

Evidence for dual mechanisms of action prediction dependent on acquired visual-motor experiences

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Running Head: visual and motor-based action prediction

Abstract

To test mechanisms underpinning action-prediction, we directly controlled experience in a dart-throwing training study. A Motor-visual group physically practised throwing darts and a Perceptual training group learnt to associate dart throw actions (occluded video clips) with landing outcomes. A final Control group did not practice. Accuracy was assessed on related prediction tests before and after practice (involving temporally occluded video clips). These tests were performed whilst additionally performing simple, action-incongruent secondary motor tasks with either the right (observed throwing arm) or left effector, in addition to an attention control task. Motor proficiency tests were also performed. While both trained groups improved their prediction accuracy after training, only the Motor-visual group showed interference associated with the right-arm secondary motor task after practice. No interference was shown for the left-arm motor task. These effects were evidenced regardless of whether predictions were made to video-stimuli or static clips. Moreover, improvements on the motor proficiency test were only shown for the Motor-visual group. These results show evidence in support of motor simulation processes during action prediction among observers with motor experience. Prediction accuracy can be achieved via non-motor processes (for the Perceptual group) but there was no evidence that physically experienced performers could effectively switch processes to maintain prediction accuracy.

Evidence for dual mechanisms of action prediction dependent on visual-motor experience

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

Because of the common neural link between motor and perceptual-based representations of the same action, the motor system seems capable of using acquired motor representations to internally simulate an observed action in order to predict its future outcome (Blakemore & Decety, 2001; Gallese & Goldman, 1998; Jeannerod, 2001; Kilner, Friston, & Frith, 2007; Schubotz, 2007; Wilson & Knoblich, 2005; Wolpert, Doya, & Kawato, 2003; see also Schutz-Bosbach & Prinz, 2007). Motor or physical practice is thought to foster the development of motor programs, or internal models, that rely on body kinematics and action outcomes more generally, to predict the actions of others. This is achieved through simulative mechanisms that map the observed action (and its effects) onto the observer's motor system (e.g., Knoblich et al.

2002; Urgesi et al., 2012). This simulation is thought to be automatic, with the closer the match between the (observed) perceptual input and the internal motor code (or program), the more accurate the prediction (Knoblich & Flach 2001). At an implicit, computational level, forward models are thought to be acquired through practice, which allow prediction of the sensory consequences of actions. When we generate a motor command, an efference copy of this motor command is fed into this forward model (predictor), allowing anticipation of what the consequences of our action should feel and look like (Miall & Wolpert, 1996). It has been suggested that these forward models can also be used to predict the outcomes of others' actions, through activation of the motor system during observation (Blakemore & Frith, 2005; Wolpert & Flanagan, 2001; Wolpert et al., 2003).

The close association between the formation of motor representations and the prediction of action outcomes suggests that motor experiences play a critical role in action prediction (Aglioti et al., 2008; Calvo-Merino et al., 2005, 2006; Urgesi et al., 2012; for a review see: Zentgraf, Munzert, Bischoff, & Newman-Norlund, 2011). This is supported by evidence showing greater activation in motor areas of the brain thought to be involved in action simulation, when people viewed action sequences that they had experience performing, rather than those they had experience observing (Calvo-Merino et al., 2005, 2006). Behavioural research has also been provided in support of this association. Groups that were trained on novel motor tasks in the absence of vision significantly improved later on related prediction tasks (Casile & Giese, 2006; Hecht et al., 2001; Mulligan & Hodges, 2014; Reithler et al., 2007). These results suggest that, once internal motor representations are formed, prediction comes about through simulation processes that utilize these internal motor representations.

Another line of evidence in support of simulation-based prediction based on the acquisition of motor representations comes from research examining the proactive nature of the human oculomotor system. Twelve-month-old infants were able to predict the action goals of observed actors, only when they had developed the ability to perform the same goal-directed action themselves (Falck-Ytter, Gredeback, & von Hofsten, 2006). In adults, observers and actors of the same task show similar patterns of visual search, with both groups showing predictive saccades (Flanagan & Johansson, 2003). Importantly, if the observer has their arms restrained during action observation, the saccades no longer show this predictive nature (Ambrosini et al., 2012). This result suggests that brain regions representing the effectors involved in the observed action are activated and used to aid in the understanding and prediction of other's movements.

In earlier work, we have shown that a secondary motor task, performed with the same arm as viewed in the action of a trained dart thrower, reduces the prediction accuracy of skilled performers to the level of a novice (Mulligan et al., 2015). Although this provided direct evidence that the motor-system was involved in decision accuracy, it did not necessarily show that predictions were a result of action-simulation. It is possible, that such a motor task interfered in a general manner, perhaps with the spatial processing of kinematic information. A stronger test about the nature of this interference effect and action-simulation would be to test prediction accuracy under conditions where two secondary motor tasks are performed. Effector-specific interference (e.g., right and left arm) during prediction accuracy, as a function of manipulated motor experience throwing darts, would provide strong evidence that motor simulative processes are directly implicated in the predictive decision processes of trained individuals.

Although action prediction may rely on the cortical neuromotor system in a general fashion, there is evidence for distinct neural representations underlying action prediction. In an fMRI study, participants had to either predict whether an action continued with accurate timing after occlusion (i.e., temporal prediction) or if the last memorized frame before occlusion continued from the same position after occlusion (static memory condition, no temporal prediction). Activation in right pre-SMA (sensorimotor areas) was shown in both conditions, indicating maintenance of an internal reference. In contrast, activation in left pre-SMA and left PMd (dorsal premotor) was only seen in the ‘prediction’ condition, and was considered indicative of simulation (Stadler et al., 2011). Behavioural evidence supporting a dual-process model of action prediction was subsequently provided, whereby evidence commensurate with real-time simulation was shown with compatible effector priming, while incompatible effector priming promoted a ‘static matching’ process (Springer, Brandstaedter & Prinz, 2013). While the results of this study provided evidence that two different processes may be involved in action prediction, the authors were unable to make any determination about the representational format (visual/motor) of these processes.

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

it was the goalkeepers' visual expertise with the penalty kicks, from a third-person perspective, that allowed them to inhibit simulation mechanisms based on body movements and switch to using visual representations, based on contextual cues, to determine ball trajectory (yet see Canal-Bruland & Schmidt, 2009, who did not show the same specificity based on player position in a handball task).

