EVIDENCE FOR THE NEUROMOTOR SIMULATION HYPOTHESIS IN ACTION

PREDICTION

by

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M.Sc., Simon Fraser University, 2009

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Kinesiology)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

May 2016

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Abstract

The overarching aim of this thesis was to further understand the processes and internal representations involved in predicting action outcomes, by manipulating information sources during learning and prediction.

Growing evidence suggests that the human motor system is activated during action observation, such that motor representations are invoked, through simulative processes that help facilitate an understanding of the unfolding action. In this work, we employed a design that manipulated visual and motor influences during learning and prediction, to try to understand; a) the types of internal representations acquired during practice, and b) how, and under what conditions, these representations are activated during prediction, and, more specifically, the conditions under which action prediction can come about through either visual- or motor-based mechanisms.

In Experiment 1 we found that a group that learned to throw darts without vision of the action performed as well, on a post-practice prediction task, as a group that practiced with full vision. These results suggested that motor practice was key to learning the skill, and vision appeared not to be important. However, it was unclear whether motor representations were formed during practice, and then simulated during action prediction, or that visual representations were formed during practice and later compared to the visual input through a perceptual matching process. In Experiment 2 we found that an incongruent secondary motor task interfered with the prediction process, reducing prediction accuracy of experts to the level of a novice with no motor experience with the task. These results implied that motor system activation was responsible for prediction accuracy, by simulating established motor representations within the observer. In Experiment 3, results showed that a group that trained

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physically, significantly improved their prediction accuracy, but performed at a pre-training level while engaging in an effector-specific, incongruent secondary motor task during prediction. In contrast, a perceptually trained group also significantly improved their prediction accuracy after practice, but did not exhibit any modulation of prediction accuracy while engaged in the secondary motor task. These results suggest that action prediction can be mediated by different processes, one motor-based and one visually-based, depending on type of training.

Preface

I was the principal investigator, primarily responsible for the research program described by this document, including experimental design, software programming, data collection, statistical analysis, and manuscript preparation for the thesis and experiments. All phases of the work were conducted under the guidance and support of my thesis supervisor Professor Nicola Hodges. My thesis committee, Professor Todd Handy and Professor Romeo Chua provided feedback on proposed and completed studies, and on thesis manuscript preparation. Dr. Keith Lohse provided advice on experimental design and statistical analysis.

All experiments were approved by the University of British Columbia Research Ethics Board under ethics certificate H10-01346.

A version of Chapter 2 has been published: Mulligan, D., & Hodges, N. J. (2014). Throwing in the dark: improved prediction of action outcomes following motor training without vision of the action. *Psychological Research*, *78*, 692–704.

A version of Chapter 3 has been published: Mulligan, D., Lohse, K. R., & Hodges, N. J. (2015). An action-incongruent secondary task modulates prediction accuracy in experienced performers: evidence for motor simulation. *Psychological Research,* doi: 10.1007/s00426-015-0672-y. A version of Chapter 4 has been published: Mulligan, D., Lohse, K. R., & Hodges, N. J. (in press). Evidence for dual mechanisms of action prediction dependent on visual-motor experiences. *Journal of Experimental Psychology: Human Perception and Performance*.

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Acknowledgements

First, I would like to sincerely thank my thesis supervisor, Dr. Nicola Hodges. Nikki, you have prepared me well, with the tools I need to succeed in this strange world of academia. You showed me how to critically analyze existing research, and to effectively use this knowledge to explore new ideas and develop my own research questions. Your attention to detail has taught me that being rigorous in experimental design, and understanding thoroughly, and early, why we are conducting a particular enquiry, is critically important for minimizing issues later on. These are just a few of the many things I have learned from you that give me confidence in the quality of my work, and in my ability to succeed as a researcher.

To my thesis committee, Dr. Romeo Chua and Dr. Todd Handy for their help at all stages of my studies. Your thoughtful examination of my work, and always interesting discussions, have helped me to better understand the breadth of this field, and the ways I can explore other avenues of research within it.

I also thank Dr. Keith Lohse for his helpful discussions during the design phases of my experiments, and for his advice on some of the more complex statistical analyses.

I would like to acknowledge my external examiner Dr. Robin Jackson, and university examiners, Dr. Miriam Spering and Dr. Alan Kingstone. Thank you so much for taking the time to examine my dissertation and for such a thorough and stimulating discussion about my work. I sincerely hope we can have more of these discussions in the future.

A big thank you to my fellow lab mates, especially Dave Hendry, Bev Larssen, Nicole Ong, April Karlinsky, Jaspreet Dhillon, Tom Coppola, Paul Campagnaro, and Shawn Hetherington. Your friendship and support is something that I will not forget. I will miss the laughter that has helped keep me sane through all of this, and I hope we can keep in touch going forward.

Finally, I would like to acknowledge, and give special thanks to two people who were instrumental in getting me to where I am today. Dr. Mark Wexler is an inspiring mentor, who saw something in me that I didn't see in myself, and encouraged me to pursue my research dream. Mark, while I am forever grateful to you for starting me on this path, I am mostly thankful for who you are, and for the way you genuinely care about your students. To Dr. Janet McCracken, who challenged me to research what I am passionate about, not what I *think* I should be researching. Janet, you gave me the confidence to change paths and pursue what I was most interested in, even though the learning challenge was much greater. You helped facilitate this at every step, and always supported me unconditionally. This is a rare thing, and I feel lucky to have you as my advisor and my friend.

Chapter 1: Introduction

The ability of humans to predict the actions of others, as well as objects, is fundamental to daily life. We navigate the highways in our automobiles, paying little notice to the precision with which we must predict the actions of other drivers and pedestrians. Similarly, expert athletes must be able to predict the actions and moves of opponents and teammates in order to be successful in their sport. But how does this ability to predict future action actually come about? A common view holds that after years of viewing a broad array of action sequences and patterns the visual system becomes better able to extract important kinematic information through improved visual search strategies and cue utilization (Abernethy & Zawi, 2007; Abernethy, Zawi, & Jackson, 2008; Williams & Davids, 1998; Williams & Ward, 2003, 2007). In this view, the visual and motor systems were considered mostly as separate and distinct components. More recently, a more nuanced view has unfolded, which suggests that motor experience, and particularly the motor system, plays a significant role in perceptual processing, and understanding the actions of others. Accordingly, vision and action are said to exist in a common representational medium, and exert reciprocal effects on each other. Briefly, evidence suggests that we are able to understand others' actions and goals, not through elaborate, inferential processes, but rather, predictably, through a system that encodes, in real-time, the observation, imagination, and production of action in a common representational domain within our own motor system (Prinz, 1997; Hommel et al., 2001). In this sense an observer's motor repertoire exerts a direct effect on their perceptual understanding, as the brain uses these motor representations to internally simulate the actions observed in others (Blakemore and Decety, 2001; Jeannerod, 2001; Wilson & Knoblich, 2005; Wolpert, Doya, & Kawato, 2003). It is these ideas of 'common-coding' and action simulation that I seek to further understand with respect to

their role in perceptual prediction. In the following section I present behavioural and neurophysiological evidence which suggests the existence of a common representational domain for perception and action in humans, and a corresponding mechanism that covertly simulates action representations generated by the self to recognise or predict the actions of others. I describe how the basic reciprocal behavioural effects that emerge between action and perception support a 'common-coding' architecture, and explain how motor simulation mechanisms, that run in real-time, help us to understand the actions and goals of others (Hamilton & Grafton, 2006; Rizzolatti, Fogassi, & Gallese, 2001; Wohlschlaeger & Bekkering, 2002), and allow us to predict their future actions (Jeannerod, 2001; Schubotz, 2007; for evidence see Knoblich & Flach, 2001; Wilson & Knoblich, 2005).

1.1 A common medium for action and perception

The idea of a common representational framework for encoding the goals and actions of others is not new. James (1890, in his ideomotor theory) suggested that, within an individual, imagining one's own action would induce the execution of the same action. In the theory of 'common coding' a common representational domain for action and perception is proposed, such that observing someone performing an action, and performing the action oneself, activates the same internal motor program (Prinz, 1997). Put another way, action execution creates a common representation between the motor program that generates the movement and the sensory effects that are produced by that movement, such that the execution of the action can influence the prediction of future effects in the actor. This process can also proceed in the opposite direction, meaning that perceiving an action can induce a similar or complementary action in the observer, and arguably assist in movement prediction (Hommel, Muesseler, Aschersleben, & Prinz, 2001).

Support for the notion of a common representational domain for the execution and observation of actions comes from behavioural research examining the reciprocal effects of action and perception on each other. If such a common medium exists, then observed and executed actions should exert effects on each other, especially in situations of tight temporal coupling, when the observed and executed actions occur concurrently. Behavioural studies looking at the effects of perception on action execution have shown that when the action observed matches the action to be executed a facilitating or priming effect on action performance occurs, whereas when the actions observed and performed do not match, action performance is degraded (Brass, Bekkering, & Prinz, 2001; Craighero, Bello, Fadiga, & Rizzolatti, 2002; Kilner, Paulignan, & Blakemore, 2003; for a review see Blakemore & Frith, 2005).

Research into the reciprocal effects of action on perception have revealed similar results to those above (Hamilton, Wolpert, & Frith, 2004; Miall et al., 2006; Wohlschlager, 2000; for a review see Schutz-Bosbach & Prinz, 2007). In the study by Miall and colleagues (2006), participants were required to perform one of two types of hand movements while spotting a hand randomly presented in a sequence of images. Reaction times were faster when the image matched the hand movement being performed (Miall et al., 2006). The reason for such effects comes from the idea that action observation and action execution are coded in the same representational medium. Thus, when these codes are congruent facilitation occurs, and when they are incongruent interference arises (yet opposite effects have also been noted, for a discussion see Thomaschke, Hopkins, & Miall, 2012).

1.2 Motor simulation: a mechanism for action perception

Related to the common coding approach is the idea of a mechanism that utilizes the observer's own motor system (Blakemore & Decety, 2001; Wilson & Knoblich, 2005) to

simulate the actions of others. This can facilitate, in real-time, an understanding of action goals (Rizzolatti & Craighero, 2004, Springer et al., 2013a, 2013b), as well as the prediction of future actions and their consequences (Aglioti et al., 2008; Ikegami & Ganesh, 2014; Knoblich & Flach, 2001; Tomeo et al., 2012; Urgesi et al., 2012; Wilson & Knoblich, 2005). For our purposes here, I define *simulation* as the covert or explicit internal reenactment of an action, without necessarily carrying out the action (Witt & Proffitt, 2008). It is a kind of representation of the future, made up of the goal of the action, the requirements needed to meet the goal, and the projected effects on the actor and the environment (Jeannerod, 2001, pS103). In computational terms, internal models of the motor commands that could produce the observed action are activated, generating a prediction of the sensory consequences of that action (Miall, 2003). The mechanisms underlying the principles of common-coding and action simulation have important implications for action understanding (Rizzolatti, Fogassi, & Gallese, 2001), the attribution of intention (Iacoboni, Molnar-Szakacs, Gallese, Buccino, Mazziotta, & Rizzolatti, 2005), and, most importantly for the work described here, action prediction (Blakemore & Frith, 2005; Wilson & Knoblich, 2005).

1.3 Neural correlates of action simulation

Over the past several decades, evidence of a neural analogue to the commoncoding/simulation framework for action understanding has been accumulating. A class of neurons was found in monkey premotor cortex that fired when the animal both *performed* and *observed* the same goal-directed grasping or holding actions (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Fogassi, Ferrari, Gesierich, Rozzi, Chersi, & Rizzolatti, 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Gallese, Fadiga, Fogassi, & Rizzolatti, 2002; Rizzolatti, Fogassi, & Gallese, 2001). These neurons have been termed *mirror neurons* because

they respond to others' actions as if they were one's own. As a result of this seminal discovery, a great deal of neurophysiological research has ensued in this area over the past two decades, and has now provided evidence for the existence of a similar system in humans (Blakemore & Decety, 2001; Caspers et al., 2010; Gazzola & Keysers, 2009; Gallese, Keysers, & Rizzolatti, 2004; Grafton, 2009; Grezes & Decety, 2001; Grezes, Passingham, & Frith, 2004; Iacoboni et al., 2001; Iacoboni et al., 2005; Mukamel et al., 2010; Rizzolatti & Craighero, 2004). As a result, there is now considerable evidence to support the idea that action observation involves a type of motor simulation in the observer, primarily based on activation of parietal (Fogassi et al., 2010; Saygin, 2007) regions of the brain during both action execution and action observation. This *Mirror Neuron System* (MNS) – also referred to as *The Action Observation Network* (AON) (Cross, Hamilton, 2006) - seems to provide the appropriate anatomical substrates to support the common links between perception and action, and the simulation mechanisms described above.

1.4 Neuro-computational implementation of action simulation

It has been suggested that when we learn we generate an internal representation or model of the action being performed (Miall, 2003). When we view someone else's action we are able to activate these predictive models in order to predict the outcomes of the other's action. At an implicit, computational level, it is suggested that, through motor practice, we acquire forward models which allow prediction of the sensory consequences of actions, based on the sending of motor commands. When we send a motor command an efference copy of this motor command is fed into a forward predictor, which allows us to predict what the action we've initiated should feel and look like. If there is a discrepancy between what was predicted and what actually

happened this will lead to the updating of our internal model. As a result, motor control/commands, as well as future predictions, become more refined (Miall, 2003; Miall & Wolpert, 1995; Wolpert & Kawato, 1998). Therefore, it might be possible that forward models are activated during perception (as an observer), such that predicted sensory (visual and proprioceptive) consequences are generated, leading to improved prediction. For example, Gentili, Papaxanthis and Pozzo (2006) have provided behavioural evidence suggestive of forward model predictions based on imagery practice only (see also Demougeot & Papaxanthis, 2011). This is interesting as in the case of imagery (like observation) no action takes place. Therefore, if a motor program is activated for these covert actions (i.e., imagery and actionobservation) like that seen for physical actions, there will be internal predictions of sensory consequences. However, the program that is planned and potentially initiated is either later inhibited and/or not of the same 'detail' or 'quality' as during action execution and, as such, is not produced. Further, evidence showing improved predictions in the outcomes of basketball free throws (Aglioti et al., 2008) and soccer penalty kicks (Makris & Urgesi, 2014), associated with neural activation indicative of internal simulation, suggests that the sensory consequences generated by these forward models may be immediately available to conscious awareness for use in predicting the outcomes of observed actions.

In terms of neural implementation of forward models, it is thought that fronto-parietal mirror neurons (MN) and areas of posterior parietal cortex (pPAR) first interact to encode the goal of the simulation, as generated via input from associated visual kinematic cues, and select the appropriate internal model based on the action to be simulated (Jeannerod, 2006). Areas activated by the observation of biological motion, such as superior temporal sulcus (STS), can then provide input to the internal model (Grezes & Decety, 2001; Grossman & Blake, 2001).

After the internal model is selected for simulation it is linked to regions involved in movement control, including primary motor cortex (M1), which encodes low-level movements and actions, premotor cortex (PM), which elaborates specific higher-level goal-directed actions, and supplementary motor areas (SMA), which are responsible for generating action plans (Shadmehr & Krakauer, 2008; Hamilton & Grafton, 2007). These areas communicate through feedforward and feedback loops, and link with the cerebellum, which is involved with temporal aspects of actions, as well as predictive aspects of internal models (Miall & Wolpert, 1996; Wolpert, Miall, & Kawato, 1998).

1.5 Evidence for motor simulation during action perception

1.5.1 Self-other identification in action prediction

According to the common-coding and simulation hypotheses, when one observes visual displays of their own action, there should be a close match between the internal representations of the action and the perceptual input. The closer the match, the better able one should be to judge the observed actions as their own. Several studies have examined whether people are better able to recognize, or predict the consequences of, their own actions, compared to those of others. Knoblich and Prinz (2001) showed that people are able to accurately differentiate between their own and others' drawings of large characters taken from different types of scripts, by following a single moving dot that retraced the character, but contained no self-identification features (Knoblich & Prinz, 2001). In terms of action prediction, participants in another study were better able to predict the landing position of a dart thrown previously by themselves to one of three areas of a dart board, even though none of the dart flight was shown. The authors suggest that prediction for self-generated actions is more accurate than predictions associated with other's actions because the stimulus activates motor simulations that produce a closer match between the

observed action and the motor commands that would have produced the action (Knoblich & Flach, 2001). More recently, a study examining predictions of ball flight direction in table tennis showed that participants were better able to predict the trajectory of their own strokes, even though none of the ball flight was shown, and video stimuli showed only point-light displays of the models. Again, the authors suggested that the prediction of action outcomes was superior for 'own' actions due to the simulation of internal motor representations that more closely matched the observed action kinematics (Bischoff et al., 2012).

1.5.2 Neuropsychological evidence

Evidence for the link between internal simulation and action performance can also be found in neurologically impaired populations. In a fascinating illustration of the link between action simulation and execution, Schwoebel and colleagues (2002) studied a patient with bilateral parietal lesions who could not refrain from physically generating imagined hand movements, while being oblivious to the movements. This impairment suggests that the action representations formed during imagination (and observation) are functionally the same as those used for physical action (Prinz, 1997), and are sufficient to induce action in the absence of inhibitory processes (Schwoebel et al., 2002). A different causal link between action recognition and execution has been seen in patients with limb or buccofacial apraxia. These patients were specifically unable to recognize the sounds of actions that they were unable to perform (Pazzaglia et al., 2008). These effects are in line with the notion that internal models used in the control of overt actions are also used in simulating the effects of such actions (Wilson & Knoblich, 2005).

1.5.3 Quantifying the roles of visual and motor experience

Previously, it was thought that, after years of visual exposure to a wide array of domainspecific action sequences, experts developed long-term memory structures made up of familiar visual patterns, chunks or templates that became quickly accessible during action perception (De Groot, 1978; Ericsson & Kintsch, 1995; Gobet & Simon, 1996; Gobet & Jackson, 2002; Hodges, Starkes, & MacMahon, 2006). The visual system became more efficient at extracting early kinematics of body motion and matched these cues to the appropriate memory structure in a kind of visual-recognition process (for sport related evidence and discussions, see Abernethy & Zawi, 2007; Abernethy, Zawi, & Jackson, 2008; Abernethy et al., 2012; Helsen et al., 2000; Williams & Davids, 1998; Williams & Ward, 2003, 2007). Early work in this area utilized recall paradigms that presented static and dynamic stimuli, representing structured and unstructured action sequences, to investigate the cognitive advantage of experts. Temporal and spatial occlusion methods have been widely employed to assess the expert advantage in predicting opponents' actions, based on the early detection of subtle kinematic cues (For a detailed review, see Starkes et al., 2001; Williams et al., 1999). Typically, in the temporal occlusion paradigm, participants would view stimuli of the early part of an action sequence, up to the point of occlusion, and would then be required to indicate how the action would end (Starkes, 1987; Williams and Burwitz, 1993).

While visual experience, on its own, may foster the development of visual representations that can be accessed during action perception, more recently, there have been suggestions that the motor system plays a primary role in action perception (Aglioti et al., 2008; Ikegami & Ganesh, 2014; Tomeo et al., 2012; Urgesi et al., 2012). Accordingly, action perception is thought to come about as early kinematic cues from the perceptual stimulus activate corresponding

internal action models (programs), that are acquired through motor-visual experience These internal models covertly simulate the observed action to aid in recognition or prediction (Jeannerod, 2001; Miall, 2003; Miall & Wolpert, 1996). However, the causal link between motor system activation and prediction accuracy has not yet been established (see below).

There have been several studies comparing 'motor-visual' experts to 'visual' experts in an effort to isolate the role of the motor system and simulation mechanisms in action perception. Calvo-Merino , Grezes, Glaser, Passingham and Haggard (2005, 2006) have shown that in action scenarios that are familiar to the observer, this familiarity is not only based on past visual knowledge and experience of seeing a similar action, but, integrally, on past *motor* experience of having performed the action. Motor-related areas of the brain showed significantly greater activation when ballet dancers viewed moves that they regularly performed rather than moves that they regularly watched (Calvo-Merino et al., 2005, 2006). Thus, observing action situations involves the viewer matching the situation not only to a perceptual memory but also to the viewer's own motor repertoire. While motor system activation was correlated with viewing familiar action sequences, direct evidence of a causal effect of motor simulation on visual recognition was lacking in these studies.

In a study examining the influence of motor and visual experience on action prediction Urgesi and colleagues (2012) showed that, after volleyball service training, a motor-visual group was better able to read the early body kinematics of an actor when making anticipatory judgments about ball direction. In contrast, although observers (i.e., visual-only group) improved in anticipatory judgments, they relied on ball flight information to make their predictions (this was the case even when clips were edited to show only ball flight or body kinematics, thus unconfounding viewing time from the type of information available, Urgesi et al., 2012). Because

only a motor-visual training group was compared with a visual-only training group it is unclear whether the ability to pick up body kinematics is strictly a function of 'motor' learning, or an interactive effect of 'visual-motor' learning. Further, no evidence of direct motor system involvement (simulation) was presented in this study.

In a related study, Aglioti et al. (2008) compared the ability of expert basketball players ("motor-visual" group), expert coaches and sports writers ("visual" group), and novices to predict the success of free throw shots from progressively occluded video clips. The expert players predicted the results of the shots significantly more accurately and earlier than those with little or no motor experience. The players relied on early kinematics of the action to make their judgments, while the expert watchers relied more on ball trajectory (later frames). The authors concluded that it was the players' motor experience that was responsible for their superior prediction accuracy. However, in a second part of the study effector-specific MEP activity from the muscles involved in shooting (thought to be a proxy of motor simulation) was shown to be generated in *both* the expert motor-visual group (players) and the expert visual group (coaches, writers) during action prediction (Aglioti et al., 2008). Thus, it is unclear whether the motor system played a causal role in predicting action outcomes for both groups, or was simply a consequence of observing the action sequences.

1.5.4 Isolating visual and motor experience during training

Behaviourally-based learning studies have been conducted in attempts to isolate motor effects on future perception, by training participants on a motor task without vision. Participants have been able to transfer motor learning effects to improvements on visual-perceptual tasks (Casile & Giese, 2006; Hecht, Vogt, & Prinz, 2001). After training on a coordinated upper-body movement in the absence of vision (blindfolded), with only verbal or haptic feedback, visual

action recognition improved to a similar level as a non-blindfolded group (Casile & Giese, 2006). The better an individual performed the motor skill, the better able they were to recognize similar visual motion patterns. It is believed that the locus of these motor effects on the recognition of action may come from motor simulation of the corresponding motor act (activation of an acquired motor program) during observation (Casile & Giese, 2006; Reithler, van Mier, Peters & Goebel, 2007). This is supported by neurophysiologic research showing overlap in the neural areas activated during acting, seeing and imagining (Decety et al, 1994; Grossman & Blake, 2001; Rizzolatti & Craighero, 2004). However, the perceptual task involved in the experiments cited above involved only recognition. That is, participants were asked if the visual representation they saw later was an accurate visual representation of the motor task they had performed earlier. In none of these studies were participants required to predict a future action outcome based on their motor-only experience during a period of training.

By isolating the visual and motor contributions to learning and subsequent prediction, and manipulating motor system activation during action prediction, the goal of my thesis has been to determine more specifically the nature of the earlier-mentioned "chunks", and whether they are based on actual visual patterns (memories) that are evoked during (active) observation of others' actions and compared to the current visual input through simple recognition processes, or are made up of motor programs (or codes) that are covertly simulated during action observation, supporting the principles of common-coding and action simulation (Jeannerod, 2001; Prinz, 1997).

