Manipulating Visual-Motor Experience to Probe for Observation-Induced After-Effects in Adaptation Learning

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Abstract

Observers can learn to move in novel, adapted environments after watching a learning or expert model. Although this is an effective practice technique, it is unclear how this learning is achieved and if observers update an internal model of their visual-motor environment, as shown through the presence of after-effects (i.e., negative carry-over effects when aiming in a normal environment following exposure to perturbed conditions). For such updating to occur via observational practice, it has been reasoned that the observer requires the motor capabilities to perform the task they are observing. To test this, we first trained 3 groups to physically move in clockwise (CW) or counterclockwise (CCW) rotated environments. When immediately returned to a normal environment, after-effects were seen. We then attempted to wash-out these effects before allowing two of these groups (CW and CCW), and a naïve observation only group, to watch a video of an actor performing in a CW environment. This observation phase was immediately followed by another test for after-effects, and a direct test of learning when aiming in the rotated environment. Consistent with previous data, there were direct learning effects due to observation. Although after-effects increased for the experienced observers, these were small and were not significantly different from a physical practice only group that did not undergo the observation phase. Therefore, even with a motor repertoire for the rotated environment, there was a lack of evidence that observational practice results in implicit (re)updating of an internal model for aiming.

Keywords: Observational learning, Practice, Motor learning, Internal models, Demonstrations, Motor resonance

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When learning a novel motor skill or when exposed to a new environment, numerous movement adjustments are needed in order to successfully complete the movement. These adjustments can be seen in soccer players learning how to pass a ball, or astronauts adapting their movements to minimal gravity in space. Commonly, these alterations do not occur immediately and practice is needed to perfect performance. There are various avenues for the types of practice that can bring about these changes. Although, physical practice is most common, it can be time consuming, energy demanding and expensive. For these reasons, other modes of practice, such as imagery and observation, have been adopted and studied with the prospect of replacing or enhancing physical practice.

While imagery and observational practice have been assumed to share neural and functional commonalities (e.g., Fadiga and Craighero 2004; Jeannerod 2001; Munzert et al. 2008), it has also been suggested that these two covert methods of practice share neural and functional similarities to physical practice (e.g., Decety et al. 1997; Grèzes and Decety 2001; Malfait et al. 2010; Munzert et al. 2008). Despite the significant evidence for shared activation patterns and processes between observation and execution of well-practiced actions, there is less agreement about the neurophysiological similarities of the processes underlying observational practice of novel actions and physical practice (e.g., Cross et al. 2006; Higuchi et al. 2012; Vogt et al. 2007). As well, there is behavioural evidence showing observational and physical practice engage different learning processes (e.g., Gruetzmacher et al. 2011; Ong and Hodges 2010; Ong et al. 2012). In this paper we evaluate the behavioural effects of observational and physical practice on adaptation learning in order to further our understanding of the differences and similarities of these different types of practice. In view of conflicting evidence of shared processes when novel versus acquired actions are observed or physically practiced, we attempt to moderate the observation process via manipulation of prior visual-motor experience and study the effects of this manipulation on measures of learning, specifically, unintentional after-effects.

Traditionally, as originally explained by Bandura (1971, 1986) in his Social Learning Theory, observational learning (where observation trials are interspersed with physical practice) was thought to be a primarily explicit, cognitively-driven process, especially during early stages of novel task learning (Ashford et al. 2007; Bandura 1971; Gentile 1998). During observational learning, the observer is assumed to create a guide or reference for imitation where the focus is on strategic processes and extraction of relevant cues (Ashford et al. 2007). Following observational practice, observers are typically better than actors at verbalizing any strategies acquired and subsequently implemented during later physical practice (e.g., Kelly et al. 2003; Ong and Hodges 2010; Ong et al. 2012). Therefore, observational practice was presumed to be a perceptual-cognitive process, done without low-level or implicit involvement of the observer's motor system (see reviews by Maslovat et al. 2010; Vogt 2002; Vogt and Thomaschke 2007).

There have been a number of motor learning studies supporting this claim that, unlike physical practice, observational practice does not engage the observer's motor system (e.g., Gruetzmacher et al. 2011; Larssen et al. 2012; Ong and Hodges 2010). One line of investigation has involved adaptation learning, whereby an individual practices moving in a novel environment (either visually- or dynamically-perturbed). Performance is subsequently measured in both this new environment, to test direct learning effects, as well as in a normal, non-rotated environment, to test for after-effects. In physical practice paradigms, these after-effects are typically short-term carry-over biases that manifest, often in spite of instructions or cues that the person has returned to a normal environment (e.g., Held 1965; Shadmehr and Mussa-Ivali 1994). Because of the unintentional nature of these after-effects, they are assumed to reflect implicit adaptation of the motor system and updating of an internal model (or motor plan) for aiming. In the internal model framework, it is the mismatch between predicted and actual sensory consequences associated with moving that leads to an updating of the relationship between these, such that the two align (e.g., Wolpert and Miall 1996; Wolpert and Flanagan 2001). Awareness of the mismatch is not needed for this alignment to occur; rather it can actually interfere (e.g., Benson et al. 2011; Kagerer et al. 1997; Ingram et al. 2000), supporting the implicit nature of this adaptation.

In early studies (e.g., Held 1965), when the participant removed prism goggles that displaced the visual field, after-effects were only seen after individuals actively initiated reaches versus passively observed their movements in the prism-shifted environment. This finding suggested that physical practice involving motor output (or efference) was needed to update an internal model of reaching. In more recent visual-motor adaptation tasks, participants that observed an actor aiming in a rotated visual-motor environment did not show after-effects in comparison to large after-effects seen in their actor counterparts

(Ong and Hodges, 2010; Ong et al. 2012). This was despite the fact that when later asked to perform in the rotated environment, observers demonstrated significant learning that was comparable to performance of participants that had physically practiced. However, performance of the observational practice group was characterized by increased between trial variability, increased reaction times and greater awareness of the size and type of rotation compared to physical practice participants, consistent with the implementation of cognitive strategies (Benson et al. 2011; Hinder et al. 2010). Although it has been suggested that internal model sensory predictions can be made without overt action (Gentili et al. 2004; Demougeot and Papaxanthis 2011; Wolpert et al. 2011) to date there is no clear evidence for this. The lack of implicit/adaptive learning seen in observers suggests that the mechanisms responsible for observational practice benefits, at least for visuo-motor adaptation tasks, are not commensurate with those of physical practice and instead are primarily strategic.

Yet despite the evidence from these visuo-motor adaptation tasks, which questions the role of implicit, motor-driven learning via observation, in other tasks there has been evidence to support the suggestion that observational learning can proceed more implicitly. For example, using a robotic, force field-generating manipulandum to perturb target aiming, observers of learning models showed savings in learning when they were later required to move with the robot (Mattar and Gribble 2005). Further, observational learning was not affected by a cognitive dual-task, but it was affected by a secondary motor task. Based on savings in learning and the pattern of interference observed, these authors concluded that observational learning took place via implicit engagement of the motor system (see also Brown et al. 2009). However, no testing of after-effects via catch trials was reported and in a later study, different to actors, observers did not show effector specificity, which is typically suggestive of motor-based encoding (Williams and Gribble 2012). On the contrary, Osman and colleagues (2005) did show that action-observation of repeating sequences was specific to the watched hand, suggesting potential motor-based activation (i.e., resonance) in the to-be-enacted hand during observation that led to effector specific learning effects. Although this observational learning result was later replicated (Bird and Heyes 2005) observers had acquired significant explicit knowledge about the repetition of the sequence, suggesting that both explicit strategies and potentially a more implicit, motor-driven type of learning occurred through action-observation. This development of parallel, yet potentially independent explicit and implicit processes, has been thought to characterize physical adaptation. In a notable study, Mazzoni and Krakauer (2006) showed how implicit, motor-driven processes continued to develop and affect learning even when they were counterproductive to the goals of the task and interfered with the implementation of an explicit strategy.

Observation of an action has also been shown to result in neural activation patterns similar to those seen during physical performance of the same action (e.g. Caspers et al. 2010; Iacoboni 2005; Rizzolatti et al. 2001). Through brain imaging and stimulation studies, a network that responds both to action-observation and execution has been identified in the human motor cortex and has been referred to as the mirror neuron system (MNS) or, more recently, the action-observation network (Cross et al. 2006). It primarily consists of the inferior parietal lobe, the inferior precentral gyrus, and the posterior part of the inferior frontal gyrus. Other areas have been implicated including the dorsal premotor cortex and the superior parietal lobe. Researchers have speculated that activation of traditionally motor areas of the brain is a result of the reproduction of the action (i.e., simulation) through stored memories or programs (Rumiati et al. 2005) and/or movement preparation (Rizzolatti and Sinigaglia, 2010). Therefore, for activation to be possible, the observed actions have to be meaningful to the observer, in terms of prior experience and/or understanding of the task (Kohler et al. 2002; Umilta et al. 2001; yet see Vogt et al. 2007).

