VISUOMOTOR ADAPTATION AND OBSERVATIONAL PRACTICE

by

Nicole Tai Tee Ong

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ABSTRACT

It has been suggested that observational practice engages neural mechanisms for movement planning and execution similar to those engaged in physical practice. In three experiments we investigated observational practice during adaptation to a novel visuomotor environment. Participants were tested in the normal visuomotor environment before and after observation, and in the novel environment after observation. In the latter, learning would be seen by immediate performance benefits from watching. In the former, negative after-effects in the normal environment would suggest an updating of internal models based on the visuomotor discordance, arguably a more robust index of learning. In Experiment 1, observers showed benefits in the novel environment, but no after-effects. Because after-effects are believed to be a result of perceived discrepancies between sensory input and predicted sensory consequences, we hypothesised that observational practice might not engage covert simulation involving motor processes to the same degree as initially implied. To more thoroughly test this idea, in Experiment 2 we encouraged more active observation (or simulation) through conditions requiring imagery and error estimation. Despite these manipulations, only actors showed after-effects. In Experiment 3, a group of observers was also passively moved during observation, to determine whether the absence of after-effects was more linked to afferent feedback instead. However, this condition still failed to yield after-effects. A second observer group actively imitated the movements of the actor during observation but this group's performance was not different from that of passive observers. Because the primary difference between actors and active-observers was the lack of self-generated visual reafference, these results strongly suggest that to update internal models, experiencing visual reafference of one's own movement is critical. We speculate that learning might have been realized in observers via a more cognitive-strategic route, as compared to actors, based on data across the three experiments showing that observers acquired more accurate explicit knowledge about the direction and size of the visuomotor perturbation, compared to actors. In conclusion, it appears that doing and seeing engage different processes which in the case of visuomotor adaptation, result in different types of learning and learning outcomes for observers and actors.

TABLE OF CONTENTS

2 Experiment One

LIST OF TABLES

LIST OF FIGURES

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1. INTRODUCTION

An indispensable method in the teaching of motor skills is the use of demonstrations. While we may teach cognitive skills, such as problem solving, in a verbal manner, it is difficult to teach a motor skill, such as batting a baseball without the use of a demonstration. Observational learning can facilitate motor learning by conveying visual cues about a desired movement or coordination pattern (Hodges, Williams, Hayes, & Breslin, 2007). Not only does this shorten the learning process considerably, learning by observation can reduce costly or potentially fatal mistakes, such as committing an error in a surgical procedure (Bandura, 1986).

1.1 Early/late mediation accounts of observational learning

In both observational learning and general skill acquisition, cognitive processes have been thought to play an important role (Bandura, 1986; Gentile, 1972). According to the social cognitive theory of observational learning (Bandura, 1986), acquisition of motor skills are governed by the following four processes: selective attention to spatial and temporal features of the action; formation and rehearsal (retention) of a cognitive representation of the action; translation of the cognitive representation into action; and motivational incentives that impact the other processes, i.e. attention, retention and execution. Importantly, to learn an observed motor skill, a cognitive representation is acquired before its execution and serves as a ‘perceptual blueprint’ that guides the execution of an action. Carroll and Bandura (1987; 1990) provided empirical support for the theory by showing that the accuracy of movement production is mediated by the accuracy or adequacy of the cognitive representation acquired. Enhanced motor learning due to greater cognitive effort involved during observational learning, such as receiving augmented feedback of the model's performance that encourages active problem solving by the observer, adds support to the view that cognitive representation is important to observational learning (Lee, Swinnen, & Serrien, 1994).

More recently, an early mediation account (Vogt, 2002; Vogt & Thomaschke, 2007) has been proposed which casts doubts on the necessity for such cognitive representation in mediating perception and action in observational learning. In the early mediation account, it is proposed that the motor system is involved during observation. In contrast, Bandura's (1986) social learning theory is considered to be a late-mediation account of observational learning where the motor system is only activated during actual movement production (see Maslovat, Hayes, Horn & Hodges, 2010). Supporting evidence for an early mediation account of observational learning is found in behavioural, brain imaging, and neurophysiological studies. Heyes and colleagues (Heyes & Foster, 2002; Bird & Heyes, 2005) showed enhanced retention of an observed motor sequence only when performed with the same effector, implying that effector-specific motor representations are formed during observational practice. Other behavioural support has been shown via interference paradigms, whereby observational learning is impaired when an irrelevant secondary motor task is performed during observational practice, but not when this irrelevant task is cognitive in nature (Mattar & Gribble, 2005).

Theoretical frameworks that would support ideas of early perception-action mediation and the role of the motor system in observation are the simulation hypothesis (Jeannerod, 1995, 2001) and the theory of common coding (Prinz, 1997). In the simulation hypothesis, it is proposed that motor imagery and observation are in fact covert actions involving processes and neural activity similar to that seen in generation of actions. As detailed below, significant support for this hypothesis has been demonstrated through studies of the neurophysiological processes that occur during imagery and observation. The common-coding approach hypothesizes that sensory codes are translated to motor codes through a common representational domain and evidence for common coding has been found in visual-motor and motor-visual priming research. For example, in visual-motor priming, an observed action can facilitate or interfere with the generation of another action depending on the congruency of the observed action to the executed action (e.g., Kilner, Paulignan, & Blakemore, 2003). Further, perceptual discrimination has been shown to be enhanced by the accompanying generation of actions that match what the actor is seeing, so termed motor-visual priming (e.g., Miall et al., 2006). The bi-directional role of perception and action is illustrated in the case of priming studies adding support to the idea that these processes share a common representational scheme.

More direct evidence supporting the idea that action and perception are governed by similar processes and that motor processes are activated during observation comes from brain imaging research, where evidence of shared neural substrates during movement observation and execution has been provided. This shared circuit of activity has been termed the human 'mirror neuron' circuit or system. Mirror neurons were first discovered in the premotor cortex of the macaque monkey (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992), which discharged both when the monkey performed and observed an action. Later on, the equivalent mirror neurons were also found in humans (e.g., Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). Neurophysiological research using transcranial magnetic stimulation (TMS) has directly implicated the involvement of the motor system during observation and motor imagery. During observation or imagery of hand gestures, increased excitability was found in the relevant hand muscles as measured by motor evoked potentials (Clark, Tremblay, & Ste-Marie, 2003). Brown and colleagues (2009) demonstrated that the application of repetitive TMS to the primary motor cortex, after a period of observational practice, adversely affected the consolidation (retention) process. As a whole, evidence for the early mediation account of observational learning appears to be growing.

1.2 Efficacy of observational practice

Learning motor skills through observation has repeatedly been shown to be a beneficial process, in comparison to control conditions where performance is assessed without previous observational experience. Researchers have reported evidence of enhanced retention or transfer (motor learning indices) supporting the efficacy of observational learning for skill acquisition. Improved retention (or "direct-effects") after observational practice has been manifested as an improvement in the performance of the observed motor task, for tasks ranging from the learning of new hand postures (Carroll & Bandura, 1990) to the learning of novel patterns of coordination between the elbow and wrists (Buchanan, Ryu, Zihlman & Wright, 2008; Hayes, Hodges, Scott, Horn & Williams, 2006) and more recently, learning to adapt to novel forces during reaching (Mattar & Gribble, 2005). Also, positive transfer as a result of observational practice in the performance of a related task has been demonstrated (Shea, Wright, Wulf & Whitacre, 2000; Hayes, Elliott & Bennett, 2009).

As discussed, the benefits seen from observational practice provide empirical backing for its application in teaching motor skills, showing that motor skills can be acquired even without physical practice or direct, response-produced feedback. Kohl and Shea (1992) concluded from their research on anticipatory tracking that indirect feedback from observational practice was just as effective as direct feedback from physical practice in achieving more advanced movement response patterns. However, the authors pointed out that as task difficulty increased, the benefit of observational practice suffered more than the benefit of physical practice, indicating that direct feedback from physical practicing was an important component for a high quality, less error-prone performance (also see Mattar & Gribble, 2005).

A number of factors appear to affect the efficacy of observational practice and/or the extent of motor involvement in observational practice. Some tasks, such as those involving dual limb coordination and the learning of new relationships between different joint pairs, do not appear to benefit from observational practice (e.g., Hodges & Franks, 2000, 2001; Maslovat, Hodges, Krigolson & Handy, submitted). After reviewing the observational learning literature, Maslovat and colleagues (2010) hypothesized that the nature or type of task moderates the effectiveness of observational practice (see also Ashford, Bennett & Davids, 2006) and arguably the extent of motor engagement during observation. For tasks that are novel and are not part of the learner's existing motor repertoire (i.e., "new" skills), observational practice has limited benefits, and those benefits that are seen appear to be more strategic in nature. Indeed, evidence from brain imaging literature supports this idea that motor expertise affects the extent of motor involvement during observation. For example, Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard (2006) compared expert male and female ballet dancers who possess similar visual familiarity with male and female ballet actions, but only motoric experience specific to their gender. Motor-related cortical activations were elicited only when dancers observed movements that they performed, rather than watched (see also Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005).

The intention of observers has also been found to affect the motor processes engaged and efficacy of observational practice. Generally, instructions to observe with the intention to imitate has activated more extensive motor-related areas in the brain (Decety et al., 1997; Grèzes, Costes, & Decety, 1998), and demonstrated more direct performance benefits compared to observers who were not required to imitate (Badets, Blandin, & Shea, 2006). There is some suggestion that the perspective of observation, first-person vs. third-person perspective, and skill level of model, expert vs. learning, will differentially affect observation or observational practice (Holmes & Calmels, 2008; McCullagh & Weiss, 2001). One potential reason for the effect of perspective is that first-person viewing promotes an egocentric manner of viewing, such that it is easier for the observer to see themselves as the agent of the action. Indeed, Maeda, Kleiner-Fisman and Pascual-Leone (2002) showed that only during first-person perspective observation were motor-evoked potentials increased corresponding to the effector-specific area of the brain responsible for the observed movement. It has been suggested that a learning model also aids observational practice as it again engages the learner more in the learning process, allowing him or her to benefit from error detection and correction procedures associated with making errors and receiving feedback. However, the effects of model type on observational practice have been fairly mixed (Lee et al., 1994). The effect of model type on learning seems to be confounded by other factors such as model similarity, type of task or availability of model's knowledge of results (McCullagh & Weiss, 2001).

1.3 Adaptation and motor learning

The adaptation paradigm is rather different from the normal type of skill learning that we witness in day-to-day situations. Adaptation studies shed light on the plasticity and nature of sensorimotor coordination (e.g., Redding & Wallace, 1996). In adaptation studies, visual or dynamical perturbations are introduced so that a sensory discrepancy is experienced, requiring modifications to motor commands and/or perception. This type of adaptation learning would be experienced when individuals are required to perform in new environments (such as with microsurgery, virtual reality and computer games, under water or in space). The benefit of using an adaptation paradigm is that it allows the examination of the extent of learning devoid of cognitive control. This is manifested by the presence of ‘after-effects’, which are unintentional remnants of compensatory movements developed in the perturbed sensorimotor environment, which continue when the participant returns to the normal environment. After-effects imply that an implicit, motorically-driven type of learning has occurred and these behavioural effects have been linked to the concept of internal models for motor control and learning.

Motor learning, as defined for these adaptation tasks, involves mastering the sensorimotor transformations or mappings relating motor commands to sensory feedback (Wigmore, Tong, & Flanagan, 2002; Ingram et al., 2000). The concept of internal models has been proposed to help understand how these transformations are realized (Wolpert, Ghahramani, & Jordan, 1995; Wolpert, 1997). Two types of models have been conceptualized: “Forward models” capture the causal relationship between inputs and outputs of the motor system in a given context. “Inverse models” act as controllers that provide the motor commands that are necessary to achieve a desired state. It has been suggested that an efference copy of the descending motor commands combined with a forward model of the relationship between the motor system and the current environment provides a prediction of the upcoming sensory consequences. This prediction affords three things: the ability for the person to distinguish self-generated movement from externally-induced sensory feedback; the control of rapid movements with limited time to process sensory feedback (termed "feedforward control") and third, learning. In this third case, learning involves an update of the forward model based on discrepancies between predicted and actual sensory consequences, leading to modifications in motor output (an update of the inverse model) and sensory predictions (Miall & Wolpert, 1996). It has been suggested that the forward model is updated before the inverse model and plays a role in the training of the inverse model (Flanagan, Vetter, Johansson, & Wolpert, 2003; Wolpert, 1997; Miall & Wolpert, 1996). In relation to internal models, researchers have considered the presence of after-effects to be an indication that the transformations between sensory input and motor output, as represented by internal models, have been updated (Shadmehr & Mussa-Ivaldi, 1994; Kagerer, Contreras-Vidal, & Stelmach, 1997; Kagerer, Bo, Contreras-Vidal & Clark, 2004; Krakauer, Ghilardi, & Ghez, 1999; Bernier, Chua, Bard, & Franks, 2006; Gandolfo, Mussa-Ivaldi, & Bizzi, 1996).

In this series of experiments, our purpose is to test the early mediation account of observational learning using a visuomotor adaptation paradigm, to determine whether motor-related processes are involved during observational practice. As discussed earlier, the adaptation paradigm allows us to examine behavioural effects without contamination from cognitive control or the use of strategy, which could be useful for assessing motor involvement in observational learning. Also, by manipulating the adaptation conditions, we hope to be able to determine the sensorimotor processes responsible for observational practice and highlight similarities or differences between observational and physical practice. At the same time, the use of observational practice in an adaptation paradigm would help elaborate upon the processes necessary for sensorimotor adaptation.

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2. EXPERIMENT ONE

Absence of after-effects for observers after watching a visuomotor adaptation[1]

Various authors have provided evidence that observation enhances performance without physical practice (e.g.; Carroll & Bandura, 1990; Buchanan, Ryu, Zihlman & Wright, 2008; Hayes, Hodges, Scott, Horn & Williams, 2006; Porro, Facchin, Fusi, Dri & Fadiga, 2007), and in combination with physical practice (e.g. Shea, Wright, Wulf & Whitacre, 2000; Blandin, Lhuisset & Proteau, 1999). A meta-analysis conducted by Ashford and colleagues (2006) showed an advantage for observational practice over physical practice alone, in approximating movement form. Researchers have also shown that observational practice can lead to qualitative changes in how movements are strategically executed, such as anticipatory tracking (Kohl & Shea, 1992), as well as how movements are scaled or parameterized (Hayes et al., 2006). These latter two were both traditionally thought to require overt practice. Most recently there has been evidence that observational practice can lead to the adoption of a new sensorimotor mapping of the task environment, in the form of adaptation to a dynamic force perturbation during observation of reaching movements (Brown, Wilson & Gribble, 2009; Mattar & Gribble, 2005). This result leads one to question any qualitative process distinctions between physical and observational practice.

Although observational practice results in enhanced performance of the motor task that is observed, termed “direct-effects”, another assessment of learning, typically used in adaptation

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studies, allows examination of the durability and persistence of the learning experience. This has been shown through the presence of compensatory actions, termed “after-effects”, in a post-practice transfer condition where such compensations are unnecessary. After-effects have been shown in participants who had physically adapted to dynamical perturbations of the limb during movement (e.g. Shadmehr & Mussa-Ivaldi, 1994; Scheidt, Reinkensmeyer, Conditt, Rymer & Mussa-Ivaldi, 2000; Kurtzer, DiZio & Lackner, 2005) and to perturbations to the visuomotor environment (e.g. Redding & Wallace, 1993, 2002; Clower & Boussaoud, 2000; Baraduc & Wolpert, 2002). Although the presence of after-effects has been well-documented with physical practice, this form of assessment has not been applied to assess the effectiveness of observational practice.

A current point of deliberation in observational learning is when in the learning process the motor system is involved; leading to the terms ‘early’ and ‘late’ (perception-action) mediation (Vogt, 2002; Vogt & Thomaschke, 2007). Conventional views of observational learning, such as the cognitive mediation hypothesis of Bandura (1986; Carroll & Bandura, 1990), are considered late mediation accounts, where motor involvement takes place during movement production itself. A cognitive representation is formed during actual observation which guides the subsequent production of, or serves as a reference-of-correctness for, movement.

Advancements in neuroscience have led to the discovery of distinct populations of cortical neurons in the premotor cortex, inferior parietal lobule and the superior temporal sulcus, which have been termed the human ‘mirror neuron system’ (see Rizzolatti & Craighero, 2004 for a review). These motor-related cortical activations, activated both during observation and execution of a movement, support the notion that motor processes are already involved at the observation stage of learning (e.g., Gallese, Fadiga, Fogassi & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese & Fogassi, 1996). Although the exact reasons for this mirror neuron circuit in the brain are debated, one proposal is that covert action simulation takes place during observation which allows for third-party understanding of an action and imitation (Jeannerod, 2006). Evidence for a human mirror neuron system supports the early mediation account of observational practice, although it is unknown whether or under what conditions this system is activated when learning new skills, and if it is activated, what role it plays in learning (in comparison to more strategic/representational routes).

Results from behavioural studies demonstrating effector specificity during observation (Heyes & Foster, 2002; Bird & Heyes, 2005) and learning of novel force dynamics (Brown et al., 2009; Mattar & Gribble, 2005) further provide support for an early mediation account of learning by observing. Beyond demonstrating that observers can acquire subtle features of movement dynamics by compensating for perturbation forces in a novel mechanical force field, Mattar and Gribble showed interference during observation with the simultaneous performance of an unrelated motor task, but not with a cognitive (arithmetic addition) task. The authors argued that performance enhancement following observation was not due to the explicit formation of strategies. Rather, they attributed the phenomenon to the direct involvement of the motor system during observation. Subsequently, Brown and colleagues showed that repetitive transcranial magnetic stimulation (TMS) over the motor cortex interfered with the retention processes between observing and acting, again suggesting a significant role of the motor system in motor learning through observation.