1.6 Two mechanisms for predicting action outcomes

Increased activity in left dorsal, pre-motor areas of the brain, as well as left pre-SMA, was observed only when participants made future predictions about actions that were briefly

occluded (Stadler et al., 2011). This is congruent with ideas discussed above that motor simulation mechanisms are involved in predictions of other's actions. Conversely, when participants were instructed to instead memorize the last seen action image before occlusion, this pattern of activation was not seen. Instead, common to both predicting and holding an actionimage in memory, activation of right pre-SMA was found. Activation in right pre-SMA was therefore thought to be indicative of maintenance or evaluations of actions, but not real-time action-simulation (Stadler et al., 2011). These results hint at the possibility that action prediction involves two types of processes – a dynamic (real-time) simulation process that uses motor representations to predict the future consequences of a simulated action (i.e., top-down perception), and a perceptual matching process that allows a comparison of internally stored images to external stimuli (bottom-up perception) (Gardner et al., 2015; Shubotz, 2007; Urgesi et al., 2010). Based on these findings, and data from an earlier study on action-verb processing, these authors (Springer & Prinz, 2010; Stadler et al., 2011) claimed that these two processes appear to run in parallel during action prediction tasks. Indeed, further evidence supporting this dual process model of action prediction, and specifically the potential separation of these processes, depending on the task demands, was subsequently provided. Priming of action observation with a compatible effector was thought to promote dynamic action simulation, as evidenced by lower error rates in temporal prediction from occluded actions, when actions, and the time interval between actions, were close. Priming with an incompatible effector (considered motor interference) appeared to hinder or prevent this real-time simulation and may have caused participants to rely on the 'static matching' of internal action images. This was evidenced by increased error rates only when the predicted poses became more dissimilar (Springer et al., 2013). The authors suggest that action incompatibility may even prevent internal simulations

because of the incompatibility between the action observed and the action produced (Hommel et al., 2001; Prinz, 1997; Springer et al., 2011; Springer et al., 2013a).

Further support for the notion that, based on contextual factors, different mechanisms may be used for predicting action outcomes, comes from research examining deceptive behavior in sports (Tomeo et al., 2012). Expert penalty kickers and goalkeepers were asked to judge the direction of video-occluded penalty kicks that had been modified to present either normal or deceptive actions. While both groups performed similarly on the normal kicks, goalkeepers were more accurate at predicting the outcomes of deceptive kicks. It was suggested that, along with their superior motor-visual expertise, goalkeepers acquired separate, perspective-specific, visual representations over years of 'observing' penalty kicks. While both groups were considered to have used their superior motor representations to simulate the observed kinematics of the kicker, up to ball contact, it was suggested that the goalkeepers were able, when presented with a deceptive action, to then inhibit any further motor involvement, and instead switch to using their established visual representations to predict the final trajectory of the kick. In contrast, because the kickers had not acquired separate visual representation of the penalty kick from a thirdperson perspective, as the goalkeepers had, they were unable to inhibit further motor system activity. Thus, only the kickers exhibited what was considered to be interference effects caused by the incongruence between the deceptive action being observed and the correct action simulated by their internal action model. The authors interpreted these results as evidence of two distinct mechanisms for predicting action outcomes (Tomeo et al., 2012). In the experiments described in this thesis I draw off the ideas put forth here, suggesting two types of prediction processes, and interference through action incompatibility, to examine the simulative mechanisms that contribute to action prediction in real time.

1.7 Thesis aims

The goal of the three main experiments that comprise this thesis was to aid in the general understanding of the processes involved in prediction of action outcomes from visual scenes. More specifically, the aim was to study how manipulations to available sources of information during learning and prediction can in turn affect perceptual judgments about the predicted outcomes of others' (and one's own) actions. Current research suggests that the human motor system plays a significant role in perceptual behavior. Growing evidence indicates that, during observation, the observer's motor repertoire is invoked, through simulation processes that help facilitate an understanding of the visual input. Mechanisms in the human brain that provide a common pathway for action and perception are thought to be responsible for this simulation process. While an increasing amount of work is being done to quantify the motor and visual contributions of prediction expertise, up to now such studies have tended to compare the visual prediction performance of motor-visual experts to visual (observer) experts and novices. As such, it is reasonable to assume that in each of such groups the participants may have had at least some expertise in both modalities (motor, visual), making it unlikely that purely motor or visual effects could be fully isolated. Further, it is unclear from current research if the motor system activation that is exhibited during action prediction contributes to prediction accuracy, or is simply a consequence of action observation.

In these thesis experiments, I employ a design that isolates visual and motor effects by training participants to perform a dart throwing task with and without vision. Participants are tested on a visual prediction task before and after various types of motor training, while motor and visual conditions are manipulated during prediction, in order to try to understand what is learned or acquired during practice, how this learning affects later prediction of others' actions,

and specifically the roles that the motor-system and visual sources of information play in later prediction.

Several other researchers have employed learning protocols without vision, in an attempt to understand the effects of the motor system on visual perception. However, in these studies only recognition of previously practiced actions have been probed, not anticipation or prediction of action outcomes. As eluded above, although there are likely commonalities between predictive judgements and recognition type judgements, there is also evidence showing that these decisions are guided by different processes (e.g., Springer et al., 2013a, b). Moreover, in a study comparing the ability of novices to either discriminate (recognize) between two action sequences, or predict the direction of a tennis shot, from the same video clips, Canal-Bruland and Williams (2010) showed that participants used different perceptual strategies (kinematics attended to) based on the instructions to either 'recognize' or 'predict' the action sequence. The authors conclude that recognition was not an integral part of, and may not underpin prediction (Canal-Bruland & Williams, 2010; Urgesi et al., 2012). In fact, the processes (simulation, visual matching) and representational formats (visual, motor) may vary, depending on context (i.e. instructions) and type of experience.

In the experiments of this thesis a dart throwing task is used in order to isolate the effects of visual and action experiences on later prediction performance of other's actions. In Experiments 1 and 3, where participants undergo practice with manipulations to the type of training experience, prediction tests are given before and after these physical or observational practice manipulations. In these prediction tests, participants were asked to estimate the landing position of a dart (top, middle or bottom third of a dart-board) under various conditions involving manipulations to a) the amount of information available to make these judgements (i.e., temporal

occlusion; static versus dynamic images), as well as b) the types of tasks performed concurrently with prediction (i.e., action or effector compatible or incompatible motor-based or attention-based secondary tasks).

In Experiment 1, two physical practice groups were compared that practiced with and without vision of the action and dart flight (all groups received outcome feedback). These groups were compared to an observation-only group and a no-practice, control group. We speculated that, if the action system was solely responsible for any subsequent improvements in predictions, that a no-vision, physical practice group would not differ from a full vision physical practice group. We also predicted that improvements in the prediction test would manifest during early temporal occlusion periods, based on the model's body kinematics, and not later where more dart flight information is available (Aglioti et al., 2008; Urgesi et al., 2012; Williams & Davids, 1998; Williams & Ward, 2003, 2007).

We found that participants who practiced a dart throwing task without vision were significantly more accurate, compared to pre-test, at later predicting the landing position of a dart thrown by another person. The no-vision group performed as well as the full-vision, motor training group on the post-training prediction task. These two groups also performed significantly more accurately than a no-training control group. An observer group was also studied and showed no improvements from pre to post testing. However, the observational group observed from a 1st-person perspective, behind the actor, yet performed the prediction tests from a side view. Because improvements in predictions have been observed in previous studies involving observational practice (e.g., Urgesi et al., 2012), it remains possible that any lack of improvement for this group could be a result of the change in visual perspective from practice to

test. This issue is partially addressed in Experiment 3, where a "side-on" perceptual-training group is included.

The results of Experiment 1 suggested that motor experience was important for prediction, and visual experience appeared not to be important. Although motor experience explained any improvements in prediction performance, it was still unclear whether the motor system was activated in a simulative way during action prediction. It was possible that during practice itself, visual sensory consequences experienced (full vision) or potentially spontaneously generated (no-vision) in the physical practice groups were used to help make predictive judgements in the test phase (more in line with a perceptual matching account of prediction).

In Experiments 2 and 3, therefore, I further studied the mechanisms, and informational resources, that allowed this predictive capability to emerge. By manipulating motor and visual information during training and prediction tests we were able to examine the processes (simulation/matching) and representational formats (motor/visual) used in predicting the sensory consequences of these action outcomes, including the possible role of motor simulation and the associated motor programs, or action codes, that are developed through motor experience. Specifically, we studied how these improved predictions are enabled as a function of past experience (Exp 2) or practice (Exp 3) through the introduction of congruent and incongruent secondary motor tasks. The aim was to attempt to interfere with any potential motor-based simulation that takes place during prediction. We expected that an incongruent motor task would interfere with prediction performance to a greater degree in motor experts or after physical practice if the motor system is needed to predict action outcomes.

Manipulations to the type of stimulus observed was also used to probe potential simulation mechanisms involved in action predictions. 'Self' and 'other' action stimuli were included in Experiment 2, given the evidence that one's own actions are more likely to prompt motor simulation and lead to more accurate predictions than predictions based on another's actions. In Experiment 2 we showed that the addition of an action-incongruent secondary motor task (pressing against a force gauge) significantly reduced prediction accuracy in the experienced group only. The effect was strongest when the experienced dart players watched themselves and no interference (or benefit) was seen if the participants were allowed to "mimic" what they were observing when making these predictions. The results of Experiment 2 supported the conclusion that action predictions require motor system involvement for accurate predictions. Although there was some indirect evidence that only a secondary motor task that was incongruent with the action interfered with prediction accuracy, effector-specific interference was not directly evaluated. This was one of the aims of Experiment 3, to test the potential action or effector specificity of these "motor" based effects on prediction accuracy, and hence for motor simulation processes.

In Experiment 1, visual experience did not significantly contribute to subsequent prediction accuracy. The Full-vision (visual-motor) group was not any better at later prediction of other's actions than the No-vision (motor-only) group, and the observation-only group did not show any pre- to post-test improvements. Further, while in Experiment 2 we were able to determine a possible role for the motor system in visual prediction of action outcomes, we still could not conclude definitively that vision during training was unimportant, not least because of the types of manipulations and measuring techniques we adopted. Therefore, one potential question concerns why visual sensory consequences did not benefit prediction accuracy, given

that in previous studies, observers and visual-motor experts have improved following practice, and have improved significantly on later predictions involving the flight of an object (Urgesi et al., 2012).

Therefore, in Experiment 3, we again directly controlled the practice experiences of participants by conducting a training study where we could give either motor-visual practice or visual-practice, what we refer to in the latter case as "perceptual training". Participants in the perceptual-training group watched from the same perspective as the test phases (i.e., side-on perspective). During the prediction tests, the same incongruent secondary motor-task used in Experiment 2 was used to probe motor processes involved in prediction accuracy (as a function of the type of training). Both a left (non-throwing) and right (throwing) arm secondary task was used in order to explore effector-specificity with respect to interference and hence motor simulation. We also wanted to understand what type of visual information was required to invoke internal simulative mechanisms. To this end we incorporated both dynamic and static (implied action) video clips in the prediction tasks.

Both training groups significantly improved their prediction accuracy after practice. However, only the Motor-visual group showed an interference effect, in the form of a significant reduction in prediction accuracy, while performing the secondary motor task with their right hand. They showed no significant decrease in prediction accuracy while performing the secondary task with their left hand. Further, the perceptual training group showed no significant decrease in prediction accuracy while performing either secondary motor task. These results suggest that, in the Motor-visual group, the motor system was involved in simulating internal action models associated with the observed action, in order to predict its outcome. In contrast, the perceptual group appears to have used a more visually-based mechanism when predicting the

outcomes of the observed action, as evidenced by a lack of motor interference while performing the secondary motor tasks. In addition, because of the differential effect of the secondary motor tasks, we conclude that motor system activation during prediction is specific to the right effector, or throwing arm. The results support the idea that action prediction can come about through two distinct mechanisms. One that relies on internal action models that simulate the observed action to provide information about the sensory consequences of the action, and another that matches observed actions to stored visual representations.

In summary, across these 3 experiments, there were a number of general questions and aims driving the research. Specifically, we were interested in if, and how, individual motor ability aids the perceptual skills involved in predicting the moves and decisions of others, and hence how (and when) the motor system is involved in the prediction process. Are people who are better able to perform a skill, better able to judge the accuracy of that skill being performed by someone else? Which informational components of an acquired skill are used by the perceptual system (i.e. are important for prediction)? How specific is motor system involvement (action-specific/effector-specific) during prediction? Theoretically, it is important to understand whether the motor system's influence on perception extends beyond the simple recognition of the same action to the prediction of future intentions or results of someone else's actions. Is the motor system always activated during prediction, or perhaps more specifically, under what conditions does the prediction of others' action involve a person's motor system?

Chapter 2: Throwing in the dark: improved prediction of action outcomes following motor training without vision of the action

2.1 Introduction

The ability to anticipate the actions of others is fundamental to human existence. This is evidenced in everyday activities like crossing the road or driving, and is most clearly highlighted in sports. But how does this ability to anticipate or predict the outcomes of others' actions actually come about? A common view holds that after years of viewing a broad array of action sequences or patterns, within a particular class of actions or motor skills (e.g. tennis, soccer), the visual system becomes better able to extract important kinematic information through improved visual search and cue utilization (e.g., Abernethy and Zawi 2007; Abernethy et al. 2008; Ward et al. 2002). Through such broad visual exposure, robust long-term memory structures are thought to be established, containing familiar patterns or 'chunks', that are quickly retrieved during decision-making (Chase and Simon 1973; de Groot 1978; Hodges et al. 2006). Although these memory structures were argued to be based on visual-motor experience (e.g., Williams and Davids 1995), the emphasis was placed on visual recognition as a primary cue, enabling expertrelated decision/anticipation advantages. More recently, it has been suggested that motor experience, specifically, plays a direct role in understanding and predicting action outcomes, and that it is this action experience that is the key factor in improved perceptual skill (Aglioti et al. 2008; Calvo-Merino et al. 2006; Casile and Giese 2006).

During action observation (for understanding, predicting, or anticipating action outcomes) the motor system seems capable of activating, in the observer, perceptual codes associated with the original motor commands that produced the same (or similar) actions

(Knoblich and Flach 2001; Knoblich et al. 2002). Perceived and executed actions are said to exist in a common representational medium and exert reciprocal influences on each other. Action execution creates a common representation between the motor commands that generate the movement and the sensory effects that are produced by that movement (Prinz 1997; Prinz and Hommel 2002). In this 'common-coding' framework it is thought that we are able to anticipate others' actions and goals, not through elaborate, inferential processes, but rather by automatically simulating the internal motor commands associated with the observed action (Blakemore and Decety 2001; Hommel et al. 2001; Jeannerod 2001; Knoblich and Flach 2001; Schubotz 2007; Wilson and Knoblich 2005). In this sense, an observer's motor repertoire exerts a direct influence on their perceptual understanding. Therefore, the closer the match between the observer's motor repertoire and the observed action, the better able they are at understanding and anticipating the sensory consequences of the unfolding action (Knoblich and Flach 2001).

Neural support for the idea of a common representational medium has come from the discovery of a class of neurons in monkey premotor cortex that are activated when the animal both performs and observes the same goal-directed grasping or holding actions (Di Pellegrino et al. 1992; Fogassi et al. 2005; Gallese et al. 1996). These neurons have been termed *mirror neurons* because they respond to others' actions as if they were one's own. Converging neurophysiologic and behavioral evidence supports the existence of a similar system in humans, primarily involving parietal cortex (inferior and superior, e.g., Fogassi et al. 2005; Iacoboni et al. 1999), inferior frontal cortex (Pobric and Hamilton 2006), and temporal cortex (medial, superior, Mukamel et al. 2010; Saygin 2007). This has been referred to as the mirror neuron system (MNS, Iacoboni et al. 2005; Rizzolatti and Craighero 2004) as well as the action-observation network (e.g., Cross et al. 2009).
Researchers have begun to more closely study the role of motor experience in action recognition and anticipation to help quantify and differentiate visual and motor influences in performance on these perceptual tasks. For example, observers are more accurate at recognising or predicting the outcomes of action sequences that are part of their own motor repertoire (Aglioti et al. 2008; Calvo-Merino et al. 2005, 2006; Knoblich and Flach 2001; Urgesi et al. 2011; Wilson and Knoblich 2005). Calvo-Merino and colleagues (2005, 2006) showed that in action scenarios that were familiar to the observer (i.e. dance specific or gender specific), motorrelated areas of the brain associated with the MNS showed significantly greater activation when dancers viewed moves that they regularly performed rather than moves of a different type of dance or that they regularly watched. They argued that observing action situations involves the viewer matching the situation not only to a perceptual memory, but importantly to the viewer's own motor representations.

Not only has motor experience been linked to brain differences during passive observation, it has also been shown to influence anticipatory decisions over and above that due to visual experience (Aglioti et al. 2008; Urgesi et al. 2011). In a study examining the influence of motor and visual expertise on action anticipation, Aglioti and colleagues (2008) compared the ability of expert basketball players, expert 'watchers' (coaches, sports' writers), and novices to anticipate the success of free-throw shots (i.e., shots made from the top of the key). Video clips showed free-throws that were progressively occluded at 10 different points. The expert players predicted the fate of the free-throws significantly earlier and more accurately than those with little or no motor experience. While the expert players used early body kinematics to make their judgments, the expert watchers primarily relied on ball trajectory. The authors suggested that the

athletes' superior motor experience was responsible for anticipating the action outcomes of others and that action simulation is inherently anticipatory in nature (Aglioti et al. 2008).

Although differences between 'visual-motor' experts and 'visual' experts support the idea that it is the motor system that is primarily responsible for differences in anticipation, in followup work, both groups showed increased electrically-induced motor evoked potentials (MEPs) in the muscles involved in shooting during observation of basket shots. This was taken as evidence that the motor system was involved in decision making for both types of experts (i.e., motor and visual). However, it is important to consider that these groups were not actually qualitatively different in their modes of experience and that both groups might more-correctly be considered motor-visual groups, with differing degrees of visual-motor and visual experience. The MEP results would support this point, in that the expert observer groups may simply be showing activation based on their own, albeit reduced, visual-motor experience, rather than pure visual experience as implied by Aglioti and colleagues (2008). It is also important to point out that athletes were also more likely to have had a different quality and quantity of visual-perceptual experiences to the other groups and that without control of this factor it remains possible that it was the athletes' enhanced visual experience that played a primary role in their superior judgments.

Therefore, based on the nature of these types of expert-novice designs, where motor and visual experiences are not strictly controlled, in addition to inconsistencies between behavioural and TMS-induced results in the study above, it is difficult to know the differential contributions of motor and visual experience to enhanced anticipatory decision making.

In a complementary study linking both cross-sectional comparisons of visual-motor experts (athletes), visual experts (fans) and novices in volleyball, as well as a training study,

Urgesi and colleagues (2011) also concluded that the motor system was key in determining anticipation accuracy. After volleyball service training, a motor-visual group improved in posttest anticipatory judgments when the stimuli (shown from first-person perspective) were based on the body kinematics of the action alone, but not when the stimuli showed only ball flight. In contrast, a group that trained by observation only, improved on anticipatory judgments to stimuli showing only ball flight, but not to stimuli showing only body kinematics of the upcoming serve (Urgesi et al. 2011). These results were similar to those seen in volleyball athletes and fans, although the athletes showed superior anticipation performance to both fans and novices in both the ball flight and body kinematics conditions. It was concluded that motor practice allows for the development of motor programs that rely on body kinematics to predict the actions of others via simulative mechanisms (see also Schutz-Bosbach and Prinz 2007; Wilson and Knoblich 2005). Urgesi et al. also argued that visual experience fosters the development of visual representations of the action that are used to generate internal models that define the visual dynamics and trajectories of objects, such as ball flight (see also Hubbard, 2005; Zago and Lacquaniti 2005). However, because only a motor-visual training group was compared with a visual-only training group, it is still unclear whether the ability to pick up body kinematics is strictly a function of 'motor' learning, or an interactive effect of 'visual-motor' learning. In other words, was it the motor experience acquired during training that was responsible for the subsequent perceptual performance of the visual-motor learning group, or was it the visual experience or a combination of both?

In the present study we sought to differentiate the independent roles of motor and visual experience on the anticipation of action outcomes through a training study where visual experience was manipulated. Learning studies have been conducted in attempts to isolate motor

training effects on future tests of perceptual recognition or recall. For example, after training on a range of movements in the absence of vision (blindfolded), with only verbal or haptic feedback, visual action recognition improved to a similar level as shown for non-blindfolded groups (Casile and Giese 2006; Hecht et al. 2001; Reithler et al. 2007). It was argued that the locus of these motor effects on the recognition of action arises from motor pattern simulation of the corresponding motor act (i.e., activation of an acquired motor program) during observation (Casile and Giese 2006; Jeannerod 2001; Reithler et al. 2007; Rizzolatti et al. 2001). However, to date, only perceptual recognition tests have been used to assess whether movement patterns that were physically practised without vision were recognised later in a visual format. Participants have not been required to anticipate or predict future action outcomes based on non-visual motor learning.

Theoretically, it is important to understand whether the motor system's influence on perceptual learning extends beyond the simple recognition of the same action to the anticipation of future intentions or results of someone else's actions. In sports and other domains, we do know that domain experts appear to encode domain specific stimuli in terms of anticipatory projections (what has been termed representational momentum, Didierjean and Marmèche 2005; Intraub, 2002). It therefore might be reasonable to suspect that motor system involvement in recognising actions automatically contains an anticipatory component, which to date has not been explicitly tested in environments where visual and motor influences are more strictly controlled. Therefore, the novel design of our study makes it the first to use visual occlusion techniques during practice to isolate the human motor system's unique contribution to the prediction of future action outcomes.

We compared anticipatory predictions about the final position of a dart thrown at a dartboard, before and following either visual-motor training, motor-action only training (no vision of the action, only feedback concerning the final landing position of the dart), visual training only (observation) or no training (control). Using video stimuli that had been edited to show only portions of the dart throwing action, we were able to compare the various training groups' predictions based on early kinematic cues to later ones based on a combination of body kinematics and dart flight.

If motor experience alone is responsible for any subsequent improvements in anticipation performance, we hypothesised that the group who practised without vision of the action would improve pre to post practice and would not differ in post-practice anticipation performance from the visual-motor training group. For both these 'motor' training groups, improvements in the anticipation test were expected to manifest during early video frames based on the thrower's body kinematics (Aglioti et al. 2008; Urgesi et al. 2011). Based on the results of the observer groups in the studies discussed above, we further predicted that an observer group would be more accurate than no-practice controls on later frames when more dart flight information is available (Aglioti et al. 2008; Urgesi et al. 2011). In this analysis of anticipatory predictions, we compared all 4 groups before and after practice, as this allowed us to compare the different types of visual, motor and visual-motor experiences to no-practice conditions. Measures of confidence were also taken during the anticipation tasks as a secondary (and potentially more subtle measure) of anticipatory performance (e.g., Jackson et al. 2009; Jackson et al. 2006). Unlike accuracy (where there is always a 33% chance of guessing correctly), this measure was not subject to probabilistic guessing and might alert to metacognitive understanding of learning/performance (e.g., Cheesman and Merikle 1984; Dienes et al. 1995).

In an attempt to balance motor learning in the two motor practice groups (motor-visual and motor-only) we established a common acquisition criteria for these groups and measured acquisition performance over two days of practice in order to make conclusions about their learning rates and performance levels at the end of practice (see Knoblich and Flach 2001). In order to study any potential motor learning benefits for the observational practice only group (i.e., perception-action transfer) we also measured motor performance throwing before and after the training and anticipation test procedures.