Here, we present a study testing how strictly visual or combined visual-motor experience affects engagement in action simulation during prediction, through manipulations to both the type of prior experience (visual/motor) and the types of secondary tasks performed during prediction. It has been argued that motor experience is required to develop motor representations that can later be simulated to generate predictions of observed actions, whereas visual experience leads to visual representations of the action that are used to define static and/or dynamic patterns of objects, such as ball flight (Urgesi et al., 2012; see also Hubbard, 2005; Zago & Lacquaniti 2005). Others, however, have suggested that the motor system can be activated during action observation, even in the absence of motor experience (e.g., Brown et al., 2009; Mattar & Gribble, 2005), referred to as the early mediation account of observational learning (Vogt & Thomaschke, 2007, Maslovat et al., 2010). As such, visual experience may still promote motor-based, simulation-type processes.

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

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

Converging lines of evidence point to an effector-specific motor mapping during action observation and prediction, based on behavioural (e.g., Brass et al., 2001; Gillmeister et al., 2008; Heyes & Leighton, 2007) and neurophysiological (e.g., Jastorff et al., 2012; Strafella & Paus, 2000; Urgesi et al., 2010) data. However, in these studies, comparisons have not been made across complementary effectors (i.e., right and left hand), which would inform about the general or specific nature of cortical activation of the motor system during action prediction. If motor system activation is specific to the trained (right) effector, suggestive of effector-specific simulation, then we hypothesised that for the group receiving physical practice, there would only be interference from the right force secondary task (i.e., throwing arm) with respect to prediction accuracy. For the perceptually-trained group, no interference was expected, from either (left or right) secondary motor task, due to the predicted absence of motor-based representations developed during training. This effector- and experience-dependent interference would also rule out interpretations of the secondary task effects as being a function of general interference in the spatial processing of action kinematics, rather than due to action simulation.

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

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

The perceptually-trained group received only static action depictions during the training phase shown at various occlusion points before dart release, with outcome feedback provided after a prediction had been made. This type of prediction training, based on static rather than dynamic clips, was thought to encourage a matching strategy between potential key body and dart kinematics and their outcomes. As such, through this training, we had hoped to maximize the chance that visually-driven representations of the action would be formed. Because of the nature of the training for the perceptually-trained group, prediction accuracy for this group could potentially decrease for the dynamic in comparison to the static stimuli, due to perceptual-specificity in training with these static stimuli only.

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

Methods

Participants

Thirty, male, volunteer students between the ages of 18 and 28 years, with normal or corrected vision, and no neurological impairment took part in the study. Participants were randomly allocated to three groups ($n=10/gp$): a “Motor-visual” training group, a “Perceptual” training group, and a “No-practice” control group. Based on our previous work with skilled darts players, we had a relatively large effect-size ($\eta_p^2 = 0.24$) for the 2-way interaction of Group with secondary-task Condition, based on a sample size of $n = 10/group$ (see Mulligan et al., 2015; yielding statistical power $> 80\%$; $\alpha = 0.05$; G*Power 3.1.9.2; Faul et al., 2007). In the current study, with the inclusion of Test time (i.e., pre vs. post-test comparisons) and hence a predicted 3-way interaction, although a reduced effect size was expected, with the high correlation between our repeated measures, power should still be above 70% based on a sample size of $n=10/group$.

All participants were self-report right-handed (and subsequently threw with their right-hand) and had no experience playing darts. All participants provided informed consent, but were blind to the hypotheses of the experiment. Ethics’ protocols for human experiments were strictly followed, as laid out by the ethics’ board of the University. Remuneration for participation was \$10 /hour.

Task and Design

There were 3 phases to the experiment consisting of pre-testing (motor proficiency and prediction tests), training across 2 practice days (Motor-visual, Perceptual or No-practice) and post-testing (prediction and motor proficiency tests). For the groups that received training, participants were required to either throw darts to one of three sections of a dart board (Motor-

visual group) or watch a video of a trained individual throw darts to three sections of a dartboard showing the beginning part of the throw only (i.e., with the outcome occluded; Perceptual group). This latter group then made predictions about the landing position of the dart and received video feedback as to the correct outcome. In the pre- and post-prediction tests, all participants predicted the landing position of a dart from temporally occluded video (pre- and post-tests) or from static clips (post-test only) after watching a model enact the beginning part of the throw. In the pre- and post-motor proficiency test, participants were asked to throw three darts at the centre of each of the three sections of the dartboard (9 darts total).

Apparatus and Stimuli

The task was modeled on earlier dart throwing studies designed to assess prediction accuracy (Knoblich & Flach 2001; Mulligan & Hodges 2014; Mulligan et al., 2015). A standard dart board was used and at regulation height and distance (i.e., participant stood at a distance of 2.37 m from the dartboard, which was placed at a height of 1.73 m from the floor to the bulls-eye). The board was divided into 3 sections (top, middle and bottom), that were formed by two horizontal lines an equal distance from the top and bottom of the dart board and from each other. In a pre- and post-test, participants were required to make predictive judgements, from videos presented in a side-on perspective, as to which of the 3 vertical sections the dart would land.

Video clips for the prediction test were created using a Cannon HV20 camera (30 fps, 33ms/frame) showing a skilled actor throwing a dart at the centre of each of three sections of a dartboard. The actor was filmed from a side-on perspective from a distance of 3 m. Three video clips were created for each of the top, middle, and bottom sections, for a total of 9 clips. The actor threw to each section until 9 clips landed in what was subjectively determined to be the centre of each section (both vertically and horizontally). Each of these clips was further edited

into 3 temporal lengths termed occlusion points (OP), each length being two frames (66 ms) longer than the previous. Three OPs for 3 clips at 3 different targets resulted in 27 total clips.

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

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

For the pre- and post-prediction tests, participants performed these tasks under one of four secondary-task conditions while viewing the dart clips; control, right-hand or left-hand force

production or tone-monitoring. For the 2 force-production tasks, a force plate sensor logger (Neulog Inc, Rochester, NY) was attached to a tall iron post and adjusted to the participant's hand position when they stood adjacent to the post with their hands at their sides (using industrial strength Velcro; see Mulligan et al., 2015 for photo). This position enabled the participant to push against the force sensor with the edge of their hand in a fist shape, keeping the rest of their arm and body relatively immobile. Participants were required to press on a force gauge, in an action-incongruent manner, while viewing the stimulus. This secondary task was designed to prevent, or interfere with, participants' ability to simulate the observed action, as the effector involved in the action would be tasked with pushing (immobilizing the arm), whereas the primary dart throwing task required extension and flexion of the elbow and wrist. In order to probe the effector-specificity of the interference effect, both a right and left force task were used (see below). The force sensor was connected to a laptop, running Neulog software, which allowed real-time monitoring and data collection. Audio files used for the tone-monitoring secondary task were created using Audacity Inc. software, v2.0.2 (Boston, MA). These were 5 s files that consisted of a 250 Hz control tone with a randomly interspersed high tone of 440 Hz, played for 100 ms on a third of the trials. We used three different temporal orders, allowing the duration of the control tone to vary from 3 s – 4.8 s before interspersing the 440 Hz tone.