The primary implication of Gribble and colleagues' research is that the processes involved during both physical and observational practice are not qualitatively different, that is the types of processes engaged are similar, even if the degree of engagement differs. A stronger test of this proposal, would be to examine whether the behavioural outcomes of physical practice and observational practice are equivalent. If direct-effects and after-effects were demonstrated following observational practice, but to a different degree compared to physical practice, it would indicate that similar learning processes were involved that differed only in their intensity. In contrast, if after-effects were present after physical practice yet absent following observational practice, different processes would seem to be implicated for the two types of practice. No attempts have been made to look at "after-effects" among observers on transfer to a normal environment in studies of adaptation learning to date.

The purpose of the current study was to test for the presence of after-effects in a group of observers following exposure to an actor adapting to a visuomotor rotation. Although we used a different task, from that in Mattar and Gribble (2005), where perturbations were applied to the visual environment rather than directly to the aiming limb, similar effects were expected. Redding and Wallace (1993; 2002) for example, have shown after-effects in actors following exposure to these perturbed environments and these after-effects have been seen in both computer-generated perturbed environments as well as following the wearing of displacement goggles (Cunningham & Welch, 1994). In order to provide discrepant information to observers during the adaptation phase, observers in our experiment saw both the actor's hand as well as the perturbation to the cursor trajectory; this means they could see the correctness (or error) of the movement under perturbed conditions. Because the actors only saw the cursor trajectory (and hence the discrepancy was alerted by proprioceptive means), any group differences could potentially be attributed to differences in the visual information provided to the actors and observers (i.e., observers also saw the movement of the hand). Therefore, a second group of actors was provided visual information of both their arm and the cursor trajectory during adaptation to the visuomotor rotation, in order to match the visual information provided to the observation group.

If action observation involves similar processes to those engaged during execution, then we should expect to see both evidence of the ability to adapt to the novel environment, and evidence of after-effects when performing under normal (non-perturbed) conditions, in both our observers and actors. The absence of after-effects in the observers only would suggest that unlike actors, observers did not update an internal model of the visuomotor environment suggesting different processes underpinning observational and physical practice.

2.1 Method

2.1.1 Participants and groups

Thirty, right-handed participants volunteered to participate and they were equally assigned to three groups; two Actor groups (with or without vision of their hand) and an Observer group. Handedness was confirmed using the ten-item version of the Edinburgh Handedness inventory (Oldfield, 1971). The Actor group with no vision of the hand (Actor-No hand; *n* = 10; mean age = 26.5, *SD* = 3.8 yr; 6 females) and Observer group (*n* = 10; mean age = 26.7, *SD* = 4.4 yr; 4 females) were randomly assigned to either one of the groups in pairs. Participants in the Actor group who saw their hand (Actor-Hand; *n* = 10; mean age = 24.0, *SD* = 3.5 yr; 6 females) were assigned last. This group was tested at a later time to control for differences in the visual information between the Actor and Observer groups. All participants reported normal or corrected-to-normal vision, no hand injury and no known neurological disorders. None of the participants had previously participated in similar adaptation studies. A remuneration of $8/hour was paid to participants for their involvement. Informed consent was obtained for all participants according to the ethical guidelines of the University of British Columbia.

2.1.2 Task and apparatus

Participants sat in a chair facing a horizontal, semi-silvered mirror, fixed 30 cm above a graphics tablet (Calcomp Drawing Board III, 225 Hz, 200 lines/cm resolution) that measured 2D position, as illustrated in Figure 2.1 (A). A PC (500 MHz Intel pentium processor) was used to run data collection (sampled at 500 Hz), reduction and analysis programs (Turbo Pascal 6.0). A monitor, set up at 30 cm above the mirror, reflected an image of the visual stimuli (targets and starting square, see Figure 2.1, B) and trajectory of the cursor onto the mirror. The cursor (a circular spot of 1.5 mm diameter) was controlled by participants using a mouse and custom-made pointing device that was attached to the right index finger. The visual stimuli consisted of a central starting square (0.5 cm inner length) and 5 radially arrayed targets (0.25 cm inner diameter) positioned 10 cm from the starting square. Targets were separated by 72°, starting at location 0° through 288° (as shown in Figure 2.1, B).

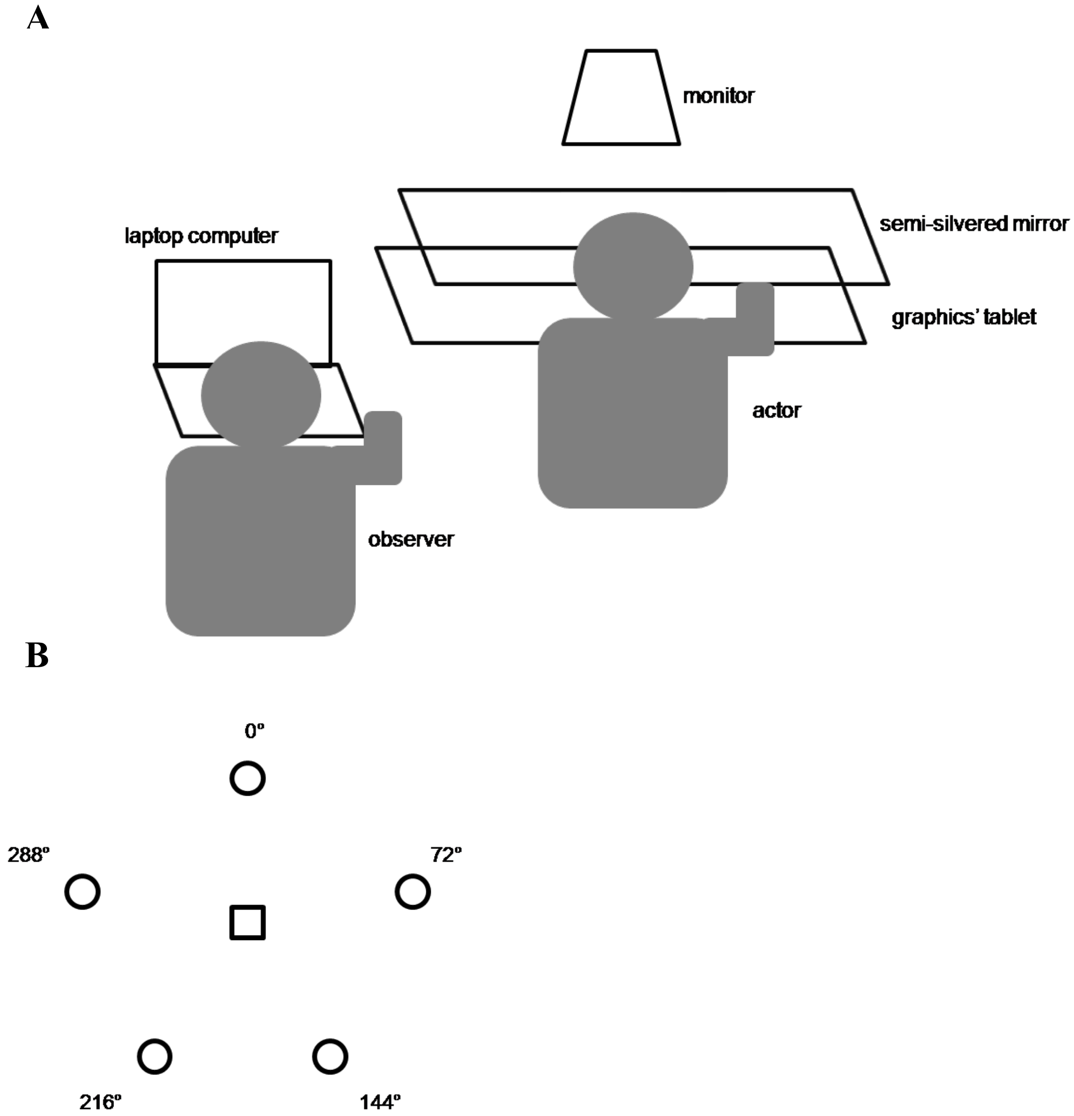

Figure 2.1 Experimental set up (A) showing the relative positions of the actor and observer and (B) an image of the 5 targets (which were depicted in green) along with the starting square (which was shown in red)

Each of the five radial targets was presented in a pseudorandom manner during a cycle of five trials. Participants had to reach for a target with their right index finger in a fast, smooth action. Instructions for the task were to make the movement as straight and uncorrected as they could. They were to move the cursor 'through' the targets at an average movement time shorter than 250 ms to prevent online correction of movement (see Bernier, Chua, Bard & Franks, 2006). If on average, participants took longer than 250 ms per trial for a cycle of five trials, the experimenter prompted them to move faster before the start of the next cycle. After coming to a stop for each trial, participants were allowed to move the cursor back to the starting square without time constraints. The next cycle began when the cursor was within the starting square for a continuous period of 700 ms. On moving the cursor back to the starting square, vision of the cursor was occluded until the cursor was within a 4 cm radius of the origin (centre of the starting square).

During the adaptation condition, the Actor-No hand group viewed the visual targets and the perturbed cursor trajectory on the mirror. The Actor-Hand group viewed the visual targets, perturbed cursor trajectory as well as the movement of their hand (alerted through panels of white light-emitting diodes attached to the underside of the semi-silvered mirror). Observers, who were yoked to the Actor-No hand group, viewed an actor's hand, along with the visual targets and perturbed cursor trajectory in real time (see Table 2.1 for further details about group differences). The observers viewed the movements of the actor on a laptop computer (Toshiba Tecra, 1.66 GHz), via a web camera (Logitech Quickcam Pro 9000) that was installed at an angle which captured both the hand and cursor movements of the actor. The size and radial distance of targets from the starting square were scaled to approximately 85 % on the laptop projection video. The observer sat directly in front of the laptop which was placed parallel to the actor during the adaptation phase of the experiment. Observers were instructed to keep their right hand stationary on the table, next to the laptop (see Figure 2.1, A).

Table 2.1 Experimental phases and their associated visuomotor conditions as a function of group

Condition/Group	*# Blocks*	*# Cycles*	*# Trials*	*Perturb*	*Cursor*	*Hand Vision*
Pretest	2	10	50	No	No	No
Adaptation:						
Actor-No hand	8	40	200	30°	Yes	No
Actor-Hand	8	40	200	30°	Yes	Yes
Observer	8	40	200	30°	Yes	Yes
First Posttest	2	10	50	No	No	No
Second Posttest[1]	2	10	50	30°	Yes	No

[1] Only the Observer group completed this condition.

2.1.3 Design and procedure

The experiment was divided into three phases; pretest, adaptation, posttests (as detailed in Table 2.1). For the first posttest, 6 of the actors in the Actor-No hand group performed this test immediately following the adaptation phase, before their yoked observer. This order was switched for the remaining four actors in the group. Before beginning the experiment, all participants were given the opportunity to familiarize themselves to the general task demands in a normal visuomotor environment for 10-20 trials (2-4 cycles). A normal visuomotor condition is where the movement of the cursor is veridical to the movement of the participant, such as when one is operating a mouse to move a cursor across a computer monitor. After familiarization, they sat for a pretest, also in a normal visuomotor environment, providing a baseline performance measure. During the adaptation phase, both groups of actors completed 200 trials (40 cycles/8 blocks) in a perturbed visuomotor environment where the cursor was rotated 30° clockwise (CW) to the starting square. Therefore, to reach each target successfully, participants had to compensate by directing their movement 30° counterclockwise (CCW) to their normal trajectory. After every 2 blocks of 50 trials (10 cycles), the actors were given a short rest.

The observers viewed the Actor-No hand group's adaptation to the visuomotor rotation during the adaptation phase and were informed before viewing that they would be required to perform under the same perturbed visuomotor rotation condition in a later posttest. During the first posttest, all groups completed 50 trials (10 cycles) in a normal visuomotor environment. They were also told before the start of the trials that this first posttest was the same as the pretest, which required participants to aim in a normal environment. The Observer group then completed a second posttest of 50 trials (10 cycles) in a 30° CW visuomotor rotation with prior knowledge that it was the same condition as the adaptation condition which they had previously watched.

At the end of the experiment, participants were asked to indicate by drawing on a diagram where they thought they had to move their hand in order to reach accurately to the 0° and 216° targets during the visuomotor rotation. This provided an indication of the participants' explicit knowledge of the direction and size of compensation of movement they had to make in the perturbed environment.

2.1.4 Data reduction and analyses

Although we prompted our participants to aim for an average movement time of 250 ms for each cycle of trials, we did not enforce this criterion strictly. To verify if online corrections occurred, a Pearson's correlation analysis was conducted on all trials for each individual. There was a relatively high correlation between constant error (CE) at peak velocity and CE at movement end, mean $r = 0.98$ for both Actor-Hand and Observer group, and mean $r = 0.87$ for the Actor-No hand group. Hence, all movement trials collected were included in the following analyses.

Displacement data collected from the graphics' tablet were filtered using a fourth-order Butterworth digital low-pass filter (10 Hz, 2 pass). Tangential velocity was obtained using the three-point differential technique.

Movement initiation was considered to be the first data point where the centre of the cursor was more than 0.25 cm from the origin. The movement end point was the point where the centre of the cursor passed a radius of 10 cm from the origin. Movement direction was measured as the angle from the origin to the position of the cursor at peak tangential velocity. Directional error of movement from the intended radial target was calculated as the difference between movement direction at peak tangential velocity and target location. A positive value or negative value for error denoted a CW or CCW directional error respectively.

Mean directional constant error was computed for each cycle of trials. Mixed-factor analyses of variance (ANOVA) were performed for aiming movements in the normal visuomotor conditions (i.e. pretest and first posttest) to test for after-effects, and under perturbed conditions, that is across practice blocks (which was the second posttest for the observers), to test for direct-effects of adaptation to the perturbation. Group (Actor-No hand, Actor-Hand, Observer) was the between-subjects' factor, while Time (pretest, first posttest); Block (each block consisted of 5 cycles) and Cycle (cycle 1 to 10, where 1 cycle was equivalent to 5 trials) were within-subject factors. Partial eta squared (η^2_p) values are reported as measures of effect size and post-hoc analyses were conducted using Tukey HSD procedures ($p <. 05$). Where violations to sphericity were observed, Greenhouse-Geisser corrections to df were applied.

2.2 Results

2.2.1 Adaptation

A 2 Group x 8 Block ANOVA was conducted on the two Actor groups' performance over the course of adaptation to the visuomotor perturbation (this was based on n = 9 for the Actor-No hand group as data were corrupted for one participant in the 5th and 6th block). As illustrated in Figure 2.2, both Actor groups improved in performance over the 8 blocks of practice. This was supported by a main effect of block, characterized by a significant linear trend component, $F(1,17) = 316.47$, $p < .001$, $\eta^2_p = .95$. There was a significant difference between the two Actor groups, $F(1,17) = 9.09$, $p < .01$, $\eta^2_p = .35$, and a two-way interaction of Group x Block that approached conventional levels of significance, $F(3.1,52.2) = 2.70$, $p = .054$, $\eta^2_p = .14$. Post-hoc analyses showed that there were no significant differences between the Actor groups for the first block and the last 3 blocks of adaptation, although all other practice blocks were different. Vision of the hand led to slower improvement for the Actor-Hand group, but it did not adversely affect their eventual level of performance in the perturbed environment.

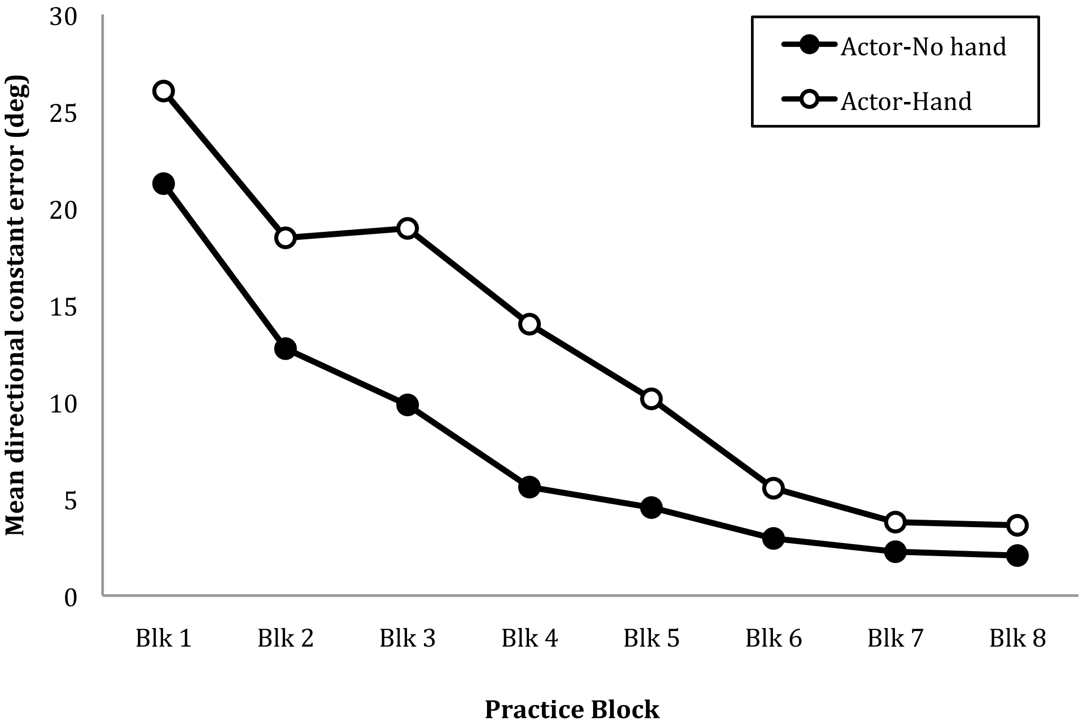

Figure 2.2 Performance error of Actor groups (Actor-No hand and Actor-Hand) over the course of adaptation to the 30° CW visuomotor rotation (a positive value means that error was in the CW direction to the intended target)

2.2.2 First posttest (after-effects)

Performance error for all groups during the pretest and the first posttest are illustrated in Figure 2.3. A 3 Group x 2 Time x 2 Block ANOVA yielded a main effect of Group, $F(2,27) = 47.72$, $p < .001$, $\eta^2_p = .80$, with the Observer group demonstrating less error overall than both Actor groups, and the Actor-No Hand group showing more error than the Actor-Hand group. There were also significant time, $F(1,27) = 220.78$, $p < .001$, $\eta^2_p = .89$ and block effects, $F(1,27) = 4.34$, $p < .05$, $\eta^2_p = .14$, showing that error increased from pretest (M = -1.7°, SD = 1.7) to posttest (M = -9.2°, SD = 7.3) and that performance on the first block (M = -5.7°, SD = 7.1) was generally more errorful than performance on the second block (M = -5.2°, SD = 5.8).