2.2 Methods

2.2.1 Participants

Forty male volunteer students between the ages of 19 and 31 yr, with normal or corrected vision, and no neurological impairment took part in the study. Participants were pseudo-randomly allocated into four groups (n=10/gp): a "No-vision of the action" motor learning group, a "Full-vision" motor learning group, an "Observer" group and a no-practice "Control" group, with the constraint that a participant in the No-vision of the action group was always tested before a participant in the Full-vision group (see procedures). They were all self-report right-handed and had no prior experience playing darts (1 or 2 times was the maximum self-reported experience allowed, but this experience had to be more than 2 years previous). All participants were briefed on the general nature of the study and provided signed consent prior to inclusion in the study. Ethics' protocols for human experiments were strictly followed, as laid out by the ethics' board of the University and the 1964 Declaration of Helsinki and its later amendments. Participants were paid \$8/hour.

2.2.2 Apparatus and stimuli

The task was modeled on an earlier dart throwing study designed to look at self-other perceptions (Knoblich and Flach 2001). Participants in this earlier experiment were proficient at recognising their own action from a side-on view, even though they had only received visual-motor experience from a first-person perspective. A standard dart board was used and height and distance regulations typically observed in the game of darts were adopted (i.e., the participant stood at a distance of 2.37 m from the dartboard, which was placed at a height of 1.73 m from the floor to the bulls-eye). Like Knoblich and Flach (2001), the board was sectioned by two horizontal lines, providing a top, middle and bottom section. Participants were either required to aim to the centre of each section and/or make anticipatory judgements concerning the landing position of a dart.

Video clips for the anticipation test were created using a Cannon HV20 camera (30 fps, 33ms/frame) showing a novice actor, after significant experience with the task, tossing a dart at each of three sections of a dartboard (that all landed near the centre of each section and that were of approximately the same duration). The actor was filmed from a side-on perspective. Six video clips were created for each section of the dart board (top, middle, bottom), for a total of 18 clips. Each of these clips was further broken down into 8 temporal lengths, each length being one frame (33 ms) different from the next. Thus, a total of 48 different clips were developed for each of the three board sections, making a total of 144 clips. Each clip showed the initial part of the dart throw (i.e., raising the arm, then arm back motion). The time for this phase of the movement was ~2 sec (M = 1930 ms, SD = 20 ms). The first occluded clip showed this initial 'setup' phase, plus one more frame (the start of the forward propulsion phase). Each of the subsequent 7 clips was 33ms (1 frame) longer. The dart left the hand in frame 4. Video editing was performed using

Sony Vegas video editing software. Clips were shown via a projector on a full length screen (Cineplex Pro, IN, U.S.A), providing an approximate life-size image. E-prime 2.0 software was used to present the stimuli and for entering responses (Psychology Software Tools, Inc., PA, USA).

During training, participants in the No-vision of the action group had their vision occluded using Plato liquid crystal occlusion goggles (Translucent Technologies, Ontario). These were operated manually by the experimenter such that vision was occluded just before the throw was initiated and was returned once the dart had landed, such that outcome feedback could be provided. Participants were instructed to stand with the dart in hand and their throwing arm by their side. Vision was then occluded. At this time the participants were required to wait ~1-2 sec before beginning their throwing action. After the dart hit the dartboard vision was returned ~1-2 sec later. In order for learning to occur it was necessary for us to provide outcome feedback to participants. In order that the feedback was equivalent in quality to that provided to the visual-motor practice group this information was given visually. Importantly, no vision of the action was ever provided during practice for the no-vision (motor-practice only) group and hence participants in this group never saw any of the perceptual stimuli used in the subsequent perceptual anticipation tests.

2.2.3 Procedure

The study took place over two days. On the first day all participants threw three darts at the 'bullseye' on the dartboard, in order to obtain a baseline measure of motor performance. This motor pre-test was limited in number in order to enable uncontaminated manipulations of motor and visual experience. The only instructions participants were provided with were with respect to how to hold the dart and how to stand facing the dart board on the line (i.e., they were instructed

to stand in the same manner as the model detailed in the video anticipation tests). Next, all participants completed the pre-practice anticipation test (144 video clips presented in a random order). After each clip ended, the final frame remained on the screen for two seconds. Via a screen prompt, participants were asked where they thought the dart would have landed (top, middle, bottom) and their confidence in their answer, ranging from '0', denoting no confidence, to '4', meaning 100 % confident (25 % intervals). During the anticipation tests participants stood facing the screen while making their predictions. They could rest at any point.

Following the anticipation pre-test, the No-vision of the action and Full-vision motor learning groups practised throwing the darts to one of the three defined areas of the dartboard. The No-vision of the action group had their vision occluded throughout the throw. The experimenter would indicate when vision was to be occluded, but the target section was always known in advance before removal of vision. When the dart struck the board the experimenter would cause the glasses to turn transparent so that outcome feedback was provided.

Participants in both physical practice groups were required to target each zone with 5 consecutive throws. The order of target blocks was determined in a pre-randomised fashion (matched across groups). Participants targeted each section for a total of 8 blocks, with 5 throws each block, for a total of 120 practice trials. Observers were yoked to participants in these two groups (n=5/group). The Observer stood slightly to the right and behind their matched physical practice counterpart. The Control group did not practise.

On the second day, approximately 24 hours later, the two physical practice groups completed a second session of practice (and observers watched their practice) until a criterion level of motor proficiency was achieved. In order to control for the amount of practice, the Fullvision group's practice schedule was determined by the No-vision of the action group's practice.

Specifically, the No-vision of the action group targeted each section of the board, starting with the top section. They were required to throw to each section until they could hit that section 5 consecutive times. They would then move to the middle and then bottom sections and complete the same requirements. This procedure was repeated twice. Participants from the Full-vision group were yoked to individual participants in the No-vision groups, in that they were required to throw the same number of darts to each section, even if they had already hit the section 5 consecutive times.

At the end of the second day of practice, all participants completed the video anticipation post-test. Again, the same 144 video trials were presented, but this time in a new random order. Testing ended with a motor proficiency post-test where participants threw 3 darts towards the centre of the dartboard (aiming for the bullseye). Participants were then fully-debriefed.

2.2.4 Data analysis

For the anticipation tests we calculated percentage accuracy scores for each of the eight temporal video periods that were presented to participants on the video clips. These were subjected to a 4 Group (Full-vision, No-vision, Observers, Control) x 2 Test (pre, post) x 8 Frame repeated measures (RM) ANOVA. Because the 4 groups varied orthogonally with respect to the type of visual-motor training of the action (none, motor-only, visual-only, visual-motor), Group was the between factor, and Test and Frame were the repeated factors. We were primarily interested in the Group x Test interaction and whether the 3 experimental groups performed with greater accuracy than the control participants on the post anticipation test. We also conducted a secondary analysis to look at percentage accuracy as a function of the dartboard section. Rather than Frame, Section (Top, Middle, Bottom) was included as our RM factor in a second ANOVA.¹

Confidence scores were also analysed for each of the eight occlusion periods that were presented to participants on the video clips. These data were subjected to a 4 Group x 2 Test (pre, post) x 8 Frame ANOVA with RM on the last two factors.

For the motor proficiency test given before and immediately following the anticipation tests, mean radial error (RE) and bivariate variable error (where BVE is based on the deviations of X and Y in relation to the target, t and the number of throws, k) were calculated.

$$BVE = \sqrt{(1/k \sum_{i=1}^{k} (X_i - X_i)^2 + (Y_i - Y_i)^2)}$$

These were subjected to a 4 Group x 2 Test (pre, post) RM ANOVA.

Acquisition accuracy data were also analyzed to enable comparisons between the two physical practice groups. Although practice amount was the same across participants on day 1 (i.e., 8 blocks of practice for each target section), on the second day, participants had different amounts of practice to each target section (matched across pairs in the two groups). Therefore we analysed day 1 and day 2 separately. Day 1 was analysed in a 2 Group x 3 Target x 8 Block RM ANOVA, with each block containing 5 throws. For day 2, we compared the overall % accuracy for each target section in a 2 Group x 3 Target x 2 Block RM ANOVA.

Partial eta squared (η_p^2) values are reported as measures of effect size, and post-hoc analyses were performed using Tukey's HSD (p < .05) when comparisons were made between three or more means. Where violations to sphericity were encountered, Greenhouse-Geisser corrections were applied.

2.3 Results

2.3.1 Anticipation accuracy

The mean percentage accuracy scores for the pre- and post-training anticipation tests are shown in Figure 2.1. The Full-vision and No-vision of action groups improved in their anticipatory predictions after the training interventions, while the Control and Observer groups did not. These effects were confirmed through statistical tests yielding a main effect of test, $F(1,36) = 52.20, p <.001, \eta_p^2 = .59$ and the predicted Group x Test interaction, F(3,36) = 19.74, $p < 0.001, \eta_p^2 = .62$. There was no group effect (F < 1). We followed up the interaction effect with post hoc comparisons. As expected, there were no significant differences between the groups in the pre-test. Importantly, on the post-test, the two motor practice groups were significantly more accurate than the Control group as well as the Observer group (all *ps*<.05). No differences were noted between the Full-vision and No-vision of action groups or between the Observer and Control groups. Comparing across the pre- and post-test, only the No-vision of action and Full-vision groups significantly improved (both *ps*<.05). There was also a main effect of frame, $F(4.92,177) = 32.09, p <.001, \eta_p^2 = .47$, which was described by a significant linear trend, $F(1,36) = 124.65, p <.001, \eta_p^2 = .78$ (see Figure 2.2). Accuracy scores increased as more vision of the throwing action and dart flight was available. There were no interaction effects for Frame involving Group or Test.



Figure 2.1 Percentage accuracy scores (and within group sds) for the anticipation test as a function of Group and Test (pre- and post-practice).



Figure 2.2 Percentage accuracy scores for the anticipation test as a function of Group, Test (pre- and post-practice) and Frame.

When we compared across sections of the board, a significant section effect was shown, F(1.44,51.97) = 77.85, p < .001, $\eta_p^2 = .68$, as well as a Section x Test interaction, F(2,72) = 5.54, p < .01, $\eta_p^2 = .13$. There were no interactions involving Group. The top section was responded to more accurately, M = 72.29% (SD = 14.41) than the bottom section, M = 35.03% (SD = 14.40). Responses to the middle section, M = 57.94% (SD = 14.99) were also significantly more accurate than those to the bottom section, but not different from the top (all *ps*<.05). The interaction between Section and Test was a result of significant improvements in accuracy across pre- and post-training, for the top and middle sections only (Top, pre: M = 67.82%, SD = 15.70; post: M = 76.77%, SD = 13.12; Middle, pre: M = 54.84%, SD = 14.84; M = 61.04%, SD = 15.13; bottom, pre: M = 34.79%, SD = 12.69; post: M = 35.26, SD = 16.11, all significant comparisons, *p*<.05).

2.3.2 Confidence measures

As shown in Figure 2.3, confidence judgments generally increased across frames as more information became available about the flight, F(7,252) = 11.46, p < .001, $\eta_p^2 = .24$. Post hoc analysis showed confidence ratings were significantly lower for frame 1 than frames 4-8 and for frame 2 in comparison to frame 8 (all ps<.05). Somewhat surprisingly, confidence actually decreased overall from the pre- to the post-test, F(1,36) = 14.62, p < .001, $\eta_p^2 = .29$. Although there was no main effect of group, F(3,36) = 2.45, p = .08, $\eta_p^2 = .17$, the predicted Group x Test interaction was observed, F(3,36) = 3.21, p = 0.034, $\eta_p^2 = .21$. This was due to a decrease in confidence for the Observer and Control groups only from pre- to post-test (both ps<.05). Despite the improved accuracy for the two motor practice groups, they did not show a significant change in confidence across the two tests. In the post-test, the Control group did not differ significantly from any of the experimental groups, only the Observer group was significantly less confident than the No-vision of action group (p < .05). There was also a Frame x Test interaction, F(7,252) = 2.24, p = 0.032, $\eta_p^2 = .06$, which on inspection of the figure was primarily due to differences in confidence across the frames in the pre-test, but less so in the post test. There were no other interactions involving Group (Frame x Group, F = 1.52; Day x Frame x Group, F =1.14).



Figure 2.3 Average confidence judgments for the anticipation tasks (pre- and post-practice) for each of the 4 groups as a function of frame.

2.3.3 Motor proficiency

As shown in Figure 2.4a (radial error) and 2.4b (bivariate variable error), the Full-vision, No-vision of action and Observer groups showed a decrease in error pre- to post training, whereas the Control group showed no change. With respect to statistics, however, for RE (Figure 2.4a) there was a main effect of Test, F(1,36) = 18.70, p < .001, $\eta_p^2 = .34$ and a Group x Test interaction, F(3,36) = 3.31, p = 0.031, $\eta_p^2 = .22$ (there was no group effect, F < 1). The groups were not significantly different in the pre-test. In the post-test, the only statistically significant difference was between the No-vision of action and Control group (p < .05), with the former showing significantly less error. Comparing across the pre and post-tests, the No-vision of action and Full-vision groups significantly reduced RE by 32 cm and 20 cm from pre to post-test respectively. A decrease of 9 cm was not significant for the Observer group (Control difference = 2 cm, ns).

For BVE (Figure 2.4b), a similar pattern of results was shown, including the Group x Test interaction, F(3,36) = 3.06, p = 0.04, $\eta_p^2 = .20$. Again the groups did not differ in the pretest, only on the post-test, where the No-vision of action group was significantly less variable than the Control group (p<.05). No other comparisons yielded significant differences. The Novision and Full-vision groups showed significant reductions in variability of 26 cm and 23 cm respectively (p<.05). While the Observer group again showed a reduction in variability (11 cm), this was not statistically significant. The Control group showed a small, but non-significant increase in variability (+ 2 cm).







Figure 2.4 (a) Mean radial error (RE) and (b) bivariate variable error (BVE) for the motor test as a function of Group and Test (pre- and post-practice). Error bars are within group SDs.

2.3.4 Acquisition of throwing accuracy

As can be seen in Figure 2.5, for day1 practice the Full-vision and No-vision of action groups improved in their motor accuracy (i.e., % success) as training progressed, although the Full-vision group was significantly more accurate on all blocks throughout practice. This was confirmed by Group, $F(1,18) = 154.56 \ p <.001$, $\eta_p^2 = .90$, Block, F(7,126) = 44.78, p <.001, $\eta_p^2 =$ = .71, and Group x Block effects, F(7,126) = 4.91, p < 0.001, $\eta_p^2 = .21$. An effect of target section that approached conventional significance was seen, F(2,36) = 3.13, p = 0.056, $\eta_p^2 = .15$. Like accuracy in the anticipation test, participants showed a trend to throw more accurately to the top section, in comparison to the bottom section, although this difference was not statistically significant after post-hoc analysis.² The Block effect was described by significant linear and quadratic components (ps < .05).

b)

As shown on the right side of Figure 2.5, with respect to day 2 practice, there were no main effects of group, F(1,18) = 3.33, p = 0.085, $\eta_p^2 = .16$ or section, F(2,36) = 1.38, p = 0.265, $\eta_p^2 = .07$, and no interaction effects involving Group (Fs < 1). There was a general improvement across the two blocks of practice on the second day, F(1,18) = 10.50, p < .01, $\eta_p^2 = .37$.



Figure 2.5 Motor training acquisition scores for the No-vision and Full-vision groups, as a function of target section (top, middle, bottom) and block for day 1 and day 2 practice.

2.4 Discussion

Participants that practiced a dart throwing task without vision of their body and dart flight were significantly more accurate, compared to pre-test, at later predicting the landing position of a dart thrown by another person. Importantly, this no-vision of action group did not differ from a full-vision motor training group on a post-training anticipation task. For both the full-vision and no-vision groups, improvements in anticipation were seen very early (frame 2 onward, see Figure 2.2) throughout the various temporal occlusion periods. Although there was a main effect of frame, with general improvements in accuracy as more dart flight became available, these improvements were not moderated by training (i.e., there were no interactions involving Group and Frame). Therefore, improvements in prediction accuracy for the motor-trained groups did not appear to be based on dart flight information. Because of this almost immediate and constant improvement in accuracy for these groups (across the frames) and the fact that the dart did not leave the model's hand until frame 4, we infer that improvements were based on early body kinematics³. These results support those based on cross-sectional comparisons of experts and novices and trained visual-motor groups (Aglioti et al., 2008; Urgesi et al. 2011). After training on a volleyball service task, a motor-visual group was more accurate at predicting the outcome of floating services when the stimuli showed the body kinematics of the action but not when the stimulus showed ball flight alone (Urgesi et al. 2011). Similarly, elite basketball players were significantly better able, than expert observers and novices, to determine the future outcomes of observed actions using only very early kinematic cues (Aglioti et al. 2008). Importantly, the two motor learning groups in our study (with and without vision of the action) also performed significantly more accurately than a no-training, control group as well as a vision training only (observer) group. There were no significant pre- and post-test differences in anticipation performance for either of these latter groups.

While our occlusion methods in practice were aimed at controlling for the influence of vision in learning, and subsequent anticipation, we also took steps to control for the amount of motor practice acquired by the two motor practice groups, in order to be able to draw conclusions about the differential effects of motor and visual information on subsequent anticipation performance. The amount of motor experience has been shown to be calibrated with improvements in visual recognition (Casile and Giese 2006; Reithler et al. 2007). Although the

no-vision of action group showed a slower learning rate over the first day of practice in our study, by the end of the first day they performed similarly to the visual-motor group, and on the second day of practice the two groups showed no statistical difference in performance. Therefore, even though the visual-motor group attained a criterion level of performance faster than the no-vision of action group and this group therefore had more "accurate" practice than the no-vision group, this did not translate into improved prediction accuracy on the subsequent anticipation test (and we found no relationship between performance during practice and later anticipation accuracy).

We were somewhat surprised that the observers in our study failed to show any benefits from watching their paired actor over two days of practice. Although there was a trend toward improvement in the motor task (suggestive of perceptual-action transfer as a result of observational practice, Hecht et al., 2001), the observers did not improve on the anticipation task across practice (at any of the occlusion periods). Their confidence also decreased on this task following 2 days of watching their motor-learning counterpart continuously throw darts to the 3 sections of the dart board that they were subsequently tested on with respect to anticipatory decisions. This may indicate awareness of a lack of learning from watching and/or an understanding that they were not performing any better (than pre-test) on the anticipation posttest (Dienes et al. 1995). Such awareness may also imply a more explicit or inferential process at work during the prediction task for this group (Allwood et al. 2000; Wright and Burton 1995). Conversely, the fact that the confidence ratings for the two motor groups did not change pre- to post-test, despite significant improvements in prediction accuracy, may suggest that, while they were also using inferential, or heuristic-based judgements prior to training, which is thought to be characterised by over-confidence early in the learning process, they exhibited a more implicit,

or unconscious prediction process post-training, and a corresponding lack of metacognitive awareness of learning improvements (Kolb and Braun 1995; Kunimoto et al. 2001: (Runeson et al. 2000; Tunney and Shanks 2003).

Although we did not expect the observers to perform similarly to the two actor groups (due to a lack of motor experience), Urgesi and colleagues (2011) showed anticipation performance improvements in observers for video clips that were based on ball flight (and not body kinematics). This lack of improvement in our study (even for the later frames, where more of the dart flight was available) could potentially be a result of incongruence between the practised and anticipation perspectives. In order to ensure that the visual information was matched to the actor's perspective the observers in our study stood behind and slightly to the side of their actor pair, promoting a first-person perspective. Urgesi and colleagues (2011) showed anticipation performance improvements in observers only in the perspective they learned in (i.e., first-person) and not in a novel, front-view (i.e., third-person). If pure visual codes are specific to perspective, then this might explain our lack of prediction advantages for the observer group (at least for the clips that included dart flight), as they viewed the test stimuli from a side view.

It has been suggested that, to affect perception, action must be tightly coupled with visual stimuli (Beets et al. 2010). However, we show that action-training in the absence of vision can have a significant positive effect on later tests of task-related visual perception. These findings are commensurate with common-coding ideas, whereby vision and action are represented in a shared representational medium. Action codes that are generated during practice (even in the absence of vision) can later be used and simulated as perceptual codes to aid in action understanding (Casile and Giese 2006; Reithler et al. 2007). Specifically, when an action is initiated, the sensory consequences associated with that action (perceptual code) are also

generated, and linked to the action codes. During anticipation, a similar perceptual code may then be activated in the observer by the perceptual input of the dart thrower, but only when action experience has been accumulated by the observer. The motor code or program, associated with the perceptual code, is automatically invoked (simulated), resulting in a prediction of the action's outcome (Knoblich et al. 2002). The closer the match between the perceptual input and the internal motor code (or program), the more accurate the prediction (Knoblich and Flach 2001).

It is thought that when we learn a motor skill we generate an internal representation, or model, of the action being performed (Miall 2003). When we view someone else's action we are able to activate this model in order to anticipate the outcomes of another's action. At an implicit, computational level, we are thought to acquire forward models which allow prediction of the sensory consequences of actions, based on the sending of motor commands. When we send a motor command, an efference copy of this motor command is fed into a forward predictor, which allows us to anticipate what the action we have initiated should feel and look like (Miall and Wolpert 1996). Whether anticipatory prediction advantages like those shown in this experiment might be guided by forward models, as has been suggested by others (e.g., Eskenazi et al. 2009), is unclear without evidence of activation of actual motor processes during anticipation. Behavioural evidence is somewhat mixed in support of such (implicit) predictive processes occurring in trained and untrained observers in the absence of action (e.g., Demougeot and Papaxanthis 2011; Lim et al. 2014; Maslovat et al. 2013; Ong et al. 2012).

Because the full-vision and no-vision of action groups did not differ in anticipation accuracy in this task, one suggestion, commensurate with common coding ideas, is that both groups generated visual codes during practice, even though one would be developed and refined

based on visual input (i.e., full-vision) and the other would be generated based only on kinesthetic feedback (no-vision). During the anticipation test, these visual codes would be matched to the video model to aid in determination of outcomes. However, the observation-only group did not improve on the anticipation test despite the fact they had access to the same visual information as the motor-visual training groups, rendering this explanation less likely.

In other studies where vision has been manipulated to study action recognition following motor training (i.e. Casile and Giese 2006; Reithler et al. 2007) no-vision and full-vision groups have also performed similarly. Kinaesthetic feedback during action execution has been shown to be sufficient (even in the absence of voluntary action planning, or visual feedback about the action or outcome) to build internal perceptual-motor contingencies that facilitate improved visual perception with respect to action recognition (e.g., Hecht et al. 2001). Therefore, it is also possible that enhanced anticipation accuracy in the post-test for the no-vision of action group in our study was due to an inter-modal association between kinaesthetic feedback and vision (what Hecht et al. 2001 refer to as visual-kinaesthetic matching) and not the generation of visual codes during practice or activation of the motor system during anticipation. We do not have definitive evidence in this experiment that active involvement of the motor system was necessary for improved prediction accuracy, and this would be difficult to show without a passively trained dart-throwing group. Hecht et al. (2001, Exp 2) showed that visual discrimination was improved through action learning with only passive kinaesthetic feedback (coupled to haptic and verbal feedback of outcomes) which might suggest that involvement of the motor system is not important. However, this was a continuous timing task that was rich in kinaesthetic feedback throughout the movement (the participants were in contact with a pendulum apparatus throughout the movement) and it might be, as suggested by the authors, that some sort of internal

timekeeper was acquired, rather than necessarily a cross-modal representation for action and perception. In our dart throwing study, such time matching strategies across practice and anticipation testing would not be possible. In darts, the action component of the task is separated from the outcome, and the required judgement in our task involved anticipation of future consequences. This anticipatory component would be more suggestive of a kind of action simulation, rather than simply a recognition (or matching) of an acquired movement profile. It is clear that further experiments are needed to determine the importance or otherwise of the motor system (and motor planning) for these action to perception effects. We are currently conducting research to determine whether a motor-based interference task inhibits anticipation accuracy for skilled darts players, in comparison to less skilled players, supportive of a low-level, simulative mechanism.