There is reason, therefore, to speculate that certain manipulations might bring about similarities between physical and observational practice, resulting in a more implicit, motor driven learning in the latter. For example, interspersing observational practice with physical practice might change the nature of the observational learning process whereby observation can elicit automatic predictions of visual sensory consequences based on this specific motor experience (referred to as forward model predictions, Wolpert and Miall 1996). Indeed, in an earlier study, a mixed observational and physical practice group (75% observational practice) showed significant after-effects that were more pronounced than a physical practice only group matched for overall practice amount (Ong et al. 2012). This outcome was despite the fact that this mixed practice group showed explicit awareness of the strategy required to aim accurately in the rotated environment, as well as a faster rate of acquisition than pure physical practice groups. Therefore, it is possible that physical experience changed the processes of observational practice (see Deakin and Proteau 2000 and Higuchi et al. 2012 for similar suggestions). Indeed, past physical practice experience has been shown to moderate motor-related activity in the brain during observation. For example, Calvo-Merino and colleagues (2005, 2006) looked at cortical activity of expert capoeira and expert ballet dancers in regions of the brain previously shown to be active during action-observation. Participants were scanned with fMRI whilst watching videos of another dancer performing in ballet or in capoeira (or in ballet only, but of the same or different gender, 2006). Greater cortical activation was seen in regions known to be involved in the MNS in dancers who observed their own dance expertise and not in the other type of dance (e.g. greater activation was seen in ballet dancers who watched another ballet dancer compared to a capoeira dancer). Gender-specific activations provided further evidence that these were specific to visual-motor experience, rather than mainly visual experience. In a specific manipulation of action experiences through a 5-week training regimen of video-game based dance sequences, fMRI measurements indicated a higher activation in areas associated with the MNS during observation of rehearsed movements compared to unrehearsed movements (Cross et al. 2006).

In the following study we manipulated previous physical practice experience to study whether a subsequent period of observational practice would be sufficient to bring about after-effects in a visual-motor adaptation paradigm. If previous visual-motor practice leads to activation of motor related areas of the brain during observation, and this activation results in functionally equivalent learning processes between action and observation, then we hypothesize that prior physical practice would allow for the development of a motor program or repertoire that can potentially be activated during subsequent observational practice. This might then allow for predictions about upcoming sensory consequences and updating of internal models for aiming as evidenced by after-effects. If we fail to see evidence of after-effects following manipulations to the previous physical experiences of the observer, this would support the proposal that observational practice and physical practice result in different types of learning, with only the latter promoting a more implicit, motor-driven learning and sensory predictions, necessary for the appearance of after-effects.

Method

Design and participants

Forty-nine naïve volunteers from the University community (*M* age = 21.64 yr, *SD* = 3.67; *F* =30) were randomly assigned to 4 groups that varied with respect to physical practice experience (Phase I) and observational practice (Phase II). The ActCW+Obs group (n = 14; F = 6), ActCCW+Obs group (n = 11; F = 5), and ActCW_only group (n = 12; F = 10) physically practiced in a visually rotated environment in Phase I.

Two of these same groups (ActCW+Obs and ActCCW+Obs) and an additional Obs_only group (n = 12; F = 9) observed an actor perform in Phase II.[1] Each participant was right-handed as determined through the Edinburgh Handedness Inventory and provided informed consent in accordance to the University's ethical guidelines. Remuneration of $15 was paid for their participation.

Apparatus

The apparatus was the same as the one from previous studies (e.g., Larssen et al. 2012; Ong et al. 2012). Participants sat in front of a custom-made system that consisted of a semi-silvered mirror fixed above a graphics' tablet (Calcomp Drawing Board VI, 200 Hz) that measured 2D displacement (see Figure 1). A monitor situated 30 cm above the mirror was used to reflect the images of the stimuli and cursor onto the mirror and hence in the same plane as movements on the graphics' tablet. The monitor was positioned within an opening of a black wooden box that was placed over the graphics' tablet and helped to create a virtual, blackened environment when participants rested their chin on a chin rest positioned just outside the box (at a height of 35.5 cm from the table-top and a distance of 30 cm from the home square). Only the side facing the participant was open in order to allow aiming movements. A custom mouse on the graphics' tablet controlled the cursor. Visual stimuli included a red "home" square in the centre of five green target circles, each placed 10 cm away from the square and separated by 72°. Each of these targets was presented one at a time in a pseudo-random order of 5 trials per cycle during testing.

During an observation phase, observers watched an edited video (filmed via a web camera, Logitech Quickcam Pro 9000) of actors adapting to the rotated environment with the rotated cursor trajectory. A fluorescent light was used to illuminate the actor's hand for making the videos, but a black-board prevented the actor from seeing their own hand.

Task and Conditions

Under movement conditions, the participant's goal was to aim quickly and accurately from the home position to one of 5 targets. This was done using their right index finger, to linearly translate a cursor trajectory through a target, producing shooting-type movements. Vision of the cursor was only available during early familiarization trials, physical and observational adaptation phases, and retention trials (as described in Table 1). We asked participants to move quickly once a target appeared, but there were no explicit reaction time (RT) constraints, and movements could begin as soon as the participant was ready. In order to prevent on-line corrections, movement times (MT) were limited to 250 ms. If these movements exceeded this time, the target would turn red after the trial as a reminder to the participants to make faster, uncorrected aiming movements. MT was measured from the onset of movement to when the target was reached.

Upon aiming past the target, participants were told to pause before returning back to the home square. In order to accurately return to the home position and begin the next trial, on-line cursor trajectory feedback was made available when participants were within a 4 cm radius of the home square. This allowed participants to control the inter-trial interval. The next trial and the appearance of the next target began when the cursor was within the home square for a continuous period of 700 ms. Vision of the hand was never available during any movement trials and return movements were not recorded.

Movement conditions were enacted in 3 different types of environments; a normal, non-rotated environment and two rotated environments where the movements of the hand corresponded to a cursor that was linearly rotated by 30° in a clockwise (CW) or counterclockwise (CCW) direction. Pretests, Posttests and Washout trials were all conducted in a known normal, non-rotated environment. The difference between the Pretest and Posttest trials and the Washout trials was that only in the latter case was cursor trajectory feedback provided (on alternating blocks of 25 trials). This cursor feedback directly corresponded to movements of the hand. The Adaptation phases and Retention trials all occurred in a visually-rotated environment. Concurrent cursor feedback was available during these rotated conditions and remained on the screen until return movements were initiated.

For the Phase II observation condition, a video was projected onto the semi-silvered mirror via the upturned monitor (see Figure 1). Participants sat in front of the mirror-box set-up in the same chair and position as during movement conditions. Participants viewed a skilled model performing the 5 target aiming task in a 30° CW rotated environment relative to the hand. The video showed the model aiming to the target such that participants viewed movements of the skilled model's lower arm and hand moving the mouse as well as the concurrent cursor trajectory. Participants were told that they would later be tested in this environment. The skilled model had received ~400 trials of practice aiming in the CW environment (see Ong et al. 2012), such that their aiming movements were relatively accurate from trial 1 onwards. The model had an average RT of 408 ms (*SD* = 87). In previous work using this adaptation protocol, both skilled and learning models have been used with almost identical outcomes (Ong and Hodges 2010; Ong et al. 2012). In this experiment, a skilled video model was chosen primarily for consistency between participants.

Procedure

All participants were tested alone. In order to become accustomed to the task constraints, before testing began, all participants were given 25 familiarization trials in the normal aiming condition with cursor trajectory feedback. The general procedure consisted of two main practice phases (Phase I and Phase II). This allowed control over the amount and type of experience with the task before observation and subsequent tests of after-effects (see Table 1). In Phase I, we manipulated physical practice experience only. Three groups of participants received physical practice (trials, t=150), whereas a fourth group did not take part in Phase I of the experiment (Obs_only). The physical practice was either of a 30° CW (ActCW+Obs and ActCW_only) or 30° CCW rotation (ActCCW+Obs). In Phase II, we manipulated observational practice only. Three groups of participants observed a video of the 30° CW rotation (t=150). The fourth group did not receive observational practice (ActCW_only) and responded to questions on a handedness questionnaire at this time. All other groups answered this questionnaire before testing began. At the end of Phase II, we assessed performance in the rotated environment during the Retention trials in order to test direct learning effects associated with the various practice conditions (t=50).

