usually notice car number plates or similar strings of information.	definitely agree	slightly agree	slightly disagree	definitely disagree
7. Other people frequently tell me that what I've said is impolite, even though I think it is polite.	definitely agree	slightly agree	slightly disagree	definitely disagree
8. When I'm reading a story, I can easily imagine what the characters might look like.	definitely agree	slightly agree	slightly disagree	definitely disagree
9. I am fascinated by dates.	definitely agree	slightly agree	slightly disagree	definitely disagree
10. In a social group, I can easily keep track of several different people's conversations.	definitely agree	slightly agree	slightly disagree	definitely disagree
11. I find social situations easy.	definitely agree	slightly agree	slightly disagree	definitely disagree
12. I tend to notice details that others do not.	definitely agree	slightly agree	slightly disagree	definitely disagree
13. I would rather go to a library than a party.	definitely agree	slightly agree	slightly disagree	definitely disagree
14. I find making up stories easy.	definitely agree	slightly agree	slightly disagree	definitely disagree
15. I find myself drawn more strongly to people than to things.	definitely agree	slightly agree	slightly disagree	definitely disagree
16. I tend to have very strong interests which I get upset about if I can't pursue.	definitely agree	slightly agree	slightly disagree	definitely disagree
17. I enjoy social chit-chat.	definitely agree	slightly agree	slightly disagree	definitely disagree
18. When I talk, it isn't always easy for others to get a word in edgeways.	definitely agree	slightly agree	slightly disagree	definitely disagree
19. I am fascinated by numbers.	definitely agree	slightly agree	slightly disagree	definitely disagree

20. When I’m reading a story, I find it difficult to work out the characters’ intentions.	definitely agree	slightly agree	slightly disagree	definitely disagree
21. I don’t particularly enjoy reading fiction.	definitely agree	slightly agree	slightly disagree	definitely disagree
22. I find it hard to make new friends.	definitely agree	slightly agree	slightly disagree	definitely disagree
23. I notice patterns in things all the time.	definitely agree	slightly agree	slightly disagree	definitely disagree
24. I would rather go to the theatre than a museum.	definitely agree	slightly agree	slightly disagree	definitely disagree
25. It does not upset me if my daily routine is disturbed.	definitely agree	slightly agree	slightly disagree	definitely disagree
26. I frequently find that I don’t know how to keep a conversation going.	definitely agree	slightly agree	slightly disagree	definitely disagree
27. I find it easy to “read between the lines” when someone is talking to me.	definitely agree	slightly agree	slightly disagree	definitely disagree
28. I usually concentrate more on the whole picture, rather than the small details.	definitely agree	slightly agree	slightly disagree	definitely disagree
29. I am not very good at remembering phone numbers.	definitely agree	slightly agree	slightly disagree	definitely disagree
30. I don’t usually notice small changes in a situation, or a person’s appearance.	definitely agree	slightly agree	slightly disagree	definitely disagree
31. I know how to tell if someone listening to me is getting bored.	definitely agree	slightly agree	slightly disagree	definitely disagree
32. I find it easy to do more than one thing at once.	definitely agree	slightly agree	slightly disagree	definitely disagree
33. When I talk on the phone, I’m not sure when it’s my turn to speak.	definitely agree	slightly agree	slightly disagree	definitely disagree
34. I enjoy doing things spontaneously.	definitely agree	slightly agree	slightly disagree	definitely disagree
35. I am often the last to understand the point of a joke.	definitely agree	slightly agree	slightly disagree	definitely disagree
36. I find it easy to work out what someone is thinking or feeling just by looking at their face.	definitely agree	slightly agree	slightly disagree	definitely disagree
37. If there is an interruption, I can switch back to what I was doing very quickly.	definitely agree	slightly agree	slightly disagree	definitely disagree
38. I am good at social chit-chat.	definitely agree	slightly agree	slightly disagree	definitely disagree
39. People often tell me that I keep going on and on	definitely	slightly	slightly	definitely

about the same thing.	agree	agree	disagree	disagree
40. When I was young, I used to enjoy playing games involving pretending with other children.	definitely agree	slightly agree	slightly disagree	definitely disagree
41. I like to collect information about categories of things (e.g. types of car, types of bird, types of train, types of plant, etc.).	definitely agree	slightly agree	slightly disagree	definitely disagree
42. I find it difficult to imagine what it would be like to be someone else.	definitely agree	slightly agree	slightly disagree	definitely disagree
43. I like to plan any activities I participate in carefully.	definitely agree	slightly agree	slightly disagree	definitely disagree
44. I enjoy social occasions.	definitely agree	slightly agree	slightly disagree	definitely disagree
45. I find it difficult to work out people's intentions.	definitely agree	slightly agree	slightly disagree	definitely disagree
46. New situations make me anxious.	definitely agree	slightly agree	slightly disagree	definitely disagree
47. I enjoy meeting new people.	definitely agree	slightly agree	slightly disagree	definitely disagree
48. I am a good diplomat.	definitely agree	slightly agree	slightly disagree	definitely disagree
49. I am not very good at remembering people's date of birth.	definitely agree	slightly agree	slightly disagree	definitely disagree
50. I find it very easy to play games with children that involve pretending.	definitely agree	slightly agree	slightly disagree	definitely disagree

Developed by:
The Autism Research Centre
University of Cambridge

REFERENCES

Abernethy, B., Gill, D. P., Parks, S. L., & Packer, S. T. (2001). Expertise and the perception of kinematic and situational probability information. *Perception*, *30*(2), 233–252. http://doi.org/10.1068/p2872

Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience*, *11*(9), 1109–1116. http://doi.org/10.1038/nn.2182

Alaerts, K., Heremans, E., Swinnen, S. P., & Wenderoth, N. (2009). How are observed actions mapped to the observer’s motor system? Influence of posture and perspective. *Neuropsychologia*, *47*(2), 415–22. http://doi.org/10.1016/j.neuropsychologia.2008.09.012

Allman, M. J. (2011). Deficits in temporal processing associated with autistic disorder. *Frontiers in Integrative Neuroscience*, *5*(March), 2. http://doi.org/10.3389/fnint.2011.00002

Allman, M. J., DeLeon, I. G., & Wearden, J. H. (2011). Psychophysical assessment of timing in individuals with autism. *American Journal on Intellectual and Developmental Disabilities*, *116*(2), 165–78. http://doi.org/10.1352/1944-7558-116.2.165

Anquetil, T., & Jeannerod, M. (2007). Simulated actions in the first and in the third person perspectives share common representations. *Brain Research*, *1130*(1), 125–9. http://doi.org/10.1016/j.brainres.2006.10.091

Ansuini, C., Giosa, L., Turella, L., Altoè, G., & Castiello, U. (2008). An object for an action, the same object for other actions: Effects on hand shaping. *Experimental Brain Research*, *185*(1), 111–119. http://doi.org/10.1007/s00221-007-1136-4

Ansuini, C., Santello, M., Massaccesi, S., Castiello, U., Ansuini, C., Santello, M., … Massaccesi, S. (2006). Effects of End-Goal on Hand Shaping. *Journal of Neurophysiology*, *95*, 2456–2465. http://doi.org/10.1152/jn.01107.2005

Austin, E. J. (2005). Personality correlates of the broader autism phenotype as assessed by the Autism Spectrum Quotient (AQ). *Personality and Individual Differences*, *38*(2), 451–460. http://doi.org/10.1016/j.paid.2004.04.022

Avenanti, A., Bueti, D., Galati, G., & Aglioti, S. M. (2005). Transcranial magnetic stimulation highlights the sensorimotor side of empathy for pain. *Nature Neuroscience*, *8*(7), 955–960.