More importantly, a significant two-way interaction was found for Group x Time, *F*(2,27) = 90.84, $p < .001$, $\eta^2_p = .87$. The groups did not differ in their pretest performance (see Figure 2.3) but they all performed significantly differently from one another in the posttest. An increase in error in the CCW direction is an indication of compensatory reaching and hence persistence of adaptation in the unperturbed posttest. Comparison of the pretest and posttest error scores for each group showed that only for the two Actor groups was there a significant increase in error, indicating the presence of after-effects. In observers, these after-effects were absent. The three-way interaction was also significant, *F*(2,27) = 9.70, $p = .001$, $\eta^2_p = .42$. Post-hoc analyses revealed that this interaction was due to an improvement in accuracy from Block 1 to 2 in the posttest for the two Actor groups only, as well as an increase in error for the Actor-Hand group from Block 1 to 2 in the pretest, which was not seen in the other groups.

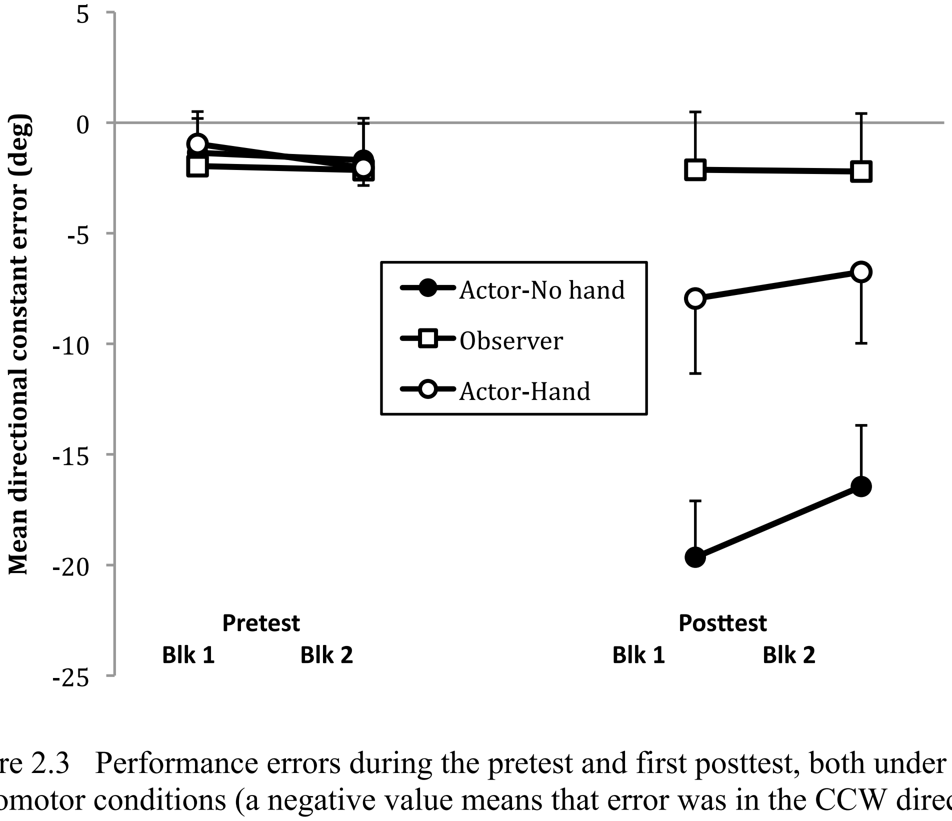

Figure 2.3 Performance errors during the pretest and first posttest, both under normal visuomotor conditions (a negative value means that error was in the CCW direction to the intended target). Error bars = *SD*

2.2.3 Second posttest (direct-effects of observation)

A 3 Group x 10 Cycle ANOVA was conducted on the first ten cycles of the Actor groups' adaptation to the 30° clockwise rotation (n = 8 for the Actor-No hand group due to one missing cycle of data for 2 participants) and the ten cycles completed by the Observer group during the second posttest. As illustrated in Figure 2.4, the Observer group was more accurate (*M* = 6.1°, *SD* = 9.1) than the Actor-No hand (*M* = 17.6°, *SD* = 6.7) and the Actor-Hand (*M* = 22.3°, *SD* = 9.0) groups, which did not differ in their performance for the first 10 cycles of adaptation. This was supported by a main effect of group, $F(2,25) = 22.86$, $p < .001$, $\eta^2_p = .65$. These results show that observation significantly benefitted subsequent performance in the same visuomotor environment as observed.

There was a significant two-way interaction of Group x Cycle which was characterized by a significant linear trend component, $F(2,25) = 4.63$, $p < .05$, $\eta^2_p = .27$. The actors demonstrated a more pronounced linear decrease in error over the ten cycles of adaptation compared to the observers. As can be seen from Figure 2.4, this was probably due to the greater accuracy shown by the observers during the first few cycles and hence the appearance of a plateauing in performance sooner than that seen in the Actor groups.

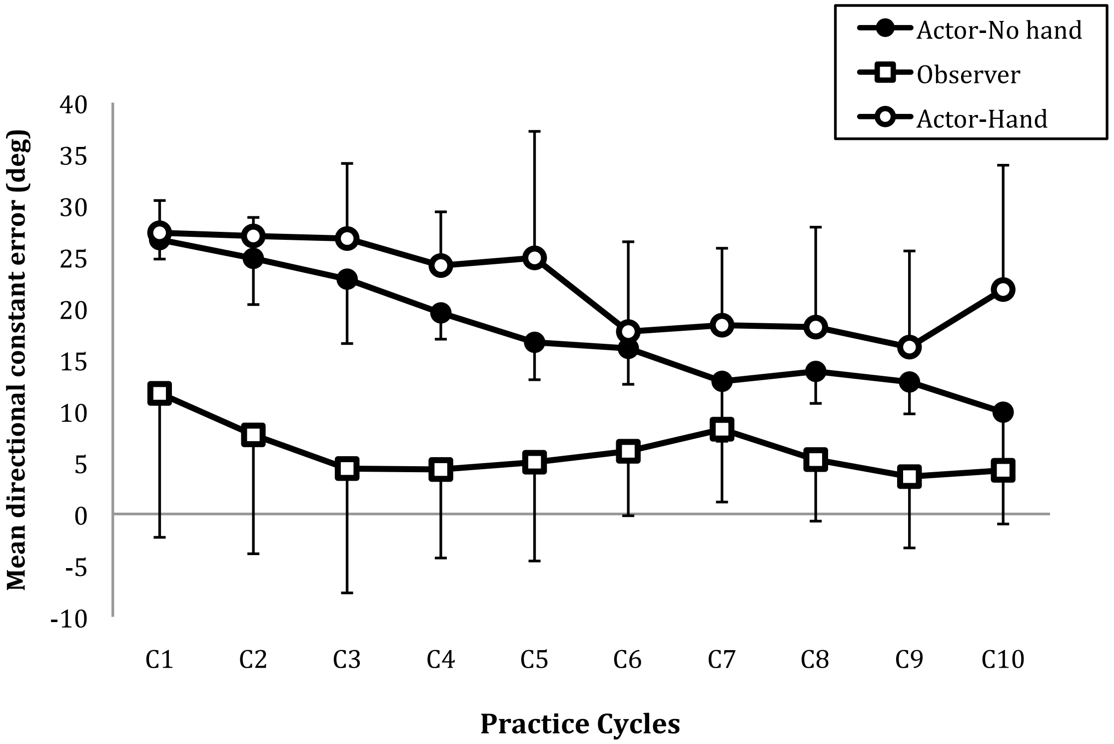

Figure 2.4 Performance errors during the second posttest for observers compared to Actor groups' first 10 cycles of adaptation to the 30° CW visuomotor rotation (a positive value means that error was in the CW direction to the intended target). Error bars = *SD*

2.2.4 Explicit knowledge

Only 4 out of 10 actors in the Actor-No hand group accurately indicated the direction of their hand movement to the target which would be needed to compensate for the visuomotor perturbation. Two actors indicated the wrong direction and the remaining 4 were inconsistent about the direction of compensation. The Observer and Actor-Hand groups were better able to report the required compensation. Eight participants in each group indicated the direction accurately whereas only two participants from each group were inconsistent about the direction of compensation. Of the participants who could indicate the direction of compensation accurately, the average size (and SD) of the reported compensations were; Actor-No hand, 13.4° (1.7); Actor-Hand, 20.1° (6.2); and Observer, 21.9° (8.7). Recall that the actual size of the perturbation was 30°. There were no apparent differences in performance error between observers who reported accurate explicit knowledge of the perturbation (pretest: *M* = -1.94, *SD* = 2.34; posttest 1: *M* = -1.77, *SD* = 2.70) and those who were incorrect or inconsistent (pretest: *M* = -2.52, *SD* = 1.98; posttest 1: *M* = -3.76, *SD* = 0.68).

2.3 Discussion

The purpose of Experiment 1 was to compare the behavioural effects of observational practice and physical practice in a visuomotor adaptation paradigm in order to make inferences about the processes governing observational practice. In support of Brown et al. (2009) and Mattar and Gribble (2005), the observers had learned to adapt to the new perturbed environment, as evidenced through their performance on the second posttest. Compared to the rate of adaptation of both actor groups during their first 50 trials, the observers were more accurate during initial physical exposure to the visuomotor perturbation. This finding speaks to positive effects of observational practice in terms of time savings on transfer to the observed visuomotor skill. These 'direct-effects' (Redding & Wallace, 1993) show that the observers had learned the transformations necessary to move their arm to the correct location in order to appear to reach accurately for the target through control of the cursor. However, it is not known how these direct-effects were realized and whether this learning was due to the activation of similar processes in both actors and observers. The more robust index of learning, i.e. after-effects, point to potential differences in processes between observational practice and physical practice. Both groups of actors showed after-effects when transferred to a normal environment, even with explicit knowledge of this transfer, but no evidence of after-effects were seen in any of our observers. These discrepancies in the behavioural effects of physical and observational practice serve to question the similarity of the processes which are purported to underlie these types of learning, and specifically the suggestion that the motor system is implicitly activated during observation (Mattar & Gribble, 2005).

The absence of after-effects in our observers cannot be attributed to the additional visual feedback of the hand for the observers alerting them to the perturbation introduced to the cursor. The Actor-Hand group, who received the same type of visual information as the observers, did show after-effects. Rather, the difference between the Actor groups and the observers must be due to the physical practice aspect of the movement, either in terms of the active sending of motor commands and the generation of an associated efference copy of the movement or in terms of the availability (and generation) of veridical sensory feedback. In other research, after-effects have been demonstrated in the absence of proprioceptive feedback. Bernier et al. (2006) showed that a deafferented person was able to adapt to a visuomotor rotation, when alerted to the visuomotor discrepancy through purely visual means. Further, this individual showed comparable after-effects to non-deafferented control participants, suggesting that experience of proprioceptive feedback is not the reason for the lack of after-effects in our Observer group. Bernier and colleagues argued that an internal model was updated due to a discordance between two sensory inputs: visual feedback and the predicted sensory consequences of these motor commands (generated from the efference copy). The absence of after-effects in our observers might therefore be attributed to the absence of this latter process and the lack of prediction of sensory consequences. However, it is also possible that the lack of afference, or self-generated visual feedback (reafference) as would be available to a deafferented individual, could be responsible for the absence of after-effects and these more general indices of learning.

There are a number of possible reasons for the differences between the Actor and Observer groups and the lack of compatible conclusions with Mattar and Gribble (2005). One difference between Mattar and Gribble's study and the present study is the extent of explicit knowledge acquired by the observers. The majority of the observers in Mattar and Gribble's study did not accumulate explicit knowledge of the mechanical forces applied to the actor in the video (as assessed through debriefing). Although visuomotor rotations do not necessarily promote learning in an explicit fashion, as shown by participants in the present Actor-No hand group (see also Werner & Bock, 2007), it appears that the manner of learning and hence the degree of explicit or implicit adaptation, is moderated by the presentation of visual feedback of the actual movements of the hand coupled with the perturbed cursor trajectory. Despite the fact that we did not directly manipulate the degree of explicit learning and hence acquisition of explicit knowledge (as did Mattar and Gribble), it appears that receiving discrepant information through visual sources resulted in a greater accumulation of explicit knowledge of the direction and size of the visuomotor rotation. This in turn moderated both the rate of acquisition and the size of the after-effect.

The reduction in after-effects, and by implication the weaker learning in the Actor-Hand group compared to the Actor-No hand group, could be explained in terms of the difficulty in adapting to the visuomotor perturbation when veridical vision of the hand is simultaneously available with the perturbed cursor trajectory. If participants can always see the trajectory of the hand then arguably the movement of the cursor may be ignored or perceived to be an erroneous representation of their hand movement. Clower and Boussaoud (2000; also see Bedford, 1999) discussed the impact of perceived error on the type of adaptation (i.e., the difficulty experienced in reverting to the original visuomotor mapping after learning a new mapping). Accordingly, the error causing the discrepancy between visual input and motor output could be perceived as an ‘internal’ or ‘external’ cause. A perceived internal error results in realignment between the sensorimotor systems leading to the appearance of after-effects while a perceived external error could result in the formation of a strategy and could make switching back to the original visuomotor mapping (lack of after-effects) easier. In this case, the discrepancy experienced between visual feedback and motor output could be attributed to an external cause instead of an intrinsic misalignment, leading to the seen reduction in after-effects.

Importantly, despite the moderation of after-effects in the Actor-Hand group, after-effects were still seen for this group, whereas no after-effects were seen for the observers. Furthermore, observers who did not show evidence of explicit knowledge pertaining to the correct rotation, did not demonstrate after-effects, nor did they differ in their performance error in the first posttest. Therefore, we would argue that the processes of learning were qualitatively different for the Observer group and more specifically that they did not involve a remapping of the relationship between sensory feedback and motor commands. There is also suggestion that the nature of the task moderates the extent of motor engagement during observation (Maslovat, Hayes, Horn & Hodges, 2010; Vogt & Thomaschke, 2007). From a review of behavioural and neurophysiological research, Maslovat et al. hypothesized that the more implicit the motor tasks or environments (i.e., requiring subtle or difficult to perceive changes in performance that are not amenable to strategic understanding), the more engaged the motor system will be during observation (i.e., early mediation). It could be argued that rule or strategy formation is more plausible for observers in visuomotor adaptations requiring limb trajectory modification, than in dynamical adaptations which entail more implicit changes in motor patterns and force activation. Therefore, the apparent lack of motor involvement in the current task could be due to the relative ease of applying cognitive strategies during observation to the acquisition of knowledge about how to move in new visuomotor environments, in comparison to more dynamic, movement perturbed tasks.

It was possible that because we did not include specific checks to ensure that our observers paid full attention to the video as Mattar and Gribble (2005) did. Our observers might have been less involved in the learning process. Therefore, the lack of motor involvement from observation might have been moderated by the degree of active involvement in the observation process. However, by yoking our observers to an actor and informing them before the observation condition that they would be assessed under the same conditions should have created a motivating learning environment. Indeed, because the observers showed significant direct-effects from watching when transferred to the perturbed environment, this would provide evidence that the observers were engaged in the task. We do not know how many trials of observation were significant to bring about these direct-effects and there is the possibility that after only a few blocks of watching, a rotational strategy could be acquired and used to advantage in the posttest. Indeed, it might be the case that the observers' attention waned once this strategy was acquired, perhaps accounting for the lack of after-effects. Without testing this more quantitative, attention hypothesis, through manipulations of the number of trials the observers watched, we are unable to rule out this possible attentional difference between the actors and observers.

In conclusion, our current findings show that observational practice is a beneficial learning tool, but that the motor system is not necessarily involved during observation. Due to behavioural differences in how performers respond to transfer tasks, following either observational or physical practice, we argue that the processes underpinning these two types of practice lead to different types of learning.

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3. EXPERIMENT TWO

Failure to update an internal model through combined observation, imagery and movement estimation[2]

In Experiment 1, we concluded that the processes underlying physical and observational practice appear to be qualitatively different, based on the absence of after-effects in observers compared to actors, despite significant direct learning advantages for observers. We hypothesized that the absence of after-effects was the result of a failure to update an internal model of the environment which could be related to either the lack of generation of an efference copy of a planned movement or the lack of afferent feedback associated with moving – either would prevent the detection of a discrepancy between predicted and actual sensory consequences. Because of existing evidence showing that proprioceptive feedback was not essential for the updating of an internal model in a deafferented individual (Bernier, Chua, Bard & Franks, 2006), based on the presence of both direct and after-effects, we speculated that the generation of efference copy and associated prediction of sensory consequences was likely to be the process missing in observers in Experiment 1. Therefore Experiment 2 was designed to try and elicit this type of process in observers through manipulations designed to make observers more actively engaged during observation and specifically to simulate the action necessary for a particular outcome through estimation and imagery. Our aim was to promote a type of learning or behavioural effect more similar to that seen in actors, merely by changing how the observation process takes place.

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[2] A version of this chapter will be submitted for publication. Ong, N. T. and Hodges, N. J. (2010). Failure to update an internal model through combined observation, imagery and movement estimation.