Immediately preceding (Pretests) and following (Posttests) both these practice phases, participants performed aiming trials in a normal environment (t=50). This allowed assessment of sensory-motor adaptation relative to normal non-rotated conditions and thus the presence of after-effects. Between the two adaptation phases, immediately before and after Posttest1 and Pretest2, respectively, we included a Washout period in the normal environment. During Washout trials, participants aimed in a known normal environment, with and without online vision of the cursor trajectory. A Washout period was included in an attempt to bring error values back to their baseline in order to test for the return of after-effects following observational practice in Phase II. The amount and schedule of Washout practice varied across participants in an attempt to ensure that errors at the end of the Washout period were on average 5° or less. All participants experienced a minimum of 50 Washout trials. The extended Washout period varied from 60-100 trials in total and the extended Washout was somewhat equivalent across groups, with ~50 % of the participants in each group receiving extended Washout. Although the amount of Washout trials varied across participants, as well as the degree to which they washed out, importantly, we measured Pretest errors without vision in the normal environment for all participants before the observation phase. This enabled within group (and between group) comparison tests of after-effects following observation.

Participants were always explicitly told when they would be moving in a normal environment and they were reminded to just aim normally to the targets. On changing to a rotated condition, participants were informed that this was a “new environment condition” and they were reminded that their task was to create a straight line with the cursor in the direction of the target. During the observational practice phase, participants were asked to observe the actor performing in a “new” environment and they were told that they would be subsequently tested for movement accuracy in the same environment.

At the end of the study, participants completed a paper and pencil strategic awareness questionnaire where they were asked to recall what they had “seen” during observation (i.e. the CW rotation). There was only one group that did not get to view the video (ActCW_only) and this group recalled what they had “done” during practice. All groups were asked to estimate and draw their hand movements relative to the already drawn cursor trajectory to each of the 5 targets (i.e., correct hand movements would be drawn 30° CCW to the cursor line).

Data reduction and analysis

Data collection, filtering, and derivation of spatial/kinematic information replicated that of previous studies (e.g., Larssen et al. 2012). To control for and reduce the number of on-line correction trials, the experimenter checked the MTs after each cycle (5 trials). If more than 2 trials in a single cycle were greater than 250 ms, that cycle of trials was repeated. Movement direction was measured as the angle from the middle of the home square to the position of the cursor at peak tangential velocity. Directional error from the intended target was calculated as the difference between movement direction at peak tangential velocity and target location. To ensure that shooting type movements were made, we performed analyses of errors at 25 %, 50 % and 100 % of the distance to the target and these yielded the same pattern of results as those reported below for peak velocity. For this reason, only peak velocity values were used for all analysis. A positive value or negative value for error denoted a CW or CCW directional error, respectively. In terms of measures of strategic awareness, errors in estimation of the rotation were computed as the directional error (in degrees) between the estimated hand trajectory to a target and the actual hand trajectory needed to reach the target. RTs were calculated for the physical adaptation trials and retention tests based on the time between target onset and movement initiation (i.e., when the cursor was more than 0.25 cm from the origin). RTs were expected to give an indication of planning time (e.g., Benson et al. 2011; Hinder et al. 2010) and any potential increase in time to plan a movement as a result of observational versus physical practice and implementation of strategic knowledge. Following data collection, trials where movement times exceeded 300 ms were excluded. Since, experimenters had already screened for unusually slow movement times during the experiment, the number of trials excluded was small (ActCW+Obs = 1.6%, ActCCW +Obs = 3.4%, ActCW_only = 1.8%, Obs_only = 3.7%).

With respect to statistical analysis we ran a number of tests to look at: 1) rate of adaptation following physical practice in Phase I; 2) after-effects following initial adaptation practice in Phase I; 3) after-effects following observational practice in Phase II and 4) direct learning/retention effects associated with observation at the end of Phase II. These analyses were conducted on mean directional constant error (CE). Analysis of direct learning/retention effects (analysis 4) was also conducted on mean RTs. Group was always the between subjects' factor.

1) Rate of acquisition during physical adaptation in Phase I was analyzed in a 3 Group (ActCW+Obs, ActCCW+Obs, ActCW_only) x 6 Block (25 trials/block) mixed ANOVA. Because the CCW group showed errors in the opposite direction to the CW groups we reversed the error sign to enable statistical comparisons.

2) After-effects following initial practice in Phase I involved a comparison of Pretest1 and Posttest1, immediately preceding and following physical practice, respectively. These were analyzed in a 3 Group (ActCW+Obs, ActCCW+Obs, ActCW_only) x 2 Test (Pretest, Posttest) x 2 Block (25 trials/block) mixed ANOVA.

3) Testing for after-effects following observational practice in Phase II was our critical analysis. We first ran an analysis without the ActCCW+Obs group (due to the potential for positive and negative after-effects in these phases). We compared the remaining 3 groups across the 2 blocks of Pretest2 and Posttest2 in a 3 Group (ActCW+Obs, ActCW_only, Obs_only) x 2 Test x 2 Block mixed ANOVA. To enable comparisons with the CCW group and to get a better appreciation of change in error (i.e., after-

effects) across individuals, we calculated and analyzed difference scores between the last block of Pretest2 and the first block of Posttest2 in a 4 Group, one-way ANOVA.

4) Direct learning/retention effects associated with observing were assessed via comparisons of the two actor-observer groups (ActCW+Obs and ActCCW+Obs) with the ActCW_only group to see if there were benefits in retention as a result of the second observation phase. This resulted in a 3 Group x 3 Test (the first 2 blocks of adaptation practice, early, the last 2 blocks of adaptation practice, late, and the 2 blocks of retention) x 2 Block mixed ANOVA. We also compared these 3 groups to the Obs_only group in retention in a 4 Group x 2 Block mixed ANOVA. Due to an omission in testing procedures, two participants from the Obs_only group did not have data for this final retention test.

We also analyzed the strategic awareness questionnaires completed at the end of testing. A 4 group one-way ANOVA was used to compare group differences in the estimated size of the rotation observed during practice (or experienced for the ActCW_only group). This was based on measurement of the subtended angle between the target and the drawn hand trajectory.

Partial eta squared (η_p^2) values are reported as measures of effect size and post hoc analyses were conducted using Tukey HSD procedures (p <. 05). Greenhouse-Geisser corrections were applied for violations to sphericity.

Results

Constant Error (CE)

1) Rate of acquisition during adaptation practice in Phase I

To allow for between group comparisons, the CE obtained for each trial of CCW performance was first converted to reflect what errors would have looked like in a CW environment. It is important to note that this procedure would potentially inflate any early acquisition errors in this group due to a pre-test bias in the opposite direction. However, the data shown for Phase I in Figure 2 (A1-A6) is not reversed.

All three groups that received physical practice of either a CW or CCW rotation, were able to successfully reduce their performance errors as evidenced by a block effect, F(4.13,70.21) = 73.61, p<.001, η_p^2 = .68. There were significant linear and quadratic trends to this effect (both ps<.001). There was also a group, F(2,37) = 152.35, p<.001, η_p^2 = .42 and Group x Block interaction, F(4.13, 70.21) = 3.32, p = .01, η_p^2 = .16. Although the ActCCW+Obs group showed more error than the other two groups (ps<.01) that did not differ from each other, the interaction showed that these differences were only manifest in the first 2 blocks of practice.

2) After-effects following initial practice in Phase I

Comparisons between the first 2 blocks of Pretest1 and the first 2 blocks of Posttest1 aiming in a normal environment yielded evidence of strong unintentional after-effects for all three physical practice groups (see Figure 2, Phase I). Aiming error of the ActCCW+Obs group was again converted for statistical analysis. The presence of after-effects was reflected statistically by a large main effect of test (Pre vs Post), $F(1,37) = 577.95$, $p < .001$, $\eta_p^2 = .94$. There was also a block effect, $F(1,37)=76.90$, $p<.001$, $\eta_p^2 = .69$, reflecting the decrease in magnitude of aiming error with continued aiming in the normal environment (especially during the second block of Posttest1, as evidenced by a Test x Block interaction, $p<.001$, see Phase I, Figure 2). The groups were significantly different, $F(2,37) = 5.29$, $p = .01$, $\eta_p^2 = .24$, which was a result of differences in Posttest1 as evidenced by a Group x Test interaction, $F(2,37) = 5.43$, $p<.01$ $\eta_p^2 = .24$. After-effects were of a smaller magnitude for the ActCCW+Obs group in comparison to both the ActCW_only and the ActCW+Obs groups (*p*s<.05). There were no other between group differences.

3) Testing for after-effects following observational practice in Phase II

Again we compared aiming performance in a normal environment immediately before (Pretest2) and after (Posttest2) a period of CW rotation observation (although the ActCW_only group did not observe the rotation). These data are presented on the right of Figure 2. In our initial analysis we did not include the ActCCW+Obs group due to positive errors in Pretest2 and an expectation of a reduction of errors in Posttest2 following a CW rotation observation (yet see the difference score analysis below).