Babiloni, C., Babiloni, F., Carducci, F., Cincotti, F., Cocozza, G., Del Percio, C., … Rossini, P. M. (2002). Human Cortical Electroencephalography (EEG) Rhythms during the Observation of Simple Aimless Movements: A High-Resolution EEG Study. *NeuroImage*, *17*(2), 559–572. http://doi.org/10.1006/nimg.2002.1192

Babiloni, C., Del Percio, C., Rossini, P. M., Marzano, N., Iacoboni, M., Infarinato, F., … Eusebi, F. (2009). Judgment of actions in experts: a high-resolution EEG study in elite athletes. *NeuroImage*, *45*(2), 512–21. http://doi.org/10.1016/j.neuroimage.2008.11.035

Babiloni, C., Marzano, N., Infarinato, F., Iacoboni, M., Rizza, G., Aschieri, P., … Del Percio, C. (2010). “Neural efficiency” of experts’ brain during judgment of actions: a high-resolution EEG study in elite and amateur karate athletes. *Behavioural Brain Research*, *207*(2), 466–75. http://doi.org/10.1016/j.bbr.2009.10.034

Bach, P., Fenton-Adams, W., & Tipper, S. P. (2014). Can’t touch this: the first-person perspective provides privileged access to predictions of sensory action outcomes. *Journal of Experimental Psychology. Human Perception and Performance*, *40*(2), 457–64. http://doi.org/10.1037/a0035348

Baess, P., Jacobsen, T., & Schroger, E. (2008). Suppression of the auditory N1 event-related potential component with unpredictable self-initiated tones: Evidence for internal forward models with dynamic stimulation. *International Journal of Psychophysiology*, *70*(2), 137–143. http://doi.org/10.1016/j.ijpsycho.2008.06.005

Baron-Cohen, S., Wheelwright, S., Skinner, R., & Martin, J. (2001). The Autism-Spectrum Quotient (AQ): Evidence from Asperger Syndrome/High-Functioning Autism, males and females, scientists and mathematicians. *Journal of Autism and Developmental Disorders*, *31*(1), 5–17. http://doi.org/10.1023/A

Bekkering, H., Wohlschläger, a, & Gattis, M. (2000). Imitation of gestures in children is goal-directed. *The Quarterly Journal of Experimental Psychology. A, Human Experimental Psychology*, *53*(1), 153–164. http://doi.org/10.1080/713755872

Bellebaum, C., & Daum, I. (2008). Learning-related changes in reward expectancy are reflected in the feedback-related negativity. *European Journal of Neuroscience*, *27*(7), 1823–1835. http://doi.org/10.1111/j.1460-9568.2008.06138.x

Bergouignan, L., Nyberg, L., & Ehrsson, H. H. (2014). Out-of-body-induced hippocampal amnesia. *Proceedings of the National Academy of Sciences*. http://doi.org/10.1073/pnas.1318801111

Bertamini, M. (1993). Memory for position and dynamic representations. *Memory & Cognition*, *21*(4), 449–57. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/8350736

Blakemore, S.-J., & Frith, C. (2005). The role of motor contagion in the prediction of action. *Neuropsychologia*, *43*(2), 260–7. http://doi.org/10.1016/j.neuropsychologia.2004.11.012

Bootsma, R. J. (1989). Accuracy of perceptual processes subserving different perception-action systems. *Quarterly Journal of Experimental Psychology*, *41A*(3), 489–500.

Botvinick, M., & Cohen, J. (1998). Rubber hands "feel" touch that eyes see. *Nature*, *391*(6669), 756. http://doi.org/10.1038/35784

Brandeis, D., & Lehmann, D. (1986). Event-related potentials of the brain and cognitive processes: Approaches and applications. *Neuropsychologia*, *24*(1), 151–168. http://doi.org/10.1016/0028-3932(86)90049-7

Brass, M., Bekkering, H., Wohlschläger, a, & Prinz, W. (2000). Compatibility between observed and executed finger movements: comparing symbolic, spatial, and imitative cues. *Brain and Cognition*, *44*(2), 124–43. http://doi.org/10.1006/brcg.2000.1225

Brass, M., & Heyes, C. (2005). Imitation: is cognitive neuroscience solving the correspondence problem? *Trends in Cognitive Sciences*, *9*(10), 489–95. http://doi.org/10.1016/j.tics.2005.08.007

Brass, M., Zysset, S., & von Cramon, D. Y. (2001). The inhibition of imitative response tendencies. *NeuroImage*, *14*(6), 1416–23. http://doi.org/10.1006/nimg.2001.0944

Brisson, J., Warreyn, P., Serres, J., Foussier, S., & Adrien-Louis, J. (2012). Motor anticipation failure in infants with autism: a retrospective analysis of feeding situations. *Autism : The International Journal of Research and Practice*, *16*(4), 420–9. http://doi.org/10.1177/1362361311423385

Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., … Parma, I.-. (2001). Action observation activates premotor and parietal areas in a somatotopic manner : an fMRI study. *European Journal of Neuroscience*, *13*, 400–404.

Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H., … Neuroscienze, D. (2004). of Hand Actions : An Event-Related fMRI Study, *42*, 323–334.

Buchanan, J. J., & Wright, D. L. (2011). Generalization of action knowledge following observational learning. *Acta Psychologica*, *136*(1), 167–78. http://doi.org/10.1016/j.actpsy.2010.11.006

Bueti, D., Bahrami, B., & Walsh, V. (2008). Sensory and Association Cortex in Time Perception. *Journal of Cognitive Neuroscience*, *20*(6), 1054–1062. http://doi.org/10.1162/jocn.2008.20060

Caggiano, V., Fogassi, L., Rizzolatti, G., Pomper, J. K., Thier, P., Giese, M. a, & Casile, A. (2011). View-based encoding of actions in mirror neurons of area f5 in macaque premotor cortex. *Current Biology : CB*, *21*(2), 144–8. http://doi.org/10.1016/j.cub.2010.12.022

Calvo-Merino, B., Glaser, D. E., Grèzes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: an FMRI study with expert dancers. *Cerebral Cortex (New York, N.Y. : 1991)*, *15*(8), 1243–9. http://doi.org/10.1093/cercor/bhi007

Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology : CB*, *16*(19), 1905–10. http://doi.org/10.1016/j.cub.2006.07.065

Cant, J. S., Westwood, D. A., Valyear, K. F., & Goodale, M. A. (2005). No evidence for visuomotor priming in a visually guided action task. *Neuropsychologia*, *43*(2 SPEC. ISS.), 216–226. http://doi.org/10.1016/j.neuropsychologia.2004.11.008

Carr, L., Iacoboni, M., Dubeau, M.-C., Mazziotta, J. C., & Lenzi, G. L. (2003). Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proceedings of the National Academy of Sciences of the United States of America*, *100*(9), 5497–502. http://doi.org/10.1073/pnas.0935845100

Casile, A., & Giese, M. a. (2006). Nonvisual motor training influences biological motion perception. *Current Biology : CB*, *16*(1), 69–74. http://doi.org/10.1016/j.cub.2005.10.071

Casile, A., & Giese, M. A. (2005). Critical features for the recognition of biological motion. *Journal of Vision*, *5*, 348–360. http://doi.org/10.1167/5.4.6

Cattaneo, L., Fabbri-Destro, M., Boria, S., Pieraccini, C., Monti, A., Cossu, G., & Rizzolatti, G. (2007). Impairment of actions chains in autism and its possible role in intention understanding. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(45), 17825–30. http://doi.org/10.1073/pnas.0706273104

Cave, C. B. (1997). Very long-lasting priming in picture naming. *Psychological Science*, *8*(4), 322–325. http://doi.org/10.1111/j.1467-9639.1991.tb00167.x

Chaminade, T., Meary, D., Orliaguet, J. P., & Decety, J. (2001). Is perceptual anticipation a motor simulation? A PET study. *Neuroreport*, *12*(17), 3669–74. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11726771

Chamley, C. P. (2003). *Rational Herds. Economic models of social learning*. New York: Cambridge University Press.