Procedures

Pre-testing.

The study took place over two days. On the first day, participants threw 3 darts at the centre of each of the three sections of the dartboard to obtain a baseline measure of motor performance. Trials in the motor pre-test were deliberately limited to reduce potential learning effects on subsequent training. Participants were required to stand and hold the darts in the same

manner as the to-be-seen video-model, that is, using a thumb and forefinger grip and with their feet aligned horizontally to the start line.

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

Force-production tasks. Participants were required to stand with their arms by their side, adjacent and to the left or right of the iron post (depending on hand condition), facing the projection screen at ~45-60° angle. They could therefore see the action unfold in approximately the same plane as the actor, without having to turn their head. They were then told to make a fist and to press against the force gauge with the elbow extended and their shoulder and wrist in a neutral position. This procedure was designed to be incompatible with the motion involved in throwing a dart, requiring activation of the same muscle groups involved in the throw, but in a different pattern (i.e., isometric versus dynamic contractions) and for a different function (i.e., the arm muscles are stabilizing and the elevator muscles of the shoulder are providing motive force whereas in the dart throw, shoulder muscles are stabilizing and the triceps are providing motive force).

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

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

additional question appeared, after the confidence question, asking participants if the tone had changed frequency during the trial.

Training.

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

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

Post-testing.

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

Data Analysis

Prediction tests.

Individual percentage accuracy for each condition (i.e., for each OP and for each Prediction condition) was calculated. Because pre and post-test measures were only available for the Dynamic stimuli, this accuracy variable was first subjected to a 3 Group (Perceptual, Motor-visual, No-practice) x 2 Test (pre, post) x 4 Prediction condition (Control, Tone, Right Force, Left Force) x 3 Occlusion Point (OP) repeated measures (RM) ANOVA, with RM on all factors except Group. Our main hypothesis concerned the 3-way interaction (independent of occlusion point). However, we included OP in the analyses to control for obvious variance associated with this ‘amount of information’ variable, and to provide indications as to where any improvements (across time) and/or between groups were evidenced. We also ran a similar analysis (with the absence of Test), comparing the prediction accuracy scores for the Static and Dynamic stimuli, which were only presented on Day 2 (post-test). Our main hypotheses here was with respect to the 3-way interaction of Group and Condition with Stimuli-type, or potentially just a 2-way interaction of Group and Condition.

Motor-proficiency tests.

Accuracy (in relation to the target centre) was measured as Mean Radial Error (MRE) across throws for a participant. Variability (in relation to the participant's average positioning) was measured as bivariate variable error (BVE) (Hancock, Butler & Fischman, 1995). To arrive at RE, X and Y coordinates were measured for each throw, using the middle of the targeted dart-board section (i.e., top, middle, bottom) as the origin (0,0). MRE and RE calculations are shown below where k = number of throws for a participant.

$$MRE = \overline{RE} = \frac{1}{k} \sum_{i=1}^k \left(\sqrt{X_i^2 + Y_i^2} \right)$$

BVE was based on the deviations of X and Y in relation to the individual's own average positioning in X and Y (termed centroid, c) and the number of throws, k , based on all throws for a participant as detailed below:

$$BVE = \sqrt{\left(\frac{1}{k}\right) \sum_{i=1}^k [(X_i - X_c)^2 + (Y_i - Y_c)^2]}$$

These measures were subjected to a 3 Group x 2 Test (pre, post) RM ANOVA.

Training data.

Data from the training phase were also analysed in order to establish improvements across practice. This was in the form of % outcome accuracy for the Motor-visual group and % verbal-response accuracy for the Perceptual group. Data were analyzed in 9 Blocks (of 15 trials), in a 2 Day x 9 Block RM ANOVA, with RM on both factors, separately for each group. A second analysis was also ran to look at an overall training effect, comparing the first 2 blocks of practice on day 1 to the last 2 blocks of practice on day 2.

For all ANOVAs, partial eta squared (η_p^2) values are reported as measures of effect size. These values provide proportional estimates of the between or within-subject variance accounted for by a particular effect (with values $>.10$ reflecting proportional variance of greater than 10% of the within or between-group variance, depending on the effect). Where violations to sphericity were encountered, Greenhouse-Geisser corrections were applied. We have focused the reporting of data on main effects and interactions related to our primary hypotheses. For secondary analyses (such as those based on occlusion point), we only report statistically significant effects. Any reporting of pairwise, follow-up comparisons as “different” or “statistically significant” was based on Tukey HSD procedures ($p < .05$).

Results

Prediction Tasks

Dynamic stimuli (pre and post-test comparisons).

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

For illustration, we have plotted the % difference in accuracy from the pre to post-test for each group and condition in Figure 2. Based on statistical analysis of % accuracy mean scores, there was a difference across the prediction conditions, $F(3,81) = 9.70, p < .001, \eta_p^2 = .26$, due to

a significant decrease in accuracy for the Right Force task compared to the other conditions. This condition effect was due primarily to the Motor-visual group during the post-test as evidenced by the predicted Group x Condition x Test interaction, $F(6,81) = 3.31, p < .01, \eta_p^2 = .20$ (i.e., ~ 20% of the within subject variance can be accounted for by this 3-way interaction). Post-hoc comparisons for the Condition x Test interaction, $F(3,81) = 5.06, p < .01, \eta_p^2 = .16$, showed that differences across the 4 conditions were only present on the post-test. Percentage accuracy in the Right Force condition was significantly less than that of the other three conditions, which did not differ from each other. The locus of this 2-way interaction was due to the Motor-visual group's post-test prediction accuracy while performing the Right Force task. Accuracy in this condition was significantly lower than in the other three conditions. No condition differences were shown in the Perceptual and No-practice groups in the post-test. However, both the Motor-visual and Perceptual groups significantly improved their prediction accuracy under all conditions, except the Right Force condition after training.

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

Dynamic vs. Static stimuli (post-test only).