There is evidence that the type of instructions and intentions of observers mediates the effectiveness and type of processes engaged during observational practice. In a positron emission tomography experiment, only when participants were assigned to a group that observed with the purpose of reproducing the actions later (imitate), compared to ‘passively’ observing, were activations along the dorsal pathway, associated with programming and visual control of skilled movements, seen (Grèzes, Costes, & Decety, 1998). Similarly, Decety and colleagues (1997) showed that only observation under instructions that emphasized watching with the purpose of imitation, rather than recognition, were brain regions activated that were involved in the planning and generation of actions. Behavioural differences have also been observed as a function of the instructional set of the observer. For example, Badets, Blandin and Shea (2006) found that the intention to later imitate influenced how learning was achieved in a sequence timing task. Observers who watched with the intention of later imitation improved more on the relative timing of the movement, in comparison to a group who had not received these instructions. These results, along with the brain imaging studies, show that the instructions and intentions of observers mediate the observation process, both in terms of what is perceived and or remembered as well as the neural processes engaged during observation. In our first experiment, although participants were informed that they would have to perform the reaching task under the same perturbed environment (i.e., the intention to imitate), it was possible that our adaptation task requiring unimanual reach movements was not as engaging or challenging as tasks requiring imitation of hand movements or sequences, perhaps leading to a more passive mode of observation.

In the following experiment, we introduced a more ‘active’ observation condition in order to keep participants maximally engaged in the task. In addition to watching with the intention of later production, participants were required to verbally estimate the trajectory of the model's hand movement. The purpose of estimating hand movement trajectory was to try to encourage a process that might have been missing in the observer group in Experiment 1, that is the sending of an efference copy and prediction of the sensory consequences associated with action. We postulated that this estimation of the model's actual hand position in relation to the perturbed cursor trajectory would promote simulation of the action by the observer leading to an updating of what has been termed the forward model (e.g. Wolpert, Ghahramani & Jordan, 1995). An updated forward model is expected to lead to accurate translation of performance errors into corresponding errors or adjustments in the motor command, leading to an updating of the inverse model and the subsequent appearance of after-effects (Miall & Wolpert, 1996).

Another way of encouraging more active simulation during observation is to engage in imagery during observation. Researchers have postulated that similar neural activities take place during covert simulations, such as motor imagery and action observation, as seen during overt execution of actions (Jeannerod 2001; 2006; Clark, Tremblay & Ste-Marie, 2003; Holmes & Calmels, 2008; Morris, Spittle & Watt, 2005; Mulder, 2007). These neural (both cortical and subcortical) activations are presumed to facilitate movement due to an increase in excitability of the corticospinal pathways or facilitate subsequent movement attempts through rehearsal of similar neural areas involved in execution (Jeannerod, 2006).

In a sequencing task requiring accuracy and speed, Gentili, Papaxanthis and Pozzo (2006) reported positive direct-effects after motor imagery practice on parameters related to movement speed, despite the fact that there was no evidence of electromyographic activity in the muscles that would be responsible for the movement during practice. Further, an eye-movement-practice-only group failed to show the same improvement as the imagery-training group. Therefore, the motor-related improvements found in the imagery-training group did not appear to be due to overt muscular activation or motor programming of eye movements. The authors reasoned that these improvements were possibly due to covert mental operations relating to the availability of an efference copy of the motor command during imagery training. They argued that this covert process allowed prediction of the sensory consequences of the movement by the forward model (Wolpert & Kawato, 1998; Flanagan, Vetter, Johansson & Wolpert, 2003) and subsequently updating of both the forward and inverse models. As discussed earlier, the forward model is believed to be updated before the inverse model and in turn serves to train or update the inverse model (Flanagan et al., 2003; Wolpert, 1997; Miall & Wolpert, 1996).

Based on Gentili and colleagues' (2006) proposition that motor imagery involves the generation of efference copies, we combined observational practice with imagery in the current experiment, where the observer would watch and imagine themselves as the agent of the action, to maximize the availability of an efference copy and its expected sensory outcome. Through encouragement of motor imagery during observation, observers now become consciously engaged in motor simulation. Because researchers have generally found motor imagery and observation in a first-person perspective to be more effective for motor learning than in a third-person-perspective (Mulder, 2007; Holmes & Calmels, 2008) we modified the apparatus in this experiment in order to promote this first-person perspective in observation and imagery. There is some behavioural evidence that advantages can be gained from combining observation with imagery practice (e.g., Ram, Riggs, Skaling, Landers & McCullagh, 2007; Zhang, Ma, Orlick & Zitzelsberger, 1992), although the mechanisms for this advantage are unclear and may be a function of increased cognitive involvement in the task (see Ram et al., 2007), rather than improved anticipation of sensory consequences related to the generation of an efference copy.

In summary, the purpose of Experiment 2 was to encourage action simulation during observation, specifically the generation of an efference copy. If after-effects are elicited in a posttest, following more ‘active’ observational practice, this finding would indicate that both the forward and inverse models have been updated. We would be able to conclude, based on data from this experiment and Experiment 1, that observational practice does not necessarily involve simulation or the generation of an efference copy, but that under more engaging conditions, this process can be encouraged. If after-effects were not elicited from active observation, we would conclude that either it is not possible to generate an efference copy of the movement in the absence of physical movement (yet see, Gentili et al., 2006) or that processes related to the sensing of afferent feedback are necessary for the updating of an internal model of the visuomotor environment.

3.1 Method

3.1.1 Participants and groups

We tested 20 participants in two groups; an observer group that engaged in ‘active’ observation involving imagery and estimation of hand trajectory (Observation-Imagery-Estimation, Observer-IE; *n* = 10; mean age = 21.6, SD = 3.0 yr; 3 females) and an actor group that physically practiced and estimated their own hand trajectory (Actor-Estimation, Actor-E; *n* = 10; mean age = 22.5, *SD* = 4.5 yr; 5 females) group. All participants were self-reported right hand dominant and were randomly assigned to either group. The observers watched a gender-neutral video display of a male trained model (i.e., an arm and hand partially encased in a brace) acting in a perturbed visuomotor environment and they were instructed to imagine and feel that it was their hand that moved while watching the video. On certain trials, observers saw only the cursor trajectory and were required to estimate the model's hand trajectory that produced the resultant cursor movement. The actors physically adapted to the perturbed visuomotor environment with vision of their hand and the cursor. On trials where only the cursor trajectory was visible, they indicated or estimated the trajectory of their hand. The Observer-IE group scored high on assessment of both general visual and kinesthetic measures of motor imagery, using the revised Movement Imagery Questionnaire (MIQ-R; Hall & Martin, 1997) before experimentation commenced. Out of a maximum score of 7 for each question (4 questions for each component), the averaged scores for the visual and kinesthetic component of the MIQ-R were 5.75 (*SD* = 1.09) and 5.80 (*SD* = 1.01) respectively.

3.1.2 Task and apparatus

The apparatus and visual stimuli were almost the same as in Experiment 1, but with a few exceptions. Instead of viewing a live model's adaptation performance, observers watched a video of a trained model.[3] The model acted in the experimental set up and received visual feedback alerting to the perturbed cursor trajectory. Previous research has shown greater movement error or variability when horizontally performed movements are represented on a vertical plane such as on a computer monitor screen (Messier & Kalaska, 1997; Bédard & Proteau, 2005) and the

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[3] From pilot work (n = 4), viewing a video of a trained model elicited direct-effects during physical adaptation, that is, low error was observed in the first 2 blocks of posttest 2 (*M* = 0.7°, *SD* = 3.8). These direct-effects were also observed in Experiment 1 with the live learning model, although participants (n =10) were not quite as accurate (*M* = 6.1°, *SD* = 7.7). Although this difference might be mediated by model type, it is likely due to breaks between watching and performing for half of the observers in Experiment 1, as their yoked actor partner performed the second posttest first. There was no evidence of after-effects (posttest 1) in either group of observers following observation of a trained, expert model (M = -1.1°, SD = 2.0) or the learning model in Experiment 1 (M = -2.2°, SD = 2.6).

use of non-aligned visuomotor coordinate planes is purported to increase the difficulty of the task because of the additional transformation required between visual input and motor output. Therefore, an additional change in this experiment was made to the orientation of the video display and the viewing position of the observer. Because there were no live models, the observers watched the video of the model seated in the actor's position (see actor's position in Figure 2.1, A) and viewed the video as reflected off a semi-silvered screen. The orientation of the visual display was now directly comparable (i.e. viewed in the horizontal plane) between the actors and observers.

To create a trained model video, one individual received 200 trials of training on the visuomotor rotation task, until he was proficient at reaching the targets accurately. Following this initial training, we recorded 8 blocks (t = 200) of reaching movements in the 30° CW rotation environment (mean constant errors: blk 1 = 2°; blk 2 = 0.6°; blk 3 = 0.5°; blk 4 = 0°; blk 5 = 0.3°; blk 6 = 0.3°; blk 7 = -0.1°; blk 8 = 0.3°). Because the observers were required to estimate the trajectory of hand movement from the cursor trajectory, we felt that this would be facilitated by having a model reach accurately to the targets so that they could easily recall the target and cursor location while they made their estimation during a pause in the video.

3.1.3 Design and procedure

The procedures were almost identical to Experiment 1, apart from the requirement of the observers to engage in imagery during observation and for both groups to provide an estimate of the model's hand trajectory on select trials. Observers were first instructed to watch the trained model video, which was projected onto the semi-silvered screen, with the intention of learning how to reach accurately in the novel environment. It was not until a scheduled break in the fifth cycle (on the 22nd trial) of the first block that the observers were given instructions to imagine that it was their hand they viewed and to try and feel that it was their hand that moved as they watched the video, even though their hand was to remain stationary on the graphics tablet at all times. They were also reminded at the beginning of each practice block to see and feel that it was their own hand that moved while watching the video.

Observers were told that on some trials, they would see only a trajectory of the cursor without the model's hand. Further, on select trials, they had to verbally indicate which out of a series of possible straight line paths depicted on the screen, provided their best estimate as to the hand movement which would produce the corresponding cursor trajectory. The trained model video was edited so that on 25 % of all trials (t = 50), only the cursor was shown. The experimenter paused the video after half of these cursor-only trials (t = 25). A "star display" of 72 straight lines was digitally presented and viewed by participants on the semi-silvered screen; each line starting at 1 cm from the origin (i.e., the start square) and extending to a circumference of 10 cm from the origin. The lines were separated by a 5° angle and represented 72 possible hand trajectories from the start square. At the termination of each line, a number from "1" to "72" was sequentially assigned in the clockwise direction with the location of the number "1" randomly assigned for each star display. Also shown on the star display was the location of the target in the preceding cursor-only trial. The observers verbally indicated the line that best estimated the model's hand trajectory. Each response was recorded by the experimenter before the video was resumed.

The actors practiced under similar conditions as detailed in Experiment 1 for the Actor-Hand group. However, practice with vision of the hand and cursor trajectory only occurred on 150 trials. For the remaining 50 trials, the actors reached for the targets with vision of the perturbed cursor trajectory only. After half of these cursor-only trials (t = 25), in a fashion similar to the observers, the actors verbally estimated, using the star display, which straight line path best represented their own hand trajectory for that trial.

To better control for movement time and prevent online corrections, all participants were instructed to move to the targets in 250 ms or less. Different to Experiment 1, the green target turned red on all trials, regardless of experimental condition or group, where the movement time exceeded 250 ms. When this happened, participants were instructed by the experimenter to move faster on subsequent trials.

The experimental phases in the current experiment matched those used in Experiment 1, with the addition of a third posttest which allowed us to test for after-effects following physical practice for the observers[4] (see Table 3.1). At the end of testing, participants were debriefed and observers were specifically asked to rate how well they performed visual and kinesthetic imagery while watching the video. Referring to the MIQ-R rating scale of "1–7", they indicated how well they were able to "see the moving hand as their own hand" and "feel the moving hand as their own hand".

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[4] From pilot work, we found after-effects in an observer in a third posttest following only 2 blocks of physical practice (posttest 3, *M* = -5.7°). However, we also tested for after-effects in two observers following 8 blocks of physical practice (comparable to the acquisition phase for the Actor groups in Experiment 1) and the after-effects observed were more pronounced (posttest 3, *M* = -13.9°).

Table 3.1 Experimental phases and their associated observational practice and visuomotor conditions as a function of group

Group/Phase	Pretest	Adaptation	Posttest 1	Physical Practice (Posttest 2)	Posttest 3
Observer_IE	Normal environ.	Observation, Imagery, Estimation	Normal environ.	30° rotation; (cursor feedback only)	Normal environ.
Actor_E		Physical Practice, Estimation			

3.1.4 Data reduction and analyses

Data collection and reduction procedures were as described in Experiment 1, except for the exclusion of 2.4 % of trials (3.0 % for Actor-E group, 1.2 % for Observer-IE group) when movement times exceeded 300 ms. Of the 144 trials we excluded from analyses, approximately 50 % were from Actor-E groups' adaptation trials (perturbed visuomotor condition; 3.7 % of actors' adaptation trials). The percentage of excluded trials ranged from 1 to 2 % for all pretest and posttest conditions for both groups, with the exception of Actor-E group's pretest, where 5.4 % of trials were excluded. Additionally, a Pearson's correlation analysis was conducted for each individual for all trials that were successfully executed in less than 300 ms. Directional error at peak velocity was highly correlated to directional error at movement end, as revealed by a mean *r* of 0.99 for the Observer-IE group and 0.98 for the Actor-E group, indicating minimal online correction during execution of the task.

Data analyses were based on procedures adopted in Experiment 1. Mean directional constant error (CE) was the main measure of performance and statistical comparisons involved mixed-factor analyses of variance (ANOVA) performed for aiming movements in the normal visuomotor conditions (i.e. pretest, first and third posttest) as well as under perturbed conditions, that is across practice blocks (adaptation for the Actor-E group and posttest 2 for the Observer-IE group). We also compared the Actor-E group from the current Experiment with the Actor-Hand group from Experiment 1, to determine whether the additional requirement to explicitly estimate error affected any of our measures of learning. Group (Observer-IE vs. Actor-E or Actor-E vs. Actor-Hand from Experiment 1) was the between-subjects' factor, while Time (pretest vs. first posttest and pretest vs. third posttest); Block (each block consisted of 5 cycles) and Cycle (cycle 1 to 10, where 1 cycle was equivalent to 5 trials) were within-subject factors.

3.2 Results

3.2.1 Adaptation

To ascertain the impact on performance for actors who estimated their own hand trajectory, a 2 Group x 8 Block ANOVA was conducted on adaptation performance of the Actor-E group in the current experiment and the Actor-Hand group from Experiment 1. There was no significant group difference or Group x Block interaction, both *F*s < 1. As predicted, there was a linear trend to the main effect of block, $F(1,18) = 113.05$, $p < .001$, $\eta^2_p = .86$, indicating improvement in accuracy of performance during the course of adaptation. The accuracy data across the 8 blocks of practice for the Actor-E and Actor-Hand groups are shown in Figure 3.1.

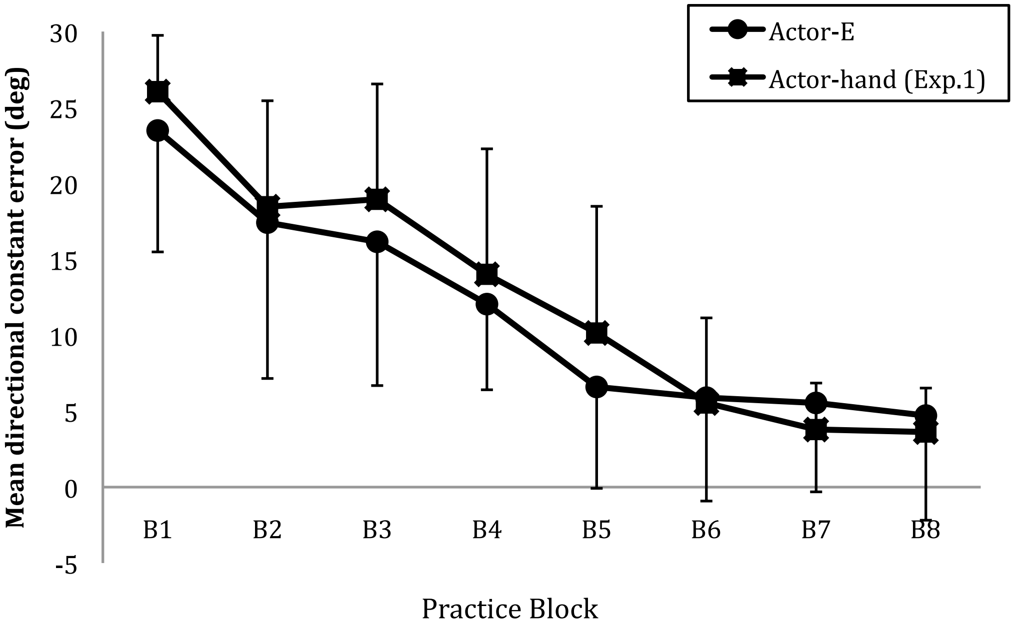

Figure 3.1 Performance error of Actor groups (Actor-E and Actor-Hand, Exp. 1) over the course of adaptation to the perturbed CW visuomotor rotation. Positive error value = error in the CW direction to the target. Error bars = *SD*

3.2.2 After-effects

Deterioration in performance accuracy or “after-effects” under normal visuomotor conditions in Posttest 1 compared to a baseline pretest performance was assessed using a 2 Group x 2 Time x 2 Block ANOVA. As illustrated in Figure 3.2, the main effects of group, $F(1,18) = 13.31, p < .01$, $\eta^2_p = .43$ and time, $F(1,18) = 45.44, p < .001$, $\eta^2_p = .72$ were significant in addition to a Group x Time, $F(1,18) = 35.50, p < .001$, $\eta^2_p = .66$ and Group x Block, $F(1,18) = 12.98, p < .01$, $\eta^2_p = .42$ interaction. Although the Actor-E group ($M = -6.35°$, $SD = 5.80$) showed more error overall than the Observer-IE group ($M = -1.69°$, $SD = 1.96$) and error was high in posttest 1 ($M = -6.19°$, $SD = 5.95$) compared to the pretest ($M = -1.85°$, $SD = 1.89$), as can be seen in Figure 3.2, these effects were due to differences between the groups in posttest 1 only. In addition, there was no significant change in error for the Observer-IE group from pretest ($M = -1.43°$, $SD = 1.43$) to posttest 1 ($M = -1.94°$, $SD = 2.39$), whereas the Actor-E group showed a significant increase in error (pretest: *M* = -2.26°, *SD* = 2.22; posttest 1: *M* = -10.44°, *SD* = 5.37). The Group x Block interaction was due to improvements in accuracy across blocks 1 and 2 for the Actor-E group only. A Time x Block interaction revealed that while accuracy did not change across the two pretest blocks (block 1: *M* = -1.63°, *SD* = 1.81; block 2: *M* = -2.07°, *SD* = 1.98), accuracy improved in posttest 1 (block 1, *M* = -6.61°, *SD* = 6.43; block 2, *M* = -5.77°, *SD* = 5.56). There was no 3-way interaction, $F < 1$.