Chan, A. W.-Y., Peelen, M. V, & Downing, P. E. (2004). The effect of viewpoint on body representation in the extrastriate body area. *Neuroreport*, *15*(15), 2407–10. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/15640765

Chartrand, T., & Bargh, J. (1999). The Chameleon Effect: The perception-behavior link and social interaction. *Journal of Personality and Social Psychology*, *76*(6), 893–910.

Chong, T. T.-J., Cunnington, R., Williams, M. a, Kanwisher, N., & Mattingley, J. B. (2008). fMRI adaptation reveals mirror neurons in human inferior parietal cortex. *Current Biology : CB*, *18*(20), 1576–80. http://doi.org/10.1016/j.cub.2008.08.068

Cochin, S., Barthelemy, C., Lejeune, B., Roux, S., & Martineau, J. (1998). Perception of motion and qEEG activity in human adults. *Electroencephalography and Clinical Neurophysiology*, *107*(4), 287–95. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9872446

Cochin, S., Barthelemy, C., & Roux, S. (1999). Observation and execution of movement : similarities demonstrated by quantified electroencephalography. *European Journal of Neuroscience*, *11*(June 1998), 1839–1842.

Conson, M., Aromino, A. R., & Trojano, L. (2010). Whose hand is this? Handedness and visual perspective modulate self/other discrimination. *Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation Cérébrale*, *206*(4), 449–53. http://doi.org/10.1007/s00221-010-2418-9

Conson, M., Mazzarella, E., & Trojano, L. (2009). Numbers are represented in egocentric space: effects of numerical cues and spatial reference frames on hand laterality judgements. *Neuroscience Letters*, *452*(2), 176–80. http://doi.org/10.1016/j.neulet.2009.01.043

Cook, R., Press, C., Dickinson, A., & Heyes, C. (2010). Acquisition of automatic imitation is sensitive to sensorimotor contingency. *Journal of Experimental Psychology: Human Perception and Performance*, *36*(4).

Costantini, M., & Haggard, P. (2007). The rubber hand illusion: sensitivity and reference frame for body ownership. *Consciousness and Cognition*, *16*(2), 229–40. http://doi.org/10.1016/j.concog.2007.01.001

Creem-Regehr, S. H., & Lee, J. N. (2005). Neural representations of graspable objects: Are tools special? *Cognitive Brain Research*, *22*(3), 457–469. http://doi.org/10.1016/j.cogbrainres.2004.10.006

Cross, E. S., Hamilton, A. F. D. C., & Grafton, S. T. (2006). Building a motor simulation de novo: observation of dance by dancers. *NeuroImage*, *31*(3), 1257–67. http://doi.org/10.1016/j.neuroimage.2006.01.033

Cross, E. S., Kraemer, D. J. M., Hamilton, A. F. D. C., Kelley, W. M., & Grafton, S. T. (2009). Sensitivity of the action observation network to physical and observational learning. *Cerebral Cortex (New York, N.Y. : 1991)*, *19*(2), 315–26. http://doi.org/10.1093/cercor/bhn083

Cross, E. S., Stadler, W., Parkinson, J., Schütz-Bosbach, S., & Prinz, W. (2011a). The influence of visual training on predicting complex action sequences. *Human Brain Mapping*, *34*(2), 467–86. http://doi.org/10.1002/hbm.21450

Cross, E. S., Stadler, W., Parkinson, J., Schütz-Bosbach, S., & Prinz, W. (2011b). The influence of visual training on predicting complex action sequences. *Human Brain Mapping*, *34*(2), 467–86. http://doi.org/10.1002/hbm.21450

Culham, J. C., & Valyear, K. F. (2006). Human parietal cortex in action. *Current Opinion in Neurobiology*, *16*(2), 205–212. http://doi.org/10.1016/j.conb.2006.03.005

David, N., Bewernick, B. H., Cohen, M. X., Newen, A., Lux, S., Fink, G. R., … Vogeley, K. (2006). Neural representations of self versus other: visual-spatial perspective taking and agency in a virtual ball-tossing game. *Journal of Cognitive Neuroscience*, *18*(6), 898–910. http://doi.org/10.1162/jocn.2006.18.6.898

de C. Hamilton, A. F., & Grafton, S. T. (2007). The motor hierarchy: from kinematics to goals and intentions. *Sensorimotor Foundations of Higher Cognition*, pp. 381. http://doi.org/DOI:10.1093/acprof:oso/9780199231447.003.0018

Decety, J., Jeannerod, M., & Prablanc, C. (1989). The timing of mentally represented actions. *Behavioural Brain Research*, *34*(1-2), 35–42. http://doi.org/10.1016/S0166-4328(89)80088-9

Denckla, M. B. (1985). Revised Neurologica; Examination for Subtle Signs. *Psychopharmacology Bulletin*, 773–800.

di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Experimental Brain Research*, *91*, 176–180.

Ehrsson, H. H., Spence, C., & Passingham, R. E. (2004). That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science (New York, N.Y.)*, *305*(5685), 875–7. http://doi.org/10.1126/science.1097011

Escera, C., Alho, K., Schröger, E., & Winkler, I. (2000). Involuntary attention and distractibility as evaluated with event-related brain potentials. *Audiology & Neuro-Otology*, *5*(3-4), 151–166. http://doi.org/10.1159/000013877

Fabbri-destro, M., Gizzonio, V., & Avanzini, P. (2013). Autism, motor dysfunctions and mirror mechanism. *Clinical Neuropsychiatry*, *10*(5), 177–187.

Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, *73*(6), 2608–2611.

Falck-Ytter, T., Gredebäck, G., & von Hofsten, C. (2006). Infants predict other people's action goals. *Nature Neuroscience*, *9*(7), 878–9. http://doi.org/10.1038/nn1729

Farrer, C., Franck, N., Georgieff, N., Frith, C. ., Decety, J., & Jeannerod, M. (2003). Modulating the experience of agency: a positron emission tomography study. *NeuroImage*, *18*(2), 324–333. http://doi.org/10.1016/S1053-8119(02)00041-1

Farrer, C., & Frith, C. D. (2002). Experiencing oneself vs another person as being the cause of an action: the neural correlates of the experience of agency. *NeuroImage*, *15*(3), 596–603. http://doi.org/10.1006/nimg.2001.1009

Farrow, D., & Abernethy, B. (2003). Do expertise and the degree of perception - action coupling affect natural anticipatory performance? *Perception*, *32*(9), 1127–1139. http://doi.org/10.1068/p3323

Feldman, R., Greenbaum, C. W., Yirmiya, N., & Mayes, L. C. (1996). Relations between cyclicity and regulation in mother-infant interaction at 3 and 9 months and cognition at 2 years. *Journal of Applied Developmental Psychology*, *17*(3), 347–365. http://doi.org/10.1016/S0193-3973(96)90031-3

Ferrandez, A. M., Hugueville, L., Lehéricy, S., Poline, J. B., Marsault, C., & Pouthas, V. (2003). Basal ganglia and supplementary motor area subtend duration perception: An fMRI study. *NeuroImage*, *19*(4), 1532–1544. http://doi.org/10.1016/S1053-8119(03)00159-9

Flanagan, J. R., & Johansson, R. S. (2003). Action plans used in action observation. *Nature*, *424*(6950), 769–71. http://doi.org/10.1038/nature01861

Flanders, M., & Cordo, P. J. (1989). Kinesthetic and visual control of a bimanual task:Specification of Direction and Amplitude. *The Jouornal of Neuroscience*, *9*(2), 447–453.

Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: from action organization to intention understanding. *Science (New York, N.Y.)*, *308*(5722), 662–7. http://doi.org/10.1126/science.1106138

Frak, V., Paulignan, Y., & Jeannerod, M. (2001). Orientation of the opposition axis in mentally simulated grasping. *Experimental Brain Research*, *136*(1), 120–127. http://doi.org/10.1007/s002210000583

Frenkel-Toledo, S., Bentin, S., Perry, A., Liebermann, D. G., & Soroker, N. (2013). Dynamics of the EEG power in the frequency and spatial domains during observation and execution of manual movements. *Brain Research*, *1509*, 43–57. http://doi.org/10.1016/j.brainres.2013.03.004

Freyd, J. J. (1983). The mental representation of movement when static stimuli are viewed. *Perception & Psychophysics*, *33*(6), 575–81. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/6622194

Freyd, J. J., & Finke, R. A. (1984). Representational momentum. *Journal of Experimental Psychology: Leanring, Memory and Cognition*, *10*(1), 126–132.

Gallagher, I. (2000). Philosophical conceptions of the self: implications for cognitive science. *Trends in Cognitive Sciences*, *4*(1), 14–21. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10637618

Gallese, V. (2005). Embodied simulation : From neurons to phenomenal experience. *Phenomenology and the Cognitive Scien*, *4*, 23–48.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain : A Journal of Neurology*, *119 (Pt 2*, 593–609. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/8800951

Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading, *2*(12), 493–501.

Gangitano, M., Mottaghy, F. M., & Pascual-Leone, a. (2001). Phase-specific modulation of cortical motor output during movement observation. *Neuroreport*, *12*(7), 1489–92. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11388435

Garofeanu, C., Króliczak, G., Goodale, M. A., & Humphrey, G. K. (2004). Naming and grasping common objects: A priming study. *Experimental Brain Research*, *159*(1), 55–64. http://doi.org/10.1007/s00221-004-1932-z

Gazzola, V., & Keysers, C. (2009). The observation and execution of actions share motor and somatosensory voxels in all tested subjects: single-subject analyses of unsmoothed fMRI data. *Cerebral Cortex (New York, N.Y. : 1991)*, *19*(6), 1239–55. http://doi.org/10.1093/cercor/bhn181

Gehring, W. J., Goss, B., Coles, M. G. H., Meyer, D. E., & Emanuel, D. (1993). A neural system for error detection and compensation. *Psychological Science*, *4*(6), 385–390. http://doi.org/10.1111/j.1467-9280.1994.tb00630.x

Gehring, W. J., & Willoughby, A. R. (2002). The Medial Frontal Cortex and the Rapid Processing of Monetary Gains and Losses. *Science*, *295*, 2279–2282. http://doi.org/10.1126/science.1066893

Gentsch, A., Ullsperger, P., & Ullsperger, M. (2009). Dissociable medial frontal negativities from a common monitoring system for self- and externally caused failure of goal achievement. *NeuroImage*, *47*(4), 2023–2030. http://doi.org/10.1016/j.neuroimage.2009.05.064

Gergely, G., & Csibra, G. (2008). Action mirroring and action understanding : an alternative account. In *Sensorymotor Foundations of Higher Cognition. Attention and Performance XXII* (pp. 435–459).

Gopher, D., & Navon, D. (1980). How is performance limited? Testing the notion of central capacity. *Acta Psychologica*, *46*(3), 161–180. http://doi.org/10.1017/CBO9781107415324.004

Gowen, E., & Miall, R. C. (2005). Behavioural aspects of cerebellar function in adults with Asperger syndrome. *Cerebellum (London, England)*, *4*(4), 279–89. http://doi.org/10.1080/14734220500355332

Graf, M., Reitzner, B., Corves, C., Casile, A., Giese, M., & Prinz, W. (2007). Predicting point-light actions in real-time. *NeuroImage*, *36 Suppl 2*, T22–32. http://doi.org/10.1016/j.neuroimage.2007.03.017

Grèzes, J., Armony, J. ., Rowe, J., & Passingham, R. . (2003). Activations related to “mirror” and “canonical” neurones in the human brain: an fMRI study. *NeuroImage*, *18*(4), 928–937. http://doi.org/10.1016/S1053-8119(03)00042-9

Griffiths, D., & Tipper, S. P. (2009). Priming of reach trajectory when observing actions: hand-centred effects. *Quarterly Journal of Experimental Psychology (2006)*, *62*(12), 2450–70. http://doi.org/10.1080/17470210903103059

Grush, R. (2004). The emulation theory of representation: motor control, imagery, and perception. *The Behavioral and Brain Sciences*, *27*(3), 377–96; discussion 396–442. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/15736871

Gusnard, D. A., Akbudak, E., Shulman, G. L., & Raichle, M. E. (2001). Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(7), 4259–64. http://doi.org/10.1073/pnas.071043098

Hamilton, A. F. D. C., Wolpert, D., & Frith, U. (2004). Your own action influences how you perceive another person's action. *Current Biology*, *14*, 493–498. http://doi.org/10.1016/j

Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., & Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(25), 15061–5. Retrieved from http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=24575&tool=pmcentrez&rendertype=abstract

Hatfield, E., Cacioppo, J., & Rapson, R. (1994). Emotional contagion. *Current Directions in Psychological Science*. http://doi.org/10.1086/322897

Heyes, C. (2001). Causes and consequences of imitation. *Trends in Cognitive Sciences*, *5*(6), 253–261. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11390296

Heyes, C. (2010). Where do mirror neurons come from? *Neuroscience and Biobehavioral Reviews*, *34*(4), 575–83. http://doi.org/10.1016/j.neubiorev.2009.11.007

Hickok, G. (2009). Eight problems for the mirror neuron theory of action understanding in monkeys and humans. *Journal of Cognitive Neuroscience*, *21*(7), 1229–43. http://doi.org/10.1162/jocn.2009.21189

Higuchi, S., Holle, H., Roberts, N., Eickhoff, S. B., & Vogt, S. (2012). Imitation and observational learning of hand actions: prefrontal involvement and connectivity. *NeuroImage*, *59*(2), 1668–83. http://doi.org/10.1016/j.neuroimage.2011.09.021

Hoekstra, R. A., Bartels, M., Cath, D. C., & Boomsma, D. I. (2008). Factor structure, reliability and criterion validity of the Autism-Spectrum Quotient (AQ): a study in Dutch population and patient groups. *Journal of Autism and Developmental Disorders*, *38*(8), 1555–66. http://doi.org/10.1007/s10803-008-0538-x

Holroyd, C. B., & Coles, M. G. (2002). The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity. *Psychol Review*, *109*(4), 679–709. http://doi.org/10.1037//0033-295X.109.4.679

Holroyd, C. B., Nieuwenhuis, S., Yeung, N., Nystrom, L., Mars, R. B., Coles, M. G. H., & Cohen, J. D. (2004). Dorsal anterior cingulate cortex shows fMRI response to internal and external error signals. *Nature Neuroscience*, *7*(5), 497–498. http://doi.org/10.1038/nn1238

Hoover, A. E. N., & Harris, L. R. (2012). Detecting delay in visual feedback of an action as a monitor of self recognition. *Experimental Brain Research*, *222*(4), 389–97. http://doi.org/10.1007/s00221-012-3224-3

Hubbard, T. L., & Bharucha, J. J. (1988). Judged displacement in apparent vertical and horizontal motion. *Perception & Psychophysics*, *44*(3), 211–21. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/3174353

Hurley, S. (2008). The shared circuits model (SCM): How control, mirroring, and simulation can enable imitation, deliberation, and mindreading, 1–58.