Comparing accuracy for both Dynamic and Static stimuli in the post-test, there was again a main effect of group, $F(1,27) = 18.53, p < .001, \eta_p^2 = .58$ and a Group x Stimuli interaction, $F(2,27) = 7.19, p = .003, \eta_p^2 = .35$ (no main effect of Stimuli, $F < 1$). Prediction accuracy decreased, only for the Motor-visual group, when viewing Static versus Dynamic stimuli (see

Figure 1A). Although the Perceptual group showed a general improvement in accuracy for the stimuli they trained on (i.e., Static) versus Dynamic, this difference was not statistically significant.

There was no 3-way interaction of Stimuli-type with Group and Condition ($F < 1$), but the predicted Group x Condition interaction was still shown when static stimuli were included, $F(6,81) = 7.75, p < .001, \eta_p^2 = .37$, accounting for a relatively large portion of the within-subject variance. Follow-up post hoc confirmed that the Motor-visual group performed worse in the Right Force task in comparison to the other conditions (showing an absolute drop in accuracy of 21% for Dynamic stimuli, comparing Control to Right Force conditions, and an absolute decrease of 11% for Static stimuli). The Perceptual group also performed worse in the Right Force task, when compared to the Control condition (showing an absolute decrease of 6% for both stimuli types), but not in comparison to the other secondary task conditions.

As illustrated in Figure 3, Stimuli-type interacted with OP, $F(2,54) = 6.45, p < .003, \eta_p^2 = .19$, but the interaction with Group was not significant, $F(4,54) = 2.15, p = .087, \eta_p^2 = .14$. Accuracy improved for both stimuli from OP1 to OP2, but only for Static stimuli was there improvement between OP2 and OP3. Comparing across stimuli, prediction accuracy at OP1 was significantly greater when participants viewed the Dynamic stimuli, while the opposite effect was seen at OP3. Prediction accuracy at OP2 did not differ.

Motor Proficiency Tasks

As shown in Figure 4A (MRE) and B (BVE), the Motor-visual and Perceptual groups showed a decrease in error pre to post training, whereas the No-practice group showed no change. For MRE, there was a main effect of test, $F(1,27) = 4.85, p = .036, \eta_p^2 = .15$ and Group x Test interaction, $F(2,27) = 3.86, p = .034, \eta_p^2 = .22$. The groups were not different in the pre-test.

In the post-test, the only difference was between the Motor-visual and No-practice group, with the former showing significantly less error (8 cm). Comparing across the pre and post-tests, the Motor-visual group significantly reduced MRE by 6 cm from pre to post-test. Decreases of 3 cm for the Perceptual group and 1.5 cm for the No-practice group were not significant.

For BVE (Figure 4B), a similar pattern of results was shown as for MRE, including a main effect of test, $F(1,27) = 17.68, p < .001, \eta_p^2 = .40$ and a Group x Test interaction, $F(2,27) = 8.09, p = .002, \eta_p^2 = .38$. Groups did not differ in the pre-test, only on the post-test, where the Motor-visual group was significantly less variable than the No-practice and Perceptual groups. Only the Motor-visual group showed a significant reduction in variability across tests.

Training Data

As shown in Figure 5, the Motor-visual group significantly improved their motor accuracy as training progressed. There was a day main effect, $F(1,9) = 42.75, p < .001, \eta_p^2 = .83$, a significant linear trend component to the block effect, $F(1,9) = 2.70, p = .003, \eta_p^2 = .65$ and no interaction. Comparisons of throwing accuracy of the first two blocks on Day 1 ($M = 43\%, SD = 5.97$) to the last two blocks on Day 2 ($M = 71\%, SD = 15.31$) in a repeated measure ANOVA, showed that accuracy improved from the start to the end of practice, $F(1,9) = 35.20, p < .001, \eta_p^2 = .80$.

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

Discussion

Our primary goal was to investigate the representational mechanisms that support action prediction. The key questions we asked were; 1) under what practice conditions is there evidence that the motor system is activated when (accurately) predicting action outcomes and 2) how specific is this activation to the observed effector (i.e., system activation) and to the type of training stimuli (i.e., dynamic video versus static clips). We used an effector specific secondary motor task in an attempt to interfere with motor system activation (simulation) during action prediction and we trained two groups either physically or perceptually.

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

interference suggests a somatotopic simulation-type process that prevents the motor system activating in an action-congruent manner to aid outcome prediction (for evidence of this effector based mapping during action observation, see Lorey et al., 2014).

In previous research it has been shown that concurrent performance by a different effector (such as the foot, rather than the hand) can affect perception, and potentially hinder simulation processes (Hamilton et al., 2004; Prinz, 1997; Springer, Brandstaedter & Prinz, 2013; Wilson & Knoblich, 2005; Springer et al., 2011). In our study, we saw neither interference nor facilitation as a result of this incongruent action with the non-throwing (left) arm. This perhaps speaks to the specificity of motor-experience in action simulation, whereby motor commands related to left-handed dart throwing were not formed for the Motor-visual group. It is however possible that the pattern of interference was a result of using the dominant right-arm. In right-hand dominant individuals, the left-hemisphere has been shown to play a greater role in motor planning (e.g., Frey 2008; Haaland et al., 2000; Janssen et al. 2010) and as such, effector-specific interference effects may reflect hemispheric asymmetry. Against this interpretation, the right-arm force task did not impact accuracy for the perceptually-trained group and in a previous study, an action-congruent task (mimicking) performed with the dominant right-arm did not interfere with prediction accuracy (Mulligan et al., 2015). A stronger test of the specificity of this interference would be to use left-handed (non-dominant) throwing as the stimuli for the prediction task, following practice with this arm.

The experimental manipulation of experience is critical for extending previous cross-sectional studies of interference (Mulligan et al., 2015; Tomeo et al., 2012). Effector-specific interference occurred only for physically trained individuals, suggesting action predictions were achieved through mechanisms that simulate (perhaps in real time), internal motor representations

of the observed action, in order to provide a prediction of its sensory consequences (Jeannerod, 2001). This supports the notion that action and perception (following physical experience) reside within a common representational medium that can exert bi-directional influences on each other (Hommel et al., 2001; Prinz, 1997).

The fact that the perceptually-trained group showed a similar improvement in outcome prediction, but no interference from either the left or right secondary motor task, gives evidence that accurate predictions can still be reached through mechanisms outside of motor simulation. In addition to a process that simulates action codes, or programs, based on the observed action, these data suggest a second, potentially more “cognitive” mechanism that works through a visual-matching process. The Perceptual training group would have built up visually-based stimulus-response associations that were then matched to the observed action stimuli to aid prediction. These processes appear to be non-motoric and not based on forward internal models as they were not susceptible to motor interference (either general or effector-specific). Much like differences seen between fans and players in sport-expertise studies (e.g., Aglioti et al., 2008), the perceptually-trained group had acquired knowledge from watching which allowed them to make quite accurate predictions about outcomes, independent of the motor system and motor experiences (see Tomeo et al., 2013; Zentgraf et al., 2011).