It is important to note that the lack of difference between no-vision of action and fullvision groups in anticipation accuracy does not necessarily mean that the processes used to aid prediction accuracy were the same in both of these groups. It may be that more subtle manipulations are needed to tap into potential advantages associated with vision during action, that might show up only after years of experience or when the testing and practice perspectives match (as suggested above for the observers, see also Urgesi et al. 2011). A possible avenue for future research would involve editing the video clips to show only dart flight (rather than a combination, as was the case here, see Urgesi et al., 2011). This would allow us to make more definite conclusions about the stimulus information underpinning the training advantages for the experimental groups in the post-training anticipation test.

One potential issue with our design was the inclusion of visual feedback of action outcomes during practice, such that vision was not completely removed from the training phase.

In the perceptual recognition studies described earlier, vision has been controlled throughout the movement (as with ours), but it has also not been presented as outcome feedback. In commoncoding terms, vision of the outcome, along with vision of the kinematics of the action, and trajectory of the object, are all visual components that can be "matched" between the observer and the performer to potentially aid in prediction (see Prinz, 1992, 1997). However, there are several reasons why we believe vision of the outcome in practice did not play a role in any kind of simulation or common-coding/matching process that may have been invoked during anticipation. First, the landing position of the dart was never shown in the anticipation test stimuli, and hence in this manner, visual experience with the stimuli was exactly controlled. Moreover, participants in the no-vision of action group had no visual feedback of the action during motor learning that could be compared to the model during the post-practice anticipation test. These participants saw nothing of the action during practice, yet they performed at a similar level of accuracy as the visual-motor group, even at the very early temporal occlusion points when only body kinematics of the action were shown. Although vision of outcome was available for the "no-vision" group in our study, this outcome feedback would have only allowed a calibration to take place between non-visual feedback during the movement and knowledge of outcome attainment. Improved visual-anticipation would have had to rely on; the kinaesthetic matching strategy discussed above, the generation of visual codes during practice or motor simulative mechanisms during the actual anticipation test.

In conclusion, we have provided evidence for improved visual-prediction following motor-only practice, when vision of the action was occluded during execution. Participants who practised throwing darts with no visual knowledge of their own action showed significant improvements in judging the outcomes of throws performed by another person. We suggest that

this improvement, which was not noted in an observation only group, but was seen in a motorvisual group, was likely a result of motor simulation during the perceptual task, which allowed the motor-action groups to predict the landing position of a dart through activation of their own motor system. Studies are currently underway in our lab to further test this hypothesis by interfering with the motor system during the perceptual decision task. Our general aim is to understand how perception-action codes are formed during practice, how they are deployed during anticipation, and the specific conditions that promote a more visual versus motoric type of matching process during action recognition and prediction.

2.5 Footnotes

1: We also converted the percent correct to the normally-distributed *d*' sensitivity measure for M-alternative forced choice tasks (Smith 1982; Stanislaw and Todorov 1999) based on the Luce (1959) choice model. A 4 Group (Full-vision, No-vision, Observers, Control) x 2 Test (pre, post) RM ANOVA was conducted on these data. These data mirrored the pattern of results observed with the unconverted % accuracy data, including the significant Group x Test interaction, F(1,36) = 19.31, p < 0.001, $\eta_p^2 = .62$. The No-vision group significantly improved their discrimination ability from d' = .59 (SD = .19) in the pre-test to d' = 1.02 (SD = .31) in the post-test. The Full-vision showed a similar pattern (Pre d' = .62 (SD = .26); Post d' = .91 (SD =.32)). The Control and Observer groups did not improve in their ability to discriminate between target sections; Control, pre d' = .66 (SD = .31); post d' = .64 (SD = .26); Observer, pre d' = .66(SD = .31); post d' = .67 (SD = .30).

2: Pearson correlations were conducted to compare i) motor proficiency scores on the final block of practice of day 2 to post-practice anticipation performance and ii) anticipation accuracy and motor performance for each target section. All of the correlations were low and

non-significant; (i), *r*(18) = -.12, *p* = .60, ii), Top, *r*(18) = -.28, *p* = .23, Middle, *r*(18) = .04, *p* = .86, Bottom, *r*(18) = -.02, *p* = .93.

3: Spearman correlations were conducted to evaluate the kinematic cues (from the model) that were best associated with an accurate dart throw. We evaluated 8 different kinematic markers (joint angles and positions), based on a centre hit on each of the 3 target sections. The kinematic measurements were taken from all video clips of the stimuli for each section of the dart board. Measurements were taken at OP2, as prediction improvements as a result of training were seen at this early occlusion point. The measurements consisted of: i) shoulder angle; ii) wrist angle; iii) elbow angle; iv) elbow vertical position (height); v) elbow horizontal position; vi) dart angle; vii) dart vertical position and viii) dart horizontal position, as measured from the top left corner of the display screen using Dartfish Software. Three kinematic cues were highly correlated with dart landing position; i) shoulder angle (r = .88, n = 18, p < .001), ii) elbow height (r = .84, n = 18, p < .001), and iii) vertical dart position (r = .68, n = 18, p < .001).

2.6 Bridging summary

In Experiment 1 we compared the perceptual prediction accuracy of a group that practiced throwing darts without vision of the action, to a motor-visual practice group, an observation-only group, and a no-practice group. Both motor practice groups significantly improved their prediction accuracy after practice. The observation-only group did not improve in prediction accuracy. These results suggested that motor practice was key to learning the skill, and that vision appeared not to be important. However, it remained unclear whether the motor system was activated, through simulative processes, during prediction, or that visual representations were formed during practice for both motor groups, and later accessed through a perceptual matching process during prediction. Thus, in Experiment 2 we wanted to further

explore the type of representations that were formed through experience, and later enabled during prediction. To this end, we used a secondary motor task, in an attempt to interfere with any motor simulation process that might be activated during prediction.

Chapter 3: An action-incongruent secondary task modulates prediction accuracy in skilled performers: evidence for motor simulation

3.1 Introduction

In many sports and games, one of the hallmarks of a skilled performer is his or her ability to predict action outcomes quickly, arguably homing in on the key components of the action that are most predictive of success. Much has been written about the perceptual-cognitive skills of athletes in sport, particularly those related to decision processes that enable prediction of an unfolding outcome (see Abernethy et al. 2012; Mann et al. 2007; Yarrow et al. 2009). Until recently, the perceptual skills exhibited by visual-motor experts in sports were presumed to be based on the acquisition of a large repertoire of visual experiences that allow for fast associations between certain cues, a memory of these stored experiences and appropriate responses (e.g., Abernethy et al. 2012; Williams and Davids 1998; Williams and Ward 2003, 2007). These ideas were based primarily on the study of cognitive tasks, such as chess (e.g., Ericsson and Kintsch 1995; Gobet 1998; Gobet and Jackson 2002), rather than motor tasks. Although for sports skills, the 'motor' component of visual-motor expertise was considered important in the development of these relevant perceptual events (e.g., Williams and Davids 1995), the emphasis was still on the acquisition of visual experiences and visual recognition processes leading to the retrieval of the appropriate action response through stored, if-then type associations (e.g., Anderson 1982; Starkes 1987). In several recent studies, this visual emphasis has shifted to one on motor experiences and the suggestion that prediction accuracy is related to a motor simulation of an observed action (e.g., Aglioti et al. 2008; Ikegami and Ganesh, 2014; Tomeo et al. 2012; Urgesi et al. 2012).

During action observation, it is thought that the observer's motor system is covertly activated, such that it 'resonates' with the observed stimuli, through simulation mechanisms that generate a visual understanding of the observed action (e.g., Blakemore and Decety 2001; Gallese and Goldman 1998; Hommel et al. 2001; Jeannerod 2001; Knoblich and Flach 2001; Schubotz 2007; Wilson and Knoblich 2005). Accordingly, perceptual codes linked to the motor command that generated the same action are activated in the observer (Blakemore and Frith 2005; Hommel et al. 2001; Wolpert et al. 2003), arguably in real time (Springer et al. 2013a, b). Perception and action are thought to exist in a common representational domain and exert bidirectional effects on each other (Prinz 1997; Prinz and Hommel 2002). Support for the idea that action and perception are subserved by common pathways comes from behavioural research showing both facilitation and interference effects during the concurrent execution and observation of congruent or incongruent movements (Brass et al. 2001; Craighero et al. 2002; Hamilton et al. 2004; Kilner et al. 2003; Miall et al. 2006; Wohlschlager 2000; for reviews see: Blakemore and Frith 2005; Schutz-Bosbach and Prinz 2007). Moreover, these effects are dependent on the observer's motor experience with the observed action (Capa et al. 2011).

There is considerable neurophysiological evidence to support the idea that action observation involves a type of motor simulation in the observer, primarily based on activation of parietal (Fogassi et al. 2005; Iacoboni et al. 1999), frontal (Pobric and Hamilton 2006), and temporal (Mukamel et al. 2010; Saygin 2007) regions of the brain during both action execution and action observation, also known as the Mirror-Neuron System or Action-Observation Network (e.g., Caspers et al. 2010; Decety et al. 1994; Gazzola and Keysers 2009; Grafton 2009; Grossman and Blake 2001; Iacoboni et al. 2005; Rizzolatti and Craighero 2004; Rizzolatti et al. 2001). Importantly, this activation is specific to the action experiences of the observer, rather

than their visual experiences (Calvo-Merino et al. 2005, 2006; Cross et al. 2006; Reithler et al. 2007).

Research examining the effects of visual-motor experience on the perception of action has shown that visual-motor 'experts' are better than novices at recognising actions that they have had more experience performing (Hohmann et al. 2011; Wilson and Knoblich 2005). Because observers are better able to recognise their own actions in comparison to the actions of others, this has been taken as further evidence that it is motor experience per se, and not visual experience, that plays the primary role in action recognition and understanding, as one would have little visual experience of their own action (Knoblich and Flach 2001; Loula et al. 2005; Repp and Knoblich 2004). Indeed, participants have improved their visual recognition performance after training on a motor task in the absence of vision (Casile and Giese 2006; Hecht et al. 2001; Reithler et al. 2007).

In several recent studies, suggestions have been made that action-simulation is not only implicated in action *recognition*, but is also the mechanism underlying the *prediction* of action outcomes (Aglioti et al. 2008; Knoblich and Flach 2001; Urgesi et al. 2012). These conclusions have been based on four lines of evidence. First, that the expert perceptual advantage in making these predictive decisions is limited to those who have acquired significant motor experiences, such as sport's performers, and not just visual experiences (e.g., fans; Aglioti et al. 2008, Urgesi et al. 2012; Williams and Davids 1995). Second, during action prediction, externally-evoked activation of the motor cortex was shown to lead to an increase in the amplitude of muscles involved in the observed action relative to baseline (Aglioti et al. 2008; Tomeo et al. 2012). Third, areas of the brain known to be part of the Action Observation Network also differentiated across novice and experts (in tennis) during prediction of action outcomes (Balser et al. 2014).

Fourth, action predictions also improved following training without vision on a dart-throwing task (Mulligan and Hodges 2014).

In summary, evidence from several research streams supports the idea that motor experience plays a role in action recognition and prediction of action outcomes. However, direct evidence that activation of the motor system is involved in action prediction is still lacking. As noted above, researchers have shown muscle-specific changes following electrical stimulation of areas of the motor cortex associated with the observed action during prediction of basketball free-throw shots (Aglioti et al. 2008) and shot direction in soccer penalty kicks (Tomeo et al. 2012), but it is still unclear if this increased activity impacts the decision process. This is further clouded by the fact that in the study by Aglioti et al. (2008) both "motor" experts and "visual" experts (coaches and writers) showed modulation of the muscles implicated in the action of shooting a basketball (i.e., wrist and hand muscles), making it difficult to attribute the superior predictive performance of the motor experts to effector-specific, motor system activation. Tomeo et al. (2012) showed a negative relationship between response accuracy and motor facilitation among kickers in a soccer penalty prediction task, but this was only for artificial, biomechanically "impossible" actions, where the body kinematics and ball were incongruent. There was no positive relationship between amplitude of MEPs (motor evoked potentials) and response accuracy for decisions made when watching congruent (normal penalty kick) actions. Similarly, using repetitive TMS (Transcranial Magnetic Stimulation) to the PMd (dorsal Premotor Cortex), some of the same group of researchers showed a decrease in prediction accuracy about the outcome of these impossible actions, but again, motor interference did not affect prediction accuracy for the congruent 'real' actions (Makris and Urgesi 2014). In addition to some potential issues with inferring predictive responses from artificially constructed

"fooling" actions (see Mann et al. 2013), it is also possible that with this type of dyad task (where a mirrored responder acting as a goal-keeper has to decide kick direction from an approaching soccer player), that any general technique which serves to disrupt or activate a specific cortical area would also interfere with the anticipated response (i.e., to move left or right) in addition to any potential simulative processes involved in watching the kickers.

Another relatively simple technique, which might help determine if motor simulation is responsible for prediction accuracy, would involve using a secondary motor task to selectively interfere with motor components of the action during prediction. The advantage of such a technique is that it is possible to determine direct costs in accuracy associated with the secondary motor task. Similar motor interference paradigms have been used in studies probing motorsystem influences on stimulus detection (e.g., Paulus et al. 2009; Witt and Proffitt 2008; Witt et al. 2010). In these studies it has generally been shown that performing a secondary motor task (e.g., ball squeezing) while viewing a stimulus, results in the modulation of perceptual estimations concerning the stimulus (Witt and Proffitt 2008).

In the current study, we adopted a dart-prediction task as our primary task, where no physical (reactive) response was required in the observer (just a judgement as to where the dart would land). Participants were required to engage in two different types of motor secondary tasks during action observation, that were either congruent to the action, what we refer to as action mimicking, or incongruent to the action, pressing against a force gauge. The latter task was designed to prevent or at least interfere with the participants' ability to simulate the observed action, as the effector involved in the action would be tasked with pushing (causing immobilization of the right arm), whereas the primary dart throwing task required extension and flexion of the elbow and wrist.

Non-experienced and experienced darts players were required to judge the final location of a thrown dart from video clips that were occluded at different time points early in the throwing motion. Participants completed the prediction task (the primary task), by itself, and while performing each of three secondary-task conditions: a force-production task, a tonemonitoring task, and a mimicry task. We expected the Experienced group to make more accurate decisions than the Non-Experienced group. Consistent with the simulation hypothesis, we predicted that the force-production task, which required an action incongruent to the one being watched, would interfere with prediction accuracy of experienced performers (directly impacting the quality of predictions). Non-experienced participants, who would have no motor experience with the task, and hence be theoretically unable to simulate the observed action, were hypothesised to show no, or minimal, interference from the force-production secondary task (Capa et al. 2011). The mimicry secondary task was not expected to produce interference for either group due to the compatible nature of the action (Christensen et al. 2011; Schutz-Bosbach and Prinz 2007; Springer et al. 2011). A lack of interference from the mimicry task would also allow for conclusions about motor-system-specific effects associated with action simulation, rather than suggesting general motor system interference. Although there has been evidence that incongruent tasks lead to more interference in the primary task than congruent tasks, it is possible that the mimicry task could interfere. For congruent actions, the action plans for both the prediction task and the secondary task are the same. Because the action and observation of the action are thought to be served by a similar common code (Hommel et al. 2001), the mimicry task could potentially render the action-code associated with the same action unavailable for perception (e.g, Hamilton et al. 2004; Wuhr and Musseler 2001). However, based on a recent review of the perception-action literature and potential for interference effects of action on

perception, Zwickel and Prinz (2012) suggest that for concurrently produced actions, where the actions are functionally related (e.g., concurrent mimicry), congruent actions are unlikely to interfere with perception. In this case, perception-action links are thought to be strengthened because the movement features become linked to the perceptual representation of the stimulus.

Evidence suggests that action recognition and prediction accuracy improve when watching oneself versus someone else perform. This is said to come about because the action being simulated in the observer is the same as that being observed (Bischoff et al. 2012; Knoblich and Flach 2001; Loula et al. 2005; Repp and Knoblich 2004). With this in mind, we used both 'self' and 'other' stimuli in the prediction tasks. We expected participants, particularly the experienced players, to show better prediction accuracy when viewing their own throws, and a corresponding increase in interference in the force-production condition due to greater motor system activation in this condition. Based on a control experiment (see below) involving visualspatial decisions (i.e., matching a rotated pattern), we were able to show that the forceproduction and tone-monitoring tasks were approximately matched with respect to attentional demands and general difficulty, suggesting that any interference from the force-production task would be due to the motor-specific nature of the task.

We also asked participants to report confidence in their predictions as a secondary measure of anticipation accuracy (see Jackson et al. 2009; Jackson et al. 2006; Mulligan and Hodges 2014). We expected that confidence would mirror the pattern of results based on prediction accuracy, with experienced participants being more confident, particularly for "Self" versus "Other" video clips. If experienced participants show awareness of the potential interfering effects of the secondary tasks, particularly the force-production task, then confidence should decrease under these conditions relative to the control.

3.2 Methods

3.2.1 Participants

Twenty-four volunteer participants, between the ages of 19 and 60 years, with normal or corrected vision, took part in the study. All participants were self-report right-handed. Half of the participants self-reported that they had never had any experience throwing darts. These were termed the Non-Experienced group (n = 12 males) who consisted of University students. The other half reported significant experience at dart playing (4-26 years experience; M = 11.6 yr, SD = 6.9) and hence these were termed the Experienced group (n=12; n=4 females). Participants in the Experienced group were recruited from adverts placed around the University, local darts' leagues and via snowball sampling. A three-dart pre-test performed on the first day (aiming for the centre of the dart board and based on mean radial error), provided an approximate measure of skill. Due to an error in video recording, it was only possible to calculate radial error for n = 10 in the Experienced group (n = 12 in the non-Experienced). The Experienced group was significantly more accurate (M = 7.09 cm, SD = 3.43; 95% CI = 4.96 – 9.21 cm) than the Non-Experienced group (M = 13.15 cm, SD = 4.50; 95% CI = 10.61 – 15.70 cm), t(20) = 3.50, p < .01, d = 1.53.

All participants gave signed consent before testing and were blind to the hypotheses of the experiment. Ethics' protocols for human experiments were strictly followed, as laid out by the ethics' board of the University. Participants were paid \$10 /hour.

3.2.2 Apparatus and stimuli

The task was modeled on an earlier dart throwing study designed to look at self-other perceptions (Knoblich and Flach 2001; see also Mulligan and Hodges 2014). Participants in the earlier experiment by Knoblich and Flach (2001) were proficient at recognising their own action from a side-on view, even though they had only received visual-motor experience from a first-
person perspective. A standard dart board was used and height and distance regulations typically observed in the game of darts were adopted (i.e., the participant stood at a distance of 2.37 m from the dartboard, which was placed at a height of 1.73 m from the floor to the bulls-eye). The board was divided into 3 sections (top, middle and bottom), that were formed by two horizontal lines an equal distance from the top and bottom of the dart board and from each other. Participants were required to make predictive judgements concerning which of the 3 sections they thought the dart would land. Because the model was shown from the side view on the video stimuli, any estimate of the horizontal trajectory of the dart would not be practical from such an angle, and was therefore not included as part of the prediction task. Further, all stimuli used were harvested from throws by the model that landed at the vertical and horizontal centre of each section (see below).

Video clips for the prediction test were created using a Cannon HV20 camera (30 fps, 33ms/frame) showing a moderately skilled actor, after significant practice with the task, throwing a dart at the centre of each of three sections of a dartboard (see Figure 3.1). The actor was filmed from a side-on perspective from a distance of 3 metres. Three video clips were created for each of the top, middle, and bottom sections, for a total of 9 clips. The actor threw to each section until 9 clips landed in what was subjectively determined to be the centre of each section (both vertically and horizontally). This requirement to aim for the centre of the section reduced any potential kinematic variability associated with differences in horizontal and vertical error within a section. Each of these clips was further edited into 4 temporal lengths termed occlusion points (OP), each length being one frame (33 ms) longer than the previous. Four OPs, for 3 clips at 3 different targets resulted in 36 total stimuli. Each clip showed the initial part of the dart throw (i.e., raising the throwing arm) which lasted approximately 2 s (M = 1930 ms, SD

= 20). The first OP showed this initial 'setup' phase, plus one more frame (+33 ms, the start of the forward propulsion phase). Each subsequent OP consisted of an additional frame. The dart left the hand at OP4. In Experiment 1, we had included 8 OPs. However, because improvements in accuracy were mostly noted for these early OP points and due to the additional conditions required to run secondary tasks, we limited the number of OP points to the first 4 in the current Experiment. The last frame of the video remained on the screen for 2 s before a decision was required. Video editing was performed using Sony Vegas and Adobe Premiere video editing software. Clips were shown via a projector on a full length screen (Cineplex Pro, IN, U.S.A), providing an approximate life-size image (~180 cm), as seen by participants from a distance of 4 metres. E-prime 2.0 software was used to present the stimuli and for entering responses (Psychology Software Tools, Inc., PA, USA).



Figure 3.1 Trial presentation: All video sequences included an initial dart preparation /set-up phase which lasted ~ 2 s. Depending on the condition the participant would then see an additional 1-4 frames (33 ms - 132 ms), corresponding to the 4 temporal occlusion points. The final frame would remain on the screen for 2 s after which point 2 prompt screens would be presented, requesting a predictive decision from the participant (top, middle or bottom) as well as a rating of confidence.

Other than for the control condition, participants performed a secondary task while viewing the dart clips. For the secondary motor task, a force sensor load cell (JR3 Inc, Woodland, CA) was attached to a tall iron post and adjusted to the participant's hand position when they stood adjacent to the post with their hands at their sides. This position enabled the participant to push against the force sensor with the edge of their hand in a fist shape, keeping the rest of their arm and body relatively immobile. The force sensor was connected to a laptop, running Labview software, which allowed real-time monitoring and data collection. Audio files used for the tone monitoring secondary task were created using Audacity Inc. software, v2.0.2 (Boston, MA). These were 5 s files that consisted of a 250 Hz control tone with a randomly interspersed high tone of 440 Hz, played for 100 ms on a third of the trials. We used three different temporal orders, allowing the duration of the control tone to vary from 3 s – 4.8 s before interspersing the 440 Hz tone.

3.2.3 Conditions and procedures

The study took place over two days (~ one week apart). On the first day, following the 3dart motor pre-test, participants made predictive decisions about the action-outcomes of the model ("Other"), whereas on the second day decisions were made about their own edited actions ("Self"). The reason for this ordering was primarily a logistical issue associated with the need to first film participants (and edit videos) in order to make the "Self" stimuli. To avoid an unnecessary third session, we filmed after testing on the first day, immediately after completing the "Other" tests. Because no feedback was provided to participants during the prediction tasks, we did not expect improvements associated with repeated testing. This was confirmed when we compared the prediction accuracy data from the first and second half of testing within each session in two repeated-measures ANOVAs, for both 'Self' and 'Other' stimuli. There were no

significant differences in performance between the first and second block of trials for either 'Self', F(1,22) = 1.16, p = .29, $\eta_p^2 = .05$ or 'Other' stimuli, F<1, nor any Group x Block interactions for either 'Self', F<1, or 'Other' stimuli, F(1, 22) = 1.97, p = .18, $\eta_p^2 = .08$.

The prediction test was completed under 4 conditions: no secondary task, forceproduction task, tone-monitoring task, and mimicry task. The mimicry condition was always completed last in order to avoid potential carry over effects associated with instructions to explicitly copy. Any possible issues associated with running the mimic condition last should be allayed by the results above, showing no practice order effects within the other 3 conditions. All other conditions were counterbalanced for order. For each test condition, 36 video clips were presented in a random order. Via a screen prompt after the video, participants were asked where they thought the dart would have landed (top, middle, bottom) and their confidence in their answer, ranging from 0 - 100 % confident based on a 5 point scale in 25 % increments. Participants stood facing the screen for all conditions, but a 3-5 min seated rest was given between conditions. Participants were presented with 4 practice trials (without prediction accuracy feedback) at the beginning of each condition.