Hurst, R. M., Mitchell, J. T., Kimbrel, N. a., Kwapil, T. K., & Nelson-Gray, R. O. (2007). Examination of the reliability and factor structure of the Autism Spectrum Quotient (AQ) in a non-clinical sample. *Personality and Individual Differences*, *43*(7), 1938–1949. http://doi.org/10.1016/j.paid.2007.06.012

Iacoboni, M., & Dapretto, M. (2006). The mirror neuron system and the consequences of its dysfunction. *Nature Reviews. Neuroscience*, *7*(12), 942–51. http://doi.org/10.1038/nrn2024

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biology*, *3*(3), e79. http://doi.org/10.1371/journal.pbio.0030079

Jackson, P. L., Meltzoff, A. N., & Decety, J. (2006). Neural circuits involved in imitation and perspective-taking. *NeuroImage*, *31*(1), 429–39. http://doi.org/10.1016/j.neuroimage.2005.11.026

Jacob, P., & Jeannerod, M. (2005). The motor theory of social cognition: a critique. *Trends in Cognitive Sciences*, *9*(1), 21–5. http://doi.org/10.1016/j.tics.2004.11.003

Jansiewicz, E. M., Goldberg, M. C., Newschaffer, C. J., Denckla, M. B., Landa, R., & Mostofsky, S. H. (2006). Motor signs distinguish children with high functioning autism and Asperger's syndrome from controls. *Journal of Autism and Developmental Disorders*, *36*(5), 613–21. http://doi.org/10.1007/s10803-006-0109-y

Jarraya, M., Amorim, M.-A., & Bardy, B. G. (2005). Optical flow and viewpoint change modulate the perception and memorization of complex motion. *Perception & Psychophysics*, *67*(6), 951–61. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/16396004

Jax, S. A., & Rosenbaum, D. a. (2007). Hand path priming in manual obstacle avoidance: evidence that the dorsal stream does not only control visually guided actions in real time. *Journal of Experimental Psychology. Human Perception and Performance*, *33*(2), 425–441. http://doi.org/10.1037/0096-1523.33.2.425

Jax, S. A., & Rosenbaum, D. A. (2009). Hand path priming in manual obstacle avoidance: rapid decay of dorsal stream information. *Neuropsychologia*, *47*(6), 1573–1577. http://doi.org/10.1016/j.neuropsychologia.2008.05.019.HAND

Jeannerod, M. (1994). The representing brain: Neural correlates of motor intention and imagery. *Behavioral and Brain Sciences*, *17*(02), 187. http://doi.org/10.1017/S0140525X00034026

Jeannerod, M. (2001). Neural simulation of action: a unifying mechanism for motor cognition. *NeuroImage*, *14*(1 Pt 2), S103–9. http://doi.org/10.1006/nimg.2001.0832

Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception & Psychophysics*, *14*(2), 201–211.

Johansson, R. S., Westling, G., Bäckström, a, & Flanagan, J. R. (2001). Eye-hand coordination in object manipulation. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *21*(17), 6917–32. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11517279

Johnson, R. J. (1993). On the neural generators of the P300 component of the event- related potential. Psychophysiology 30, 90-97. *Psychophysiology*, *30*, 90–97.

Johnson-Frey, S. H. (2004). The neural bases of complex tool use in humans. *Trends in Cognitive Sciences*, *8*(2), 71–78. http://doi.org/10.1016/j.tics.2003.12.002

Johnson-Frey, S. H., Maloof, F. R., Newman-Norlund, R., Farrer, C., Inati, S., & Grafton, S. T. (2003). Actions or hand-object interactions? Human inferior frontal cortex and action observation. *Neuron*, *39*(6), 1053–8. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12971903

Kahneman, D. (1973). *Attention and effort*. *The American Journal of Psychology* (Vol. 88). http://doi.org/10.2307/1421603

Kelly, R. L., & Wheaton, L. A. (2013). Differential mechanisms of action understanding in left and right-handed subjects: the role of perspective and handedness. *Frontiers in Psychology*, *4*(December), 1–8. http://doi.org/10.3389/fpsyg.2013.00957

Kerzel, D. (2002). A matter of design: No representational momentum without predictability. *Visual Cognition*, *9*(1-2), 66–80. http://doi.org/10.1080/13506280143000322

Ketelaars, C., Horwitz, E., Sytema, S., Bos, J., Wiersma, D., Minderaa, R., & Hartman, C. A. (2008). Brief report: Adults with mild autism spectrum disorders (ASD): Scores on the autism spectrum quotient (AQ) and comorbid psychopathology. *Journal of Autism and Developmental Disorders*, *38*(1), 176–180. http://doi.org/10.1007/s10803-007-0358-4

Keysers, C., & Perrett, D. I. (2004). Demystifying social cognition: a Hebbian perspective. *Trends in Cognitive Sciences*, *8*(11), 501–7. http://doi.org/10.1016/j.tics.2004.09.005

Kilner_Friston_Mirrorness.pdf. (n.d.).

Kilner, J. M. (2009). Dissociable functional roles of the human action-observation network (Commentary on E. S. Cross et al.). *The European Journal of Neuroscience*, *30*(7), 1382. http://doi.org/10.1111/j.1460-9568.2009.06958.x

Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: an account of the mirror neuron system. *Cognitive Process*, *8*(3), 159–66. http://doi.org/10.1007/s10339-007-0170-2

Kilner, J. M., Marchant, J. L., & Frith, C. D. (2006). Modulation of the mirror system by social relevance. *Social Cognitive and Affective Neuroscience*, *1*(2), 143–8. http://doi.org/10.1093/scan/nsl017

Kilner, J. M., Neal, A., Weiskopf, N., Friston, K. J., & Frith, C. D. (2009). Evidence of mirror neurons in human inferior frontal gyrus. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *29*(32), 10153–9. http://doi.org/10.1523/JNEUROSCI.2668-09.2009

Kilner, J. M., Vargas, C., Duval, S., Blakemore, S.-J., & Sirigu, A. (2004). Motor activation prior to observation of a predicted movement. *Nature Neuroscience*, *7*(12), 1299–301. http://doi.org/10.1038/nn1355

Knoblich, G., & Flach, R. (2001). Predicting the effects of actions: interactions of perception and action. *Psychological Science*, *12*(6), 467–72. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11760133

Knolle, F., Schröger, E., Baess, P., & Kotz, S. a. (2012). The cerebellum generates motor-to-auditory predictions: ERP lesion evidence. *Journal of Cognitive Neuroscience*, *24*(3), 698–706. http://doi.org/10.1162/jocn_a_00167

Knolle, F., Schröger, E., & Kotz, S. a. (2013). Prediction errors in self- and externally-generated deviants. *Biological Psychology*, *92*(2), 410–6. http://doi.org/10.1016/j.biopsycho.2012.11.017

Koban, L., Pourtois, G., Bediou, B., & Vuilleumier, P. (2012). Effects of social context and predictive relevance on action outcome monitoring. *Cognitive, Affective, & Behavioral Neuroscience*, *12*(3), 460–478. http://doi.org/10.3758/s13415-012-0091-0

Koban, L., Pourtois, G., Vocat, R., & Vuilleumier, P. (2010). When your errors make me lose or win: Event-related potentials to observed errors of cooperators and competitors. *Social Neuroscience*, *5*(4), 360–374. http://doi.org/10.1080/17470911003651547

Kobza, S., & Bellebaum, C. (2013). Mediofrontal event-related potentials following observed actions reflect an action prediction error. *European Journal of Neuroscience*, *37*(9), 1435–1440. http://doi.org/10.1111/ejn.12138

Kourtzi, Z., & Shiffrar, M. (1997). One-Shot view invariance in a moving world. *Psychological Science*, *8*(6), 461–466.