In the motor learning literature, there is some debate about whether observational training, in the absence of motor experience, is sufficient to activate motor codes that can subsequently directly transfer to motor execution (so termed early mediation; see for example Vogt & Thomaschke, 2007; Maslovat et al., 2010). In visuomotor adaptation studies, observational practice has not been sufficient to update internal, sensorimotor models of the action, as evidenced by an absence of unintentional motor after-effects, despite direct learning

benefits, in these tasks (e.g., Larssen et al., 2012; Lim et al., 2014; Ong & Hodges, 2010; Ong et al., 2012). Learning through watching appears to be more a strategically-driven process in the absence of any physical practice, at least for tasks that require novel sensorimotor relationships. Although there are benefits to be gained from observing others, arguably the motor system is not involved in this process until enactment.

These results and explanations are somewhat congruent with recent evidence from temporal prediction tasks that have led to proposals that action prediction can occur via two different processes; a simulation-based process, known as ‘dynamic updating’ and a perceptually-driven process, termed ‘static matching’ (Springer, Parkinson & Prinz, 2013). However, these authors were unable to speak to the representational format of these two processes with respect to whether they relied on motor- or visually-based representations or simulations. Because we controlled motor experience, and subsequently showed a differential effect of the secondary motor task as a function of this experience, it is likely that the Motor-visual group engaged in dynamic updating via motor representations. The Perceptual group may have engaged in dynamic updating or static matching, with either being underpinned by a visual representational format.

Dynamic updating was suggested to be the default process in action prediction tasks, with static matching only occurring when dynamic updating was interfered with in some way (Springer, Brandstaedter & Prinz, 2013; Springer, Parkinson & Prinz, 2013; Tomeo et al., 2012). Although we did not probe the time-course of predictions (such as through response time measures), it does appear that this effector-specific incongruent secondary task disrupted this dynamic process for the Motor-visual group, perhaps forcing them to instead turn to a ‘static’, visually-based process. Indeed, in one study where participants were primed with an incongruent

effector (i.e., hand rather than foot), temporal predictions were shown to reflect this static matching process rather than dynamic updating (Springer, Brandstaedter & Prinz, 2013). Based on our data, however, we reason that it is unlikely that the Motor-visual group was able to effectively switch prediction strategies as a function of the task demands. Although this group performed above chance, even while performing the right force secondary task, accuracy under this condition was not better than pre-test performance (or control group accuracy), where arguably no (or only weak) perceptual or motor-based representations existed. Neither did their accuracy match that of the perceptually-trained group. These results suggest that the Motor-visual group did not develop separate, purely visual representations, and was thus unable to switch to a visual matching strategy to solve the prediction task. By contrast, in the Springer et al. (2013) study, the task involved simple movements that participants had wide experience both performing and observing. Similarly, in the Tomeo et al. (2012) study, the goalkeepers had extensive, purely visual experience anticipating, from the same perspective that the stimuli were presented. Based on these differences, we hypothesize that visual experiences would need to be acquired independently from motor experience, in a manner specific to the perspective where testing would take place, for physically trained participants to maintain prediction accuracy under force-interference conditions.

Additional support for the proposal that action predictions, for the Motor-visual group, were primarily a function of a motor-based process following action experience is evidenced by the motor-proficiency task data. The Motor-visual training group significantly improved in dart throwing ability after training, while the perceptually-trained group did not show significant improvements. This improvement in motor ability for the physically trained group serves as a validity check that this group developed motor representations (internal models) that could later

be used to simulate the observed action during prediction. In contrast, the Perceptual group presumably did not acquire these motor-based internal models required for motor simulation, but instead developed visual representations that they were able to use in a visual matching process during prediction.

Our overall theoretical premise is that the development of motor representations (and motor simulation processes) are responsible for the predictive and interference effects seen in our study. However, it is important to consider an alternative explanations for our data, such as one based on inter-modal transfer. In a study involving active and passively-guided training on a rhythmic arm movement task without vision, participants improved on later visual judgements of similar movements (Hecht et al., 2001). Because participants performed equally well in the active and passive conditions, the authors suggested that participants were matching kinesthetic signals formed during motor practice to the visual afferents presented in the perceptual test (i.e., inter-modal matching). An explanation based on motor representations was a less likely candidate due to the absence of preparation and the need for action programming in the passively trained group. Thus, it may be the case that pressing on the force plate in our study caused kinesthetic (proprioceptive) interference, disrupting the kinesthetic-visual, inter-modal matching process during prediction. Indeed, in a study where actors were asked to lift boxes, and were told either the correct or incorrect weight of the box, two individuals with a complete loss of cutaneous touch and proprioception, were unable to judge the mismatch between action preparation and action execution experienced by the observed actors (Bosbach, Cole, Prinz, & Knoblich, 2005). In order to experimentally untangle the differential effects of motor and kinesthetic representations on action prediction, it would be necessary to de-couple the active motor component from the kinesthetic component of the secondary force task, perhaps by

passively engaging the participant's hand with the force plate or through vibration or nerve stimulation techniques).

It is important to point out that, during training, the Perceptual group in our study only watched static clips of a dart-throwing action and hence any “motor” based representations or transfer might be limited by the nature of the perceptual training stimuli. There are two critical points to make with respect to this idea. First, in previous work, prediction accuracy did not improve from pre- to post-test following only action-observation training, where individuals watched all the (dynamic) practice trials of a matched actor (Mulligan & Hodges, 2014). Second, in the current experiment, prediction accuracy was only weakly moderated by the type of stimuli (i.e., Static or Dynamic). Even though the Perceptual group only viewed static clips during training, they did not show a significant decrease in prediction accuracy for the dynamic videos. Moreover, although the Motor-visual group showed a significant decrease in accuracy for the Static versus Dynamic stimuli in the post-test, the Right-force secondary task interfered with prediction accuracy in both stimuli conditions. These results indicate that the Motor-visual group was able to use static images that only implied motion to activate motor-based simulation mechanisms and in general that any interference effects (or lack thereof), noted in our study, were not specific to the type of stimuli used to train the Perceptual group.