The groups were significantly different, $F(2,35) = 10.67$, $p<.001$, $\eta_p^2 = 0.38$ as a result of persistent after-effects (from Phase I testing) demonstrated in Pretest2. As expected based on previous studies, the Obs_only group showed no biased aiming in the direction of the observed CW rotation before or after practice. This group was significantly less errorful than the ActCW+Obs and ActCW_only groups, which did not differ from each other. Importantly, yet against predictions, the test main effect was not significant, $F(1,35) = 2.89$, $p = .098$, $\eta_p^2 =.08$, nor the Group x Test interaction, $F(2,35) = 1.71$, $p =.20$, $\eta_p^2 = .09$. The absence of an interaction shows a lack of after-effects as a result of the act and observe intervention. There was no block effect ($F<1$), but there was a Group x Block interaction, $F(2,35) = 5.48$, $p<.01$, $\eta_p^2 =.24$.

Although errors decreased across the 2 testing blocks for the two ActCW groups, they increased for the Obs_only group. However, none of these differences were statistically significant.[2,3]

Due to the potential significance of after-effects in our physically experienced observers we ran further analyses on the difference scores across the first block of Posttest2 and last block of Pretest2 in Phase II. First we counted the number of participants in each group to show an increase in error (suggestive of after-effects) from the last block of Pretest2 to the first block of Posttest2. For the ActCW+Obs group, 11/14 (71 %) showed an increase in error, in the predicted direction. Ten people showed an increase of more than 1° (range = 1.39 – 6.18°, one person showed an increase of 11.32°) and 2 showed a decrease of >1° (-1.42 to -1.55°). For the ActCW_only group, 9/12 (75 %) also showed an increase in error in the predicted direction. Six people showed an increase of >1° (range = 1.01-5.11°) and 2 people showed a decrease in error of >1°(-1.54 to -1.81). For the Obs_only group, 4/12 (33 %) showed an increase in error, although only 1 person by more than 1° (2.60°) and 5/12 showed a decrease of >1° (-1.95 to -3.37°). For the ActCCW+Obs group, 6/11 (55 %) showed a reduction in the size of their after-effect in the opposite (yet predicted) direction, although only 2 people showed a reduction of more than 1° (1.38, 3.57°) and 4 showed an increase of >1°(-1.23 to – 5.16°).

Statistical analysis of the difference scores yielded a significant group effect, $F(3,45) = 4.22$, $p = .01$, $\eta_p^2 = 0.22$. The CW physically-experienced observer group (ActCW+Obs, $M_{diff} = -2.31°$) was significantly different from the Obs_only group ($M_{diff} = + 0.97°$, p=.01). Importantly, however, they did not differ statistically from the ActCW_only group who did not observe the CW rotation (ActCW_only, $M_{diff} = -.98$, p =.55). No other group differences were statistically significant (ActCCW+Obs, $M_{diff} = +.35°$).

Based on these data it appears likely that any increase in after-effects was a result of persistent after-effects from acting in the same environment (i.e., incomplete washout), rather than being due to the observation phase. Further, when we looked at those individuals in the ActCW+Obs group who had showed a more complete washout (based on Pretest2 aiming errors of less than 5°, M = -3.38°, n = 7) and hence had potentially more room to increase errors following observation, the Posttest constant error averaged only -5.34° (i.e., comparable to the rest of the group).

4) Direct learning/retention effects associated with observing

We first compared errors across 3 phases of adaptation exposure in the CW environment (early Adaptation practice and late Adaptation practice in Phase I and Retention in Phase II, see Figure 2). This resulted in a comparison of 3 groups (the Obs_only group was excluded from this analysis). There was a benefit in retention for the group that watched what they had previously physically practiced, ActCW+Obs (i.e., direct learning effects from observing). This was shown by a significant group effect, F(2,37) = 14.25, p<.001, η_p^2 = .46 and a Group x Test interaction, F(4,37) = 4.99, p =.001, η_p^2 = .23. As above, early in practice, the ActCCW+Obs group had significantly higher error than the ActCW_only and ActCW+Obs groups (ps<.05, based on sign-adjusted CE values), however the groups were not different late in adaptation practice. Following a period of observation of the CW environment, the ActCW+Obs performed with significantly less error in retention than the other 2 groups (p<.05), which did not differ from each other. Therefore, there was evidence that the observation phase had a positive, direct learning effect. Significant test, F(2,37) = 55.77, p<.001, η_p^2 = .62 and block main effects, F(1,37) = 27.36, p<.001, η_p^2 = .45, were due to reductions in errors for all groups across practice blocks and test phases (early vs. late adaptation). There was no 3-way interaction.

A separate analysis of performance during the 2 blocks of the retention phase (the right panel of Figure 2) for all 4 groups showed significant main effects for group, F(3,43) = 2.89, p = .046, η_p^2 = .17 and block, F(1,43) = 9.21, p<.01, η_p^2 = .18 (and no interaction, F = 1.82). Tukey post-hoc analysis did not yield significant differences, although the ActCW+Obs group showed a trend to be more accurate than the ActCW_only (p =.077) and ActCCW+Obs (p = .071) groups. Importantly, the Obs_only group did not differ from the physical practice groups, showing direct benefits from watching.

Reaction Times

To determine how observation affected reaction times (RTs), as a proxy of planning and implementation of cognitive strategies, we performed an analysis on mean RTs when participants were physically acting in the CW environment (i.e., early and late Adaptation practice and Retention). These data are displayed in Table 2. As evidenced by a test phase effect, F(2,37) = 21.55, p<.001, η_p^2 =.39, RTs significantly decreased across adaptation in Phase I (i.e., early vs. late) and significantly increased from late adaptation in Phase I to retention in Phase II (both ps<.05). They also decreased across blocks, F(1,37) =34.57, p<.001, η_p^2 = .50, except during late adaptation in Phase I (Test x Block, F(2,37) = 4.32, p = .017, η_p^2 = .11). Although there was no significant group effect (F =1.29), there was a Group x Test interaction, F(4,37) = 2.78, p = .03, η_p^2 = .14. The ActCCW+Obs group had longer RTs early in adaptation relative to both of the CW practice groups (p<.05), however the groups were not statistically different in late adaptation. In the CW retention test following the period of observation, the ActCCW+Obs group had significantly longer RTs than the ActCW_only group. In accordance with predictions, only the two observe groups (ActCW+Obs and ActCCW+Obs) increased their RTs from late adaptation to retention.

Strategic Awareness

The data corresponding to explicit awareness of the type and size of the rotation observed (or experienced during physical practice for the ActCW_only group) is reported in Table 3(as an average across all 5 targets). In addition to poor accuracy in estimating the size of the rotation, only 2 out of 9 subjects in the ActCW_only group were able to consistently identify the correct direction of the experienced rotation during physical practice. Groups that watched the video in Phase II were more accurate in estimating the correct direction of the rotation, such that between 75 % (ObsCW_only) to 100 % of participants (ActCW+Obs), drew the direction of the rotation correctly for all 5 targets. With respect to the estimated size of the rotation, again all groups that observed the video of the actor performing in the CW environment were more accurate in judging the size of the rotation than the ActCW_only group. This was evidenced by a group effect, F(3,43) = 9.36, p<.001, η_p^2 = .40 and significant post hoc differences between the ActCW_only group and the 3 observer groups (who did not differ from one another).

Discussion

In this experiment we investigated whether previous visual-motor experience could change the observation process during adaptation practice and lead to a more implicit, motor-driven type of learning as evidenced by the presence of unintentional after-effects. Similar to previous findings, participants who physically practiced in a novel, rotated environment learned implicitly, as indicated by large unintentional after-effects when transferred back to the normal environment. This suggests that their motor system had been updated such that a new internal model for aiming was being erroneously activated in the normal aiming trials. Also in accord with previous experiments (e.g., Ong and Hodges 2010; Ong et al. 2012), naïve observers showed no after-effects as a result of observational practice, despite the fact that they had learned from watching and performed well on direct tests of learning in the rotated environment. Importantly, we did not show convincing evidence that observational practice could bring about (increased) after-effects, even once a motor repertoire for performing in this environment had been established. Additional observational practice following earlier physical practice (and Washout trials) did not lead to increased after-effects relative to a group that physically practiced but did not observe.