Kourtzi, Z., & Shiffrar, M. (1999). Dynamic representations of human body movement. *Perception*, *28*(1), 49–62. http://doi.org/10.1068/p2870

Kourtzi, Z., & Shiffrar, M. (1999). The visual representation of three-dimensional, rotating objects. *Acta Psychologica*, *102*(2-3), 265–292. http://doi.org/10.1016/S0001-6918(98)00056-0

Kraskov, A., Dancause, N., Quallo, M. M., Shepherd, S., & Lemon, R. N. (2009). Corticospinal neurons in macaque ventral premotor cortex with mirror properties: a potential mechanism for action suppression? *Neuron*, *64*(6), 922–30. http://doi.org/10.1016/j.neuron.2009.12.010

Land, M. F., & Furneaux, S. (1997). The knowledge base of the oculomotor system. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 352(1358), 1231–1239. http://doi.org/10.1098/rstb.1997.0105

Leary, M. R., & Hill, D. a. (1996). Moving on: autism and movement disturbance. *Mental Retardation*, *34*(1), 39–53.

Leslie, K. R., Johnson-Frey, S. H., & Grafton, S. T. (2004). Functional imaging of face and hand imitation: towards a motor theory of empathy. *NeuroImage*, *21*(2), 601–7. http://doi.org/10.1016/j.neuroimage.2003.09.038

Lewis, P. A., & Miall, R. C. (2003). Distinct systems for automatic and cognitively controlled time measurement: evidence from neuroimaging. *Current Opinion in Neurobiology*, *13*(2), 250–255. http://doi.org/10.1016/S0959-4388(03)00036-9

Linden, D. E. J. (2005). The P300: Where in the Brain Is It Produced and What Does It Tell Us? *The Neuroscientist*, *11*(6), 563–576. http://doi.org/10.1177/1073858405280524

Lindgren, R. (2012). Generating a learning stance through perspective-taking in a virtual environment. *Computers in Human Behavior*, *28*(4), 1130–1139. http://doi.org/10.1016/j.chb.2012.01.021

Loula, F., Prasad, S., Harber, K., & Shiffrar, M. (2005). Recognizing people from their movement. *Journal of Experimental Psychology. Human Perception and Performance*, *31*(1), 210–20. http://doi.org/10.1037/0096-1523.31.1.210

Macar, F., Anton, J.-L. L., Bonnet, M., & Vidal, F. (2004). Timing functions of the supplementary motor area: an event-related fMRI study. *Brain Research*, *21*, 206–215. http://doi.org/10.1016/j.cogbrainres.2004.01.005

Maeda, F., Kleiner-Fisman, G., & Pascual-Leone, A. (2002). Motor Facilitation While Observing Hand Actions : Specificity of the Effect and Role of Observer's Orientation. *Journal of Neurophysiology*, *87*, 1329–1335.

Mahon, B. Z., & Caramazza, A. (2005). The orchestration of the sensory-motor systems: Clues from Neuropsychology. *Cognitive Neuropsychology*, *22*(3), 480–494. http://doi.org/10.1080/02643290442000446

Marshall, P. J., Young, T., & Meltzoff, A. N. (2011). Neural correlates of action observation and execution in 14-month-old infants: an event-related EEG desynchronization study. *Developmental Science*, *14*(3), 474–480. http://doi.org/10.1111/j.1467-7687.2010.00991.x.Neural

Martineau, J., Schmitz, C., Assaiante, C., Blanc, R., & Barthélémy, C. (2004). Impairment of a cortical event-related desynchronisation during a bimanual load-lifting task in children with autistic disorder. *Neuroscience Letters*, *367*(3), 298–303. http://doi.org/10.1016/j.neulet.2004.06.018

Mauk, M. D., & Buonomano, D. V. (2004). The neural basis of temporal processing. *Annual Review of Neuroscience*, *27*, 307–40. http://doi.org/10.1146/annurev.neuro.27.070203.144247

McGuire, P. K., Silbersweig, D. a, & Frith, C. D. (1996). Functional neuroanatomy of verbal self-monitoring. *Brain : A Journal of Neurology*, *119 (Pt 3*, 907–17. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/8673501

Miall, R. C. (2003). Connecting mirror neurons and forward models. *Neuroreport*, *14*(17), 2135–7. http://doi.org/10.1097/01.wnr.0000098751.87269.77

Miall, R. C., Weir, D. J., Wolpert, D. M., & Stein, J. F. (1993). Is the cerebellum a smith predictor? *Journal of Motor Behavior*, *25*(3), 203–16. http://doi.org/10.1080/00222895.1993.9942050

Miall, R. C., & Wolpert, D. M. (1996). Forward models for physiological motor control. *Neural Networks*, *9*(8), 1265–1279.

Miltner, W. H. R., Brauer, J., Hecht, H., Trippe, R., & Coles, M. G. H. (2004). Parallel brain activity for self-generated and observed errors. *Errors, Conflicts, and the Brain: Current Opinions on Performance Monitoring*, (October 2015), 124–129. Retrieved from http://www.uni-jena.de/unijenamedia/Miltner_ERN_04.pdf

Molnar-Szakacs, I., Kaplan, J., Greenfield, P. M., & Iacoboni, M. (2006). Observing complex action sequences: The role of the fronto-parietal mirror neuron system. *NeuroImage*, *33*(3), 923–35. http://doi.org/10.1016/j.neuroimage.2006.07.035

Morrison, I., Tipper, S. P., Fenton-Adams, W. L., & Bach, P. (2013). "Feeling" others' painful actions: the sensorimotor integration of pain and action information. *Human Brain Mapping*, *34*(8), 1982–98. http://doi.org/10.1002/hbm.22040

Muthukumaraswamy, S. D., & Johnson, B. W. (2004). Primary motor cortex activation during action observation revealed by wavelet analysis of the EEG. *Clinical Neurophysiology : Official Journal of the International Federation of Clinical Neurophysiology*, *115*(8), 1760–6. http://doi.org/10.1016/j.clinph.2004.03.004

Muthukumaraswamy, S. D., Johnson, B. W., & McNair, N. a. (2004). Mu rhythm modulation during observation of an object-directed grasp. *Brain Research. Cognitive Brain Research*, *19*(2), 195–201. http://doi.org/10.1016/j.cogbrainres.2003.12.001

Nishitani, N., & Hari, R. (2000). Temporal dynamics of cortical representation. *Proceedings of the National Academy of Sciences*, *97*(2), 913–918.

O'Brien, F., & Cousineau, D. (2014). Representing Error bars in within-subject designs in typical software packages. *The Quantitative Methods for Psychology*, *10*(1), 56–67.

Oberman, L. M., & Ramachandran, V. S. (2008). How do shared circuits develop? *Behavioural and Brain Sciences*, *31*(1), 34–35.