There was sufficient reason to suspect that both types of stimuli would produce a similar pattern of results in our study as perceptual effects, such as action embodiment (Bach & Tipper, 2006) and representational momentum (e.g., Hubbard & Bharucha, 1988) have been shown to occur in response to both actual motion and apparent or implied motion (i.e., static clips) (Munger & Owens, 2004). That is, action observation in general appears to elicit forward predictions in the observer, at least when the observer has experience with the stimuli (either

motor or visual, see also Hubbard, 2014; Wilson et al. 2010). Therefore, although there was a decrease in accuracy going from dynamic to static clips (for the Motor-visual group), the patterns of interference remained. This would suggest that the simulation that takes place does not need to be directly matched, temporally or spatially, to the unfolding action. However, it is worth pointing out that for the early occluded clips (OP1), some benefits were noted for the Motor-visual group in the Dynamic versus Static condition (see Figure 3), potentially highlighting a minimum amount of implied movement necessary for simulation to occur.

To summarise, we have shown that a group that was trained to throw darts at specific areas of a dartboard, significantly improved in predicting the outcomes of occluded dart throws shown on video (both dynamic clips and static frames). Importantly, this physically trained group also exhibited a significant reduction in prediction accuracy, to pre-practice levels, while concurrently performing an incongruent secondary motor task with the trained (right) effector. A second group, that was perceptually-trained to associate occluded dart throws with outcomes, improved similarly to the motor trained group on the prediction test, but displayed no reduction in prediction accuracy under any of the secondary task conditions. These results strongly suggest two distinct paths to predicting action outcomes; one motor-based and one visually-based. Individuals with motor training were able to utilise acquired motor representations to simulate observed actions to aid in prediction, and that, as evidenced by the interference effects shown while performing the right, but not the left, secondary motor task, these representations were effector-specific. In contrast, the fact that the perceptually-trained group was able to solve the prediction task with similar accuracy, yet showed no interference from the secondary tasks (and no statistically significant improvement in dart throwing ability), suggests that motor representations were generally not formed by this group during training and thus were not usable

during action prediction. Instead, visual representations were acquired, which allowed for a visual matching process during prediction. For this group, the observed throwing action was likely matched to an internal visual representation of the appropriate outcome of the observed throw. By experimentally manipulating dart-throwing experience and effector-specificity in secondary tasks during on-line predictions, these results suggest separable motoric and visual processes that support action prediction. Despite both visual and motor-experiences (albeit coupled) for physically trained participants, there was no evidence that these individuals could effectively switch between processes to maintain prediction accuracy. This makes sense as this group presumably did not develop separate, purely visual representations, as they had no opportunity to engage in any perceptual or observational learning (*cf.*, Tomeo et al., 2012; Urgesi et al., 2012). Whether separate visual training over the short term could facilitate switching between processes for a physically trained group remains to be tested.

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Figure Headings

Fig. 1A-C. Mean percentage accuracy scores for each group (**A** = Motor-visual, **B** = Perceptual, **C** = No-practice) as a function of prediction condition and test phase (pre or post). Error-bars show between-subject SDs

Fig. 2. Difference between post- and pre-test % accuracy for each secondary task condition when watching Dynamic stimuli, as a function of group. Error-bars show between-subject SDs

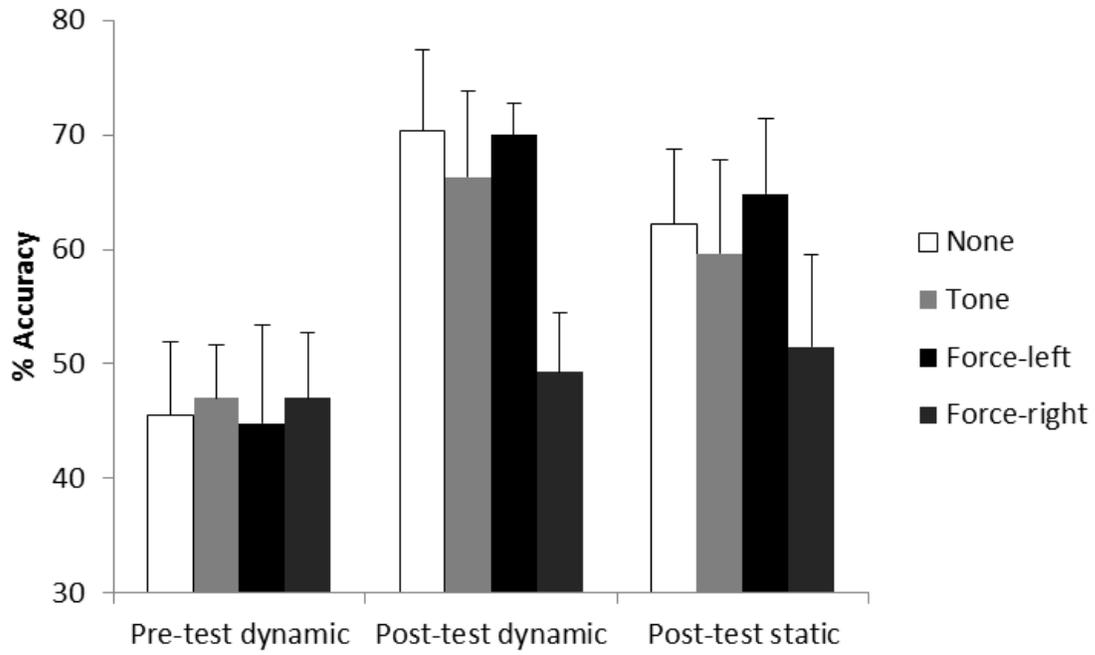
Fig. 3. Mean percentage accuracy for each group as a function of test phase (pre or post), stimulus-type (with Dynamic “dyn” stimuli in both test phases and Static just in the post-test) and occlusion point (OP). Error-bars show between-subject SDs

Fig. 4A & B. Mean radial error (**A**) and bivariate variable error (**B**) for the motor test as a function of Group and Test (pre- and post-practice). Error bars show between-subject SDs.