3.2.3.1 Force-production task

Participants were required to stand with their arms by their side adjacent and to the left of the iron post, facing the projection screen at ~45-60° angle. They could therefore see the action unfold in approximately the same plane as the actor, without having to turn their head (see Figure 3.2). They were then told to make a fist and to press against the force gauge with the elbow extended and their shoulder and wrist in a neutral position. This procedure was designed to be incompatible with the motion involved in throwing a dart, requiring activation of the same muscle groups involved in the throw, but in a different pattern (i.e., isometric versus dynamic

contractions) and for a different function (e.g., the arm muscles are stabilizing and the elevator muscles of the shoulder are providing motive force whereas in the dart throw, shoulder muscles are stabilizing and the triceps are providing motive force).



Figure 3.2 A view of the task setup for the force-production task. Participants were required to press on the force gauge with their right hand in a fist position while viewing the video stimuli in approximately the same plane as the observed action. Although not shown in the picture, participants could also see the dartboard on the wall to the far right of this picture.

Participants first completed a maximal force test to calculate a 15 % maximum force for the force-production task. Fifteen percent was considered a low force threshold (based on pilot testing in the control experiment, see below), that was relatively easy to maintain for the duration of a trial and throughout the testing condition. Participants pressed as hard as possible against the force sensor with their dominant right hand for 4 s, three times. From the average of these readings, 15 % average force was calculated. Participants next practised producing 15 % of their maximum force. The experimenter was able to monitor force output relative to the criterion in

real time in all trials. During the practice trials only, participants were given feedback when pressing against the load cell during the trial. This was provided intermittently such that they were told when they had reached the criterion and when they varied from the force by more than ~1 Newton. During testing, a screen appeared before each trial prompting the experimenter to press a key to continue testing. The participant also saw this screen and they were instructed to begin pressing against the load cell when this prompt screen appeared (~1s before the video began). They were instructed to maintain the force until the video clip had finished and the video-prompted questions appeared. This was to make sure that they maintained force through the entire clip, but stopped pressing before they had to respond with their answer. During experimental trials, force was monitored by the experimenter and if the participant veered from the required force on a trial, feedback was provided at the end of the trial.

3.2.3.2 Tone monitoring task

A control tone was presented on every trial, and the participant's task was to determine whether there had been a change in the tone. On 66 % of the trials, participants heard a continuous 250 Hz control tone for 5s duration, from the point when the experimenter initiated the trial, until the question asking the participant about dart location appeared on the screen. On the remaining trials, which were administered randomly throughout the condition, a 440 Hz tone was interspersed with the control tone for 100 ms. The tone started to play when the video clip started and stopped when the questions appeared on the screen. An additional question appeared, after the confidence question, asking participants if the tone had changed frequency during the trial.

3.2.3.3 Mimicry task

Participants were asked to hold a dart as if they were going to throw it. They were instructed to use the dart to 'mimic' the dart throw on the screen in a way that would help them "understand what was happening on the screen". They were advised that, during each trial, they could also view the real dartboard on the wall and could imagine themselves throwing the dart. Participants were not required to try to precisely match the temporal or kinematic aspects of the model's action.

At the end of the first day all participants were videotaped throwing darts so that video clips of their own action could serve as stimuli for the "Self" prediction tests on Day 2. Participants aimed for the centre of each section until three successful throws were obtained for each section (top/middle/bottom). The videos of these throws were subsequently edited, creating twelve clips for each section of the board, corresponding to the 4 occlusion points for each throw (36 clips in total). Participants returned approximately one week later and performed the prediction tasks in the same order, this time viewing stimuli of their own action.

3.2.3.4 Control experiment using visuospatial rotations

To ensure that the attentional demands of the force-production and tone-monitoring tasks were low and approximately matched, we first compared 12 different participants (9 male), all right-handed, on a visuospatial rotation task. This task was chosen because it required participants to make visual-spatial decisions and to make a decision based on a 3 choice protocol (thereby matching aspects of the main dart-throwing task). Participants viewed a single unrotated pattern on a screen (made up of intersecting horizontal and vertical bars of different widths), with 3 rotated patterns shown directly below (see Cooper and Podgorny 1976; Shepard and Cooper 1982 for similar tasks). Only one of these patterns was the same as the single, un-

rotated pattern. Participants were instructed to match the single pattern with the correctly matched rotated pattern. These decisions were made under either single-task, tone-monitoring or force-production conditions (as detailed above). There were 108 trials in total. With respect to accuracy, there were no significant differences across conditions (Force = 67.59%, *SD* = 14.62; Tone = 65.97%, *SD* = 10.47; Control = 62.96%, *SD* = 15.04, F<1), confirming the low attentional requirements of these tasks and a lack of difference between the Force and Tone monitoring conditions.

3.2.4 Data analysis

3.2.4.1 Prediction accuracy and confidence

We calculated percentage accuracy scores for each of the four occlusion points (OP) and these were subjected to a 2 Group (Non-Experienced, Experienced) x 4 Condition (Control, Tone, Force, Mimic) x 2 Model (Other, Self) x 4 OP repeated measures (RM) ANOVA. Condition, Model and OP were RM factors. The same analysis was conducted on the % confidence scores. Partial eta squared (η_p^2) values are reported as measures of effect size, and Tukey's HSD post hoc tests were used to compare differences involving more than 2 means (p<.05). Where violations to sphericity were encountered, Greenhouse-Geisser corrections were applied.

3.2.4.2 Secondary task accuracy

Median force, for both the "Other" and "Self" conditions, was calculated as a measure of secondary task accuracy. Median values were chosen due to the fact that data were continually tracked during this condition, which would involve ramping up and ramping down between trials. The median values were compared to the required values (based on 15 % of maximum force). We also ran correlations on the % force output and prediction accuracy for the "Other"

and "Self" conditions for the Non-Experienced and Experienced participants to determine any potential trade-offs. For the tone-monitoring secondary task we summed any trials that were identified incorrectly (either tone miss or misidentification of a tone change). This was repeated for "Other" and "Self" conditions and any errors were reported as a percentage of the total number of trials. Correlations were also run on these data and prediction accuracy.

3.3 Results

3.3.1 Action prediction accuracy

Percentage accuracy data are shown in Figure 3.3a (Other) and b (Self) as a function of condition and skill group (Also see Figure 3.4). As predicted, Experienced participants were more accurate than the Non-Experienced participants, F(1,22) = 14.87, p = .001, $\eta_p^2 = .40$. There was a difference across conditions, F(3,66) = 5.71, p = .002, $\eta_p^2 = .21$, due to a significant decrease in accuracy for the force-production task compared to the other conditions. The condition effect was due primarily to the Experienced performers, as supported by a Group x Condition interaction, F(3,66) = 7.03, p < .001, $\eta_p^2 = .24$. Post hoc comparisons confirmed that only the Experienced group performed worse in the force-production task in comparison to the other three conditions. The Experienced group also performed significantly more accurately than the Non-Experienced group under all conditions except the force-production task, where their accuracy did not differ from the Non-Experienced group.



B



Figure 3.3 Percentage accuracy for Other-judgments (A) and Self-judgments (B) as a function of group and condition. Error-bars show between-subject SDs



B



Figure 3.4 Percentage accuracy for Other-judgments (A) and Self-judgments (B) as a function of condition and group. Error-bars show between-subject SDs

Although participants were less accurate when viewing stimuli of the "Other" model versus "Self", F(1,22) = 5.06, p = .035, $\eta_p^2 = .19$, there were no significant interactions involving Group and Model-type (F values between .03 and 1.45). Prediction accuracy for the 4 test conditions did, however, depend on Model-type, F(3,66) = 4.00, p = .011, $\eta_p^2 = .15$. For "Self" stimuli, accuracy during the force task was significantly impaired relative to the other three conditions, which did not differ from each other. No differences were seen for the "Other" condition. Participants were more accurate when viewing themselves, compared to the model, under all conditions except the force-production task.

To determine when differences emerged while watching the action, we also looked at the effects of Occlusion Point (OP). There were differences in accuracy as a function of OP, F(3,66) = 14.76, p < .001, $\eta_p^2 = .40$, as well as a Group x OP interaction, F(3,66) = 3.16, p = .030, $\eta_p^2 = .13$. As would be expected, accuracy significantly increased from OP1 (M = 48.67%, SD = 7.96) to OP2 (M = 53.41%, SD = 7.65) and also from OP2 to OP3 (M = 57.29%, SD = 7.42). The interaction was mostly due to the lack of any change in accuracy for the Non-Experienced group from OP2-4 (OP2 = 51.39\%, OP3 = 51.85\%, OP4 = 54.28\%) in comparison to OP1 (41.90\%), whereas the Experienced group showed improvements for OPs 3 (62.73\%) and 4 (62.38\%) in comparison to OPs1 (55.44\%) and 2 (55.54\%).

3.3.2 Confidence

Confidence data are shown in Figures 3.5a (Other) and b (Self) as a function of occlusion point. Despite a trend for higher confidence ratings from the Experienced (M = 68.35%, SD = 11.33) versus Non-Experienced (M = 61.55%, SD = 11.33) groups, this difference was not statistically significant, F(1,22) = 1.91, p = .18, $\eta_p^2 = .08$. Similarly, although there was a trend for "Self" ratings to be higher than "Other" ratings, these too were not statistically different,

 $F(1,22) = 3.31, p = .083, \eta_p^2 = .13.$ Confidence differed as a function of condition, $F(3,66) = 10.29, p < .001, \eta_p^2 = .32$, with confidence significantly higher under the Mimicry condition (M = 68.04%; SD = 8.19) compared to the other three conditions (control, M = 63.43%, SD = 8.35; tone, M = 64.66%, SD = 8.21; force, M = 63.67%, SD = 8.16), which were not different from each other. However, there were no Group or Model-type interactions with Condition. Confidence generally increased across OPs as more information became available, $F(1.3,28.5) = 74.93, p < .001, \eta_p^2 = .77$, such that confidence significantly increased at each occlusion point (ps < .001, see Figure 3.5). There was also a Group x OP interaction, $F(3,66) = 3.12, p = .032, \eta_p^2 = .12$. The Experienced and Non-Experienced participants were significantly different from each other at all OPs, except OP4, where confidence was above 70% for both groups.



B

A



Figure 3.5 Percentage confidence for Other-judgments (A) and Self-judgments (B) as a function of group and occlusion point. Error-bars show between-subject SDs

3.3.3 Secondary task accuracy

With respect to the force (motor) task, participants were required to maintain 15 % of their max force during the trial. The Non-Experienced participants achieved a mean of 14.34 % (SD = 2.64) and 16.13% (SD = 3.46) for the "Other" and "Self" conditions respectively. Experienced participants achieved a mean of 17.04 % (SD = 2.46) for the "Other" condition and 14.69 % (SD = 1.68) for the "Self" condition. Comparing statistically across the force data for the 2 groups and 2 (Other and Self) model-type conditions, there were no main effects of group or model-type (Fs<1). However, there was a significant interaction, F(1,22) = 10.19, p < .01, $\eta_p^2 =$.32. The Experienced participants exerted more force (than required) in the "Other" condition compared to the "Self" (wherein the latter they were more accurate). The Non-Experienced group showed the reverse (i.e., more force was exerted in the "Self" condition versus the "Other"). We also ran correlations between prediction accuracy and % force values for the "Self" and "Other" conditions, given the difficulty in interpreting the % force values. Importantly, these yielded low and non-statistically significant correlations, speaking against any force-for-accuracy trade-offs (Experienced: Other, r = .0003; Self, r = -.16; Non-Experienced: Other, r = .17, Self, r = .15).

For the tone monitoring task errors overall were low (<3% of trials). The Non-Experienced group made more errors (M = 3.94 %, SD = 4.66) than the Experienced group (M = 2.78 %, SD = 3.35) on the "Other" condition. For the "Self" condition there were fewer errors generally (Non-Experienced, M = 2.78%, SD = 3.35; Experienced, M = 2.55%, SD = 4.18). An ANOVA conducted on the error data did not yield any statistically significant group-related effects (all Fs<1). As with the force data, correlations were performed between prediction accuracy and % of tone monitoring errors for the "Self" and "Other" conditions. These were

generally low and non-statistically significant particularly for the Experienced group (Other, r = -.09; Self, r = -.10) compared to the Non-Experienced group (Other, r = -.43, Self, r = -.37).

3.4 Discussion

We tested whether the predictive decisions of skilled performers would be directly impaired by a secondary motor task that would prevent or interfere with any potential involvement of the motor system in the prediction process. This manipulation was designed to test the proposal that a simulation-type mechanism is responsible for the prediction of action outcomes in humans, which involves a low-level activation of the motor system in the observer (Blakemore and Decety 2001; Gallese and Goldman 1998; Jeannerod 2001; Schubotz 2007; Wilson and Knoblich 2005). We also tested the specificity of this effect, through manipulation of the action required of the primary effector. Either a congruent (mimicry) or incongruent action (isometric force production) was required whilst watching dart throwing actions performed with the same arm. In support of this action-specific simulation account, while viewing action sequences performed by themselves and another person, skilled darts players were susceptible to motor interference from a force task that used the same effector in an incompatible configuration. This interference effect took the form of a significant reduction in accuracy predicting the landing position of a thrown dart. This effect was not seen in a Non-Experienced group. Indeed, the Experienced group showed superior prediction accuracy under all conditions except the force-production task, where their performance was reduced to the level of the Non-Experienced group.

These results provide evidence for active engagement of the human motor system during the prediction of action outcomes among experienced performers and support the idea that action and perception share a common representational medium (Hommel et al. 2001; Prinz 1997). It

appears that motor experience plays a direct role in modulating the prediction of action outcomes, through mechanisms that work in real time to simulate the observed action to aid in prediction of its sensory consequences (Springer et al. 2013a, b).

The mimicry secondary task, which required a congruent action (actively copying the observed dart throw), did not interfere with, nor aid the decisions of the skilled or novice participants, although it was performed with the highest degree of confidence. Previous studies involving the concurrent performance and observation of action have likewise shown no interference effects as a result of performing actions congruent to observed stimuli (e.g., Bouquet et al. 2007; Kilner et al. 2003). The high confidence scores suggest that participants perceived this congruent action as helpful to their decision process, although this did not translate into improved prediction accuracy. Because this condition was always performed last, we questioned if the increased confidence might be a practice effect. However, correct feedback was never provided to participants during testing (and hence there would be no error signal on which to base a change in confidence), such that we have no reason to think that the high(er) confidence levels in the mimicry task were a result of practice. Moreover, when we compared statistically across the other three conditions, there was no evidence of an order effect with respect to confidence ratings (F < 1).

According to common-coding principles, individuals may utilize the same motor representations used in performing an action for predicting the outcome of the same action observed in someone else (Hommel et al. 2001; Prinz 1997). This is thought to take place internally via motor simulation processes. However, the requirement to *internally* simulate an observed action may not be necessary while executing a congruent action (i.e. our mimic condition). As such, performing a concurrent action could provide the same real-time

representations needed to predict the outcome of the observed action, eliminating the need for an additional internal simulation process (Springer et al. 2011). This may explain the lack of interference for the Experienced participants when they performed the mimic condition. Conversely, for the incongruent condition (i.e. the force condition), because the motor representations used for initiating the (incongruent) action are different from those of the action being observed, these incongruent motor representations are not used (or available) to predict the outcome of the observed action. Instead, internal simulation processes are invoked in this case, but these motor representations are then partially interfered with by the motor representations from the (incongruent) executed (force) action (Springer et al. 2011; Springer et al. 2013).

Several lines of evidence converge in this study to support the suggestion that the predictions of the skilled participants were based on a motor simulation of the dart-throwing action, and that interference from the force production task was due to action-specific motor engagement and not alternative mechanisms (such as increased attention or visual-spatial processing). Participants generally made more accurate predictions when viewing "Self" stimuli versus "Other" stimuli and the interference effects observed for the force production task were more pronounced for the "Self" condition. These results are congruent with the hypothesis that self-stimuli are more likely to promote action simulation than observation of a stranger's actions (Knoblich and Prinz 2001), which has shown to be true even when participants are unaware that they are watching themselves (Bischoff et al. 2012). There is also evidence that predictions made on the basis of "Self" actions (e.g. Bischoff et al. 2012), lead to increased brain activation in regions of the medial Frontal Cortex, associated with implicit self-processing, as well as areas of the Inferior Parietal Lobe, thought to involve internal models and the processing of self-other kinematics (Lorey et al. 2009; Pilgramm et al. 2009; Ruby and Decety, 2003). The fact that

explicit awareness of one's own actions was not needed for simulation to occur in these prior studies, and we did see evidence of simulation with awareness, suggests that awareness is not likely to be a moderator of this process.

Both the force task and the tone task required low-level monitoring of a secondary stimulus during action observation and hence were approximately matched for attentional demands. This was confirmed by: i) a lack of difference in prediction accuracy between these tasks for the Non-Experienced group, even though this group's performance was above chance, and hence there was room for deterioration, ii) a lack of effect associated with these secondary tasks in the control experiment involving a 3 choice decision on a visual-spatial rotation task (akin to the decisions required in the dart prediction task), iii) no detriments in prediction accuracy associated with the secondary tone monitoring task in the main experiment, showing that attention demands for the Experienced participants in the experimental task were not higher than for Non-Experienced and, iv) the mimic task did not interfere with prediction accuracy, even though it was similar in execution (right handed forward motion) to the force-production task. This latter effect associated with the mimic task, further points to an action-specific role of this interference effect, and by extension, of the simulation process.

In the sport expertise literature, considerable emphasis has been placed on the importance of acquiring a repertoire of visual experiences to account for the expert advantage in making fast and accurate predictive decisions. Although the motor system was thought to moderate the effects of visually stored memories (i.e., altering how they were encoded and retrieved), until quite recently, this system was not thought to impact directly on the decision process. With the demonstration that muscles of the arm involved in basketball shooting were moderated when action decisions were required about the fate of a basketball free-throw shot (Aglioti et al. 2008),

researchers began considering a more direct role for the motor system in predicting action outcomes. Neuro-physiological changes in motor system activity during action prediction have been demonstrated, but it has not been clear if this activity was directly involved in generating predictions or was a consequence of action observation (Aglioti et al. 2008) or action response (Tomeo et al. 2012). Here we show that the requirements to perform an action-incongruent motor task to that being observed, impairs action prediction, and that this interference is only seen among individuals with acquired motor experience.

In summary, these results lead us to conclude that predicting action outcomes from a video display of another person leads to a motor-based simulation of the observed action in the observer. Although we are unable to say whether motor system activation is essential to accurate prediction across contexts, we have strong evidence that interference with the effector and muscles involved in a discrete and rather simple motor action (involving only one effector) significantly impairs prediction accuracy amongst performers with considerable experience in the observed action. Testing the role of the motor system in more complex actions using this type of methodology is potentially more challenging, due to the difficulty in isolating effector-specific roles. For example, a tennis serve involves movement of the whole body, and there is evidence that predictive decisions are based on various features of the action as it unfolds, such as the hips, shoulders and finally arm and racket position (e.g., Cañal-Bruland et al. 2011; Ward et al. 2002). However, it may be possible to use such an economical and simple paradigm as this secondary task methodology to test how predictive decisions are made when occlusion points are tied to key information sources (such as the hip area ~240-180 ms before ball-racket contact).

In sports that require a response to anticipatory decisions, especially when this response might be opposite to the seen action, it is less clear how (or if) such an incongruent action would

interfere with decisions. Perhaps a mechanism exists to inhibit such interference in these types of interactive scenarios. Alternatively, rather than invoking only a motor simulation of the observed action, decisions may, under certain circumstances, come about via a more visual-based process. In line with this notion, it has been suggested that both visual- and motor-based processes are utilized by experts when anticipating the outcomes of observed actions (Tomeo et al. 2012; Urgesi et al. 2012). Accordingly, perceptual experience is said to build internal models that define the motion of objects in the environment, creating visually-based predictive representations of the observed action (Hubbard 2005; Motes et al. 2008; Zago and Lacquaniti 2005). In contrast, motor experience develops predictive internal models, based on acquired motor commands that are thought to be simulated during the observation of similar action sequences (Flach et al. 2004; Ramnani and Miall 2004). The fact that the Non-Experienced group performed at ~50 % accuracy, rather than closer to 33% (chance), suggests that their predictions were based on these visual experiences with moving objects. This is underscored by the fact that the secondary motor task failed to degrade performance for the Non-Experienced group. Similarly, motor interference reduced the skilled performers' accuracy to that of the novices (~ 50 %) rather than to chance levels (33 %).

It has also been suggested that the motor system may be able to re-purpose internal models of particular biological motion to make predictions about other similarly-structured motion (e.g., Grosjean et al. 2009). Indeed, it has been demonstrated that areas within the ventral Pre-motor Cortex, previously thought to only be activated via established motor representations, are active when predicting actions unrelated to one's motor repertoire (Schubotz and von Cramon 2003, 2004; Wolfensteller, Schubotz and von Crammon 2007; for a review see: Zentgraf et al. 2011). Therefore, visual-motor experience with throwing objects in general might have

aided prediction. As a result, in addition to producing noisier, less-accurate predictions, these more-generic representations may also have been less susceptible to effector-specific interference effects.

While previous researchers have shown interference effects from motor secondary tasks during action recognition and discrimination (Paulus et al. 2009; Witt and Proffitt 2008; Witt et al. 2010), our results show, for the first time, that the *prediction* of future action outcomes is also subject to interference from a secondary task that either inhibits, or interferes with, in an action-specific way, motor areas that would be implicated in the observed action. As such, these data provide further insights into the role, and specificity, of the motor system in predicting the sensory consequences of others' actions, and the kinds of simulative mechanisms that may facilitate such predictions in real time.

3.5 Bridging summary

In Experiment 2 we determined that the concurrent execution of an incongruent secondary motor task interfered with the prediction process, reducing prediction accuracy to the level of novices with no motor experience on the task. These results suggested that motor system simulation was responsible for action prediction accuracy. The effect was action-specific, as a congruent (mimicry) secondary task did not interfere with prediction accuracy. However, the tasks were not specifically matched with respect to attention demands, and because the motor task was only performed with the effector specific to the action (i.e., the right throwing arm), we do not know whether motor-system interference was specific to the action and the observed effector. This was examined in Experiment 3, by comparisons of the same action-incongruent secondary motor task, performed with both the right and left arms.

From Experiment 1, visual experience (either through throwing darts and getting response-produced feedback, or through action-observation in a first-person perspective), did not positively aid prediction accuracy. It was unclear whether this was potentially a result of visual perspective, the method of training and/or reflective of the role of vision in action prediction. Therefore, to return to the question of whether visual-only training can improve prediction accuracy in people learning to throw darts (and whether accuracy is affected by secondary motor tasks), we included a perceptual-training group in Experiment 3 who practiced under conditions where the trained perspective and the test perspective matched (through video clips shown from the same (side-on) perspective as the prediction test stimuli). Moreover, the perceptual-training group was also asked to make predictions in response to occluded video stimuli, and received feedback about their accuracy. This manipulation of the type of experience; either visual or visual-motor (which was not controlled in Experiment 2), allowed us to establish the role of motor system activation during action prediction as a function of the type of visual/motor experience. Thus, in Experiment 3 we undertook a training study, where we trained one group to throw darts (Motor-visual practice), while a second group undertook perceptual training (Visualonly practice), where they were taught to make associations between dart flight stimuli and dart board outcomes. Our goal was to explore whether accuracy in predictive decisions is mediated by simulative-type mechanisms only when the performer has had motor experience with the observed action.