Oosterhof, N. N., Tipper, S. P., & Downing, P. E. (2012). Viewpoint (in)dependence of action representations: an MVPA study. *Journal of Cognitive Neuroscience*, *24*(4), 975–89. http://doi.org/10.1162/jocn_a_00195

Parkinson, J., Springer, A., & Prinz, W. (2011). Can you see me in the snow? Action simulation aids the detection of visually degraded human motion. *Quarterly Journal of Experimental Psychology (2006)*, *64*(8), 1463–72. http://doi.org/10.1080/17470218.2011.594895

Parkinson, J., Springer, A., & Prinz, W. (2012). Before, during and after you disappear: aspects of timing and dynamic updating of the real-time action simulation of human motions. *Psychological Research*, *76*(4), 421–33. http://doi.org/10.1007/s00426-012-0422-3

Pavani, F., Spence, C., & Driver, J. (2000). Visual Capture of Touch: Out-of-the-Body Experiences With Rubber Gloves. *Psychological Science*, *11*(5), 353–359. http://doi.org/10.1111/1467-9280.00270

Peirce, J. W. (2007). PsychoPy-Psychophysics software in Python. *Journal of Neuroscience Methods*, *162*(1-2), 8–13. http://doi.org/10.1016/j.jneumeth.2006.11.017

Peirce, J. W. (2008). Generating stimuli for neuroscience using PsychoPy. *Frontiers in Neuroinformatics*, *2*(January), 1–8. http://doi.org/10.3389/neuro.11.010.2008

Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. *Electroencephalography and Clinical Neurophysiology*, *72*(2), 184–187. http://doi.org/10.1016/0013-4694(89)90180-6

Perry, A., & Bentin, S. (2009). Mirror activity in the human brain while observing hand movements: a comparison between EEG desynchronization in the mu-range and previous fMRI results. *Brain Research*, *1282*, 126–32. http://doi.org/10.1016/j.brainres.2009.05.059

Pfurtscheller, G., Brunner, C., Schlögl, a, & Lopes da Silva, F. H. (2006). Mu rhythm (de)synchronization and EEG single-trial classification of different motor imagery tasks. *NeuroImage*, *31*(1), 153–9. http://doi.org/10.1016/j.neuroimage.2005.12.003

Pineda, J. a. (2005). The functional significance of mu rhythms: translating “seeing” and “hearing” into “doing”. *Brain Research. Brain Research Reviews*, *50*(1), 57–68. http://doi.org/10.1016/j.brainresrev.2005.04.005

Pisella, L., Binkofski, F., Lasek, K., Toni, I., & Rossetti, Y. (2006). No double-dissociation between optic ataxia and visual agnosia: Multiple sub-streams for multiple visuo-manual integrations. *Neuropsychologia*, *44*(13), 2734–2748. http://doi.org/10.1016/j.neuropsychologia.2006.03.027

Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, *118*, 2128–2148. http://doi.org/10.1016/j.clinph.2007.04.019

Portella, C., S., M., F., P., M., C., A.T., S., A., S.-C., … Arias-Carrion O. (2014). Differences in early and late stages of information processing between slow versus fast participants. *International Archives of Medicine*, *7*(49), 1–8. http://doi.org/10.1186/1755-7682-7-49

Poulton, E. C. (1982). Influential companions: Effects of one strategy on another in the within-subjects designs of cognitive psychology. *Psychological Bulletin*, *91*(3), 673–690. http://doi.org/10.1037//0033-2909.91.3.673

Pouthas, V., George, N., Poline, J.-B., Pfeuty, M., Vandemoorteele, P.-F., Hugueville, L., … Renault, B. (2005). Neural network involved in time perception: an fMRI study comparing long and short interval estimation. *Human Brain Mapping*, *25*(4), 433–41. http://doi.org/10.1002/hbm.20126

Press, C., Heyes, C., & Kilner, J. M. (2011). Learning to understand others' actions. *Biology Letters*, *7*(3), 457–460. http://doi.org/10.1098/rsbl.2010.0850

Prinz, W. (1997). Perception and Action Planning, *9*(September 1995).

Prinz, W. (2006). What re-enactment earns us. *Cortex*, *42*, 515–517.

Prinz, W., & Rapinett, G. (2008). Filling the Gap : Dynamic Representation of Occluded Action. In F. Morganti, A. Carassa, & G. Riva (Eds.), *Enacting Intersubjectivity: A Cognitive and Social Perspective on the Study of Interactions* (pp. 223–236). Amsterdam: IOS Press.

Ramnani, N., & Miall, R. C. (2004). A system in the human brain for predicting the actions of others. *Nature Neuroscience*, *7*(1), 85–90. http://doi.org/10.1038/nn1168

Rao, S. M., Mayer, a R., & Harrington, D. L. (2001). The evolution of brain activation during temporal processing. *Nature Neuroscience*, *4*(3), 317–23. http://doi.org/10.1038/85191

Reed, C. L., & Vinson, N. G. (1996). Conceptual effects on representational momentum. *Journal of Experimental Psychology. Human Perception and Performance*, *22*(4), 839–50. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/8756955

Rinehart, N. J., Bradshaw, J. L., Brereton, a V, & Tonge, B. J. (2001). Movement preparation in high-functioning autism and Asperger disorder: a serial choice reaction time task involving motor reprogramming. *Journal of Autism and Developmental Disorders*, *31*(1), 79–88. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11439757

Rizzolatti, G., & Arbib, M. A. (1998). Language within our grasp. *Trends in Neurosciences*, *21*, 188–194.

Rizzolatti, G., Camarda, L., Fogassi, M., Gentilucci, G., Luppino, G., & Matelli, M. (1988). Functional organization of inferior area 6. *Experimental Brain Research*, *71*, 491–507. http://doi.org/10.1007/BF00248742

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, *27*, 169–92. http://doi.org/10.1146/annurev.neuro.27.070203.144230

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, *3*(2), 131–141. http://doi.org/10.1016/0926-6410(95)00038-0

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews. Neuroscience*, *2*(September), 1–10.

Rizzolatti, G., Fogassi, L., & Gallese, V. (2002). Motor and cognitive functions of the ventral premotor cortex. *Current Opinion in Neurobiology*, *12*(2), 149–54. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12015230

Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nature Reviews. Neuroscience*, *11*(4), 264–74. http://doi.org/10.1038/nrn2805

Rotman, G., Troje, N. F., Johansson, R. S., & Flanagan, J. R. (2006). Eye movements when observing predictable and unpredictable actions. *Journal of Neurophysiology*, *96*(3), 1358–69. http://doi.org/10.1152/jn.00227.2006

Ruby, P., & Decety, J. (2001). Effect of subjective perspective taking during simulation of action: a PET investigation of agency. *Nature Neuroscience*, *4*(5), 546–50. http://doi.org/10.1038/87510

Rushworth, M. F. S., Behrens, T. E. J., & Johansen-Berg, H. (2006). Connection patterns distinguish 3 regions of human parietal cortex. *Cerebral Cortex*, *16*(10), 1418–1430. http://doi.org/10.1093/cercor/bhj079

Saunders, J. a, & Knill, D. C. (2003). Humans use continuous visual feedback from the hand to control fast reaching movements. *Experimental Brain Research*, *152*(3), 341–52. http://doi.org/10.1007/s00221-003-1525-2

Saxe, R., Jamal, N., & Powell, L. (2006). My body or yours? The effect of visual perspective on cortical body representations. *Cerebral Cortex (New York, N.Y. : 1991)*, *16*(2), 178–82. http://doi.org/10.1093/cercor/bhi095

Schmitz, C., Martineau, J., Barthélémy, C., & Assaiante, C. (2003). Motor control and children with autism: deficit of anticipatory function? *Neuroscience Letters*, *348*(1), 17–20. http://doi.org/10.1016/S0304-3940(03)00644-X

Schubotz, R. I. (2004). Human premotor cortex : Beyond motor performance. In *MPI Series in Human Cognitive and Brain Sciences* (Vol. 50). Max Planck Institute ofHuman Cognitive and Brain Sciences.