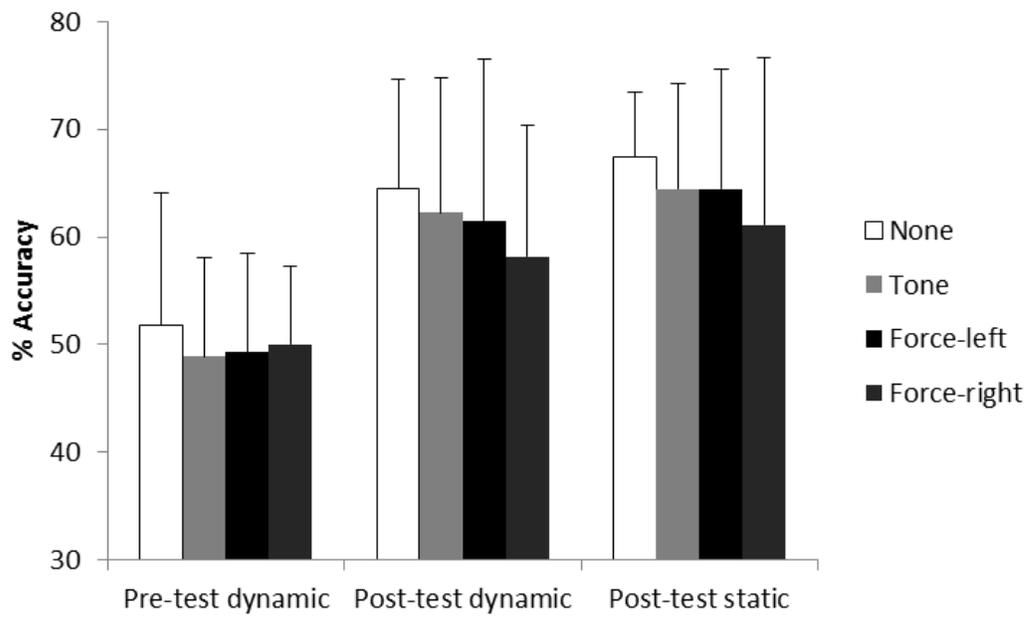
Fig. 5. Motor and Perceptual practice acquisition data as a function of practice block.