Recall that we tested experienced observers (who had prior physical experience in either the same environment as subsequently observed, or an opposite environment) for after-effects in a second Posttest. The physically experienced observers showed an increase in error of ~ 2° from the second Pretest to the second Posttest following observation. Although ~70% of participants in this group showed an increase of >1°, this increase was small in comparison to typical after-effects seen following physical practice (~15°). Perhaps more important, these experienced observers did not differ from the ActCW_only group that did not undertake observational practice. Again, over 70% of participants in this group showed an increase in error, half of which increased by >1°. Moreover, the ActCCW+Obs group did not show after-effects in the opposite direction to that seen in Posttest1. Although just over half of the participants in this group showed a reduction in the size of their after-effect in the opposite (yet predicted) direction, only 2 people showed an increase of more than 1°. Therefore, although there are trends in the data that might lead us to conclude that observation is moderated by prior physical exposure (given that the ActCW and ActCCW showed a different pattern of data), the lack of difference between the experienced observers and the control, ActCW_only, group does not support the conclusion that previous visual-motor experience modulates later observation in a significant manner needed to produce unintentional after-effects, which would have been reflective of (re)updating of internal models of aiming.

As with previous studies, there was a benefit of watching what had been previously practiced. This can be seen by the ActCW+Obs group's performance during retention testing in the rotated environment. This group performed significantly more accurately during retention than the other 2 groups who had either just physical practice in the CW environment (ActCW_only), or only previous physical practice in the CCW environment (ActCCW+Obs). This would support the contention that observational practice is a beneficial practice method, but that it works in a qualitatively different way to improve learning than that engendered through physical practice. In an earlier study we also showed that a mix of both physical and observational practice (25% physical and 75% observational practice) aided performance in the adapted environment and led to larger after-effects than physical practice alone (Ong et al. 2012). Because a significant increase in after-effects was not seen here as a result of observational practice, even though participants experienced these two modes of practice, we surmise that (some) physical experience in the adapted environment is needed immediately prior to testing for after-effects for updating of an internal model to occur. Perhaps if we had given our groups some physical exposure to the CW rotated environment immediately following observation and then tested for after-effects, it might have been possible to see significantly increased after-effects after only a few trials of physical practice. These results would indicate that self-produced physical movement and subsequent re-afference (i.e., self-generated sensory consequences) during the movement is needed to re-update the previously learned internal model for aiming.

Evaluation of the RTs and strategic recall data point to the fact that observation promoted a more strategically-driven learning process than that adopted following only physical practice (e.g., Benson et al. 2011). RTs increased for the ActCW+Obs group from the end of adaptation practice in Phase I to the start of retention in Phase II, even though this group performed in the same environment. Increases in RT across the same period were not noted for the no-observation, ActCW_only group. Although it is also possible that the observation phase served to interfere with recall of the previously acquired adaptation (leading to increases in RT for the observers), in previous work, similar high RT values were shown when participants were tested after an observation only phase (e.g., Larssen et al. 2012). This suggests that observation prompted a more strategic, planned action than that adopted before observational exposure (see Fernandez-Ruiz et al. 2011; Hinder et al. 2010). The observer groups were also better able to recall and detail what the rotation looked like during observational practice than the no-observation group. In previous adaptation studies, strategic knowledge has not been enough to remove after-effects (e.g., Mazzoni and Krakauer 2006), although it has been suggested to play a role in modifying them (Hinder et al. 2010). For example, when individuals practiced in a visual-motor environment with continued vision of their hand (that explicitly alerted to the direction and magnitude of the rotation), after-effects were reduced by about a third in comparison to a no hand-vision group (Ong and Hodges 2010). The reduction in after-effects in this earlier study might have also been moderated by the higher errors seen in practice (i.e., reduced adaptation), in addition to strategic modulation. Therefore, it is not the adoption of strategies per se that prevents implicit adaptation, but rather the absence of self-movement and arguably the sending of a motor command and associated low level predictions of associated action consequences (see Mazzoni and Krakauer, 2006; Taylor and Ivry 2011).

We had reason to think that the development of some sort of motor repertoire of visual-motor experience prior to observation would result in a different type of learning than that typically found to be engendered by observational practice of novel adapted environments. Calvo-Merino et al. (2005, 2006) have shown motor-related patterns of activation in the motor cortex during observation of dance specific moves. They argued that these activations were a result of motor experiences specific to the observers that allowed a resonance (i.e. a similar type of activation in the brain as experienced when acting) when already acquired actions were subsequently observed. In these experiments, participants were not given any instructions about re-enacting what they had seen, suggesting that this resonance was somewhat automatic. However, following significant reductions in error on a relatively simple adaptation task in the current experiment (arguably indicative of visual-motor expertise), we did not find evidence that the subsequent observation process had significantly changed, becoming more “motor” driven.

It is possible that the experienced actors had reason to doubt that they would be tested in the rotated environment, because following physical exposure they had immediately been transferred to a normal environment. Moreover, the lack of awareness of the rotation experienced in Phase I (physical practice) and its relation to Phase II (observational practice) might have also modified any potential transfer benefits from observing. The presence of direct learning effects, however, calls into question these two conclusions, in that positive transfer was seen following observation, suggesting that some learning had occurred. It is also possible that we did not give enough practice to our participants (either visual-motor or observational) to bring about after-effects in the second Posttest. Yet significant improvements in accuracy following 150 trials of physical practice were seen, with large after-effects that were comparable to those seen in previous studies. As well, the Obs_only group did show benefits of watching when finally tested in the CW environment, as inferred from a lack of significant difference from the other 3 physical practice groups. It does, however, remain a possibility that for purely visually-based information to affect learning in an implicit, motor-driven manner, more exposure is needed and potentially more sensitive tests of after-effects. This exposure might also be with respect to the within trial duration and preview times for the observers, who might need longer to activate motor plans than their actor counterparts. It is also possible that increased activation in motor-related areas of the brain during observation (or motor resonance) is not necessarily indicative of motor resonance at a functional level. Perhaps if we had performed neurophysiological scans on our participants we too might have seen some changes in activation circuits in the brain associated with MNS activation (see Malfait et al. 2010). Importantly, even with such high-level changes, it might indeed be the case that these activations are not strong or significant enough to be manifested at a behavioural level (see Maslovat et al. 2013). In fact, in a study of guitar chord observation and execution, although observation engaged activation in areas of the brain associated with the MNS, similar to that of physical practice and immediate imitation, observational practice was not as effective behaviourally as these two latter conditions and differences in cortical activations were shown that were related to a lack of execution-related processing (Higuchi et al. 2012).

One issue in the design of our experiment might have been with respect to the persistence of after-effects despite attempts to washout these effects following physical practice. Other researchers have also shown evidence that after-effects are relatively persistent even after washout (e.g., Hatada et al. 2006; Klapp et al. 1974). As shown through the differences in Pretest1 and Pretest2 data, because small after-effects were still present before observation, it might have been difficult to bring about significant after-effects as a result of observation. In the only experiment to date that has reported compensatory after-effects as a result of observing someone continually miss a target, these effects were of a very small magnitude (~1-2°) and only seen during a proprioceptive (in the absence of both target and limb vision) reach straight ahead (Ronchi et al. 2011). No after-effects were seen when the target remained visible (which is how they are typically assessed). Because, the average size of the errors in our experiment, before and after observation was ~5°, additional after-effect errors would have been difficult to detect. After-effects following physical practice are typically about 15°. Furthermore, in a group of 6 people we tested who physically practiced in both phases of the experiment, the average after-effect following a second phase of practice was ~20°[3]. As such, there was still significant room for an increase in error to be seen following an observation period. As others have suggested, washout might actually interfere with any consolidation processes associated with previous experience (e.g., Hinder et al. 2007; Krakauer 2009). So it remains possible that the washout phase removed any or most of the benefits physical practice had on observation. We would only be able to get at this issue by removing Washout tests and instead looking to see if the observation phase serves to increase already large after-effects. This appears to be a less powerful design as it relies on the presence of larger after-effects (relative to groups who do not watch).

In studies of observational practice during adaptation to novel environments there has been no documented evidence of after-effects. Participants do show subsequent savings when aiming in novel environments following observational practice (e.g., Mattar and Gribble 2005; Ong and Hodges 2010; Ong et al 2012), but evidence for internal model updating has not been shown. Effector specificity has been taken as evidence for motor system activation following observation, yet again, no effector specificity was shown following observational practice in a force field environment (Williams and Gribble 2012). This finding again suggests that observational learning in these types of tasks is not necessarily driven by motor resonance and arguably forward model predictions. The only study that we are aware of where after-effects following observation exposure has been shown was under conditions where participants watched a person consistently miss (aim to the right of a target) when reaching to horizontally displayed targets (Ronchi et al. 2011). This was not an observational practice study per se as the watched actor did not change in their error and were consistently wrong (except in Exp 2 where one group did improve with practice but no subsequent after-effects were then shown). When after-effects were observed, they were very small (~1-2°) and this bias did not increase when the size of the discrepancy increased (different to what would be expected as a result of physical practice, e.g., Henriques and Cressman 2012; Salomonczyk et al. 2011). Compensatory errors were also seen when visual judgments were required (in Exp. 1), which are typically expected to be in the opposite direction (c.f., Hatada et al. 2006). Therefore, rather than a motor-driven adaptation based on forward model predictions, like that seen during physical enactment and physical practice, these previously observed small after-effects following observation of target misses, might be a design artifact or suggestive of a different process in response to repeated missing. Experiments are underway to test whether observation of intentional errors (misses) are dealt with differently by an observer than observation of correct performance.