A second analysis was conducted to determine whether after-effects would be seen in the Observer-IE group following the two blocks of physical practice. These data are also illustrated on the far right of Figure 3.2. A 2 Group x 2 Time x 2 Block ANOVA on pretest and posttest 3 CE this time revealed no significant group differences, $F(1,18) = 2.12$, $p = .16$, and no Group x Time interaction, $F(1,18) = 1.98$, $p = .18$. The size of after-effects elicited from the Observer-IE group (posttest 3: *M* = -9.11°, *SD* = 2.87) after only two blocks of physical practice (i.e. posttest 2) was not significantly different from the after-effects shown by the Actor-E group in posttest 3 (*M* = -11.90°, *SD* = 5.57).

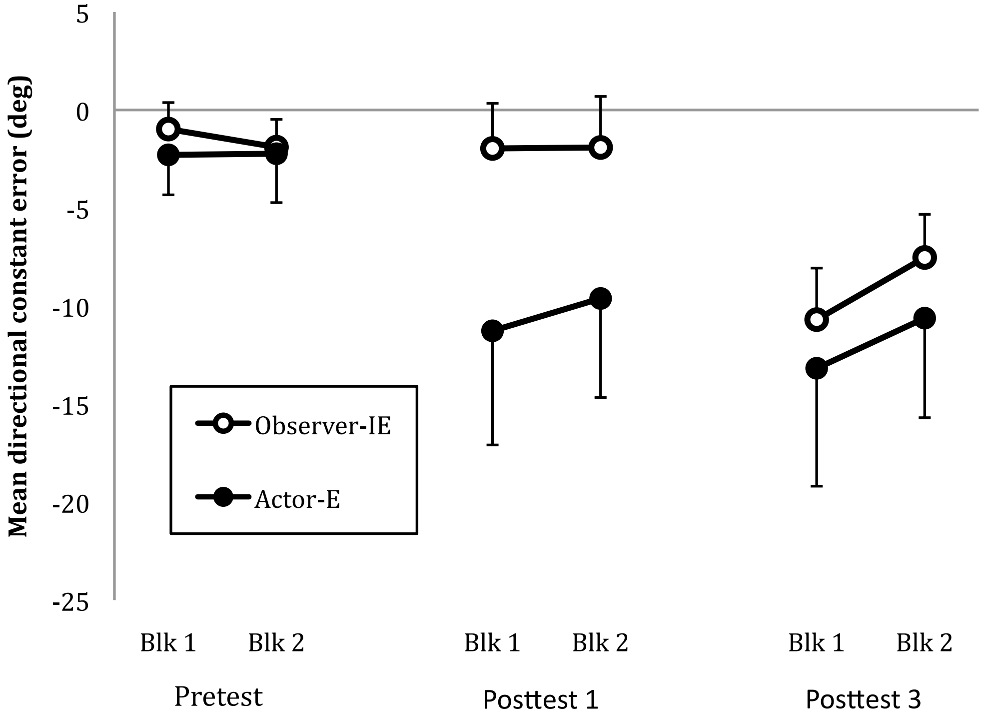

Figure 3.2 Performance errors during pretest, posttest 1 and posttest 3, all under normal visuomotor conditions. Negative error value = error in the CCW direction to target. Error bars = *SD*

3.2.3 Direct-effects

The level and rate of adaptation to the perturbed visuomotor environment as a function of group was compared using a 2 Group x 10 Cycle ANOVA. The first 10 cycles from the Actor-E group's practice trials and 10 cycles conducted during posttest 2 for the Observer-IE group were compared. These data are displayed in Figure 3.3. The main effect of group, $F(1,18) = 44.32$, $p < .001$, $\eta^2_p = .71$, revealed that the Observer-IE group (*M, CE* = -1.59°, *SD* = 7.84) was significantly more accurate than the Actor-E group (*M, CE* = 20.46°, *SD* = 10.76). A significant linear trend, as depicted in Figure 3.3, was found for the main effect of cycle, $F(1,18) = 8.27$, $p = .01$, $\eta^2_p = .32$, in addition to a Group x Cycle interaction, $F(4.5,81.9) = 2.62$, $p < .05$, $\eta^2_p = .13$. From inspection of the means, this appears to be due to the more pronounced and consistent decrease in error across the first 10 cycles for the Actor-E group in comparison to the Observer-

IE group who maintained low error (between 0º and -5º) from as early as the second cycle of adaptation.

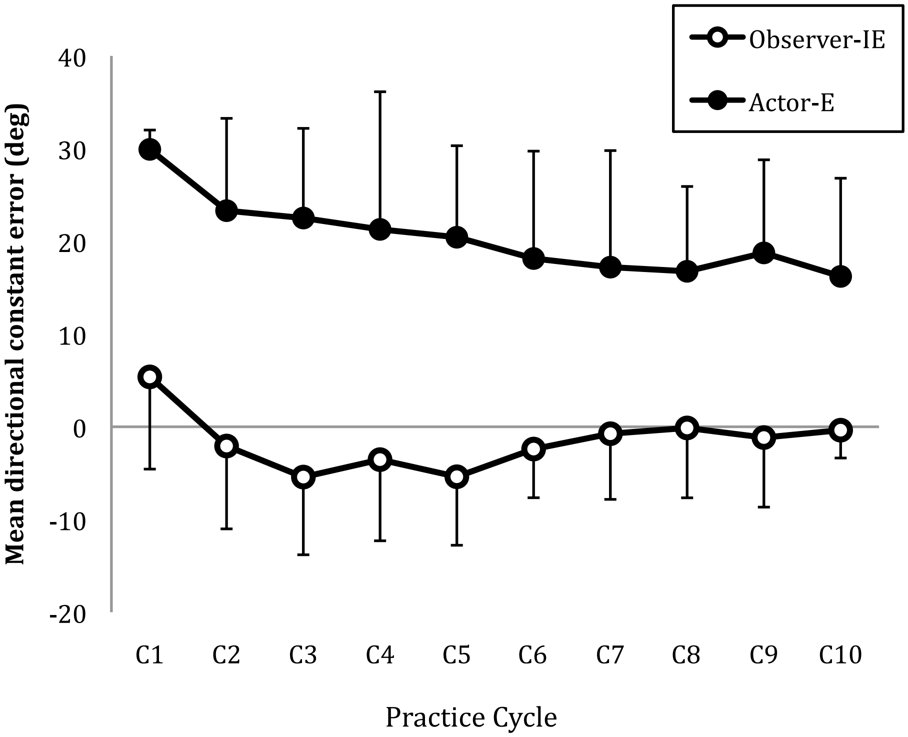

Figure 3.3 Performance errors during the posttest 2 for Observer-IE group and the first 10 cycles of adaptation for Actor-E group. Positive error value = error in the CW direction to the target. Error bars = *SD*

3.2.4 Estimation of hand trajectory

Overall, both groups underestimated the degree of hand movement trajectory in the CCW direction, shown by the positive error in estimation detailed in Figure 3.4. A significant cubic trend was found for the main effect of block, with estimation error highest at block 1, lowest at block 2 and peaking again at block 6, $F(1,18) = 15.10, p = .001, \eta^2_p = .46$. There was no significant main effect of group, $F < 1$. Rather, the Group x Block interaction was significant, $F(4.1,72.9) = 12.45, p < .001, \eta^2_p = .41$. Post-hoc tests on the this interaction showed that the Actor-E group estimated hand trajectories more accurately than the Observer-IE group only in the first block (Actor-E: *M, CE* = 7.93, *SD* = 11.15; Observer-IE: *M, CE* = 30.50, *SD* = 16.57). In blocks 5, 6 and 8, the Observer-IE group was more accurate than the Actor-E group as shown in Figure 3.4, while for the rest of the blocks, the two groups did not differ in estimation accuracy.

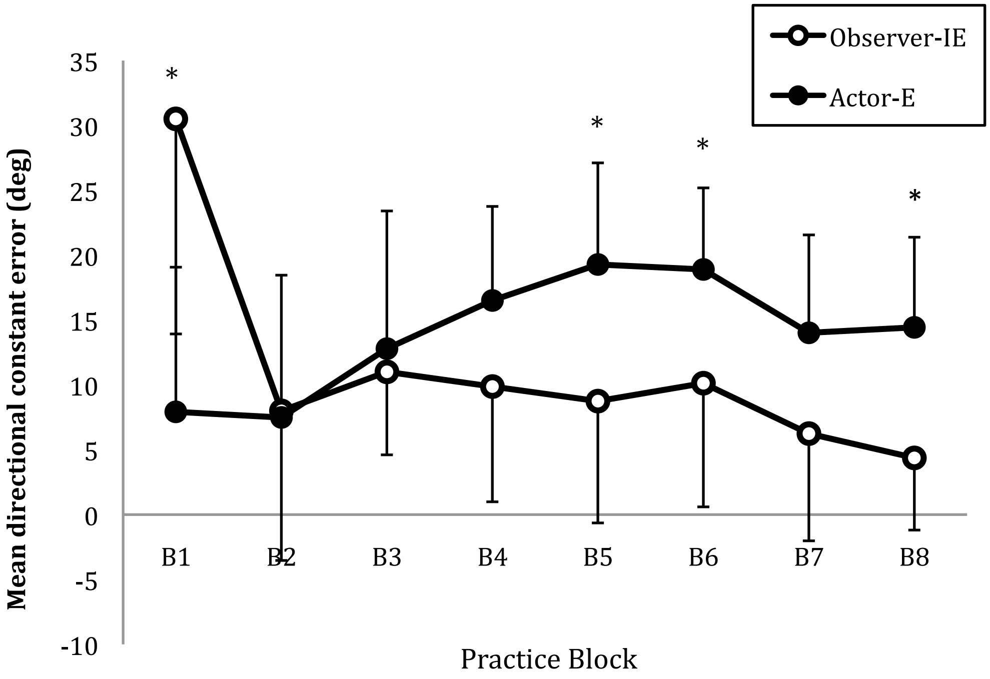

Figure 3.4 Movement estimation error of Observer-IE and Actor-E groups over the course of adaptation where observers imaged and viewed a trained model, and actors adapted to the visuomotor perturbation. Positive error value = estimation error in the CW direction of the actual hand trajectory. * = $p < .05$ (based on comparisons of the two groups at each block, using Tukey HSD post-hoc tests carried out on the interaction). Error bars = *SD*

A paired t-test analysis was also conducted to compare the Actor-E group's actual performance error and the corresponding estimation error for each of the eight blocks of adaptation. These data are illustrated in Figure 3.5. Significant differences were found for block 1, $t(9) = 5.33$, $p < .001$, and block 2, $t(9) = 2.82$, $p < .05$, where performance error was greater than estimation error, and blocks 5 to 8 where estimation error was greater than performance error, $p < .001$ except block 7, $p < .01$. From visual inspection of the results, there appears to be an inverse relationship between the actors' physical adaptation error to estimation error of their own hand trajectory.

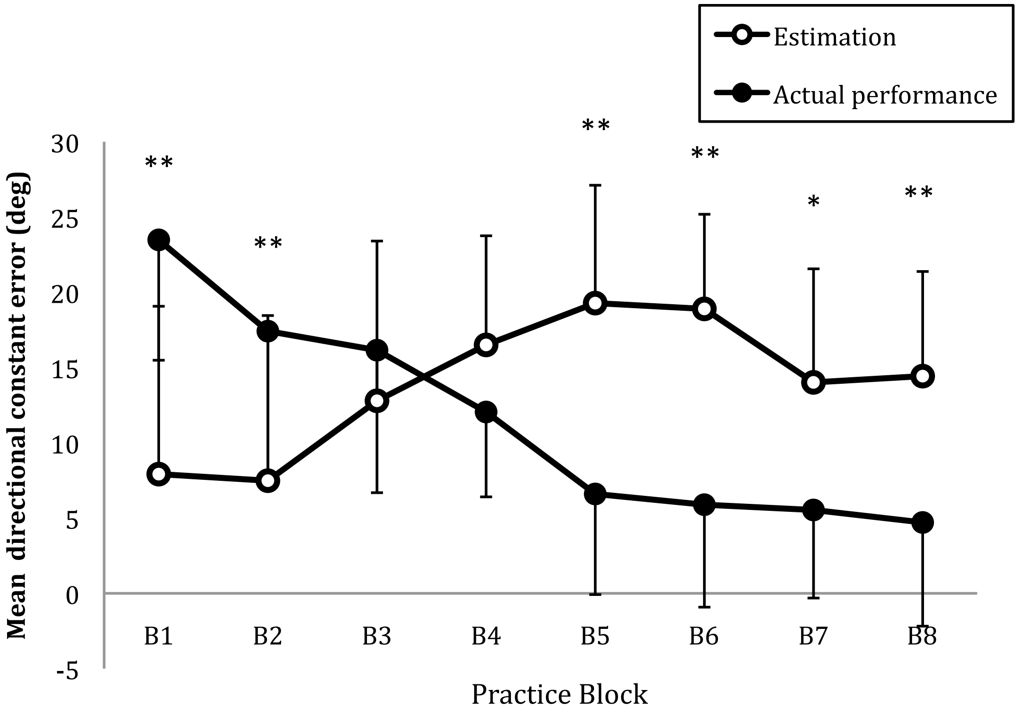

Figure 3.5 A comparison between movement estimation error and actual performance error for the Actor-E group. Positive error value = error in the CW direction. * = *p* < .01, ** = *p* < .001 (based on paired t-tests). Error bars = *SD*

3.2.5 Self-report of imagery ability

At the end of the experiment, the Observer-IE group indicated a self-rating for their ability to imagine visually and kinesthetically that it was their own hand that moved in the video. The self-rated scores were compared to the averaged MIQ-R scores for the visual and kinesthetic components in a paired t-test. There was no difference between the averaged MIQ-R score (5.75, *SD* = 1.09) and self-rating (5.50, *SD* = 1.43) for the visual imagery component, $p > .05$, whereas there was a significant difference (MIQ-R: *M* = 5.80, *SD* = 1.01; Self-rating: *M* = 4.60, *SD* = 1.35) for the kinesthetic imagery component, $t(9) = 2.83$, $p < .05$.

3.3 Discussion

In this experiment, all participants engaged in estimation of hand movements based on the rotated cursor trajectory. An actor group was compared to an ‘active’ observation group who was additionally encouraged to engage in imagery during the observation period. We expected that this more active type of observation encouraged by the estimation trials and imagery would lead to increased simulation of the movements during observation and aid in the generation of some sort of efference copy of the movement. As with Experiment 1, we expected the observer group to show learning as evidenced by direct-effects when allowed to perform in the perturbed environment (i.e., in comparison to early practice trials for the actors). Unlike Experiment 1, we expected the observer group to show evidence of after-effects when asked to perform in a normal environment following observation trials. The requirement to consciously engage in estimation and imagery during observation was expected to lead to increased simulation of the movement and an eventual updating of the internal models thought to be responsible for these after-effects.

As predicted, similar to the positive direct learning effects we found in Experiment 1, the observers were more accurate than the actors on their initial performance of the task in the perturbed visuomotor environment. The observers also became more accurate in their estimation of the model’s hand movement over the course of adaptation. The observation of a trained accurate model in the current experiment did not appear to adversely affect performance as evidenced by the much lower constant error observed during Posttest 2 (*M* = -1.6°) compared to the observer group of Experiment 1 (*M* = 6.1°). Based on these data, we believe that the current conditions are optimal for learning through observation.

Although after-effects were absent in the first posttest, we showed in Posttest 3 of the current experiment that even after only two blocks (50 trials) of physical practice in the new environment, the observers showed after-effects similar to those seen in the actor group following 250 trials. Therefore additional processes associated with physically moving are necessary for the appearance of after effects, even though we do not know how many trials are necessary and it may be that only one or two would be sufficient to lead to updating of internal models. In addition, we did not test for after-effects in our actor group following only two blocks of trials in order to determine how beneficial the observational practice conditions were for later physical performance in the perturbed environment. These would both be important additions for future investigations.

Despite manipulations to the observational practice condition, after-effects were only present for the actors and were not seen for the observers. The absence of after-effects indicates that the mapping between sensory feedback and motor commands, or an internal model, was not updated. If we believe that the conditions above did promote the sending of an efference copy as a result of watching and imaging (see Gentili et al., 2006), then it would appear that the generation of efference copies alone is not responsible for after-effects. Other differences between the actors and observers need to be considered in order to understand the behavioural differences between the two groups and to relate these to control processes (as discussed below). From brain imaging, neurophysiological and behavioural studies, there is considerable evidence pointing to the involvement of the motor system during action observation (e.g., Strafella & Paus, 2000; Rizzolatti et al., 1996; Mattar & Gribble, 2005) and motor imagery (e.g., Jeannerod, 2001; Fadiga et al., 1999; Yue & Cole, 1992). Brown and colleagues (2009) showed that the primary motor cortex, identified as the cortical region most directly linked to descending corticospinal tracts and motoneurons (Jeannerod, 2006), was implicated in motor learning by observation. This was shown by negative performance effects when this region was prevented from operating (via repetitive TMS) during the retention interval. Such evidence for motor-related cortical activity as a result of observation and imagery suggests that efference copies might be generated during these covert simulations. Rather, the absence of after-effects (hence updating of internal models) could instead be related to processes typically involved in self-generated movements. Further experiments are needed to test these hypotheses, where participants actively imitate while watching, controlling for the sensory feedback that is received.