Chapter 4: Evidence for multiple mechanisms of action prediction dependent on visual-motor experience

4.1 Introduction

Recent evidence suggests that the human motor system is involved in predicting the outcome of observed actions (e.g., Aglioti et al, 2008; Ikegami & Ganesh, 2014; Mulligan et al., 2015). This claim is supported by the idea that a common representational system underlies perception and action (James, 1890; Prinz & Hommel, 2002) and that action perception and action execution have a shared neurophysiological base (e.g., Blakemore & Decety, 2001; Caspers et al., 2010; Grafton, 2009; Rizzolatti & Craighero, 2004). In the current experiment, we consider how action prediction processes depend on motor and perceptual experience, specifically testing whether the same predictive accuracy can be achieved, based on the same stimuli, via different prediction processes (i.e., one motor-based, one visually-based). To date, differential processes, despite similar accuracy levels, have not been shown as a result of manipulations to visual-motor experience. This would provide strong evidence that prediction of action outcomes is driven by at least two pathways that do and do not depend on motor system activation (and experience) during the prediction processe.

Motor practice is thought to foster the development of motor programs or internal models that rely on body kinematics and action outcomes more generally, to predict the actions of others. This is thought to be achieved via simulative mechanisms that map the observed action (and its effects) onto the observer's motor system (e.g., Knoblich et al. 2002; Urgesi et al., 2012). This simulation is thought to be automatic, with the closer the match between the (observed) perceptual input and the internal motor code (or program), the more accurate the prediction

(Knoblich & Flach 2001). At an implicit, computational level, forward models are thought to be acquired through practice, which allow prediction of the sensory consequences of actions. When we generate a motor command, an efference copy of this motor command is fed into this forward model (predictor), allowing anticipation of what the consequences of our action should feel and look like (Miall & Wolpert, 1996). It has been suggested that these forward models can also be used to predict the outcomes of others' actions, through activation of the motor system during observation (Blakemore & Frith, 2005; Wolpert & Flanagan, 2001; Wolpert et al., 2003). One line of evidence in support of this motor-based prediction is work showing that visual gaze is similar among observers and actors of the same task, with both groups showing predictive saccades (Flanagan & Johansson, 2003). Importantly, if the observer has their arms restrained during action observation, the saccades no longer show this predictive nature (Ambrosini et al., 2012). This result suggests that brain regions representing the effectors involved in the observed action are activated and used to aid in the understanding and prediction of other's movements.

In prior work, we have shown that a secondary motor task, performed with the same arm as viewed in the action of a trained dart thrower, reduces the prediction accuracy of skilled performers to the level of a novice (Mulligan et al., 2015). Although this provided direct evidence that the motor-system was involved in decision accuracy, it did not necessarily show that predictions were a result of action-simulation. It is possible, that such a motor task interfered with spatial processing of kinematic information, rather than necessarily simulative mechanisms. A stronger test about the nature of this interference effect would be to test prediction accuracy under conditions where the secondary motor task is performed with both arms. Effector-specific interference during prediction accuracy, as a function of manipulated motor experience throwing

darts, would provide strong evidence that motor simulative processes are directly implicated in the predictive decision processes of trained individuals.

Although action prediction may rely on the cortical neuromotor system in a general fashion, there is evidence for distinct neural representations underlying action prediction. In an fMRI study, participants had to either predict whether an action continued with accurate timing after occlusion or if the last memorized frame before occlusion continued from the same position after occlusion ('freezing' condition). Activation in right pre-SMA (sensorimotor areas) was shown in both conditions, indicating maintenance of an internal reference (a requirement of both conditions). In contrast, activation in left pre-SMA and left PMd (dorsal premotor) was only seen in the 'prediction' condition, and was considered indicative of simulation (Stadler et al., 2011). Behavioural evidence supporting a dual-process model of action prediction was subsequently provided, whereby evidence commensurate with real-time simulation was shown with compatible effector priming, while incompatible effector priming promoted a 'static matching' process (Springer, Brandstaedter & Prinz, 2013). While the results of this study provided evidence that two different processes may be involved in action prediction, the authors were unable to make any determination about the representational format (visual/motor) of these processes.

Other evidence supporting the idea that action prediction involves at least two different processes was shown in a study comparing the ability of experienced soccer goalkeepers and kickers to determine the trajectory of penalty kicks (Tomeo et al., 2012). Kickers were more likely to be fooled, than goalkeepers, by deceptive kicks (those showing incongruence between the initial kinematics at ball contact and the resultant ball trajectory). Further, the kickers exhibited similar activation of cortical motor representations related to the kicking limb while

viewing congruent and incongruent (deceptive) actions, whereas the goalkeepers showed reduced activation in these areas while observing incongruent actions. The authors suggested that it was the goalkeepers` visual expertise with the penalty kicks, from a third-person perspective, that allowed them to inhibit simulation mechanisms based on body movements and switch to using visual representations, based on contextual cues, to determine ball trajectory.

Here, we present a study testing how strictly visual or combined visual-motor experience affects engagement in action simulation during prediction, through manipulations to both the type of prior experience (visual/motor) and the types of secondary tasks performed during prediction. It has been argued that motor experience is required to develop motor representations that can later be simulated to generate predictions of observed actions, whereas visual experience leads to visual representations of the action that are used to define static and/or dynamic patterns of objects, such as ball flight (Urgesi et al., 2012; see also Hubbard, 2005; Zago & Lacquaniti 2005). Others, however, have suggested that the motor system can be activated during action observation, even in the absence of motor experience (e.g., Brown et al., 2009; Mattar & Gribble, 2006), referred to as the early mediation account of observational learning (Vogt & Thomaschke, 2007). As such, visual experience may still promote motor-based, simulation-type processes.

We physically trained one group of participants to improve in their spatial accuracy at throwing darts (motor-visual training). Another group received only perceptual training, where they practised associating static action pictures of occluded dart throws with their outcomes. Before and after training, participants made predictions about the spatial accuracy of the landing position of a thrown dart, from video clips that were occluded at different temporal points early in the action. Importantly, during some of these prediction tasks, participants were additionally

required to perform either a secondary motor task (pushing against a force gauge), with either their throwing or non-throwing arm or a non-motor based, attention control task.

Converging lines of evidence point to an effector-specific motor mapping during action observation and prediction, based on behavioural (e.g., Brass et al., 2001; Gillmeister et al., 2008; Heyes & Leighton, 2007) and neurophysiological (e.g., Jastorff et al., 2010; Strafella & Paus, 2000; Urgesi et al., 2010) data. However, in these studies, comparisons have not been made across complementary effectors (i.e., right and left hand), which would inform about the general or specific nature of cortical activation of the motor system during action prediction. If motor system activation is specific to the trained (right) effector, suggestive of effector-specific simulation, then we hypothesised that for the group receiving physical practice, there would only be interference from the right force secondary task (i.e., throwing arm) with respect to prediction accuracy. For the perceptually-trained group, no interference was expected, from either (left or right) secondary motor task, due to the predicted absence of motor-based representations developed during training. This effector- and experience-dependent interference would also rule out interpretations of the secondary task effects as being a function of general interference in the spatial processing of action kinematics, rather than due to action simulation.

In helping to understand the nature of the visual information required to invoke internal simulation mechanisms, we also compared across static and dynamic stimuli pertaining to the last frame of the action (up to the point of occlusion) or the unfolding of the action respectively. In prior work, we had presented a dynamic video clip that ended with a 2 s static display of the last frame (Mulligan & Hodges, 2014; Mulligan et al., 2015). As such, we were unable to determine whether improvements or interference in predictions were associated with the unfolding of the action or static, mid-action depictions. There is neurophysiological evidence that

dynamic and static stimuli engage the motor system similarly (David & Senior, 2000; Kourtzi & Kanwisher, 2000; Olson et al., 2003). Interference effects associated with viewing of congruent and incongruent actions on action execution, can arise from viewing both dynamic (Brass et al., 2001; Kilner et al., 2003) and static (Craighero et al., 2002; Vogt et al., 2003) actions, although direct comparisons have not been made. In comparing these 2 types of stimuli in the current experiment, we are able to determine the magnitude of interference associated with the secondary-motor tasks. This manipulation provides insight into the simulation process and whether a direct temporal matching, encouraged by dynamic stimuli, results in more accurate predictions and potentially greater interference from the secondary motor task than a process based on a snapshot of information. However, we expected prediction accuracy for the perceptually-trained group would actually decrease for the dynamic clips, in comparison to the static stimuli, due to perceptual-specificity in training with these static stimuli only.

A motor-proficiency task was also given pre- and post-training to assess any potential transfer benefits associated with the perceptual-training. Any positive transfer, in the absence of motor-based interference in prediction accuracy, would be assumed to be strategically realised (e.g., knowing how to hold and position the dart to achieve accuracy).

4.2 Methods

4.2.1 Participants

Thirty, male, volunteer students between the ages of 18 and 28 years, with normal or corrected vision, and no neurological impairment took part in the study. Participants were randomly allocated to three groups (n=10/gp): a "Motor-visual" training group, a "Perceptual" training group, and a "No-Practice" control group. All participants were self-report right-handed (and subsequently threw with their right-hand) and had no experience playing darts. All

participants provided informed consent, but were blind to the hypotheses of the experiment. Ethics' protocols for human experiments were strictly followed, as laid out by the ethics' board of the University. Remuneration for participation was \$10 /hour.

4.2.2 Task and design

There were 3 phases to the experiment consisting of pre-testing (motor proficiency and prediction tests), training across 2 practice days (motor-visual, perceptual or no-training) and post-testing (prediction and motor proficiency tests). For the groups that received training, participants were required to either throw darts to one of three sections of a dart board (motor-visual group) or watch a video of a trained individual throw darts to three sections of a dart-board with the outcome occluded (perceptual group). This latter group also made predictions about the landing position of the dart and received video feedback as to the correct outcome. In the pre- and post-prediction tests, all participants were required to predict the landing position of a dart from temporally occluded video (pre- and post-tests) or from static clips (post-test only) after watching a model enact part of a throw. In the pre- and post-motor proficiency test, participants were asked to throw three darts at the centre of each of the three sections of the dartboard (9 darts total).

4.2.3 Apparatus and stimuli

The task was modeled on earlier dart throwing studies designed to assess prediction accuracy (Knoblich & Flach 2001; Mulligan & Hodges 2014; Mulligan et al., 2015). A standard dart board was used and at regulation height and distance (i.e., participant stood at a distance of 2.37 m from the dartboard, which was placed at a height of 1.73 m from the floor to the bullseye). The board was divided into 3 sections (top, middle and bottom), that were formed by two horizontal lines an equal distance from the top and bottom of the dart board and from each other.

In a pre- and post-test, participants were required to make predictive judgements, from videos presented in a side-on perspective, as to which of the 3 vertical sections the dart would land.

Video clips for the prediction test were created using a Cannon HV20 camera (30 fps, 33ms/frame) showing a skilled actor throwing a dart at the centre of each of three sections of a dartboard. The actor was filmed from a side-on perspective from a distance of 3 m. Three video clips were created for each of the top, middle, and bottom sections, for a total of 9 clips. The actor threw to each section until 9 clips landed in what was subjectively determined to be the centre of each section (both vertically and horizontally). Each of these clips was further edited into 3 temporal lengths termed occlusion points (OP), each length being two frames (66 ms) longer than the previous. Three OPs for 3 clips at 3 different targets resulted in 27 total clips.

The video clips were modified to be either "Dynamic" video stimuli or "Static" clips. For the prediction tests, the Dynamic videos showed the initial part of the dart throw (i.e., raising the throwing arm) which lasted approximately 2 s (M = 1930 ms, SD = 20). Depending on the occlusion point (OP), this initial 'setup' phase was shown, plus 2 more frames (+66 ms, OP1), 4 more frames (+132 ms, OP2), or 6 more frames (+199 ms, OP3). The dart left the hand at OP2. The last frame of the video (either OP1, 2 or 3) remained on the screen for 2 s before a decision was required. The Dynamic video clips were used in the pre- and post-test prediction tasks. The Static clips were only used in the post-test prediction task (primarily because of time constraints associated with the number of conditions during pre-testing and repetition of stimuli). These static images were of the final frame, shown for 2 s (i.e., the frame corresponding to OP1, 2 or 3). A separate, third set of 27 Static clips, with the same actor, was created for the Perceptual group during training. These clips were edited based on the same parameters as above.

All Dynamic and Static clips included the dartboard in the stimuli. Video editing was performed using Sony Vegas and Adobe Premiere video editing software. Clips were shown via a projector on a full length screen (Cineplex Pro, IN, U.S.A), providing an approximate life-size image (~180 cm), as seen by participants from a distance of 4 m. E-prime 2.0 software was used to present the stimuli and for entering participant responses (Psychology Software Tools, Inc., PA, USA).

For the pre- and post-prediction tests, participants performed these tasks under one of four secondary-task conditions while viewing the dart clips; control, right-hand or left-hand force production or tone-monitoring. For the 2 force-production tasks, a force plate sensor logger (Neulog Inc, Rochester, NY) was attached to a tall iron post and adjusted to the participant's hand position when they stood adjacent to the post with their hands at their sides (using industrial strength Velcro; see Mulligan et al., 2015 for photo). This position enabled the participant to push against the force sensor with the edge of their hand in a fist shape, keeping the rest of their arm and body relatively immobile. Participants were required to press on a force gauge, in an action-incongruent manner, while viewing the stimulus. This secondary task was designed to prevent, or interfere with, participants' ability to simulate the observed action, as the effector involved in the action would be tasked with pushing (immobilizing the arm), whereas the primary dart throwing task required extension and flexion of the elbow and wrist. In order to probe the effector-specificity of the interference effect, both a right and left force task were used (see below). The force sensor was connected to a laptop, running Neulog software, which allowed real-time monitoring and data collection. Audio files used for the tone-monitoring secondary task were created using Audacity Inc. software, v2.0.2 (Boston, MA). These were 5 s files that consisted of a 250 Hz control tone with a randomly interspersed high tone of 440 Hz,

played for 100 ms on a third of the trials. We used three different temporal orders, allowing the duration of the control tone to vary from 3 s - 4.8 s before interspersing the 440 Hz tone.

4.2.4 Procedures

4.2.4.1 Pre-testing

The study took place over two days. On the first day, participants threw 3 darts at the centre of each of the three sections of the dartboard to obtain a baseline measure of motor performance. Trials in the motor pre-test were deliberately limited to reduce potential learning effects on subsequent training. Participants were required to stand and hold the darts in the same manner as the to-be-seen video-model, that is, using a thumb and forefinger grip and with their feet aligned horizontally to the start line.

The prediction test was completed under 4 conditions: no secondary task, forceproduction task using the left hand, force-production task using the right hand, and tonemonitoring task. All conditions were counterbalanced for order, and matched across groups. For each test condition, 27 video clips were presented in a random order. Via a screen prompt after the video, participants were asked where they thought the dart would have landed (top, middle, bottom) and their confidence in their answer, ranging from 0 - 100 % confident based on a 5 point scale in 25 % increments. Participants stood facing the screen for all conditions, but a 3-5 min seated rest was given between conditions. Participants were presented with 4 practice trials (without prediction accuracy feedback) at the start of each condition. No outcome feedback was provided on any trial.

4.2.4.1.1 Force-production tasks

Participants were required to stand with their arms by their side, adjacent and to the left or right of the iron post (depending on hand condition), facing the projection screen at \sim 45-60°

angle. They could therefore see the action unfold in approximately the same plane as the actor, without having to turn their head. They were then told to make a fist and to press against the force gauge with the elbow extended and their shoulder and wrist in a neutral position. This procedure was designed to be incompatible with the motion involved in throwing a dart, requiring activation of the same muscle groups involved in the throw, but in a different pattern (i.e., isometric versus dynamic contractions) and for a different function (i.e., the arm muscles are stabilizing and the elevator muscles of the shoulder are providing motive force whereas in the dart throw, shoulder muscles are stabilizing and the triceps are providing motive force).

For both the left and right arm conditions, participants first completed a maximal force test to calculate a 15 % force. Fifteen percent was considered a low force threshold that was relatively easy to maintain for the duration of a trial and throughout the testing condition (Mulligan et al., 2015). Participants pressed as hard as possible against the force sensor with their respective hand for 4 s, three times. From the average of these readings, 15 % average force was calculated. Participants next practised producing 15 % of their maximum force. The experimenter was able to monitor force output relative to the criterion in real time in all trials. During the practice trials only, participants were given feedback when pressing against the force plate during the trial. This was provided intermittently such that they were told when they had reached the criterion and when they varied from the force by more than ~1 N. During testing, a screen appeared before each trial prompting the experimenter to press a key to continue testing. The participant also saw this prompt and began pressing against the force plate when this prompt screen appeared (~1s before the video began), maintaining the force until the video clip had finished and the video-prompted questions appeared. This was to ensure that force was maintained throughout the entire clip, but not during the response. During experimental trials,

force was monitored by the experimenter and if the participant veered from the required force on a trial, feedback was provided at the end of the trial.

4.2.4.1.2 Tone monitoring task

A control tone was presented on every trial and the participant's task was to determine whether there had been a change in the tone. On 66 % of the trials, participants heard a continuous 250 Hz control tone for 5s duration, from the point when the experimenter initiated the trial, until the question asking the participant about dart location appeared on the screen. On the remaining trials, which were administered randomly throughout the condition, a 440 Hz tone was interspersed with the control tone for 100 ms. An additional question appeared, after the confidence question, asking participants if the tone had changed frequency during the trial.

4.2.4.2 Training

4.2.4.2.1 Perceptual training

The Perceptual group was required to make visual associations between static occluded images and outcomes. Participants were shown static images of partially completed dart throws on the large projection screen, just as they would be presented in the pre- and post-prediction tests. After each clip presentation they were asked where they thought the dart would land on the dartboard. After answering, they were presented with a close-up picture of a dartboard for 2 s showing the correct location of the landing position of the dart. The original static image corresponding to the feedback was then shown again for 2 s. Participants completed 135 practice trials on the first day and 24 hours later on a second day (total = 270 trials). The order of trials was randomised for each participant for both outcome location and occlusion point (OP). An equal number of trials were presented from each of the three sections of the dart board, along with an equal distribution of the three OPs.

4.2.4.2.2 Motor-visual training

Participants in the Motor-visual group were required to throw to one of the three sections of the board on each trial, as instructed by the experimenter. The order of the targets was random and pre-determined, such that it was the same order for each participant. Practice was conducted in blocks of 5 trials, after which the participant would collect the 5 darts from the dartboard and await instruction from the experimenter as to which sections to target next before each throw. Participants in this group practised a total of 27 blocks (135 trials) on each day across two consecutive days. There was an equal distribution of throws to each of the three sections of the dart board.

4.2.4.3 **Post-testing**

At the end of the second day of practice, all participants first completed the video (Dynamic) prediction post-test. The same 27 video trials as shown in the pre-test were presented under each of the 4 conditions, which were also given in the same order as in the pre-test. Following predictions to Dynamic stimuli, the procedure was repeated with the Static stimuli (i.e., the same 4 conditions which were repeated in the same order). Testing on day 2 ended with a motor proficiency post-test, where participants threw 3 darts towards the centre of each of the three sections of the dartboard. Participants were then fully-debriefed.

4.2.5 Data analysis

4.2.5.1 **Prediction tests**

Individual percentage accuracy for each condition (i.e., for each OP and for each Prediction condition) were calculated. These dependent variables were subjected to a 3 Group (Perceptual, Motor-visual, No-Practice) x 2 Test (pre, post) x 4 Prediction condition (Control, Tone, Right Force, Left Force) x 3 Occlusion Point (OP) repeated measures (RM) ANOVA, with
RM on all factors except Group. We also ran a similar analysis (with the absence of Test), comparing the prediction accuracy scores for the Static and Dynamic stimuli, which were only presented on Day 2 (post-test).

4.2.5.2 Motor-proficiency tests

Mean radial error (RE) and bivariate variable error (BVE) were calculated. BVE was based on the deviations of X and Y in relation to the target and the number of throws (see Hancock, Butler & Fischman, 1995). These measures were subjected to a 3 Group x 2 Test (pre, post) RM ANOVA.

4.2.5.3 Relationships between prediction tasks and motor proficiency

Partial correlations (controlling for group) were calculated to assess the relationship between motor proficiency (i.e., size of the reduction in RE and BVE from pre- to post-practice), and; a) % prediction accuracy, as determined by subtracting pre-test accuracy from post-test accuracy to yield a positive value (Dynamic stimuli only), and b) Post-test interference, as determined by subtracting the Right Force condition from the control condition (Dynamic and Static stimuli).

4.2.5.4 Training data

Data from the training phase were also analysed in order to establish improvements across practice. This was in the form of % outcome accuracy for the Motor-visual group and % verbal-response accuracy for the Perceptual group. Data were analyzed in 15 trial blocks in a 2 Day x 9 Block RM ANOVA, with RM on both factors, separately for each group. A second analysis was also ran to look at an overall training effect, comparing the first 2 blocks of practice on day 1 to the last 2 blocks of practice on day 2. For all ANOVAs, partial eta squared (η_p^2) values are reported as measures of effect size, and post-hoc analyses were performed based on Tukey's HSD (p < .05). Where violations to sphericity were encountered, Greenhouse-Geisser corrections were applied.

4.3 Results

4.3.1 Prediction tasks

4.3.1.1 Dynamic stimuli (pre and post-test comparisons)

Mean percentage accuracy scores are shown in Figure 4.1a (Motor-visual), b (Perceptual), and c (No-Practice). When viewing the Dynamic stimuli, the Motor-visual and Perceptual training groups improved in their predictions after the training interventions, while the No-Practice group did not. These effects were confirmed through a main effect of group, F(2,27) = 6.34, p <.01, $\eta_p^2 = .32$, test, F(1,27) = 75.26, p <.001, $\eta_p^2 = .74$ and the predicted Group x Test interaction, F(2,27) = 31.65, p < 0.001, $\eta_p^2 = .70$. In the post-test, the two practice groups were significantly more accurate than the No-Practice group, but were not different from each other. Only the practice groups significantly improved across the test phase.





A





Figure 4.1 Mean percentage accuracy scores for each group (A = Motor-visual, B = Perceptual, C = No-Practice) as a function of prediction condition and test phase (pre or post). Error-bars show between-subject SDs

For illustration, we have plotted the % difference in accuracy from the pre to post-test for each group and condition in Figure 4.2. Based on statistical analysis of % accuracy mean scores, there was a difference across the prediction conditions, F(3,81) = 9.70, p < .001, $\eta_p^2 = .26$, due to a significant decrease in accuracy for the Right Force task compared to the other conditions. This condition effect was due primarily to the Motor-visual group during the post-test as evidenced by the predicted Group x Condition x Test interaction, F(6,81) = 3.31, p < .01, $\eta_p^2 = .20$ (i.e., ~ 20% of the within subject variance can be accounted for by this 3-way interaction). Post-hoc comparisons for the Condition x Test interaction, F(3,81) = 5.06, p < .01, $\eta_p^2 = .16$, showed that differences across the 4 conditions were only present on the post-test. Percentage accuracy in the Right Force condition was significantly less than that of the other three conditions, which did not

differ from each other. The locus of this 2-way interaction was due to the Motor-visual group's post-test prediction accuracy while performing the Right Force task. Accuracy in this condition was significantly lower than in the other three conditions. No condition differences were shown in the Perceptual and No-training groups in the post-test. However, both the Motor-visual and Perceptual groups significantly improved their prediction accuracy under all conditions, except the Right Force condition after training.



Figure 4.2 Difference between post- and pre-test % accuracy for each secondary task condition when watching Dynamic stimuli, as a function of group. Error-bars show between-subject SDs

There was also a main effect of Occlusion Point (OP), F(2,54) = 8.80, p < .001, $\eta_p^2 = .25$. As expected, accuracy improved as more vision of the throw was available between OP1 (M = 47.78%, SD = 4.74) and OP2 (M = 56.67%, SD = 4.68). However, there was no general improvement from OP2 to OP3 (M = 54.31%, SD = 5.78). There were no significant interaction effects for OP involving Group, Test or Condition (F values between .02 and 1.17).