In conclusion, we argue that observational practice results in a different type of learning than that seen during physical practice, with the former promoting a primarily strategically-driven, explicit learning process. Arguably, physical practice relies on low-level, sensory predictions and implicit comparisons between the estimated hand trajectory and the executed trajectory. There has been little evidence, at least in these visuomotor adaptation tasks, that implicit estimates of hand trajectory are made when participants observe, even when they observe with the intention to learn, or importantly, even when they have had previous physical practice and hence possess a motor repertoire that would potentially allow for such an estimation process. This goes against the speculative proposal that observation results in the sending of motor commands that have corresponding efference copies allowing for implicit motor prediction (Wolpert et al. 2011).

Despite some recent claims that observational learning is implicit (Mattar and Gribble 2005; Osman et al. 2005) and engages the motor system (what Vogt and Tomaschke 2007 have referred to as ‘early mediation’ learning) we have not found evidence to support this contention, at least in these types of visual-motor adaptation learning environments. In other research involving motor sequence learning, similar negative conclusions have been reached regarding the processes underpinning observational practice (e.g., Gruetzmacher et al. 2011) as well as some of our other work involving bi-manual coordination learning from demonstrations (e.g., Hodges and Franks 2001; Maslovat et al. 2010). Although motor resonance may be observed in MNS cortical areas following visual-motor experience, arguably these activations are not significant enough to change the process of observational learning, which still proceeds in a more explicit, strategically-driven fashion, rather than an implicit fashion.

Footnotes

1. There were originally n=12 participants in the ActCCW+Obs group, but during the analysis stage one individual was removed due to unusually low errors in practice and subsequent knowledge that they had participated in a previous, similar experiment. We tested a couple more participants in our primary condition (ActCW+Obs) to allow greater confidence in our conclusions.
2. We also looked at after-effects on a smaller time scale (i.e., a cycle of 5 trials, rather than a 25 trial block), to see if potential after-effects dissipated quickly. There was no evidence that this was the case with after-effects remaining relatively consistent within a 25 trial block. We ran a 4 Group x 2 Block x 5 Cycle Repeated Measures ANOVA. None of the effects involving cycle were significant ($F<1$ for the cycle main effect).
3. Based on a Reviewer's suggestion we considered the possibility that after-effects in Phase II might be reduced for a group who had 2 phases of CW physical practice, potentially as a result of the additional blocks of washout interspersed before the second test for after-effects. This raises the possibility that the small after-effects we saw from our previous ActCW groups (ActCW+Obs; ActCW_only) would have been observed even after a second physical practice phase. Testing of 6 individuals ActCW+ActCW who underwent the same washout procedures showed this not to be the case. After-effects following a second phase of physical practice were M = -20.88° (Block1) and M = -15.49° (Block2), similar to the size of the after-effects after the first physical practice block (Block1, M = -20.40 and Block2, M = -14.65°). These values were of a significantly greater magnitude than those seen by the groups who had only one phase of CW physical practice and they were also commensurate with the Posttest1 data from these two groups (ActCW_only and ActCW+Obs).

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References

Ashford D, Davids K, Bennett SJ (2007) Observational modeling effects for movement dynamics and movement outcome 5 measures across differing task constraints: A meta-analysis. J Mot Behav 38: 185-205

Bandura A (1971) Analysis of modeling processes. In: Bandura A (ed) Psychological modeling: Conflicting theories. Adline-Atherton, Chicago, pp 1-62

Bandura A (1986) Social foundations of thought and action: a social cognitive theory. Prentice Hall, Englewood Cliffs, NJ

Benson BL, Anguera JA, Seidler RD (2011) A spatial strategy reduces error but interferes with sensorimotor adaptation. J of Neurophys 105: 2843-2851.

Bird G, Heyes C (2005) Effector-dependent learning by observation of a finger movement sequence. J Exp Psychol Hum Percept Perform 31: 262–275.

Brown LE, Wilson ET, Gribble PL (2009) Repetitive transcranial magnetic stimulation to the primary motor cortex interferes with motor learning by observing. J Cog Neurosci 21(5): 1013-1022. doi:10.1162/jocn.2009.21079

Calvo-Merino B, Glaser DE, Grezes J, Passingham RE, Haggard P (2005) Action observation and acquired motor skills: an fMRI study with expert dancers. Cereb Cortex 15(8): 1243-1249. doi: 10.1093/cercor/bhi007

Calvo-Merino B, Grezes J, Glaser DE, Passingham RE, Haggard P (2006) Seeing or doing? Influence of visual and motor familiarity in action observation. Curr Biol 16(19): 1905-1910. doi: 10.1016/j.cub.2006.07.065

Caspers S, Zilles K, Laird AR, Eickhoff SB (2010) ALE meta-analysis of action observation and imitation in the human brain. NeuroImage 50: 1148-1167.

Cross ES, Hamilton A, Grafton ST (2006) Building a motor simulation de novo: Observation of dance by dancers. NeuroImage 31 : 1257-1267

Deakin JM, Proteau L (2000) The role of scheduling in learning through observation. J Mot Behav 32(3) : 268-276.

Decety J, Grèzes J, Costes N, Perani D, Jeannerod M, Procyk E, Grassi F, Fazio F (1997) Brain activity during observation of actions. Influence of action content and subject's strategy. Brain 120: 1763–1777.

Demougeot L, Papaxanthis C (2011) Muscle fatigue affects mental simulation of action. J Neurosci 31(29): 10712-10720. Doi: 10.1523/jneurosci.6032-10.2011

Fadiga L, Craighero L (2004) Electrophysiology of Action Representation. J Clin Neurophysiol 21(3): 157-169.

Fernandez-Ruiz J, Wong W, Armstrong IT, Flanagan J (2011) Relation between reaction time and reach errors during visuomotor adaptation. Behav Brain Res 219:8–14

Gentile AM (1998) Implicit and explicit processes during acquisition of functional skills. Scand J Occup Ther 5: 7-16

Gentili R, Cahouet V, Ballay Y, Papaxanthis C (2004) Inertial properties of the arm are accurately predicted during motor imagery. Behav Brain Res 155(2): 231-239. doi: 10.1016/j.bbr.2004.04.027

Grèzes J, Decety J (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. Hum Brain Mapp 12: 1-19. doi: 10.1002/1097-0193(200101)12:1<1::AID-HBM10>3.0.CO;2-V.

Gruetzmacher N, Panzer S, Blandin Y, Shea CH (2011) Observation and physical practice: coding of simple motor sequences. Q J Exp Psychol 64(6): 1111-1123. doi: 10.1080/17470218.2010.543286.

Hatada Y, Miall RC, Rossetti Y (2006). Two waves of a long-lasting aftereffect of prism adaptation measured over 7 days. Exp Brain Res 169:417-426.

Held R (1965) Plasticity in sensory-motor systems. Sci Am 213: 84-94

Henriques DYP, Cressman EK (2012) Visuomotor adaptation and proprioceptive recalibration. J of Motor Behav 44: 435-444.

Hinder MR, Riek S, Tresilian JR, De Rugy A, Carson RG (2010) Real-time error detection but not error correction drives automatic visuomotor adaptation. Exp Brain Res 201:191-207

Hinder MR, Walk L, Woolley DG, Riek S, Carson RG (2007) The interference effects of non-rotated versus counter-rotated trials in visuomotor adaptation. Exp Brain Res 180:629–640

Higuchi S, Holle H, Roberts N, Eickhoff SB, Vogt S (2012) Imitation and observational learning of hand actions: Prefrontal involvement and connectivity. NeuroImage 59: 1668-1683.

Hodges NJ, Franks IM (2001) Learning a coordination skill: interactive effects of instruction and feedback. Res Q Exer Sport 72: 132-142.

Iacoboni M (2005) Neural mechanisms of imitation. Curr Opin Neurobiol 15: 632-637.

Ingram HA, van Donkelaar P, Cole J, Vercher J-L, Gauthier GM & Miall RC (2000) The role of proprioception and attention in a visuomotor adaptation task. Exp Brain Res 132: 114-126.

Jeannerod M (2001) Neural simulation of action: a unifying mechanism for motor cognition. Neuroimage 14(1 Pt 2):S103-109. doi: 10.1006/nimg.2001.0832

Kagerer FA, Contreras-Vidal JL, Stelmach GE (1997) Adaptation to gradual as compared with sudden visuo-motor distortions. Exp Brain Res 115: 557-561.