In contrast to Experiment 1, both actors and observers were required to engage in explicit movement estimation in the current experiment. It was possible that this more explicit mode of practice would change the mode of learning, failing to engage the implicit motor system which has been shown to adapt to such visuomotor rotations (Mazzoni & Krakauer, 2006), and hence might prevent after-effects in both actors and observers. In addition, this explicit estimation might have positively benefited the Actor-E group in this experiment, encouraging them to pick up the rotation more quickly and adapt sooner to the visuomotor perturbation. Despite these various predictions related to the explicit estimation of movement, there was no evidence that this condition affected performance for the actors. There were no significant differences between the rate and level of adaptation for the present Actor-E group and the Actor-Hand group from Experiment 1. One possible explanation for the similarity in performance between the two actor groups could be due to the fact that estimation-error feedback was not provided. The Actor-E participants might therefore not be as explicitly aware of the direction and extent of the visuomotor perturbation as they would be had feedback been provided. Also, the Actor-E group’s estimation error appeared to be inversely related to their physical-adaptation error in the perturbed environment. The more accurate they were in guiding the cursor towards the visual targets in the perturbed environment, the more inaccurate they were in their estimation of their own hand movement. This disparity between explicit knowledge of the corresponding hand trajectory given the cursor feedback, and physical performance of the task, suggests that the present actors were implicitly adapting to the visuomotor perturbation at least later in practice.

In contrast to the actors, during the adaptation (observation) phase, there was evidence that the observers were more explicitly aware of the size and type of cursor rotation. Except for the first block, observers were generally as accurate, or more accurate, at estimating hand trajectory than actors. Although this might reflect differences in the mode of learning, suggesting a more explicit, strategic route for the observers, it is important to note that whereas the observers viewed a well trained model and hence estimated the hand movement on highly accurate performance trials (where the cursor was directed at or close to the targets), the perturbed environment was novel to the actors and hence estimations were made on less accurate and more variable performance trials. However, in Experiment 1 we also found evidence from a post-experiment debrief that the observers were better able to give explicit information about the size and direction of the rotation than the actors, suggesting that at least in part, learning for the observers was more guided by strategic, explicit means.

Earlier, we suggested that the availability of an efference copy may not be the only process to evaluate for the lack of after-effects we have shown in the two experiments. The presence of after-effects in adaptation paradigms may be attributed to three components: an efference copy of the motor commands (from which sensory outcomes are predicted via an internal model), proprioceptive feedback and visual feedback. Because of the data from these first two experiments and the lack of after-effects following conditions that would be expected to promote the sending of an efference copy (and prediction of sensory consequences), it is necessary to explore other differences between observers and actors that could be the cause of these differences.

Self-generated movements involve proprioceptive feedback or afference, as well as reafference about how the movement felt and looked. Reafference is the experience of sensory effects as a result of self-produced movements (von Holst, 1954; Held, 1965). To experience discordance between predicted sensory outcome and actual sensory feedback, and hence produce after-effects, it is possible that the feedback might have to be proprioceptive (rather than just visual) and/or self-generated. Bernier and colleagues (2006) showed that a deafferented individual, in the absence of proprioception, demonstrated a similar rate and magnitude of adaptation under visuomotor conditions similar to those experienced by healthy participants. Importantly, besides similarity in direct-effects, comparable after-effects were elicited from the deafferented individual in a posttest. Because proprioceptive feedback did not seem necessary for the updating of an internal model for this deafferented individual, we did not think that this process was responsible for the differences between our actors and observers. However, because control processes involved in reaching in participants without such disorders might be different from individuals who have become used to moving without proprioceptive sensory feedback, the absence of proprioceptive feedback remains a possible reason for the lack of after-effects in our observers. One additional difference between a deafferented individual and observers is that the deafferented individual still moved to the target and hence was the agent of the actions. It might also be the case that this self-generation process, and the experience of reafference (i.e., knowing that the sensory feedback was a result of self-generated action), could account for the difference between the observers and actors with respect to after-effects. Furthermore, observers reported a low self-rating for kinesthetic imagery in this task in comparison to visual imagery and other motor skills. We speculate that this could also be related to the difficulties experienced due to the lack of proprioceptive feedback while participants were engaged in imagery.

To determine the impact of actual sensory feedback on visuomotor adaptation in observers, we propose a third experiment that would entail observation with proprioceptive afference, or with reafferent signals associated with active movement. This requirement to actively move to imitate movements while watching would have the additional benefit of allowing us to test again the importance of efference copies in the generation of after-effects. Because active movement takes place, we would expect the generation of efference copies and prediction of the sensory consequences of motor output.

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4. EXPERIMENT THREE

Imitation does not lead to after-effects suggesting that visual reafference is required to update the internal model during visuomotor adaptation[5]

In Experiment 1, we assessed whether observational practice would result in behavioural effects comparable to those found with physical practice of a visuomotor rotation. Although there were direct learning benefits to observers, as evidenced by a significant reduction in movement error for observers when compared to actors' initial adaptation performance, different from actors, no significant after-effects were present. This latter finding would suggest that different learning processes are involved in observational and physical practice. We hypothesized that the lack of after-effects might be related to the generation of efference copies of (covert) motor commands as a result of observation. Therefore, in Experiment 2, observational practice was combined with imagery and movement estimation in order to optimize conditions for action simulation (what we call 'active' observation) and hence promote the generation of efference copies. Although positive direct-effects were again observed as a result of observational practice, after-effects were again absent from the active observation group in Experiment 2. The lack of after-effects would suggest that observational practice does not lead to updating of the observer's internal model of the environment, as there is no evidence of a change in the intrinsic relationship between motor commands and visual input.

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[5] A version of this chapter will be submitted for publication. Ong, N. T. and Hodges, N. J. (2010). Imitation does not lead to after-effects suggesting that visual reafference is required to update the internal model during visuomotor adaptation.

Although we cannot confirm that the hypothesized efference copies were indeed generated during our active observation condition, existing research corroborates the involvement of the motor system during covert simulation, such as in action observation and imagery, where similar patterns of motor cortical activity are seen during observation and imagery as observed when actions are actually executed (Jeannerod, 2001, 2006; Morris, Spittle & Watt, 2005; Holmes & Calmels, 2008; Mulder, 2007). Further, there is behavioural evidence showing improvements following imagery practice in the absence of corresponding muscle activity, in movement features related to force and speed (Gentili, Papaxanthis & Pozzo, 2006). This finding has been taken to suggest that motor processes related to efference copies, and the prediction of sensory consequences, can be generated during imagery practice.

It is said that a discrepancy between predicted and actual sensory consequences is crucial to the updating of an internal model (Miall & Wolpert, 1996; Wolpert, Ghahramani & Jordan, 1995; Wolpert, 1997; Bernier, Chua, Bard & Franks, 2006). Indeed, several researchers have attributed the presence of after-effects in a normal sensorimotor environment, after a period of practising in a perturbed environment, to an updating of this internal model (e.g., Shadmehr & Mussa-Ivaldi, 1994; Redding & Wallace, 1993). Because we were unable to bring about after-effects in observers after encouraging the generation of an efference copy through active simulation (imagery and movement estimation), we speculate that the failure to observe after-effects and hence an updating of an internal model for movement might instead be due to differences in sensory feedback or processes related to sensory feedback between actors and observers. This might be the absence of proprioceptive feedback (or afference), or the absence of what has been termed ‘reafference’ (either proprioceptive or visual). Reafference is the experience of sensory effects as a result of self-produced movement (von Holst, 1954, Held

1965). As discussed at the end of Experiment 2, actors' self-generated movements involve proprioceptive feedback or afference, as well as reafference about how the movement felt and looked. Except for the video of the model's hand movement and corresponding cursor feedback providing visual afference to observers, other components of sensory input, that is proprioceptive afference/reafference and visual reafference, were unavailable to observers in the previous experiments.

In the current experiment, we examined observational practice conditions in the presence of feedback about the movement that was either self- or externally generated. In the latter case, externally generated proprioceptive feedback was achieved through passive hand responses. The observers' hand was moved to imitate the hand movement of the video model. Without actual self-generated execution of movement, these observers received proprioceptive afference relating to the kinematic and dynamic properties of their own hand movement as well as visual afference of the discrepancy between the video model's hand response and the perturbed cursor trajectory.

A second group of observers actively imitated the movements of the video model, and as such, through overt execution and the sending of actual motor commands to the end effector, efference copies would be available through active movement and the experience of proprioceptive reafference would be felt. As with other experiments, and still different from actors, these observers would perceive externally generated visual afference.

The importance of reafference for motor adaptation was originally highlighted by Held and Hein (1958; 1963; Held, 1965). According to their 'reafference hypothesis', active movement provides crucial information for adaptation. For instance, Held and Hein (1958) presented participants with a series of crosses whose locations they were required to mark during pretest and posttest with their hidden hand. Between pretest and posttest, participants viewed their passively or actively moved hand through a laterally-displacing prism. Based on the result that there were significant after-effects only in the active movement condition, the authors concluded that self-generated movement is necessary for adaptation. Other researchers have also shown that planning, execution or reproduction of reaching movements to targets are superior in the active generation, rather than the passive movement condition (Coslett et al., 2008; Laufer et al., 2001). Interestingly, Held and his colleagues presented a model for perceptual adaptation that resembled the concept of a forward model later proposed by Wolpert and colleagues (e.g., Wolpert et al., 1995; Miall & Wolpert, 1996). The analogy lies in the necessary condition of a discrepancy between motor output and sensory input that provides the impetus for adaptation or an updating of the internal model specifying this relationship. Evidence put forth by Held and colleagues further emphasizes that the sensory input needs to be reafferent signals from self-produced movement.

Since this time, there has been debate regarding the necessity of active movement for adaptation. For example, Singer and Day (1966) did not show differences in after-effects after a period of prism adaptation where active, self-generated responses were compared to passive responses externally generated by the experimenter or the participants' non-tested arm. Both types of movement resulted in adaptation and after-effects. As discussed by Welch (1978), the disparity in findings could be related to the saliency of information pointing to the discrepancy between predicted and actual sensory outcomes. For example, visual features such as the existence of contours or targets had been found to negate behavioural differences between passive and active adaptation, due to the enhanced visual-proprioceptive discrepancy experienced by participants (Melamed et al., 1973). It has also been proposed that (stronger) after-effects associated with active over passive movement may be attributed to the greater amount of proprioceptive information one receives from active movement (see review by Welch, 1986; Kornheiser, 1976).

If after-effects were elicited from both groups of observers, it would indicate that proprioceptive afference is necessary and sufficient sensory input for the updating of an internal model in a healthy individual (cf. Bernier et al., 2006). Observational practice, in the absence of this source of afferent information, would therefore fail to provide the same sort of learning experience as physical practice even though similar cortical processes might be involved engaging the motor system during observation. If after-effects were elicited only in observers who actively moved, it would emphasize the importance of self-generated action and proprioceptive reafference for visuomotor adaptation. Therefore, only conditions which promote imitation during observation, rather than more passive observation, would be recommended for more robust learning effects as indicated by the presence of after-effects following visuomotor adaptation. This finding would suggest that observation alone does not covertly engage the same motor processes associated with physically moving. Should after-effects be absent in both conditions, it would suggest that visual reafference, a source of information lacking due to the observers' viewing of a model, is necessary for visuomotor adaptation. As above, this finding would suggest that observation alone does not covertly engage the same sensorimotor processes as activated during movement. In this last scenario, there would be no observational practice situation where after-effects would be expected, as the visual discrepancy would always be alerted by another individual or model. We would therefore conclude that observational practice and physical practice promote different types of learning due to the absence of self-generated visual feedback.

4.1 Method

4.1.1 Participants and groups

Self-reported right-hand dominant participants were recruited and randomly assigned to one of two observation conditions (n = 5/group), one involving active movement (Active-copying; 2 females; *M* age = 26.2, *SD* = 3.3 yr) and one involving passive movement (Passive-copying; 2 females; *M* age = 23.4, *SD* = 7.0 yr). In both conditions, observers watched a video (as detailed in Experiment 2) of a trained model adapting to a perturbed visuomotor environment and imitated the hand movement of the model.

4.1.2 Task and apparatus

The task, apparatus and visual stimuli were the same as in Experiment 2, except that the video model's hand movement remained visible in all trials and no hand estimation was required (t = 200).

4.1.3 Design and procedure

The procedures were almost identical to the procedures for observers in Experiment 2, apart from modifications to the adaptation phase (see Table 4.1). As with the first two experiments, participants were instructed before the adaptation phase to watch the video with the intention of learning how to reach accurately in the novel environment. For this experiment, they were then given further instructions directing them to either imitate the hand movements of the video model (Active-copying group) or to relax and have their hand passively moved by the experimenter to trace the trajectory of the hand movements of the video model (Passive-copying group). Vision of their own hand movement was occluded from view. When testing the Passive-copying participants, the experimenter stood to the right of the participant in a position that permitted her vision of the video playback during adaptation. Supporting the participants' arm by the elbow and applying pressure to the participants' right index finger, the experimenter moved the hand to imitate the model's hand movement. Participants in the Active-copying condition were asked to copy the model and therefore, not move in advance of the model. They were specifically asked to wait to see where the hand had moved before copying the movement. If there was movement in advance of the model's movement, as determined by the experimenter, participants were instructed to 'slow down' and the instructions to wait were again repeated. At the beginning of each block, participants were reminded to pay attention to both the hand movement of the model and the trajectory of the cursor in order to learn how to direct the cursor to the targets like the model.

At the end of the experiment, participants indicated the direction and size of movement compensations they were required to make in order to accurately aim for the targets. The Passive-copying group was also asked how well they thought their hand responses matched the hand movement of the video model and this was judged by the participants to be accurate between 80 and 90% of the time.

Table 4.1 Experimental phases and their associated observational practice and visuomotor conditions as a function of group

Group/Phase	Pretest	Adaptation	Posttest 1	Readaptation (Posttest 2)	Posttest 3
Passive-copying observers	Normal environ.	Observation, Passive movement	Normal environ.	30° rotation; (cursor feedback only)	Normal environ.
Active-copying observers		Observation, Active movement			

4.1.4 Data reduction and analyses

Performance data collected for the Actor-Hand group from Experiment 1 (*n* = 10) was included in the following analyses to enable comparisons with the current observation/copying conditions. As with Experiment 2, trials with movement times greater than 300 ms were excluded from analyses for both Passive-copying and Active-copying groups, only for the normal visuomotor conditions (i.e., pretests and posttests). This resulted in the exclusion of 3.2 % of trials for the Passive-copying group and 0.6 % of trials for the Active-copying group. Pearson's correlation analysis conducted for each participant for trials that were completed in less than 300 ms showed high correlation between CE at peak velocity and CE at movement end, mean *r* = 0.99 for the Passive-copying group and 0.98 for the Active-copying group, indicating minimal online correction. Because the movement time constraint was not as strictly enforced in Experiment 1, all trials for the Actor-hand group were included in the current analyses. Again there was little evidence of online correction in the Actor-hand group, according to the high mean correlation of 0.98 that was found between CE at peak velocity and movement end.

Mixed-factor analyses of variance (ANOVA) were conducted on mean directional CE in the normal visuomotor conditions (i.e. pretest, first and third posttest) as well as under perturbed conditions (posttest 2). Group (Actor-Hand, Active-copying, Passive-copying) was the between-subjects' factor, while Time (pretest vs. first posttest; pretest vs. third posttest), Block (each block consisted of 5 cycles) and Cycle (cycle 1 to 10, where 1 cycle was equivalent to 5 trials) were within-subject factors.

4.2 Results

4.2.1 After-effects

The assessment of after-effects was conducted using a 3 Group x 2 Time (pretest vs. posttest 1) x 2 Block ANOVA. These data are illustrated in Figure 4.1. The main effects of group, $F(2,17) = 4.01, p < .05, \eta^2_p = .32$ and time, $F(1,17) = 14.25, p < .01, \eta^2_p = .46$, were significant, but there was also a Group x Time, $F(2,17) = 17.29, p < .001, \eta^2_p = .67$, and a three-way interaction, $F(2,17) = 3.70, p < .05, \eta^2_p = .30$. The important Group x Time interaction was a result of a significant increase in error across pretest to posttest 1 for the Actor-hand group only (pretest, $M = -1.50°$, $SD = 1.17$; posttest 1, $M = -7.35°$, $SD = 3.28$). There were no significant differences between the three groups in the pretest; only in the posttest did the Actor-Hand group show more error than the Passive-copying group only. The Active-copying group was not significantly different from either group. The three-way interaction was mainly due to increased error across the two pretest blocks for the Actor-hand group, but a decrease in error across the two blocks for the same group in the posttest.