4.3.1.2 Dynamic vs static stimuli (post-test)

Comparing accuracy for both Dynamic and Static stimuli in the post-test, there was again a main effect of group, F(2,27) = 18.53, p < .001, $\eta_p^2 = .58$ and a Group x Stimuli interaction, F(2,27) = 7.19, p = .003, $\eta_p^2 = .35$ (no main effect of Stimuli, F < 1). Prediction accuracy decreased, only for the Motor-visual group, when viewing Static versus Dynamic stimuli (see Figure 4.1A). Although the Perceptual group showed a general improvement in accuracy for the stimuli they trained on (i.e., Static) versus Dynamic, this difference was not statistically significant.

Although there were no interactions with Stimuli-type involving Group and Condition (*F* values between .41 and 1.14), a Group x Condition interaction was still shown, F(6,81) = 7.75, p < .001, $\eta_p^2 = .37$. Follow-up post hocs confirmed that the Motor-visual group performed worse in the Right Force task in comparison to the other conditions (showing an absolute drop in accuracy of 21% for Dynamic stimuli, comparing Control to Right Force conditions, and an absolute decrease of 11% for Static stimuli). The Perceptual group also performed worse in the Right Force task, when compared to the Control condition (showing an absolute decrease of 6% for both stimuli types), but not in comparison to the other secondary task conditions.

Stimuli-type interacted with OP, F(2,54) = 6.45, p < .003, $\eta_p^2 = .19$ (see Figure 4.3). For Dynamic stimuli, accuracy did not improve between OP2 (M = 61.20%, SD = 5.91) and OP3 (M = 58.70%, SD = 8.34), but it did for the Static stimuli (OP2, M = 58.80%, SD = 6.13; OP3, M = 64.63%, SD = 5.50). When comparing across stimuli, prediction accuracy at OP1 was significantly greater when participants viewed the Dynamic (M = 52.50%, SD = 7.08), compared to the Static stimuli, (M = 46.68%, SD = 4.77), while the opposite effect was seen at OP3. Prediction accuracy at OP2 did not differ. The interaction with Group approached conventional

levels of significance, F(4,54) = 2.15, p = .087, $\eta_p^2 = .14$. As illustrated in Figure 4.3, the Perceptual group generally showed an improvement in accuracy across each OP for both Static and Dynamic clips, whereas the Motor-visual and No-practice groups, showed this improvement most noticeably for the Static stimuli. Differences across stimuli-type for the Motor-visual group were most evident for OP1, where improvements as a function of practice were only noted for Dynamic stimuli⁴.



Figure 4.3 Mean percentage accuracy for each group as a function of test phase (pre or post), stimulus-type (with Dynamic "dyn" stimuli in both test phases and Static in the post-test only) and occlusion point (OP).

4.3.2 Motor proficiency tasks

As shown in Figure 4.4a (RE) and b (BVE), the Motor-visual and Perceptual groups showed a decrease in error pre to post training, whereas the No-Practice group showed no change. For RE, the group effect approached conventional levels of significance, F(2,27) = 3.25, p = .054, $\eta_p^2 = .19$ and there was a main effect of test, F(1,27) = 4.85, p = .036, $\eta_p^2 = .15$ and Group x Test interaction, F(2,27) = 3.86, p = .034, $\eta_p^2 = .22$. The groups were not different in the pre-test. In the post-test, the only difference was between the Motor-visual and No-Practice group, with the former showing significantly less error (8 cm). Comparing across the pre and post-tests, the Motor-visual group significantly reduced RE by 6 cm from pre to post-test. Decreases of 3 cm for the Perceptual group and 1.5 cm for the No-Practice group were not significant.



Figure 4.4 Mean radial error (A) and bivariate variable error (B) for the motor test as a function of Group and Test (pre- and post-practice). Error bars show between-subject SDs.

For BVE (Figure 4.4b), a similar pattern of results was shown, including a main effect of test, F(1,27) = 17.68, p < .001, $\eta_p^2 = .40$ and a Group x Test interaction, F(2,27) = 8.09, p = .002, $\eta_p^2 = .38$ (no group effect, F(2,27) = 2.70, p = .085, $\eta_p^2 = .18$). Groups did not differ in the pretest, only on the post-test, where the Motor-visual group was significantly less variable than the No-Practice and Perceptual groups. Only the Motor-visual group showed a significant reduction in variability across tests.

4.3.3 Relationships between prediction tasks and motor proficiency

4.3.3.1 Prediction accuracy

For Dynamic stimuli, a larger reduction in RE (Figure 4.5a) across pre and post-tests was not significantly correlated with improvements (post minus pre-test) in prediction accuracy under the control condition, after controlling for group, $r_p(27) = .26$, p = .18. However, larger reductions in BVE (Figure 4.5b) were correlated with improvement in prediction accuracy, r_p (27) = .52, p = .004. As prediction accuracy improved over test-phase, so did consistency in throwing.



Figure 4.5 Scatter plots showing the relationship between change in error (RE and BVE) on the motor proficiency test across pre and post-tests and A-B) Change in % prediction accuracy (post-pre) and C-F) Interference effect associated with the Right-Force task in the post-test, as compared to Control condition (C-D = Dynamic stimuli, E-F = Static stimuli). Trend lines are not adjusted for group.

4.3.3.2 Interference effect

Reductions in RE (Figure 4.5c) were not significantly correlated with motor interference in the prediction tasks for Dynamic stimuli, r_p (27) = .29, p = .13, but they were for Static stimuli, r_p (27) = .41,p = .03 (Figure 4.5e). There was also a relationship between BVE reduction across test-phases and the interference effect while viewing Dynamic stimuli, r_p (27) = .53, p = .003 (Figure 4.5d) but not significantly for Static stimuli, r_p (27) = .34, p = .070 (Figure 4.5f). In general, after controlling for group, a greater improvement on the motor proficiency task (reduction in error) was generally related to a larger interference effect in the post-test.

4.3.4 Training data

As shown in Figure 4.6, the Motor-visual group significantly improved their motor accuracy as training progressed. There was a day main effect, F(1,9) = 42.75, p < .001, $\eta_p^2 = .83$ and a significant linear trend component to the block effect, F(1,9) = 2.70, p = .003, $\eta_p^2 = .65$. There was no interaction. An ANOVA comparing throwing accuracy of the first two Blocks on Day 1 (M = 43%, SD = 5.97) to the last two Blocks on Day 2 (M = 71%, SD = 15.31), showed that accuracy improved from the start to the end of practice, F(1,9) = 35.20, p < .001, $\eta_p^2 = .80$.



Figure 4.6 Motor and Perceptual practice acquisition data as a function of practice block.

For the Perceptual training group, we were only able to analyse data from 8 participants due to software collection errors. Despite trends for improvement in prediction accuracy, the Day, F(1,7) = 4.11, p = .082, $\eta_p^2 = .37$, and Block, F(8,56) = 2.01, p = .062, $\eta_p^2 = .22$ effects were not statistically significant (and no interaction, F < 1). However, a comparison of the first 2 blocks of practice on day 1 (M = 50.42%, SD = 8.44) to the last 2 blocks on day 2 (M = 69.58%, SD = 14.96), indexed improvements from the start to the end of practice, F(1,9) = 8.21, p = .024, $\eta_p^2 = .54$.

4.4 Discussion

Our primary goal was to investigate the representational mechanisms that support action prediction. The key questions we asked were under what conditions is the motor system activated when (accurately) predicting action outcomes and how specific is this activation to the observed effector (i.e., system activation) and to the type of training stimuli (i.e., dynamic video versus static clips). We used an effector specific secondary motor task in an attempt to interfere with motor system activation (simulation) during action prediction and we trained two groups either physically or perceptually.

Both training groups significantly improved in prediction accuracy (and in comparison to a No-Practice control group). Importantly, however, only the Motor-visual group was significantly affected by the right-arm force task in the post-test. This group showed a significant decrease in prediction accuracy of 21% under Dynamic stimuli conditions, compared to the control condition (in relative terms this was a 30% decrease). No such decrement in prediction accuracy was shown while performing the same force-task with their left arm (less than 1%). The Perceptual group showed no significant decrease in prediction accuracy with either effector, when compared to the control condition (\sim 3-6%). These results support the suggestion that the motor system is activated and directly involved in the prediction of action outcomes, but only in observers with motor experience performing the observed action (see also Aglioti et al., 2008; Urgesi et al., 2012). Because of the differential effects as a function of the type of training, the motor-based interference cannot simply be with the spatial encoding /interpretation of body kinematics (as both groups must interpret kinematic information). Moreover, the effector specific nature of these effects suggests that the interference is not a general motor-based interference (see also Aglioti et al., 2008). Rather, effector-specific interference suggests a somatotopic simulation-type process that prevents the motor system activating in an action-congruent manner to aid outcome prediction.

In previous research it has been shown that concurrent performance by a different effector (such as the foot, rather than the hand) can affect perception, and potentially hinder simulation processes (Hamilton et al., 2004; Prinz, 1997; Springer, Brandstaedter & Prinz, 2013;

Wilson & Knoblich, 2005; Springer et al., 2011). In our study, we saw neither interference nor facilitation as a result of this incongruent action with the non-throwing (left) arm. This perhaps speaks to the specificity of motor-experience in action simulation, whereby motor commands related to left-handed dart throwing were not formed for the Motor-visual group. It is however possible that the pattern of interference was a result of using the dominant right-arm. In right-hand dominant individuals, the left-hemisphere has been shown to play a greater role in motor planning (e.g., Frey 2008; Haaland et al., 2000; Janssen et al. 2009) and as such, effector-specific interference effects may reflect hemispheric asymmetry. Against this interpretation, the right-arm force task did not impact accuracy for the Perceptually-trained group and in a previous study, an action-congruent task (mimicking) performed with the dominant right-arm did not interfere with prediction accuracy (Mulligan et al., 2015). However, a stronger test of the specificity of this interference would be to use left-handed (non-dominant) throwing as the stimuli for the prediction task, following practice with this arm.

The experimental manipulation of experience is critical for extending previous crosssectional studies of interference (Mulligan et al., 2015; Tomeo et al., 2012). Effector-specific interference occurred only for physically trained individuals, suggesting action predictions were achieved through mechanisms that simulate (perhaps in real time), internal motor representations of the observed action, in order to provide a prediction of its sensory consequences (Jeannerod, 2001). This supports the notion that action and perception (following physical experience) reside within a common representational medium that can exert bi-directional influences on each other (Hommel et al., 2001; Prinz, 1997).

The fact that the perceptually-trained group showed a similar improvement in outcome prediction, but no interference from either the left or right secondary motor task, suggests that

accurate predictions can still be reached through mechanisms outside of motor simulation. In addition to a process that simulates action codes, or programs, based on the observed action, these data suggest a second, potentially more "cognitive" mechanism that works through a visual-matching process. The Perceptual training group would have built up visually-based stimulus-response associations that were then matched to the observed action stimuli to aid prediction. These processes appear to be non-motoric as they were not susceptible to motor interference (either general or effector-specific).

In the motor learning literature, there is some debate about whether action observation, in the absence of motor experience, is sufficient to activate motor codes that can subsequently directly transfer to motor execution (so termed early mediation; see for example Vogt & Thomascheke, 2008; Maslovat et al., 2010). In visuomotor adaptation studies, action observation has not been sufficient to update internal, sensorimotor models of the action, as evidenced by an absence of unintentional motor after-effects, despite direct learning benefits, in these tasks (e.g., Larssen et al., 2012; Lim et al., 2014; Ong & Hodges, 2010; Ong et al., 2012). Learning through watching appears to be more a strategically-driven process in the absence of any physical practice, for tasks that require novel sensorimotor relationships. Although there are benefits to be gained from observing others, arguably the motor system is not involved in this process until enactment.

These results and explanations are somewhat congruent with recent evidence from temporal prediction tasks that have led the authors to propose that action prediction can occur via two different processes. A simulation-based process, known as 'dynamic updating', and a perceptually-driven process, termed 'static matching' (Springer, Parkinson & Prinz, 2013). However, these authors were unable to speak to the representational format of these two

processes with respect to whether they relied on motor- or visually-based representations or simulations. Because we controlled motor experience, and subsequently showed a differential effect of the secondary motor task as a function of this experience, it is likely that the Motorvisual group engaged in dynamic updating via motor representations. The Perceptual group may have engaged in dynamic updating or static matching, with either being underpinned by a visual representational format.

Dynamic updating was suggested to be the default process in action prediction tasks, with static matching only occurring when dynamic updating was interfered with in some way (Springer, Brandstaedter & Prinz, 2013 Springer, Parkinson & Prinz, 2013; Tomeo et al., 2012). Although we did not probe the time-course of predictions (such as through response time measures), it does appear that this effector-specific incongruent secondary task disrupted this dynamic process for the Motor-visual group, perhaps forcing them to instead turn to a 'static', visually-based process. Indeed, in one study where participants were primed with an incongruent effector (i.e., hand rather than foot), temporal predictions were more in line with a static matching process than dynamic updating (Springer, Brandstaedter & Prinz, 2013). Based on the data, however, we reason that it is unlikely that the Motor-visual group was able to effectively switch prediction strategies as a function of the task demands. Although this group performed above chance, even while performing the right force secondary task, accuracy under this condition was not better than pre-test performance (or control group accuracy), where arguably no (or only weak) perceptual or motor-based representations existed. Neither did their accuracy match that of the Perceptually-trained group.

Additional support for the proposal that action predictions were primarily a function of a motor-based process following action experience is evidenced by the motor-proficiency task

data. The Motor-visual training group significantly improved in dart throwing ability after training, while the Perceptually-trained group did not show significant improvements. This improvement in motor ability for the physically trained group serves as a validity check that this group developed motor representations (internal models) that could later be used to simulate the observed action during prediction. In contrast, the Perceptual group presumably did not acquire these motor-based internal models required for motor simulation, but instead developed visual representations that they were able to use in a visual matching process during prediction. Interestingly, correlations between improvements in motor proficiency and improvements in prediction accuracy as well as the degree of motor-based interference were seen, even after controlling for group effects. This suggests that these group effects were perhaps not universal across individuals. Inspection of Figure 4.5C-F shows that some individuals in the perceptuallytrained group (circle symbols) may have been basing their prediction accuracy on a motor-based process (particularly for the Dynamic stimuli). Individuals in this group who showed the most reduction in error on the motor proficiency test also showed the largest interference effect. It will be necessary in future work to further probe prediction processes in this group, testing more individuals to hopefully alert to factors that may lead to motor improvements in the absence of physical practice.

It is important to point out that the Perceptual-group in our study only watched static clips of a dart-throwing action and hence any "motor" based transfer might be limited by the nature of the stimuli. There are, however, two critical points to make with respect to this idea. First, in previous work, prediction accuracy did not improve from pre- to post-test following only action-observation training, where individuals watched all the (dynamic) practice trials of a matched actor (Mulligan & Hodges, 2014). Second, in the current experiment, prediction

accuracy was only weakly moderated by the type of stimuli (i.e., Static or Dynamic). Even though the Perceptual group only viewed static clips during training, they did not show a significant decrease in prediction accuracy for the dynamic videos. Moreover, although the Motor-visual group showed a significant decrease in accuracy for the Static versus Dynamic stimuli in the post-test, the Right-force secondary task interfered with prediction accuracy in both stimuli conditions. These results indicate that the Motor-visual group was able to use static images that only implied motion to activate motor-based simulation mechanisms and in general that these effects are not specific to the type of stimuli used to train the Perceptual group.

There was sufficient reason to suspect that both types of stimuli would produce a similar pattern of results in our study as perceptual effects, such as action embodiment (Bach &Tipper, 2006) and representational momentum (e.g., Hubbard & Bharucha, 1988) have been shown to occur in response to both actual motion and apparent or implied motion (i.e., static clips) (Munger & Owens, 2004). That is, action observation in general appears to elicit forward predictions in the observer, at least when the observer has experience with the stimuli (either motor or visual, see also Hubbard, 2014; Wilson et al. 2010). Therefore, although there was a decrease in accuracy going from dynamic to static clips (for the Motor-visual group), the patterns of interference remained. This would suggest that the simulation that takes place does not need to be directly matched, temporally or spatially, to the unfolding action. However, it is worth pointing out that for the early occluded clips (OP1), some benefits were noted for the Motor-visual group in the Dynamic versus Static condition (see Figure 4.3), potentially highlighting a minimum amount of implied movement necessary for simulation to occur.

To summarise, we have shown that a group that was trained to throw darts at specific areas of a dartboard, significantly improved in predicting the outcomes of occluded dart throws

shown on video (both dynamic clips and static frames). Importantly, this group also exhibited a significant reduction in prediction accuracy, to pre-practice levels, but only while concurrently performing an incongruent secondary motor task with the trained (right) effector. A second group, that was perceptually trained to associate occluded dart throws with outcomes, improved similarly to the motor trained group on the prediction test, but displayed no reduction in prediction accuracy under any of the secondary task conditions. These results strongly suggest two distinct paths to predicting action outcomes; one motor-based and one visually-based. Individuals with motor training were able to utilise acquired motor representations to simulate observed actions to aid in prediction, and that, as evidenced by the interference effects shown while performing the right, but not the left, secondary motor task, these representations were effector-specific. The fact that the perceptually-trained group was able to solve the prediction task with similar accuracy, yet showed no interference from the secondary tasks (and no statistically significant improvement in dart throwing ability), suggests that motor representations were generally not formed by this group during training and thus were not usable during action prediction. Instead, visual representations were acquired, which allowed for a visual matching process during prediction. For this group, the observed throwing action was likely matched to an internal visual representation of the appropriate outcome of the observed throw. By experimentally manipulating dart-throwing experience and effector-specificity in secondary tasks during on-line predictions, these results suggest separable motoric and visual processes that support action prediction. Despite both visual and motor-experiences for physically trained participants, there was no evidence that individuals could effectively switch between processes to maintain prediction accuracy.

4.5 Footnote

4: Generally confidence increased from pre- to post-test (for the training groups only) and as more information became available, that is for OP2 and 3 vs OP1 and for Dynamic versus Static stimuli. The increase in confidence with time was more pronounced for the Perceptualtraining group.

Chapter 5: General discussion

5.1 Theoretical overview and summary of research results

The ability to effectively predict action outcomes was previously thought to come about through a process that draws on large banks of perceptual action sequences that are acquired over years of motor-visual experience. During action prediction, these visual-based patterns were thought to be compared to observed actions, using a type of cognitive matching process (Abernethy et al., 2008; Gobet & Simon, 1996; Starkes, 1987; Starkes et al., 2001; Williams & Davids; 1995, 1998). More recently, researchers have suggested that the human motor system is highly involved in these predictive processes. As such, it is thought that observed action activates the motor system, in a top-down fashion, as it maps the observed action onto acquired motor representations (internal models) through a type of covert simulation process in order to provide an understanding of the sensory consequences associated with the observed action (Aglioti et al, 2008; Gallese, 2005; Ikegami & Ganesh, 2014; Jeannerod, 2001; Miall, 2003; Tomeo et al., 2012; Urgesi et al., 2012). Support for the idea of motor involvement in action prediction comes from the suggestion that action and perception exist in a common representational domain, and can exert influence on each other (Hommel et al., 2001; Prinz, 1997). Evidence for a neural homologue to this system comes from research showing cortical areas of the brain that are similarly activated during the observation and execution of the same action sequences (Fogassi et al., 2005; Gallese et al., 2002; Rizzolatti et al., 2001). Motor experience plays a primary role in action prediction, such that, during observation, these motor areas become active, running internal models of the perceived action to aid prediction (Aglioti et al., 2008; Ikegami & Ganesh, 2014; Tomeo et al., 2012; Urgesi et al., 2012).

Research examining the role of the motor system in visual prediction has relied on comparisons between motor-visual and visual experts (e.g., Aglioti et al., 2008; Urgesi et al., 2012). While these studies have shown performance advantages for motor-visual experts, the differential contributions of motor-visual compared to visual-only experiences is unclear because of the difficulty in finding 'purely' visual experts. Further, in studies where vision has been completely isolated, the tasks have involved recognition or discrimination-type decisions (Casile & Giese, 2006; Hecht et al., 2001; Reithler et al., 2007), not decisions that involve predicting future action outcomes. Although it has been established that areas of the brain responsible for action production are activated during action prediction (Aglioti et al., 2008; Makris et al., 2014; Tomeo et al., 2012), it is unclear what role these activations play in the prediction of action outcomes.

In my first experiment, I trained a full-vision group and a no-vision group to throw darts at three sections of a dartboard. I also trained an observation-only group, who viewed the action from behind the physical performer. Pre- and post-practice, participants were required to predict the final position of occluded dart throws. We predicted that if the motor system was solely responsible for prediction accuracy, both motor groups would significantly improve their prediction accuracy after training, and the no-vision group would perform the same as the fullvision group. Based on previous studies (Ong & Hodges, 2010; Ong et al., 2012), we also expected the observation-only group to improve in prediction accuracy after observational practice, without necessarily developing internal motor representations.

The results from Experiment 1 showed that, compared to the observation group and a nopractice control group, the two motor groups significantly improved their prediction accuracy, to the same degree, after training. They also showed similar, significant improvements in motor

proficiency after training. The observation group did not show post-practice improvements in either prediction accuracy or motor skill. While these results suggested that motor experience was responsible for improvements in prediction accuracy, and visual experience did not appear to be important, it was unclear what type of processes are actually involved in prediction. An alternative explanation to one based on motor-based simulation, might suggest that, during training, visual representations were generated and later recalled to help in prediction decisions, through a kind of perceptual matching process that did not involve the motor system. Overall, our results were not able to provide any direct evidence that the motor system was activated in a simulative way during these predictive decisions.

In Experiment 2, I wanted to further study the mechanisms and informational resources responsible for predictive skill. Specifically, the aim was to interfere with any potential motor system simulation during prediction to determine if simulative processes were active during prediction. I compared experienced and inexperienced dart players on the prediction task, while they performed congruent and incongruent secondary motor tasks. We hypothesized that, if acquired motor representations were simulated and used for predicting action outcomes, there would be a decrease in prediction accuracy for the experienced group when they performed the incongruent secondary task.

The results from Experiment 2 showed that, in the no-secondary-task condition, the experienced group performed significantly more accurately than the inexperienced group on the prediction task. However, while performing the incongruent secondary task, the experienced group's accuracy level significantly decreased, to that of the inexperienced group. The inexperienced group showed no such decrement while performing the incongruent secondary task. Both groups were more accurate when viewing stimuli depicting their own action. We

concluded that predicting action outcomes requires motor system activation, and this activation appears to be action-specific. However, it was unclear if motor system activation (simulation) is essential to accurate prediction in all contexts. The results also left unresolved, the question of the role that vision may play (i.e. the development of visual representations) in the training period.

Experiment 3 was driven by the suggestion that, depending on context, different processes may be used during prediction – a motor-based simulation process, based on acquired motor representations, and a visual-based 'matching' process, based on acquired visual representations (Springer et al., 2013a, b). Thus, my aim in Experiment 3 was to further understand the specificity of motor system involvement in action prediction. Specifically, I wanted to understand whether the motor system is always involved in such predictions, or if other mechanisms may be employed, depending on contextual factors. I explored the notion that action prediction can come about through two processes – one motor-driven, and one visuallydriven – by investigating if, and how, visual or motor experience might affect the tendency to utilize one or other of these processes during action prediction.