Schubotz, R. I. (2007). Prediction of external events with our motor system: towards a new framework. *Trends in Cognitive Sciences*, *11*(5), 211–218. http://doi.org/10.1016/j.tics.2007.02.006

Schubotz, R. I. (2007). Prediction of external events with our motor system: towards a new framework. *Trends in Cognitive Sciences*, *11*(5), 211–8. http://doi.org/10.1016/j.tics.2007.02.006

Schubotz, R. I., Friederici, A. D., & von Cramon, D. Y. (2000). Time perception and motor timing: a common cortical and subcortical basis revealed by fMRI. *NeuroImage*, *11*(1), 1–12. http://doi.org/10.1006/nimg.1999.0514

Schubotz, R. I., & von Cramon, D. Y. (2002). Predicting perceptual events activates corresponding motor schemes in lateral premotor cortex: an fMRI study. *NeuroImage*, *15*(4), 787–96. http://doi.org/10.1006/nimg.2001.1043

Schubotz, R. I., & von Cramon, D. Y. (2004). Sequences of abstract nonbiological stimuli share ventral premotor cortex with action observation and imagery. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *24*(24), 5467–74. http://doi.org/10.1523/JNEUROSCI.1169-04.2004

Schubotz, R. I., von Cramon, D. Y., & Lohmann, G. (2003). Auditory what, where, and when: a sensory somatotopy in lateral premotor cortex. *NeuroImage*, *20*(1), 173–185. http://doi.org/10.1016/S1053-8119(03)00218-0

Schütz-Bosbach, S., Mancini, B., Aglioti, S. M., & Haggard, P. (2006). Self and other in the human motor system. *Current Biology : CB*, *16*(18), 1830–4. http://doi.org/10.1016/j.cub.2006.07.048

Sebanz, N., & Shiffrar, M. (2009). Detecting deception in a bluffing body: the role of expertise. *Psychonomic Bulletin & Review*, *16*(1), 170–5. http://doi.org/10.3758/PBR.16.1.170

Shmuelof, L., & Zohary, E. (2006). A mirror representation of others' actions in the human anterior parietal cortex. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *26*(38), 9736–42. http://doi.org/10.1523/JNEUROSCI.1836-06.2006

Southgate, V., Johnson, M. H., Osborne, T., & Csibra, G. (2009). Predictive motor activation during action observation in human infants. *Biology Letters*, *5*(6), 769–72. http://doi.org/10.1098/rsbl.2009.0474

Sparenberg, P., Springer, A., & Prinz, W. (2012). Predicting others' actions: evidence for a constant time delay in action simulation. *Psychological Research*, *76*(1), 41–9. http://doi.org/10.1007/s00426-011-0321-z

Spence, S. a, Brooks, D. J., Hirsch, S. R., Liddle, P. F., Meehan, J., & Grasby, P. M. (1997). A PET study of voluntary movement in schizophrenic patients experiencing passivity phenomena (delusions of alien control). *Brain : A Journal of Neurology*, *120 (Pt 1*(1997), 1997–2011. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9397017

Sperry, R. W. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion, 482–489.

Springer, A., Brandstädter, S., Liepelt, R., Birngruber, T., Giese, M., Mechsner, F., & Prinz, W. (2011). Motor execution affects action prediction. *Brain and Cognition*, *76*(1), 26–36. http://doi.org/10.1016/j.bandc.2011.03.007

Stadler, W., Ott, D. V. M., Springer, A., Schubotz, R. I., Schütz-Bosbach, S., & Prinz, W. (2012). Repetitive TMS suggests a role of the human dorsal premotor cortex in action prediction. *Frontiers in Human Neuroscience*, *6*(February), 20. http://doi.org/10.3389/fnhum.2012.00020

Stadler, W., Schubotz, R. I., von Cramon, D. Y., Springer, A., Graf, M., & Prinz, W. (2011). Predicting and memorizing observed action: differential premotor cortex involvement. *Human Brain Mapping*, *32*(5), 677–87. http://doi.org/10.1002/hbm.20949

Stewart, M. E., & Austin, E. J. (2009). The structure of the Autism-Spectrum Quotient (AQ): Evidence from a student sample in Scotland. *Personality and Individual Differences*, *47*(3), 224–228. http://doi.org/10.1016/j.paid.2009.03.004

Thornton, I., & Hayes, A. (2004). *Anticipating action in complex scenes*. *Visual Cognition* (Vol. 11). http://doi.org/10.1080/13506280344000374

Thornton, I. M., & Hubbard, T. L. (2002). Representational momentum: New findings, new directions. *Visual Cognition*, *9*(1-2), 1–7. http://doi.org/10.1080/13506280143000430

Tipper, S. P., & Bach, P. (2008). Your own actions influence how you perceive other people: A misattribution of action appraisals. *Journal of Experimental Social Psychology*, *44*(4-2), 1082–1090. http://doi.org/10.1016/j.jesp.2007.11.005

Tipples, J., Brattan, V., & Johnston, P. (2013). Neural bases for individual differences in the subjective experience of short durations (less than 2 seconds). *PloS One*, *8*(1), e54669. http://doi.org/10.1371/journal.pone.0054669

Tregellas, J. R., Davalos, D. B., & Rojas, D. C. (2006). Effect of task difficulty on the functional anatomy of temporal processing. *NeuroImage*, *32*(1), 307–315. http://doi.org/10.1016/j.neuroimage.2006.02.036

Tsakiris, M., & Haggard, P. (2005). The rubber hand illusion revisited: visuotactile integration and self-attribution. *Journal of Experimental Psychology. Human Perception and Performance*, *31*(1), 80–91. http://doi.org/10.1037/0096-1523.31.1.80

Umiltà, M. a, Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., & Rizzolatti, G. (2001). I know what you are doing. a neurophysiological study. *Neuron*, *31*(1), 155–65. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11498058

Urgesi, C., Savonitto, M. M., Fabbro, F., & Aglioti, S. M. (2012). Long- and short-term plastic modeling of action prediction abilities in volleyball. *Psychological Research*, *76*(4), 542–60. http://doi.org/10.1007/s00426-011-0383-y

van Baaren, R. B., Holland, R. W., Kawakami, K., & van Knippenberg, A. (2004). Mimicry and prosocial behavior. *Psychological Science*, *15*(1), 71–74. http://doi.org/10.1111/j.0963-7214.2004.01501012.x

van Schie, H. T., Mars, R. B., Coles, M. G. H., & Bekkering, H. (2004). Modulation of activity in medial frontal and motor cortices during error observation. *Nature Neuroscience*, *7*(5), 549–554. http://doi.org/10.1038/nn1239

Verfaillie, K. (1993). Orientation-dependent priming effects in the perception of biological motion. *Journal of Experimental Psychology*, *19*(5), 992–1013.

Verfaillie, K., & Daems, A. (2002). Representing and anticipating human actions in vision. *Visual Cognition*, *9*(1/2), 217–232.

Wearden, J. . (1991). Do humans possess an internal clock with scalar timing properties? *Learning and Motivation*, *22*(1-2), 59–83. http://doi.org/10.1016/0023-9690(91)90017-3

Wicker, B., Keysers, C., Plailly, J., Royet, J. P., Gallese, V., & Rizzolatti, G. (2003). Both of us disgusted in My insula: the common neural basis of seeing and feeling disgust. *Neuron*, *40*(3), 655–64. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/14642287

Wilson, M., & Knoblich, G. (2005). The case for motor involvement in perceiving conspecifics. *Psychological Bulletin*, *131*(3), 460–73. http://doi.org/10.1037/0033-2909.131.3.460

Wolpert, D. M., & Flanagan, J. R. (2001). Motor prediction. *Current Biology : CB*, *11*(18), R729–32. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12546789

Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience*, *3 Suppl*(november), 1212–7. http://doi.org/10.1038/81497

Yirmiya, N., Gamliel, I., Pilowsky, T., Feldman, R., Baron-Cohen, S., & Sigman, M. (2006). The development of siblings of children with autism at 4 and 14 months: Social engagement, communication, and cognition. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, *47*(5), 511–523. http://doi.org/10.1111/j.1469-7610.2005.01528.x