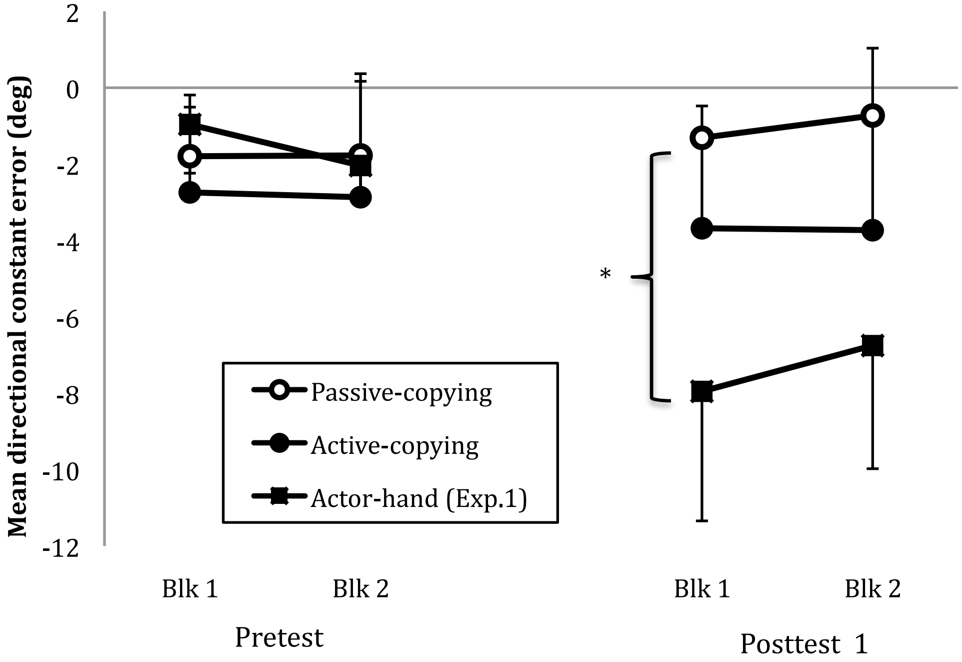

Figure 4.1 Performance errors during the pretest and posttest 1, both under normal visuomotor conditions, for the Passive-copy group, Active-copying group and Actor-hand group from Experiment 1. Negative error value = error in the CCW direction to the target. * = $p < .05$ (based on between group Tukey HSD post-hoc comparisons of Group x Time interaction). Error bars = *SD*

4.2.2 Direct-effects

The level and rate of adaptation of the two observer groups were compared to the Actor-hand group during the 10 cycles of posttest 2 for the observer groups, and the first 10 cycles of adaptation for the Actor-hand group. These data are illustrated in Figure 4.2. A 3 Group x 10 Cycle ANOVA confirmed the fact that observation with imitation aided performance as evidenced by a main effect of group, $F(2,17) = 25.83$, $p < .001$, $\eta^2_p = .75$. Both observer groups (Passive-copying: *M, CE* = 2.72°, *SD* = 12.67; Active-copying: *M, CE* = -0.84°, *SD* = 10.30) were significantly more accurate than the Actor-hand group (*M, CE* = 22.25°, *SD* = 9.01), but they were not significantly different from each other. A significant linear trend component for the main effect of cycle, $F(1,17) = 10.14$, $p < .01$, $\eta^2_p = .37$, was a result of a general linear decrease in error across the first 10 cycles. There was no significant interaction effect.

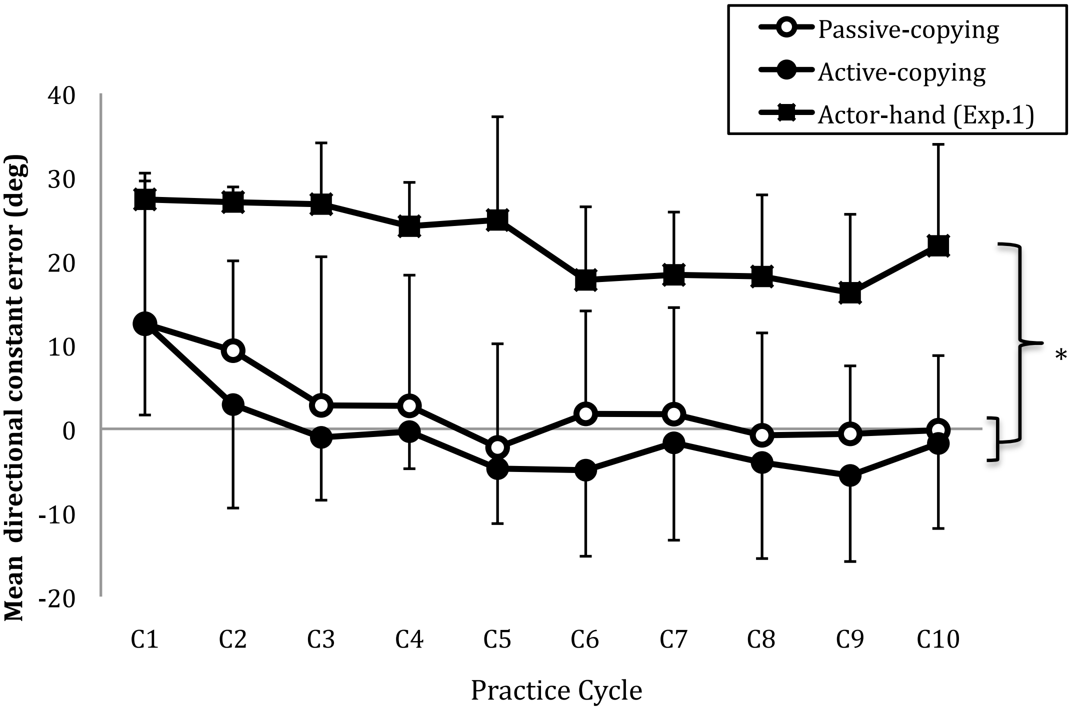

Figure 4.2 Performance errors during posttest 2 for both Passive-copying and Active-copying groups, in comparison to the Actor-hand group's first 10 cycles of adaptation to the visuomotor perturbation in Experiment 1. Positive error value = error in the CW direction to the target. * = $p < .05$ (based on Tukey HSD post-hoc comparisons of group means). Error bars = *SD*

4.2.3 Explicit knowledge

Eight out of ten participants in the Actor-Hand group consistently reported the correct direction of hand movement required to accurately guide the perturbed cursor to the target, as reported in Experiment 1. All observers in the current experiment (active or passive-copying) consistently reported the correct direction of compensation. Of these participants who were aware of the correct direction, the average size (and SD) of the reported compensations for the groups were; Actor-Hand, 20.1° (6.2); Passive-copying, 24.5° (4.5); Active-copying, 20.8º (6.2) showing that all participants, irrespective of group, had gained approximately correct explicit knowledge of the direction and size (i.e., 30°) of the perturbation.

4.3 Discussion

The purpose of the current experiment was to determine the necessary conditions for after-effects in order to understand differences in learning processes between observation and physical practice. Observation conditions coupled with sensory feedback (both passively felt and actively generated) provided a mechanism to determine the conditions necessary for after-effects and the updating of internal models or motor commands presumed to underlie visuomotor adaptation.

As with previous experiments conducted with observers (see Experiment 1 and 2; Mattar & Gribble, 2005), positive direct-effects as a result of watching a model were shown for the current observer groups. Again, despite the fact that this was an accurate model (cf., Mattar & Gribble, 2005), participants were able to determine how to move their limb in order to aim for the target in the perturbed environment. When both groups of observers were physically exposed to the visuomotor rotation in Posttest 2, which was the first time they viewed perturbed cursor feedback from their own hand responses, they performed significantly more accurately than actors without any previous observation experience. The magnitude of direct-effects of the two observer groups were not significantly different, showing that the addition of actively moving (and sensing) while watching a model did not benefit performance accuracy over the passively moving condition.

Importantly, this experiment was conducted in an attempt to bring about after-effects in observers and hence isolate the processes that cause these more robust learning indices and differentiate actors and observers. As discussed in Experiments 1 and 2, Bernier and colleagues (2006) showed that a deafferented individual was able to learn a visuomotor rotation similar to the one participants were exposed to in our experiment, and in addition, this individual showed evidence of after-effects, suggesting that proprioception is not necessary for adaptation. Due to the possibility that control processes in healthy individuals are different from that of a deafferented individual, there was reason to suspect that proprioceptive feedback might have been the source of information missing in our observers in order to bring about after-effects. Our results showed that participants who observed a video model and were passively moved to imitate the hand movement of the model did not demonstrate any evidence of after-effects. From this finding, we infer that sensory feedback or afference alerting participants to the visuomotor discrepancy (both visual and proprioceptive) is not sufficient to lead to the updating of motor commands inferred through the appearance of after-effects when participants perform in a non-perturbed environment.

Active-copying observers, compared to the passive-copying observers, received response-produced proprioceptive feedback (i.e., reafference) as a result of generating the movement. They also were involved in the sending of motor commands and the associated production of an efference copy. Yet, after-effects were also absent from this group. According to our predictions, the absence of after-effects in both groups of observers implies that visual reafference, a motor-related process resulting in the production of sensory feedback unavailable to the observers, is crucial for robust visuomotor adaptation as seen through after-effects (what others have referred to as true adaptation; Welch, 1986). The observers were aware that the visual afference they received was externally-produced feedback, as they watched a video of the trained model's hand and the perturbed cursor trajectory that resulted from the model's movement. Arguably, this awareness, or at least the lack of congruency between actual and seen movements, led to different activation of processes responsible for adaptation. Bernier and colleagues' (2006) results also support the finding that visual reafference could be essential for visuomotor adaptation. Despite not having any proprioceptive feedback, the deafferented individual from this study was the agent generating motor commands (and efference copies) that cause movements and received visual reafference as a consequence of self-produced responses.

We also need to consider an alternative explanation for the absence of after-effects in these observers based on two further differences between these observers and actors. The observers who passively moved or actively moved to imitate the movements of the model were not required to decide or plan where to move in order to aim accurately in the perturbed environment. The actor groups from the previous two experiments were actively involved in the planning processes necessary for movement execution. It is therefore possible that this cognitive process could account for differences between the groups. However, based on results from Experiment 2, we do not think this is a likely explanation for the absence of after-effects. In Experiment 2, observers who were explicitly involved in deciding or planning where movements should be made also failed to show evidence that an internal model had been updated in the form of after-effects.

The lack of after-effects in observers could also be accounted for by the time delay during imitation, between the model's hand response and corresponding cursor trajectory to the actual hand response of the observers. The existing time delay could aggravate the problem of agency, especially since the visual cursor feedback occurred before active or passive movements were made. Potentially, if there were no delay between the observers' hand response and the perturbed cursor feedback, the observer may be able to overcome the awareness that they were receiving externally-produced cursor feedback, and be more likely to associate this feedback to their own hand response. Under these conditions, we would expect that similar motor processes would be engaged as a result of observation. Welch (1972) conducted a visuomotor adaptation study where participants were required to adapt their non-visible finger pointing movement so that an experimenter's finger, which was always displaced at a fixed distance away from their finger, would appear to coincide with the target. One group was explicitly informed that they were viewing the experimenter's finger, while another group was made to believe that the discrepancy between felt and seen position of 'their' finger was due to prism distortion. Surprisingly, informed participants demonstrated significant after-effects, though the magnitude was smaller than the after-effects shown by the misinformed participants. Although adaptation was moderated by the knowledge that visual and proprioceptive feedback did not emanate from the same object (i.e. the same finger), this study showed that it is difficult to overcome the inherent assumption of identity between felt and seen limb position (also see "rubber hand illusion", IJsselsteijn, de Kort & Haans, 2006). Therefore, it is possible that after-effects might be elicited if passive movements were timed to correspond in synchrony with the model's hand movement or if active movements were made at the same time as the model's but were guided along the correct trajectory (Cressman & Henriques, 2009).

Along with increasing sample size to ensure these effects, or lack of after-effects, are reliable, conditions which make visual afference seem or feel like visual reafference would be important future steps. In many training environments, observational learning takes place concurrently with physical practice. It is a common experience for a performer to both watch and attempt to imitate at the same time. We had expected that this coupling of conditions would be most beneficial for learning, as compared to other observational practice conditions assessed in this series of experiments, and also most likely to elicit after-effects. However, as noted above, participants in the active-copying group were not more accurate than participants who were only passively guided in the perturbed environment, and neither group showed after-effects.

There is evidence in the literature that passive guidance can lead to significant performance improvements, but not when the guidance is removed (e.g., Crespo & Reinkensmeyer, 2008; Lynch et al., 2005; Volpe et al., 2005). In this experiment, there were no detrimental effects associated with the removal of guidance in the 'readaptation' phase (i.e. posttest 2) of the experiment. We did not compare the observers in the readaptation phase to actors who had physically practiced and then also completed a second adaptation phase, in order to determine how equitable the observation and guidance conditions were to physical practice. It would be important to know whether observation and passive copying conditions could substitute for physical practice, which would be important when participants are unable, perhaps due to safety reasons or injury, to practice physically.

In summary, the passive and active copying observers learned the visuomotor adaptation, as evidenced by significant learning benefits (direct-effects), in comparison to actors without previous observation experience. It is clear that the observers had acquired the knowledge about what to do and where to move in order to move accurately in the perturbed environment. Although we have not directly assessed how these learning benefits were realized or what processes underlie these direct-effects, it would appear that the manifestation of this learning is independent of modifications to the inherent visuomotor mapping or internal model. It might be that with observational practice, a separate and independent internal model may be acquired (e.g., Cunningham & Welch, 1994). It might also be that these direct-effects in observers are realized by more conscious, strategic means, than realized by actors. Indeed, these two ideas might be intertwined, such that separate models of the environment may be realized through motor system involvement or more explicit means of learning.

We showed that proprioceptive feedback, coupled with observational practice, is not sufficient to bring about after-effects and hence provide a more robust index of learning. There was no evidence that participants updated their internal model for reaching movements so that they would continue to show evidence of learning when transferred back to a normal environment. Further, even when observers were able to imitate the movements of the model, and hence produce the movements needed to guide the cursor to the target (i.e., initiate movements and receive proprioceptive feedback associated with self-production of these movements), there was no evidence of after-effects. Only when participants physically practiced and experienced the visual reafference (perturbed cursor trajectory) were after-effects observed. These results are somewhat in agreement with the reafference hypothesis proposed by Held and Hein (1958; 1963) that passive movement is insufficient to lead to sensorimotor adaptation. Visual feedback as a result of one's own movement appears to be necessary for visuomotor adaptation and that the absence of this process in observers leads to different behavioural outcomes as a result of practice and arguably qualitatively different learning processes.

4.4 References

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5. GENERAL DISCUSSION

There is little doubt about the benefits of observational practice, in tandem with physical practice, or in lieu of physical practice, for the purpose of rehabilitation, injury prevention or cost-savings. Extensive research conducted on the topic has shown time-savings in acquisition or enhanced performance of motor skills, such as seen in movement form (e.g., Ashford, Bennett & Davids, 2006), timing (e.g., Vogt, 1996), and sequencing of actions (e.g., Heyes & Foster, 2002). More recently, with the advent of brain imaging techniques and electrophysiological equipment, scientists have been able to delve into the physical structures and substrates of the central nervous system that were previously inaccessible to inspection. Increasingly, research attention has been directed at determining the cortical areas and understanding the processes that are involved in observation and observational learning (Rizzolatti, Fadiga, Gallese & Fogassi, 1996; Calvo-Merino, Glaser, Grèzes, Passingham & Haggard, 2005; Calvo-Merino, Grèzes, Glaser, Passingham & Haggard, 2006; Cross, Hamilton & Grafton, 2006).

5.1 Theoretical recap and rationale

Traditionally, observational leaning was believed to be mediated mainly by cognitive processes, as outlined by Bandura and associates (Bandura, 1986; Carroll & Bandura, 1987, 1990). More recently, motoric processes have been implicated in the perception-action mediation of observational learning. Theoretical support for the involvement of motor structures during the observation process has been provided by various authors, including Jeannerod (1995, 2001, 2006) who proposed a ‘simulation’ hypothesis implicating motor-related cortical areas during action observation and imagery and the common coding approach (Prinz, 1997), where perception and action are believed to be processed and accessed in a common format. These theoretical ideas are supported by cortical evidence for what has been referred to as a ‘mirror neuron system’ in humans (Rizzolatti & Craighero, 2004). Both action observation and motor imagery have been found to activate cortical structures, for instance in the primary motor cortex, premotor cortex, parietal cortex, basal ganglia, and cerebellum (for a review, see Jeannerod, 2001), in similar patterns to the cortical activity found during actual execution of actions. Behaviourally, there is also indirect evidence that the motor system is actually involved during action observation for later production (Mattar & Gribble, 2005) as well as during imagery practice of novel motor sequences requiring both accuracy and speed (Gentili, Papaxanthis & Pozzo, 2006). In both these experiments, subtle movement dynamics, such as force and inertia, which had been thought to require physical practice, were shown to be enhanced through both observation and imagery. Further, Mattar and Gribble found that when observational practice was combined with a secondary, irrelevant motor task, interference to learning occurred whereas interference was absent with an irrelevant cognitive task. These findings have been taken to suggest that the motor system is activated during the observation phase (termed ‘early mediation’; Vogt, 2002; Vogt & Thomaschke, 2007) and that learning benefits are not exclusively the result of more cognitive, strategic processes, where the motor system only plays a role once physical practice ensues (i.e., late mediation).

Our purpose in these experiments was to evaluate the evidence that observational practice engages qualitatively similar processes during learning as those engaged during physical practice. Our goal was to evaluate behavioural outcomes associated with learning during visuomotor adaptation, in order to make inferences about the sensorimotor processes governing these types of learning conditions. The visuomotor adaptation paradigm allowed us to isolate sensorimotor processes that were likely responsible for differences (or similarities) in behavioural outcomes for the two types of practice. There are two distinct types of behavioural outcomes or effects associated with adaptation learning. The first effect, known as direct-effects, is improvement in performance of a skill after a period of practice. In the case of observational practice, positive direct-effects would be evidenced by increased accuracy in initial performance of the observed skill, in comparison to initial performance of the same skill without this period of observational practice. The second effect, which is considered an implicit and more robust assessment of learning, is after-effects. These effects are unintentional compensatory actions that persist after exposure to a perturbed environment, even though participants are conscious that the environment has reverted back to normal. In adaptation literature, the presence of after-effects is considered to be an indication that the mapping or transformation between sensory input and motor output has changed, and/or that the internal model of the sensorimotor system has been updated.

For skillful or accurate performance of movements, one has to acquire and maintain reliable sensorimotor mappings. That is, specific motor outputs become associated with specific sensory inputs. Wolpert and his colleagues (Wolpert, Ghahramani & Jordan, 1995; Wolpert, 1997; Wolpert & Kawato, 1998; Miall & Wolpert, 1996; Flanagan, Vetter, Johansson & Wolpert, 2003) presented the concept of internal models in order to provide a theoretical description of how motor learning takes place in terms of these sensorimotor relations. It is believed that for motor learning to occur, a discrepancy has to be experienced between expected sensory consequences and actual sensory consequences. Hypothetically, a copy of the motor commands is generated, termed an efference copy, which interacts with the forward internal model to give a prediction of the sensory consequences of an action (also termed “feedforward” process). When discrepancies are experienced, both the forward and inverse internal models are updated, so that motor commands are essentially modified to suit the new sensorimotor mapping. As mentioned, after-effects indicate that internal models have been updated and hence this theoretical link was expected to shed some light on our questions concerning the processes governing observational practice.