Figure 1

A



B



C

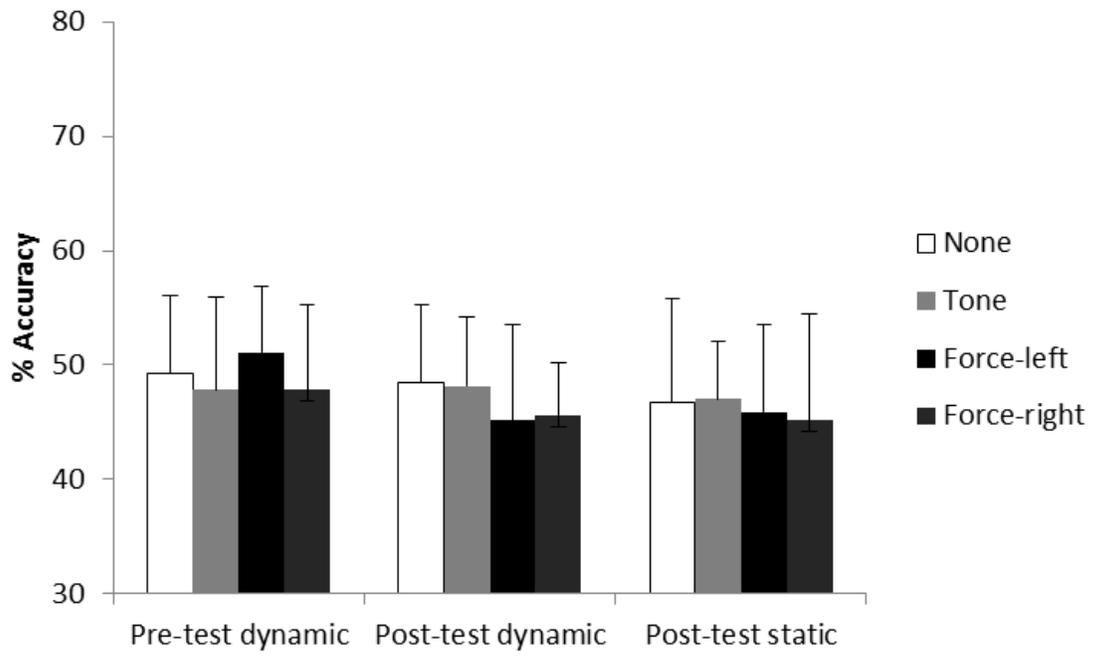


Figure 2

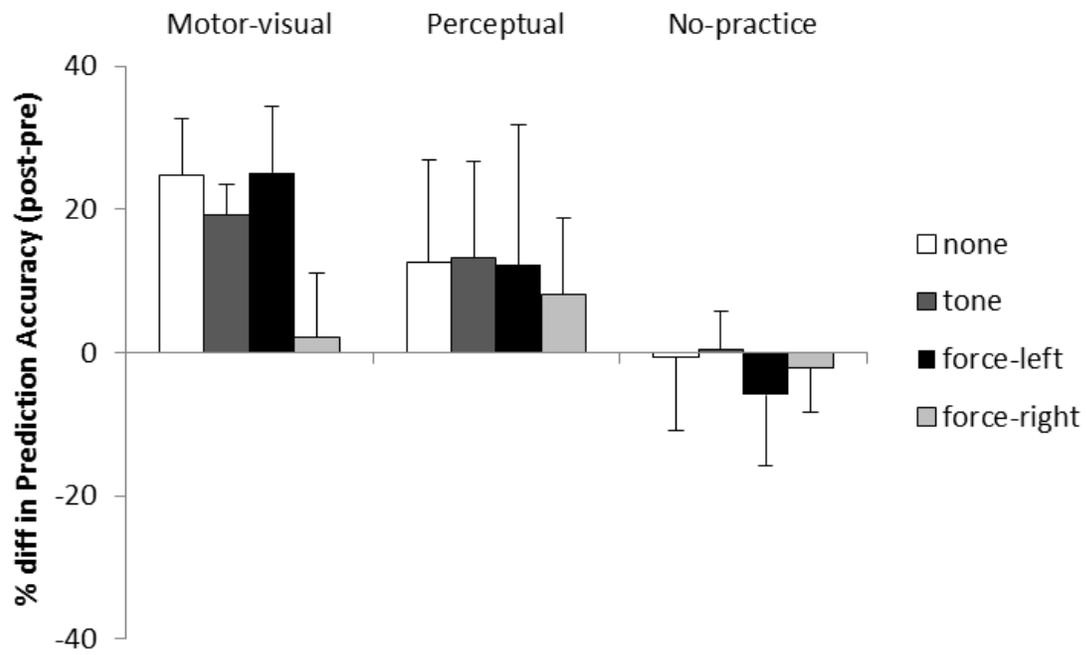


Figure 3

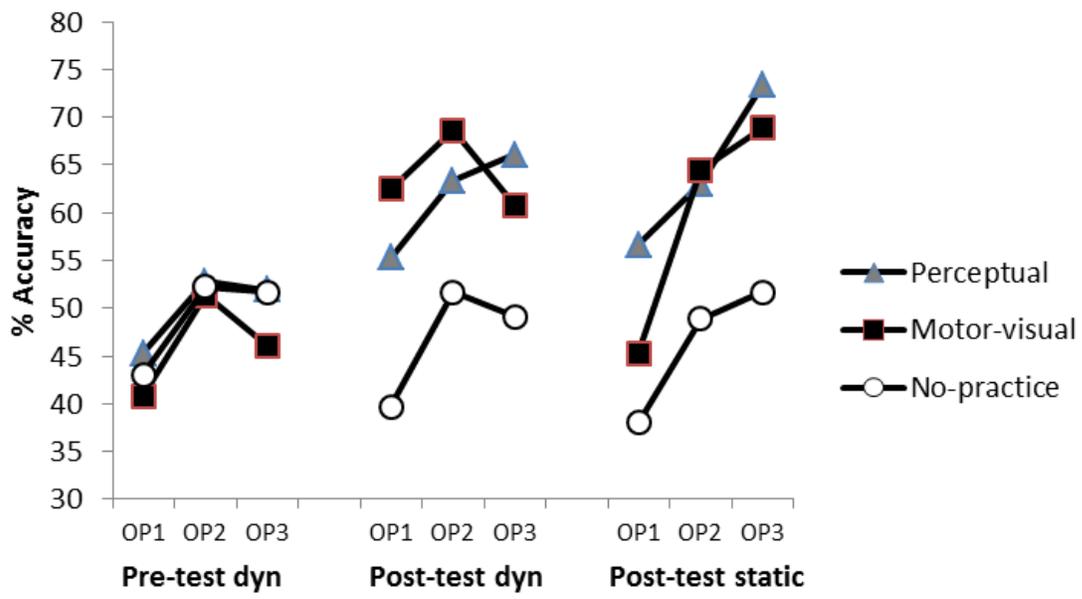
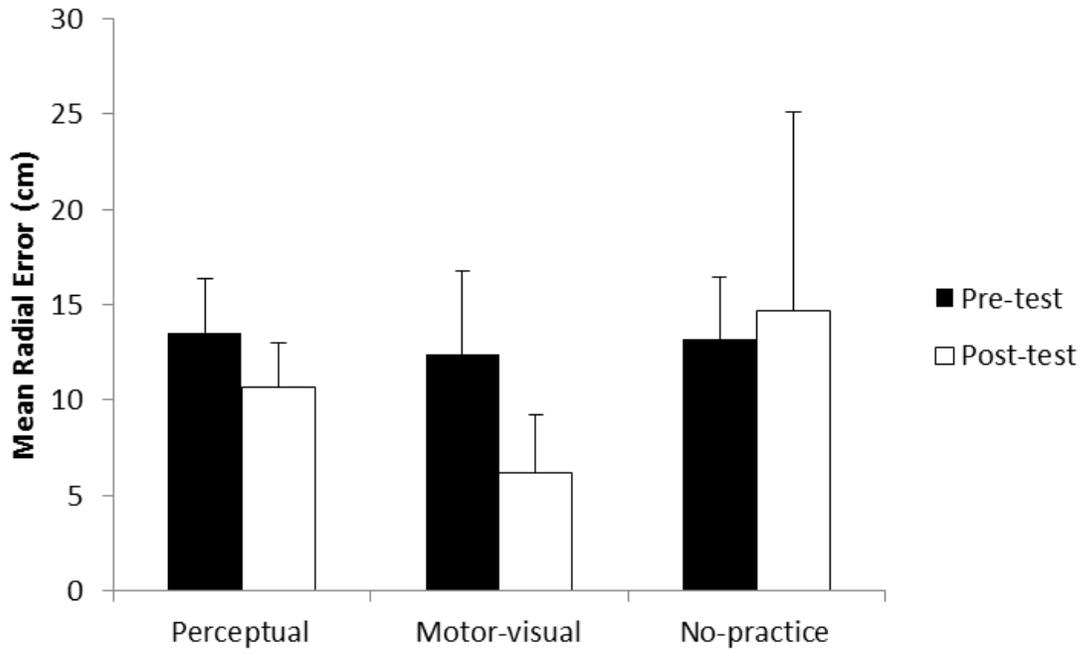


Figure 4

A



B

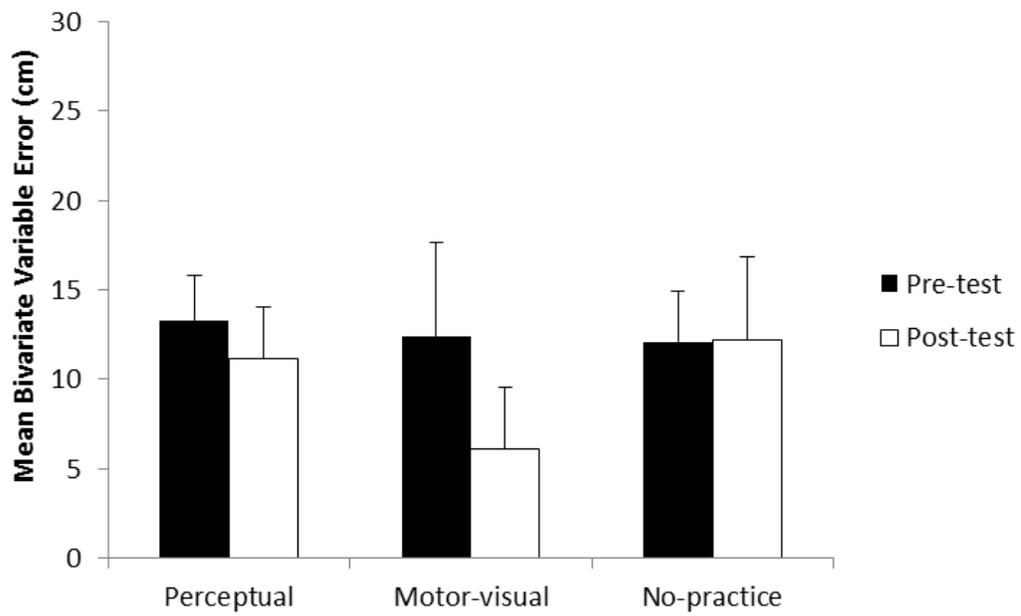


Figure 5