Kelly SW, Burton AM, Riedel B, Lynch E (2003). Sequence learning by action and observation: Evidence for separate mechanisms. Br Jn of Psychology 94: 355-372. doi: 10.1348/000712603767876271

Klapp ST, Nordell SA, Hoekenga KC, Patton CB (1974) Long-lasting aftereffect of brief prism exposure. Percep Psychophys 15: 399-400.

Kohler E, Keysers C, Umilta MA, Fogassi L, Gallese V, Rizzolatti G (2002) Hearing sounds, understanding actions: Action representation in mirror neurons. Science 297: 846-848.

Krakauer JW (2009) Motor learning and consolidation: the case of visuomotor rotation. Adv Exp Med Biol 629: 405-521. doi: 10.1007/978-0-387-77064-2_21

Larssen BC, Ong NT, and Hodges NJ (2012) Watch and learn: seeing is better than doing when acquiring consecutive motor tasks. PLoS ONE 7(6): e38938. doi: 10.1371/journal.pone.0038938

Malfait N, Valyear KF, Culham JC, Anton JL, Brown LE, Gribble PL (2010) fMRI activation during observation of others' reach errors. J Cog Neurosci 22: 1493-1503.

Maslovat D, Chua R, Hodges NJ (2013) When unintended movements "leak" out: A startling acoustic stimulus can elicit a prepared response during motor imagery and action observation. Neuropsych 5: 838-844. doi: 10.1016/j.neuropsychologia.2013.01.016

Maslovat D, Hodges NJ, Krigolson OE, Handy TC (2010) Observational practice benefits are limited to perceptual improvements in the acquisition of a novel coordination skill. Exp Brain Res 204: 119-130. doi: 10.1007/s00221-010-2302-7

Mattar AA, Gribble PL (2005) Motor learning by observing. Neuron 46: 153–160. doi: 10.1016/j.neuron.2005.02.009.

Mazzoni P, Krakauer JW (2006) An implicit plan overrides an explicit strategy during visuomotor adaptation. J Neurosci 26: 3642-3645.

Munzert J, Zentgraf K, Stark R, Vaitl D (2008) Neural activation in cognitive motor processes: comparing motor imagery and observation of gymnastic movements. Exp Brain Res 188: 437-444. doi: 10.1007/s00221-008-1376-y

Ong NT, Hodges NJ (2010) Absence of after-effects for observers after watching a visuomotor adaptation. Exp Brain Res 205: 325-334. doi: 10.1007/s00221-010-2366-4

Ong NT, Larssen BC, Hodges NJ (2012) In the absence of physical practice, observation and imagery do not result in updating of internal models for aiming. Exp Brain Res 218: 9-19. doi: 10.1007/s00221-011-2996-1

Osman M, Bird G, Heyes C (2005). Action observation supports effector-dependent learning of finger movement sequences. Exp Brain Res 165, 19–27. doi: 10.1007/s00221-005-2275-0.

Rizzolatti G, Fogassi L, Gallese V (2001) Neurophysiological mechanisms underlying the understanding and imitation of action. Nat Neurosci 2: 661–670.

Rizzolatti G, Sinigaglia C (2010) The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. Nat Rev Neurosci 11: 264-274.

Ronchi R, Revol P, Katayama M, Rossetti Y, Farnè A (2011) Seeing your error alters my pointing: observing systematic pointing errors induces sensori-motor after-effects. PLoS One: 6:e21070. doi: 10.1371/journal.pone.0021070.

Rumiati RI, Weiss PH, Tessari A, Assmus A, Zilles K, Herzog H, Fink GR (2005) Common and differential neural mechanisms supporting imitation of meaningful and meaningless actions. J Cog Neurosci 17: 1420-1431

Salomonczyk D, Cressman EK, Henriques DY (2011). Proprioceptive recalibration following prolonged training and increasing distortions in visuomotor adaptation. Neuropsych 49: 3053-362

Shadmehr R, Mussa-Ivaldi FA (1994) Adaptive representation of dynamics during learning a motor task. J Neurosci 14: 3208-3224

Taylor JA & Ivry RB (2011) Flexible cognitive strategies during motor learning. PLoS Comp Bio: 7(2):e1001096.

Umilta MA, Kohler E, Gallese V, Fogassi L, Fadiga L, Keysers C, Rizzolatti G (2001) I know what you are doing: A neurophysiological study. Neuron 31: 155-165

Vogt S (2002) Visuomotor couplings in object-oriented and imitative actions. In Meltzoff AN & Prinz W (Eds.), The imitative mind: Development, evolution, and brain bases. Cambridge University Press, Cambridge, pp. 206-220

Vogt S, Buccino G, Wohlschläger AM, Canessa N, Shah NJ, Zilles K, Eickhoff SB, Freund H-J, Rizzolatti G, Fink GR (2007) Prefrontal involvement in imitation learning of hand actions: effects of practice and expertise. NeuroImage 37: 1371-1383

Vogt S, Thomaschke R (2007) From visuo-motor interactions to imitation learning: behavioural and brain imaging studies. J Sports Sci 25: 3-23

Williams A, Gribble PL (2012) Observed effector-independent motor learning by observing. J Neurophys 107: 1564-1570

Wolpert DM, Diedrichsen J, Flanagan JR (2011) Principles of sensorimotor learning. Nat Rev Neurosci 12: 739-751

Wolpert DM, Flanagan JR (2001) Motor prediction. Curr Biol 11(18): R729-732. doi: 10.1016/S0960-9822(01)00432-8

Wolpert DM, Miall RC (1996) Forward models for physiological motor control. Neural Net 9: 1265-1279. doi: 10.1016/S0893-6080(96)00035-4

Table 1: Procedural table showing the chronology of testing conditions, number of trials, act or observe experiences, the type of environment/rotation (none, clockwise, CW or counterclockwise, CCW, all 30°) and the available visual feedback (N = No, Y = Yes) for each condition and for all four groups.

Condition/Gp	# Trials	Act/Observe	Rotation	Concurrent Feedback	
				Cursor	Hand
Familiarization	25	Act	none	Y	N
PHASE I					
Pretest1	50	Act	none	N	N
Adaptation practice:					
ActCW+Obs	150	Act	CW	Y	N
ActCCW+Obs	150	Act	CCW	Y	N
ActCW_only	150	Act	CW	Y	N
Posttest1	50	Act	none	N	N
Washout	50(minimum)	Act	none	Y/N	N
PHASE II					
Pretest2	50	Act	none	N	N
Observation practice:					
ActCW+Obs	150	Obs	CW	Y	Y
ActCCW+Obs	150	Obs	CW	Y	Y
ActCW_only	-	-	-	-	-
Obs_only*	150	Obs	CW	Y	Y
Posttest2	50	Act	none	N	N
Retention	50	Act	CW	Y	N

* The "Obs_only" group only completed Phase II of testing. In all conditions, the next target was visible once the cursor was within the home square for 700 ms and remained visible until the end of the trial (movement cessation).

Table 2: Group Mean RT data (ms, and between subject SDs) as a function of Group, Test phase and Block

Test Phase	Early Adaptation		Late Adaptation		Retention	
Group /Block	A1	A2	A5	A6	A7	A8
ActCW+Obs	438.56 (60)	405.28 (67)	364.35 (48)	372.39 (52)	480.61 (99)	426.62 (103)
ActCCW+Obs	498.75 (78)	475.22 (77)	423.68 (66)	396.94 (63)	513.50 (103)	464.85 (74)
ActCW_only	443.95 (108)	414.06 (133)	407.06 (115)	392.82 (106)	433.64 (141)	399.72 (111)
Obs_only	-	-	-	-	465.63 (91)	445.10 (108)