5.2 Experimental results

In our first experiment we tested whether observational and physical practice do indeed lead to comparable behavioural outcomes, as suggested by Mattar and Gribble (2005), when participants are required to learn how to move in an altered environment. In addition to measuring direct-effects from watching we also tested for after-effects in both actors and observers. If comparable behavioural effects are seen as a result of the two types of practice, then one hypothesis would be that these types of practice both engage similar processes and support the idea of motor simulation (or activation) during observation. Specifically, if observers simulate the action such that some sort of efference copy is generated, there would be a discrepancy between predicted and actual sensory (visual) consequences leading to an updating of the internal model. Therefore, we would expect to see similar after-effects in actors and observers. In this first experiment, although we showed significant direct-effects as a result of watching, after-effects only emerged following physical practice but not from observational practice. Therefore, we concluded that different processes were likely responsible for the two types of practice, that is as a result of doing as compared to seeing.

In order to probe what it was about ‘doing’ that led to these behavioural differences, two further experiments were conducted. We hypothesized that the lack of after-effects in observers, an indicator that there had been no updating of an internal model of the environment, was due to the lack of an efference copy and its feedforward processes. If observers are not engaging their motor system during observation then there would also not be any feedforward process and expectation of sensory outcomes. Although there is tentative evidence to suggest that covert simulation (i.e., imagery, Gentili et al., 2006) does lead to the generation of an efference copy, despite the fact that no overt action has occurred, this is still hypothetical and there is no evidence that this is the same for observation. Therefore, in a second experiment, we sought to encourage covert simulation and increase the engagement of the observer during observational practice. Pilot data with only observation conditions where observers were also asked to estimate the hand movement based on vision of the perturbed cursor (i.e., to encourage action simulation), did not lead to after-effects. Therefore, we set up the experiment to combine imagery with observation, in addition to requiring explicit movement estimation. Despite the combination of observation and imagery, after-effects were still absent in the observer group, although again the observers showed significant direct-effects as a result of this practice. This latter learning benefit, similar to that seen in Experiment 1, might suggest that learning was mediated by more cognitive/strategic means rather than more implicit and motoric processes. There was evidence in both experiments that some observers were more explicitly aware of the size and direction of the visuomotor rotation than actors, as assessed through debriefing in Experiment 1 and movement estimation during practice in Experiment 2. It is also possible that direct-effects in the absence of after-effects were related to the absence of sensory input pertaining to how the movement felt, that is, a source of feedback indicating a discrepancy between predicted and actual sensory consequences.

Therefore, in the final experiment we examined two observation conditions, one of which required observers to actively imitate the model's actions. In this condition, observers were expected to generate an efference copy and engage in feedforward processing. In addition, this group would actively generate proprioceptive feedback (reafference) associated with moving. Comparing this group to observers who were passively moved to imitate the model's actions then allowed us to determine whether proprioceptive feedback was the reason for the lack of after-effects and the difference between actors and observers in these experiments. Surprisingly, despite the additional efferent and afferent processes for the actively imitating observers, no signs of after-effects were found. Our results corroborate the suggestions offered by Bernier, Chua, Bard and Franks (2006) that proprioception does not appear to be necessary for visuomotor adaptation, although having this sensory information could aid adaptation (Welch, 1978). By default, the results from this last experiment led us to conclude that processes related to the active generation of visual feedback (reafference), the primary difference between actors and observers, was the cause of these behavioural differences, that is, the absence of after-effects. Unless visual feedback is self-generated (i.e., visual reafference), or perhaps seems like self-generated feedback, in this case the perturbed cursor trajectory, then they will not update their motor commands and internal models of the environment responsible for after-effects. This lack of motoric involvement in the production of sensory feedback, might also have the effect of promoting a more explicit mode of learning for the observer.

In order to try and understand how learning was achieved in the observers, as different from the actors, we need to look in more depth at the reasons for the positive direct-effects as a result of observational practice in all three experiments.

5.3 Discussion of experimental results

In comparison to actors who did not receive previous visual experience, observers were more accurate in performance when first exposed to the novel environment, suggesting important benefits as a result of observational practice. We suggest two potential reasons for these positive benefits in the absence of after-effects; the application of an acquired cognitive strategy through watching, which would not impact implicitly on performance in the normal environment, or the acquisition of multiple internal models of the visuomotor environment (which might or might not be mediated by explicit knowledge).

Previously we described a study where an irrelevant secondary cognitive task did not interfere with the direct-effects associated with observational practice of moving in a novel dynamic environment (Mattar & Gribble, 2005). The majority of observers reported not having explicit knowledge of the familiarity between the felt perturbation and seen perturbation during a post-experiment interview. The authors therefore concluded that observers did not rely on an explicit rule or strategy in order to benefit later performance and that learning was achieved via more implicit, motorically induced means. Qualitative, post-experiment assessment in Experiment 1 and estimation analysis in Experiment 2 of participants' explicit knowledge of the rotation in our experiments indicated that the observers were more explicitly aware than the actors of the hand responses required for accurate performance in the perturbed visuomotor environment. This finding suggests that in our case (cf. Mattar & Gribble, 2005), observational practice did prompt a more explicit mode of learning than that engendered by moving, at least for this type of task, and that this mode of learning might have prevented unintentional after-effects when performing in a normal, non-altered environment.

There were two observers (out of 10) in the first experiment that failed to show explicit knowledge concerning the direction and size of the visuomotor rotation (and hence performed more like actors in terms of their explicit knowledge). However, these observers showed no signs of after-effects. This would indicate that a more explicit mode of practice was not responsible for the behavioural differences in after-effects between actors and observers, although obviously this requires further testing. Indeed, when explicit knowledge has been manipulated for actors during visuomotor adaptation (e.g., Mazzoni & Krakauer, 2006) there has been suggestive evidence that learning still proceeds implicitly, in parallel with the explicit implementation of knowledge early in the learning process. The explicit strategy helped the actors to perform accurately (by reaching 45º CW) in the new environment during the initial period of practice, but with more practice the actors began to make increasingly large errors in the CW direction, meaning that they overcompensated for the visuomotor perturbation. The after-effects later seen in this actor group were similar to a control actor group that did not employ an explicit strategy. These results suggest that an implicit adaptation process occurred during exposure to the new environment, regardless of explicit knowledge and early implementation of a strategy. To further test the importance and role of explicit knowledge accumulation in observational learning, as well as the importance of implicit learning, an obvious next step would be to engage observers in a secondary cognitive task, using an interference paradigm similar to that used by Mattar and Gribble (2005). It would be critical that the cognitive task is challenging enough to preclude the accumulation of explicit knowledge during observation. If this method serves to decrease knowledge of the visuomotor rotation, without affecting direct performance benefits, then this would confirm the hypothesis that learning can be achieved via implicit, more motorically driven means, through watching. If this mode of practice brings about after-effects in observers then we would conclude that explicit knowledge prevents the implicit updating of motor commands in order to generalize movements to new situations and/or encourages the generation of multiple internal models of different environments.

It is important to also consider the role of the task in mediating the effects seen in our experiments and the mode of learning that is encouraged. It might be the case that visuomotor adaptation is more accessible to explicit, rule formation than ‘dynamic’ adaptation. According to Maslovat and colleagues (2010), the nature of movement or type of task to be acquired may moderate the extent of motor engagement during observation. Hence, the more implicit (or difficult) a task or environment, such as a novel mechanical environment, the more engaged will be the motor system during observation. Previous researchers (e.g., Kohl & Shea, 1992; Mattar & Gribble, 2005) demonstrated that additional physical practice was required for observers to achieve an accurate and high quality performance. However, in our experiments, involving a visuomotor perturbation, observers appeared to have mastered the task without this additional physical practice, as evidenced by the near zero error in their initial reaching performance in the perturbed environment (especially in Experiment 2: mean constant error = -1.6º) The type of task can also be categorized as ‘new’ or ‘learned’, depending on motor experience or expertise. We define ‘new’ to be skills or sequences of actions requiring novel motor patterns or patterns of coordination and ‘learned’ skills to be sequences of actions that are already acquired or practiced. Evidence from brain imaging literature (Calvo-Merino et al., 2005; 2006; Cross et al., 2006) suggests that the extent of motor-related (e.g., mirror neuron circuit) activation during observation is dependent on motor expertise. Observation of 'learned' skills appears to result in greater motor-related activity, although conflicting results have been shown by other researchers (Buccino et al., 2004; Vogt et al., 2007). In adaptation paradigms, one might consider the task of adapting to dynamical perturbations for the first time to be 'new', while adapting to initial visuomotor perturbations to be a more simple modification of the mapping between existing representations of external and internal coordinates or space. Before any modification to this mapping, performers already possess the motor patterns or coordination necessary for movement execution. It is plausible then, since movements performed during visuomotor adaptation are already part of an observer's motor repertoire, that observational practice would naturally lead to a more explicit mode of learning and formation of cognitive rules and strategies.

A final consideration when implementing or engaging in observational practice is the impact of the type of model (trained or learning) on the effectiveness of learning. As discussed in the introduction, there is evidence that a learning model might be more beneficial for observational learning than a trained model (see Adams, 1986), due to the advantages associated with being involved in the error-detection and correction processes of the learner and hence the additional engagement this type of learning could provide. In the three experiments reported here, we did not find any differential effects as a function of model type (live learning model in Experiment 1 and trained video model in Experiments 2 and 3). It is possible that the type of model most effective for observational learning is task dependent, and that only for skills where some sort of (cognitive) strategy is not obvious, such as dynamic learning (see Mattar & Gribble, 2005), would a learning model provide more subtle information to aid learning.

An alternative, though possibly related, hypothesis to consider for our results pertains to the idea that observers are able to hold/acquire multiple internal models of the visuomotor environment. This is different from actors. We have shown that physical practice in a novel visuomotor environment leads to an updating of the existing internal model, suggesting that actors are able to maintain only a single internal model of the visuomotor environment. Data in support of this idea, especially if the competing visuomotor mapping is an equal but opposite perturbation to an already acquired internal model, has been shown by a number of authors (Krakauer, Ghilardi & Ghez, 1999; Tong, Wolpert & Flanagan, 2002; for dynamical perturbations, see Karniel & Mussa-Ivaldi, 2002; Caithness et al., 2004). However, there has been some evidence showing that in certain conditions it is possible to hold multiple internal models of the visuomotor environment (e.g., Wolpert & Kawato, 1998; Krakauer, Ghez & Ghilardi, 2005; Wada et al., 2003; Osu, Hirai, Yoshioka & Kawato, 2004; Cunningham & Welch, 1994). Cunningham and Welch showed that after an extended period of alternating practice between two different visuomotor environments, the magnitude of after-effects caused by switching between mappings decreased over time, and performance accuracy in the alternate environment improved, indicating that participants had mastered both environments and were capable of acquiring and maintaining more than one internal model.

It has been suggested that the failure to acquire multiple internal models might be related to factors such as insufficient practice/time, non-randomized practice, or ineffective contextual information or cues to distinguish the internal models from one another (Wada et al., 2003; Osu et al., 2004; Krakauer, 2009). In our experiment, for the actors, salient contextual distinctions separating the normal from the altered visuomotor environment might have been lacking. This would have led to the presence of after-effects, indicating that the existing internal model had been updated as a result of practice. Because the conditions of watching were more different or distinct from those of doing, especially the absence of visual reafferent feedback, it might have been easier for observers to acquire and maintain a separate internal model of the novel visuomotor environment, without modifying their existing veridical internal model. We speculate that the acquisition of a distinct internal model is related to action simulation and covert neural rehearsal (motor-related activations that one might associate with the hypothetical efference copy), whereas the retuning or updating of an existing internal model seems to require both efferent and reafferent signals.

In the adaptation paradigm, it has been argued that the presence of after-effects demonstrates more robust learning over direct performance benefits (direct-effects), even when performers are aware of this change in environment. The presence of after-effects has been termed “true” adaptation (Welch, 1978, 1986). Despite the positive connotation associated with after-effects, with respect to indices of learning, such after-effects or negative transfer of learning in everyday motor behaviour would not be considered an effective way of learning. To function skillfully and effectively, it would be an advantage to produce movement effects exactly the way they are envisioned. The negative transfer elicited from adaptation and mastering a new skill is undesired retrograde interference to a learned skill, that is, losing the ability to perform a learned skill. In typical motor learning, desired generalization or positive transfer of learning is demonstrated from one’s capacity to apply aspects of learned skills to new ones more effectively. Considering that observational practice does not affect one’s capacity to perform in the normal visuomotor environment while a novel one is being practiced or learned, this effect (or absence of an effect) could be considered a beneficial finding associated with observational practice conditions.

Across the three experiments we varied the amount and type of information available to observers when they were watching actors perform in the altered visuomotor environment. As such, it is possible to make claims about the relative benefits of the various observation conditions for immediate performance benefits when physically experiencing the perturbation for the first time. Specifically, in Experiment 2 and 3, where the conditions of practice were the same with respect to the video display, orientation and skillfulness of the model, the direct-effects attained in the absence of movement (CE, $M = -1.6^{o}$) were similar to those observed when actual movement and proprioception were included (CE, $M = -0.8^{o}$). Therefore, observational practice (perhaps in combination with imagery) is a strong learning tool that would be expected to have benefits for learning in a number of conditions, even when active movement is not possible (such as in rehabilitation). There is evidence that observational practice in combination with physical practice is as beneficial for skill retention and more beneficial for transfer of learning than physical practice on its own in an anticipatory tracking task (Shea, Wright, Wulf & Whitacre, 2000). It has also been shown that although observational practice was inferior to physical practice when direct-effects were measured (i.e., retention performance), observational practice was as effective in a transfer task (Hayes, Elliott & Bennett, 2009). Hence, replacing some physical training with observational practice could reduce training costs and the likelihood of physical injury or fatigue. In our experiments we showed evidence in favour of this method of training in the form of positive direct-effects, although we also judged these benefits in terms of negative transfer (after-effects) when returned to the normal environment. After a period of observational practice ($t = 200$), observers were physically exposed to the perturbed environment for the first time for just 50 trials (in posttest 2). In addition to the positive direct-effects remarked upon above, on transfer back again to the normal environment (posttest 3), significant after-effects were now seen in the observer groups despite the relatively small amount of physical practice (Experiments 2 and 3). However, we acknowledge that comparisons will need to be made to actors who are physically exposed to the perturbation for just 50 trials in order to determine the potential benefits associated with observational practice and the relative size of the after-effects as a result of the combination of observational and physical practice.

5.4 Summary and conclusions

Adaptation paradigms have been useful for assessing the nature of sensorimotor coordination and the adaptability or plasticity of the sensorimotor system when discrepancies in sensory inputs are experienced. Using this paradigm, we first examined whether there were differences between behavioural outcomes of observational and physical practice. While positive direct-effects have been typically reported with observational practice, no research has examined after-effects with observational practice to date. Researchers have also related the presence of after-effects in adaptation studies to the concept of internal models and sensorimotor processes that are thought to be involved in the updating of internal models (Wolpert et al., 1995; Miall & Wolpert, 1996; Wolpert, 1997). The lack of after-effects in observers but presence of after-effects in actors from Experiment 1 suggested that different processes underlie the two types of practice. Based on internal models, because visual feedback was available to observers, we hypothesized that motor simulation or generation of an efference copy was missing during observational practice. This hypothesis was examined in Experiment 2 where observation was combined with imagery and an explicit estimation of movement in order to further encourage covert motor simulation and the expectation of sensory consequences. In Experiment 3, observers actively (and passively) imitated the model during observational practice. After-effects were absent in both Experiments 2 and 3 as well. These results imply that motor simulation, or the generation of efference copies, may not be the reason for differences between actors and observers with respect to after-effects. Even when the motor system was directly activated when observers actively imitated the movements of the model (which would be expected to engage feedforward processes), no after-effects were seen.

We concluded that in order for after-effects to appear, hence signaling an updating of the internal model or “true” visuomotor adaptation, self-produced movement and its associated visual reafferent feedback seems to be a necessary feature. During action observation, the motor system has been shown to be activated (see Jeannerod, 2001 for a review) but this activity may be different from the type of activity seen during sensorimotor integration when execution of movement takes place with self-generated feedback. One way of further testing this reafference hypothesis and the role of motor input in generating the feedback, is to try to elicit after-effects by making visual feedback seem as close as possible to visual reafference. This could be achieved by synchronizing the timing of visual feedback to the active-copying observers' movement. From the persistent lack of after-effects in observers from the three experiments, we concluded that processes underlying observational practice and physical practice lead to different types of learning. Testing the reafference hypothesis would allow more concrete conclusions about the sensorimotor processes that are similar or different during observation and actual movement.

It might also be an advantage in future research to more directly test the role of motor involvement during observational practice through repetitive TMS to areas of the brain involved in motor execution. Although evidence exists from brain imaging studies (see Jeannerod, 2001 for review) that the motor system is implicated during observational practice, caution must be taken when interpreting such motor-related activation. These patterns of motor-related activity do not necessarily explain observational learning benefits. If typical direct-effects seen as a result of observational practice are eliminated with the implementation of repetitive TMS, it would suggest that the motor processes are indeed responsible for observational learning benefits, hence supporting the early mediation account of observational learning. Another way to test the early vs. late mediation account is to implement a secondary cognitive task during observational practice to help confirm or refute some of the conclusions we have made from these three experiments and offer more insight into the processes involved in observational practice. Better understanding of the processes that underpin observational practice and 'how' this learning is achieved or enhanced will enable practitioners and learners to construct more effective skill training and rehabilitation programmes.

5.5 References

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