We trained a motor-visual group, who learned to throw to different sections of the dart board, and a visual group, who learned to make perceptual associations between static images of dart throwing actions and outcomes. The perceptual training group allowed us to address the issue concerning the importance, or unimportance, of visual experience in prediction. Related to this question, recall that the observational learning group from Experiment 1 showed no improvement in prediction accuracy. We speculated that this may be because they observed the actor from a first-person perspective, yet performed the prediction task from a side view. In contrast, all the motor-visual groups in our studies showed superior performance on the

prediction tasks, even though they were presented in a side perspective, while performers would only have experience in a first-person perspective. Indeed, perceptual experience seems to be highly viewpoint dependent, whereas motor experience is thought to be independent of viewpoint (Canal-Bruland & Schmidt, 2009; Tomeo et al., 2012). Common-coding principles state that the production of one's own actions, and the perception of others' actions, share a common representational domain, and because the observer and the actor do not share the same perspective, these common motor representations must be viewpoint independent (Knoblich & Flach, 2001; Urgesi et al., 2012). To address this possible issue, the perceptual group in Experiment 3 both trained, and performed the prediction tasks, using stimuli shown from the side view.

While the results of Experiment 2 showed that motor system involvement in action prediction is action-specific, we were also interested in further exploring how observed actions are mapped to the motor system. Specifically, we wondered if motor system activation was specific only to the effector involved in the action (right hand), or if activation also involved the complementary effector (left hand), implying wider system involvement. To explore these two alternatives we utilized both a right and left hand secondary motor task.

Finally, I wanted to understand the nature of the information required to invoke internal simulation mechanisms, given that, in Experiments 1 and 2, the videos contained both dynamic actions and static presentation of the final action frame at the corresponding occlusion point. To this end I incorporated both static (implied action) and dynamic (video) stimuli. We predicted that the motor-visual group would use their acquired motor representations to simulate the observed action, and would significantly improve in their prediction accuracy, while viewing both types of stimuli. We further expected right hand secondary motor task interference for both

types of stimuli, but made no specific predictions involving the left hand secondary motor task. We expected prediction accuracy to improve for the perceptual group, to a greater degree while viewing static stimuli (the stimuli they had trained on). We also hypothesized that, because the perceptual group would not have acquired motor representations during training, they would not experience interference under either secondary motor task condition.

The results from Experiment 3 showed that the perceptual and motor-visual groups significantly improved their prediction accuracy after training, and while both groups performed equally on the static clips, the motor-visual group performed significantly more accurately than the perceptual group on the dynamic stimuli. Motor interference, in the form of significantly reduced prediction accuracy, was only observed in the motor-visual group, and only while performing the right hand secondary motor task. Both static and dynamic images were subject to interference. These results provide evidence that two different types of processes were used to arrive at accurate predictions. We suggest that the motor-visual group utilized motor simulation mechanisms, as evidenced by the interference effects, while the perceptual group used a kind of perceptual matching process, drawing off visual-based representations, which were not vulnerable to secondary task interference. The results also revealed that implied motion (from the static stimuli) was sufficient to trigger motor system simulation (congruent with other action embodiment research, Bach & Tipper, 2006; David & Senior, 2000; Kourtzi & Kanwisher, 2000; Olson et al., 2003). By incorporating both right and left hand secondary motor tasks we were able to conclude that, under these task conditions, the observed actions are mapped in an effector-specific manner. Finally, our results suggest that even short-term training can promote the development of both motor and visual representations that can be used to effectively predict action outcomes.

To summarize, the purpose of interfering with the motor system during the anticipation phase (by having participants perform a secondary task) was to help us to better understand; a) whether judgments, during prediction, are based on the simulation of a motor program from the observer's motor repertoire, or are based on stored visual representations that are recalled and compared to the visual input during prediction, or both; b) the conditions under which these motor and visual representations are formed during training, and; c) the specificity of motor system activation during prediction. Both congruent and incongruent secondary motor tasks were designed to allow a better understanding of the action-specific nature of any activated simulation process. Similarly, employing incongruent secondary task conditions for both right and left hands allowed insight into the effector-specificity of the simulation mechanism.

5.2 Theoretical interpretations

The overarching goal of this thesis was to understand the mechanisms and informational resources involved in predicting action outcomes. Specifically, I was interested in the type of representations that are formed during learning, and how these representations are utilized during prediction. The work was premised on the notion that action prediction involves mapping an observed action onto the observer's acquired internal motor representations, which are then covertly simulated to provide a prediction of the sensory consequences associated with those internal motor 'programs' (Jeannerod, 2001; Miall, 2003). This implies that action and perception are linked, and reside within the same representational space (Hommel et al, 2001; Prinz, 1997). As such, action codes (motor programs) generated during training, even in the absence of vision, can later be called upon (simulated) to aid in action understanding (Casile & Giese, 2006; Reithler et al., 2007). This is what our results showed in Experiment 1, where a group trained on a motor task, without vision of the action, later improved significantly on

visually-driven prediction tests associated with the practiced motor skill. Computationally, it is thought that when we learn a motor skill we develop an internal motor representation (forward model) of the action, which is activated when we move, in order to provide a prediction of the outcome of our action, ahead of its completion. There is evidence to suggest that these forward models may even be activated (simulated) in the absence of movement, in order to generate predictions of imagined actions, or the actions of others (Gentili et al., 2006; Papaxanthis et al., 2002). However, we could not definitively say that the predictions generated by the no-vision group in Experiment 1 were the result of simulative mechanisms that utilize forward models, without direct evidence showing activation of motor processes during prediction.

Alternatively, we might speculate that, rather than motor representations even being formed during practice, and then later simulated, it might be possible that visual representations were spontaneously formed instead (even in the no-vision group), and were later retrieved and matched to the observed model-stimuli to aid prediction. Thus, while we were able to show, generally, that motor experience was important for action prediction, the results of Experiment 1 did not allow us to claim a causal link between motor simulation and action prediction, or even if motor representations were formed during practice.

Experiment 2 was primarily designed to investigate direct evidence of motor system activation (simulation) during action prediction, and determine if that activation has a causative effect on action prediction. When compared to an inexperienced group, as well as to a control condition where no secondary motor task was employed during prediction, an experienced group showed a significant reduction in prediction accuracy, while performing the secondary task. The experienced group, however, showed no decrement in prediction accuracy while performing a motor secondary task that was congruent with (mimicked) the action being observed. We

concluded that the experienced group was able to use their acquired motor repertoire to simulate the action being observed in order to generate a prediction of the future consequences of the observed action.

In Experiment 3, a motor-visually trained group and a perceptually trained group both significantly improved their prediction accuracy similarly after practice (Urgesi et al., 2012), with only the motor-visual group showing interference, in the form of significantly reduced accuracy, while performing the right force secondary motor task. We surmised that two different processes were at play during action prediction. One, used by the motor-visual group, that simulates acquired internal motor representations of the observed action to predict its sensory consequences (Gallese, 2005; Jeannerod, 2001), and another, used by the perceptual group, that matches stored visual representations to the observed stimuli to aid prediction (Springer et al., 2013a, b).

Next I will examine the collective results presented by these studies, using a framework which proposes that action prediction is supported by multiple processes (Aglioti et al., 2008; Springer et al., 2013a, b; Tomeo et al., 2012; Urgesi et al., 2012). Using this framework, and the experimental methods developed in this thesis, I explore new protocols that might be used to understand in more detail the development of internal motor and visual representations, and the interplay between the two during acquisition and action prediction.

5.2.1 Two paths to action prediction

As described above, for observers, there may be multiple mechanisms involved in action prediction. The first involves a motor-driven process that simulates an observed action, drawing off acquired internal action models that run, in real time, (Blakemore & Frith, 2005; Flanagan & Johansson, 2003; Grush, 2004; Kilner et al., 2007; Miall, 2003), generating top-down predictions

of an unfolding action (see Wilson & Knoblich, 2005, for a review). Based on the Theory of Event Coding (TEC), and common-coding principles in general (Hommel et al., 2001; Prinz, 1997), it has been suggested that the functional overlap between perceived and planned (or simulated) actions may provide a framework for predicting action outcomes by mapping observed actions onto one's own established motor representations (Jeannerod, 2001; Gallese, 2005). Further, it has been shown that concurrently executed and perceived actions that are incongruent may severely interfere with internal simulations (Prinz, 1997; Wilson & Knoblich, 2005).

The second process used in action prediction involves a kind of visually-based, perceptual matching mechanism, whereby internal visual representations, acquired separately from motor-visual experience, are matched with an observed stimulus to aid in prediction (Springer et al., 2013a, b; Tomeo et al., 2012; Urgesi et al., 2012). Other studies have provided behavioral and neurophysiological support for the notion of such a dual-process model of action prediction (Aglioti et al., 2008; Makris et al., 2014; Tomeo et al., 2012; Urgesi et al., 2012). In a study examining the contributions of motor and visual experience to predictive processes (judging the direction of penalty kicks) in soccer kickers and goalkeepers, it was suggested that, while both kickers and goalkeepers acquired visual-motor expertise, in the form of internal motor representations, only goalkeepers further acquired separate visual processing strategies (internal visual representations, specific to the third-person viewing perspective of the penalty kick). It is thought that internal motor simulations run an internal model based on congruency. That is, the simulation reflects the "honest" or true outcome of the observed action, ignoring deceptive kinematic cues (Tomeo et al., 2012). Thus, interference is created from the presence of an incongruent observed action. When faced with incongruent contextual cues (in the form of

deceptive actions), goalkeepers were able to inhibit internal motor simulation processes that were based on body kinematics, and switch to a perceptual process that involved matching visual cues to stored visual representations. As a result, their prediction accuracy was significantly greater than that of the kickers, for deceptive actions, and remained above chance. It was concluded that their separate visual experience with frontal views of penalty kicks provided goalkeepers with the ability to more efficiently utilize these visual cues to predict the kicker's actions, and because these visual representations are not linked to performing the task (penalty kick), they are not susceptible to interference (Tomeo et al., 2012).

Another study examined the notion that action prediction may come about through multiple mechanisms, and that these mechanisms operate separately based on task demands. Priming action observation with a compatible effector was considered to promote action simulation, as shown by lower error rates in predicting occluded actions, when the actual time interval between pre- and post-occlusion actions matched the presented post-occlusion action pose. Priming with an incompatible effector (considered motor interference) hindered or prevented simulation, as evidenced by an increase in prediction errors. This incompatible priming was thought to cause participants to covertly switch from using simulation mechanisms to matching internal visual images to the presented stimuli. This was supported by the fact that, although prediction accuracy was reduced, they were still able to maintain an accuracy rate of approximately 87%, compared to 92% under compatible effector priming (Springer et al., 2013a).

From Experiment 3, we suggest that, because dart throwing was a novel skill for the participants to learn, the motor-visual group would have acquired new motor representations (internal models) through practice, linking motor and perceptual codes. These representations

would be vulnerable to interference. However, unlike the goalkeepers described above (Tomeo et al., 2012), it is improbable that the motor-visual darts group would have also acquired separate purely visual representations, as they would have had very little observational experience of dart throwing. This could explain the fact that this group's accuracy scores dropped to pre-test levels, under conditions of interference. Similar to the kickers in the soccer study by Tomeo et al (2012), participants in the motor-visual group may have been unable to inhibit the action representations invoked by the incongruent action, and thus were unable to switch to a more visually-guided processing of important contextual cues (i.e. dart flight). Conversely, it is reasonable to assume that the perceptual training group in Experiment 3 would have developed purely visual representations, linked to the side perspective (the same as the prediction test stimuli), but would have acquired no internal motor representations. As a result, the perceptual group was able to perform the prediction task accurately, presumably using a type of perceptual matching process. The fact that this group did not experience a decrease in prediction accuracy under dual task conditions, suggests that motor representations were not used (or available) during prediction.

While we believe the above explanations have merit, we have no definitive evidence that they are a true reflection of the mechanisms involved. We might, however, suggest a manipulation that could be used to probe these processes further, in an effort to verify our hypotheses. Using the ideas of Springer et al, and Tomeo et al, it might be informative to again train a motor-visual group the same way as in Experiment 3. After administering the prediction post-tests, which would presumably show interference while participants performed the right force secondary task, we would train this (motor-visual) group the same way we trained the perceptual group in Experiment 3. We would expect that participants would now have acquired

separate visual representations (based on matching the side view), as we believe the perceptual group in Experiment 3 did. We would then test this group under all the same prediction test conditions. We would expect this group to be able to solve the prediction task (similar to the goalkeepers) by switching from using motor simulation processes, to using visual matching processes, based on the newly acquired internal visual representations. That is, the participants should now show no interference while performing the right force secondary task, similar to the goalkeepers in the study by Tomeo et al. (2012). Similarly, we could train a perceptual group, as per the protocol from Experiment 3, then test them under all the same conditions, expecting no interference (as per Experiment 3). Next we would train them to throw darts, using the same training methods used for the motor-visual group in Experiment 3. Finally we would re-test them under all the same prediction conditions. Because they too should now have both types of representations (Tomeo et al., 2012), we also expect them to still be able to use visual processing methods to solve the prediction tasks without interference.

In terms of the performance of the skilled darts players in Experiment 2, based on the dual-process model outlined earlier, we might have expected these individuals to have performed in a similar manner as the goalkeepers in the previously mentioned study (Tomeo et al., 2012). However, they performed more like the motor-visual group in Experiment 3, showing accuracy levels that were reduced to novice levels, when they performed the right force secondary task. There are several possible interpretations of this result that may not be mutually exclusive. First, although we might expect these participants to have acquired some form of purely visual representations along with the motor representations that we believe they did acquire, it is somewhat unclear as to what those visual representations would consist of. In considering the goalkeeper situation, it is possible that the visual representations that were formed by the

goalkeepers came about through a pressured requirement to react, from a third-person perspective to the kinematics of the approaching kicker, as well as the trajectory of the ball. Thus, these visual representations (goalkeeper) would consist of mostly front-facing elements (Tomeo et al., 2012; Urgesi et al., 2012). Darts players do not face the same pressure to react to a thrown dart (at least not under normal circumstances!). Therefore, it is somewhat unclear what type of characteristics, if any, would make up visual representations of a dart throw, acquired through experience.

In one sense, the results of Experiment 2 would suggest that no visual representations are formed during the acquisition of darts expertise, separate from those formed as part of the internal action model. At least it seems likely, from our data, that any separate visual representations that may have been formed do not reflect a side-view perspective, that is, the perspective that matches that of the prediction task. If they did, then we would have expected participants to have been able to switch, as the goalkeepers were thought to have done, to visually-based processes in order to solve the task. It may be more plausible that this group of skilled darts players could have formed separate visual representations from a first-person perspective. This would provide a more parsimonious explanation of the results for this group. Under this scenario, it would be reasonable to suggest that the reason why this group was unable to switch to a more visually-based prediction process was because the participants' acquired visual representations did not correspond to the perspective of the prediction task. This would also explain the results of the observation group from Experiment 1, who failed to improve on the prediction task presented from a side-view perspective, after observational practice from a first-person perspective.

The questions surrounding the performance of the observational group in Experiment 1 were answered, to some degree, in Experiment 3, where we trained a similar non-motor group perceptually, from the same side perspective as the prediction task, although they were specifically trained to make predictions, using the same task they were later tested on. There are two other ways in which we could examine this issue through further experiments. First, an observational group, like that from Experiment 1, could observe the action from the side perspective, matching the prediction task. Second, we could potentially use a prediction task that presented a first-person perspective, similar to others (Springer et al., 2011, 2013a; Urgesi et al., 2012). This later manipulation would also allow for reassessment of the results of skilled darts players in Experiment 2, as the perspective of the prediction task would now match the perspective, arguably, most likely to have spawned, in the first place, separate visual representations (not coupled to internal action models) during the acquisition of expertise (see Tomeo et al., 2012). As a result, we might then expect the skilled players to be able to switch to a more visually-based prediction process, and thus show less, or no, interference from the secondary motor task.

From the results of Experiment 1, we could not say whether motor system activation was responsible for action prediction, based on the results from the two motor practice groups. While we are confident, based on the results for a similar group in Experiment 3, that the motor-visual group acquired motor representations and used them through simulative mechanisms during prediction, it is still unclear whether motor representations, visual representations, or both were formed during practice for the no-vision group. Re-running Experiment 3 with a no-vision practice group, and using our interference tasks should be able to shed light on this issue.
There remains the question as to why the groups that experienced interference saw their accuracy levels drop to ~50%, rather than to chance levels. There might be several reasons why these scores were above chance. First, these results might be due to the idea that the motor system may be able to utilize generic models of objects in motion to make predictions about similarly structured human action sequences (Grosjean et al., 2009; Shubotz, 2007; Wolfensteller et al., 2007). Presumably, in this case, any simulation of the motor system would not be effector-specific, and thus, while generating noisier and less accurate predictions, would also not be susceptible to interference effects (Pezzulo et al., 2013). Alternatively, these predictions might have come about as the result of the activation of acquired representations that are visually-based models of the general motion of objects in the environment (Hubbard 2005; Motes et al. 2008; Zago and Lacquaniti 2005).

As a proxy of prediction accuracy, measures were taken of participants' confidence in their predictive capability (Jackson et al., 2009; Jackson et al., 2006). For the motor experienced groups, confidence ratings did not relate to prediction accuracy scores (at least at the group level). In Experiment 2, the confidence scores for the Experienced group were not significantly different from those of the novice group, even though their accuracy scores were significantly higher. Similarly, in the two training studies (Exp1 and Exp3), the physical training groups showed no difference in confidence levels pre- to post-test, despite the fact that their accuracy scores improved significantly. Further, even though participants with acquired motor experience exhibited a significant decrement in prediction accuracy when performing the right effectorincongruent secondary task (Exp2 and Exp3), they showed no corresponding decrease in confidence.

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In contrast to the groups with acquired motor experience, the groups that received visual training (Observation group, Exp1; Perceptual training group, Exp3) showed confidence scores that better aligned with their prediction accuracy. The perceptually-trained group in Experiment 3 showed a significant increase in confidence ratings pre- to post-test (which matched what was seen in their prediction accuracy data). The Observer group in Experiment 1, that did not improve their prediction accuracy after two days of observational practice, also did not show an improvement in confidence and, in fact, showed a significant decrease from pre- to post-test.

These results suggest that predictions made using simulative (motor) mechanisms (i.e., for the motor practice/experienced groups) are more implicit in nature, providing little or no metacognitive awareness concerning predictive capability (Kolb & Braun 1995; Kunimoto et al. 2001; Runeson et al. 2000; Tunney & Shanks, 2003). Conversely, predictions that draw off acquired visual representations may be more explicit, allowing the observer some insight into their own (bad or good) performance (Allwood et al. 2000; Dienes et al. 1995; Wright & Burton 1995). As such, confidence ratings may alert to the kind of mechanisms involved in predicting the outcome of an observed action.

5.3 Future work

While we were arguably able to build 'motor-visual' and 'visual-only' representations separately in different groups, others, using expertise paradigms, have been studying the acquisition and utilization of these different representations within the *same* individual (Tomeo et al., 2012: Makris et al., 2014). As was touched on earlier, in terms of future work in this area, it would be fruitful to try to establish, through short-term training techniques, both motor-visual and visual-only representations within the same individual, as was seen in the expert Goalkeepers, described by Tomeo et al. (2012). We would be interested in understanding

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whether participants would still experience interference from a secondary motor task during prediction, and would they be able to switch to using visual representations to solve the prediction task. Similarly, we could ask what the 'default' process is under these controlled training conditions. It has been suggested, based on behavioral and neurophysiological evidence, that motor simulation is the default process during action prediction in experts (Springer et al., 2011; 2013a, b; Tomeo et al., 2012). It is unclear whether the same situation would emerge through short-term training. As part of this potential study, after separate sessions of physical and perceptual training within the same group, secondary motor tasks could be employed, while recording neural activation through the application of fMRI. For the Goalkeepers described earlier, fMRI results showed that, during prediction, activation in motor areas was somatotopically modulated (reduced) after ball strike, leaving the authors to suggest that participants shifted to the use of visual representations at that point (Tomeo et al., 2012). If we gave a group physical training, as well as separate perceptual training, would they show this same cortical modulation during prediction, and switch to using a more visually-based type of prediction when presented with interference? Would the order of training matter to whether they switched or not? Would participants continue to 'simulate' based on body kinematic cues, and only switch based on flight information, or would they switch to using visual representations even when presented with stimuli showing both kinematic and flight information? These questions could be examined by presenting stimuli with either kinematic or flight information, or both together (Urgesi et al., 2012). The results of this exploration could have implications for developing skill acquisition programs, in terms of their emphasis on physical and perceptual training, and the timing of each training modality.

We showed that several kinematic measurements were closely correlated with accurate dart throws. It would be interesting to use eye-tracking information to examine whether these kinematic cues are actually used during prediction, and how this might change over time, as a motor skill is acquired. Linked to the idea that action prediction can come about through several different mechanisms, it would also be informative to explore whether, and how, gaze characteristics change, based on the type of mechanism employed during prediction (simulation/visual matching) (Flanagan & Johansson, 2003).

Research examining the temporal nature of action simulation suggests that simulation occurs in real-time (Demougeot & Papazanthis, 2011; Flanagan & Johansson, 2003; Graf et al., 2007; Papazanthis et al., 2002; Parkinson et al., 2012; Rotman et al., 2006; Springer et al., 2013a, b). Another methodological paradigm that might be of value in exploring the temporal dynamics of action simulation would involve manipulating the speed of dynamic stimuli presented during an action prediction task. If simulation is only activated by real-time dynamic stimuli (video), notwithstanding the fact that we showed that observing static stimuli of implied motion resulted in interference effects, it might be of interest to determine if video stimuli presented in slow-motion (or faster than real-time) would hinder motor simulation (i.e. not produce interference effects from a secondary motor task). That is, could a change in the speed of the stimulus presentation invoke a switch to the use of visual representations to solve the prediction task? Further, eye-tracking could again be used, in this case to examine any shifts in the predictive nature of the gaze profile based on changes in stimuli speed.

5.4 Summary

The experimental results presented in this thesis suggest that the human motor system is activated when predicting the outcomes of others' actions, and has a direct effect on prediction accuracy. We conclude that during skill acquisition the motor commands that produce action, and the consequences of that action, are linked together within a common representational medium (Prinz, 1997; Hommel et al., 2001). The neural correlate of this 'common' representation may be found in mirror neurons, which are activated in the same way when both executing and observing the same action (Rizzolatti & Craighero, 2004).

In neuro-computational terms, skill acquisition may be thought of as the formation of inverse and forward models. When an action is required, it is suggested that an inverse model generates the appropriate motor command, based on the current state of the system and the desired outcome. At the same time, an efference copy of this command is sent to the forward model, which generates a prediction of the sensory consequences of the action. This prediction of the outcome of the action is then compared to the actual sensory feedback (afference) from the action, and the inverse model (motor command) is then updated. Over time, through practice, the inverse model becomes more refined (Miall, 2003).

During action prediction, internal models may be activated by observed stimuli in a similar way, but the motor command is not generated in this case. As such, the efference copy of the motor command is thought to be simulated during action observation, producing a prediction of the action's outcome. In the studies described in this thesis we found that when we interfere with the motor system, by having participants perform a secondary motor task during action prediction, the simulation mechanism breaks down, as indicated by a modulation (reduction) in prediction accuracy. We have shown that this effect is action-specific, as evidenced by a decrement in prediction accuracy when performing an incongruent, but not congruent, secondary action. We further saw that the simulation process is effector-specific, as indicated by a

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significant decrease in outcome prediction, only when participants performed the incongruent secondary motor task with the throwing effector, not the opposite effector.

Importantly, we have also shown that separate visual representations, independent of the motor-visual representations acquired through physical practice, may be acquired through perceptual practice. These representations seem to lie outside the motor system, and, as such, are impervious to motor interference, providing the observer with an alternate mechanism for predicting action outcomes (Tomeo et al., 2012; Urgesi et al., 2012; Mulligan et al., 2015). By controlling visual and motor influences on skill acquisition, we have been able to characterize their differential effects on action prediction, along with the corresponding processes and representations that underlie such effects.

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