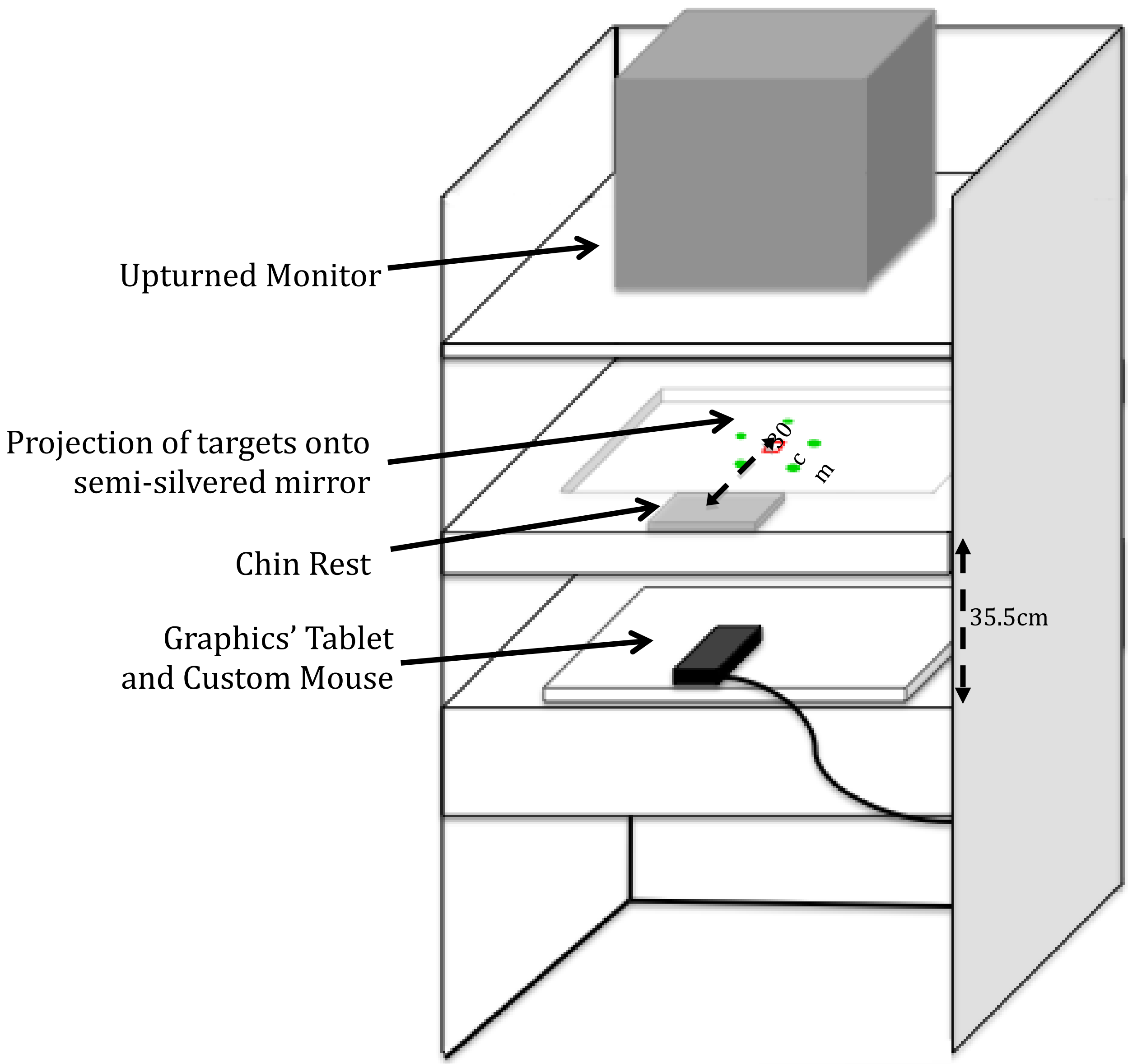
Table 3: Number of participants who consistently reported (on paper and pen schematic diagrams of the target display) the correct direction (direction correct) of the target rotation for all 5 targets, along with the mean measured angle of the rotation (°) from the diagrams and between target SDs (i.e., VE°) across the 5 targets (between-subject SDs). Participants always observed a 30°CW rotation.

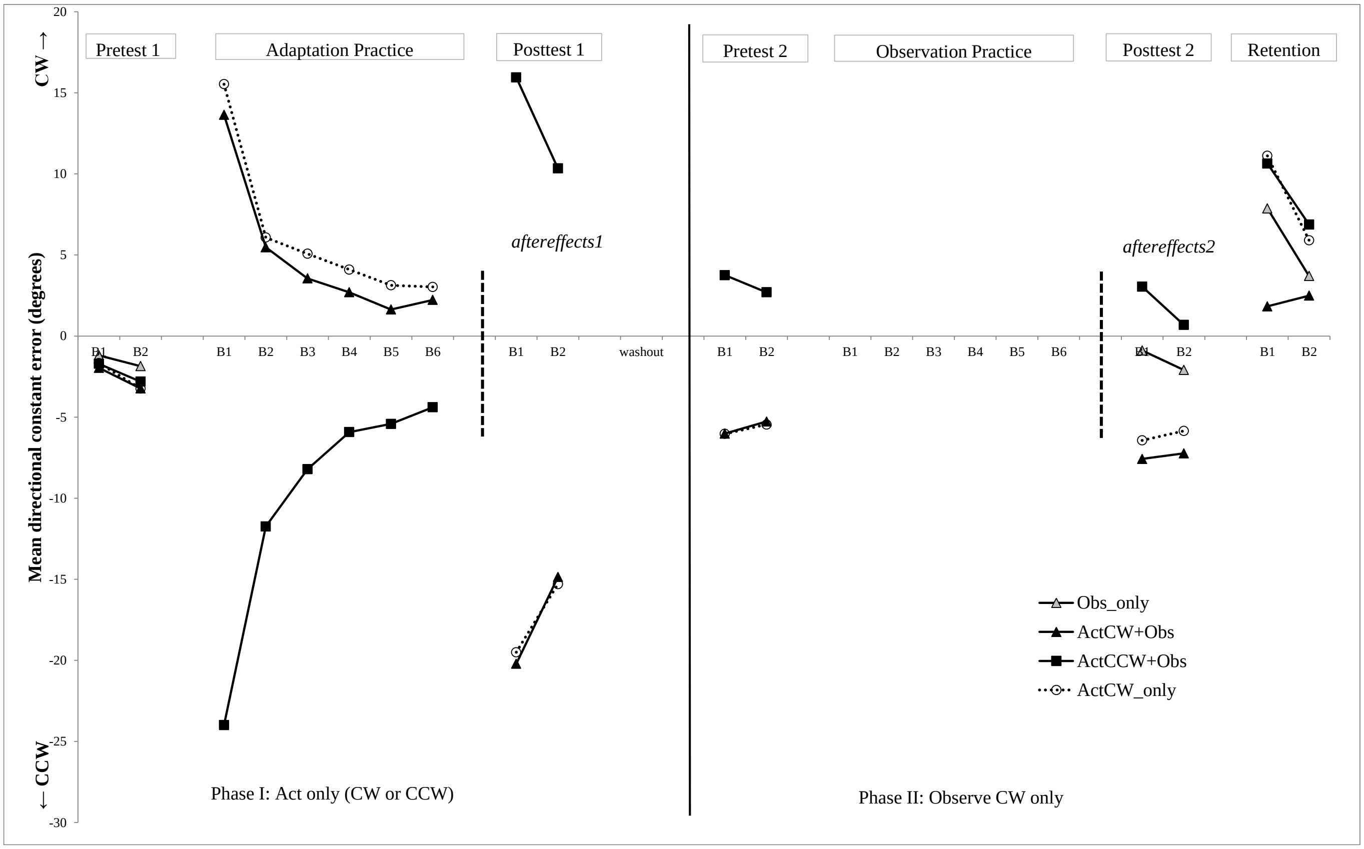
Group	Direction correct (n)	Mean Angle° (SD)	Mean VE° (SD)
ActCW+Obs	14/14	28.82 (9.94)	3.08 (3.86)
ActCCW+Obs	9/11	28.91 (9.63)	5.47 (7.32)
ActCW_only	2/10	7.90 (7.25)	15.18 (10.52)
Obs_only	9/12	22.36 (13.52)	8.07 (10.96)

Figure heading

Fig 1: A schematic of the apparatus used during the physical aiming and observation conditions.

Fig 2: Mean directional constant error (degrees) for the 4 different groups across the 2 phases of the experiment. Group means are plotted as a function of block (B) for each experimental condition. Positive error values represent error in the CW direction, and negative values represent error in the CCW direction. Phase I consisted of adaptation physical practice (6 blocks of 25 trials/block, either in a clockwise, CW or counterclockwise, CCW environment). In Phase II, participants only observed a CW rotation. Pretests and Posttests in a normal, no vision environment, were conducted in both Phases of the experiment to allow for tests of after-effects following physical (after-effects1) and observational (after-effects2) practice. We also tested participants in the adapted environment at the end of Phase II (2 block retention test in a CW environment). We have marked on the figure when "Washout" trials occurred, which was normal aiming with vision, as well as the observational practice phase, which consisted of 150 trials in the CW environment. The dashed lines signal when tests for after-effects were conducted.


Upturned Monitor
Projection of targets onto semi-silvered mirror
30 cm
Chin Rest
Graphics' Tablet and Custom Mouse
35.5cm



Pretest 1
Adaptation Practice
Posttest 1
Pretest 2
Observation Practice
Posttest 2
Retention
CW →
← CCW
Mean directional constant error (degrees)
20
15
10
5
0
-5
-10
-15
-20
-25
-30
B1
B2
B3
B4
B5
B6
washout
aftereffects1
aftereffects2
Obs_only
ActCW+Obs
ActCCW+Obs
ActCW_only
Phase I: Act only (CW or CCW)
Phase II: Observe CW only