Effector-specific improvements in action prediction in left-handed individuals after short-term physical practice

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PRE-PRINT VERSION…. PUBLISHED IN CORTEX (online 8th June 2024):
https://www.sciencedirect.com/science/article/pii/S0010945224001680

https://doi.org/10.1016/j.cortex.2024.05.017

(there may be a few minor differences from the final version, which is an open-source publication)

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Highlights

- Short-term motor experience in an observed task improves prediction accuracy
- Observed actions are represented differently depending on perceived handedness
- Outcome prediction accuracy in throwing improved after effector-specific practice
- An effector-specific motor task interfered with prediction accuracy after practice
- Prediction accuracy is effector-specific in LH individuals

Abstract

Research has established the influence of short-term physical practice for enhancing action prediction in right-handed (RH) individuals. In addition to benefits of physical practice for these later assessed perceptual-cognitive skills, effector-specific interference has been shown through action-incongruent secondary tasks (motor interference tasks). Here we investigated this experience-driven facilitation of action predictions and effector-specific interference in left-handed (LH) novices, before and after practicing a dart throwing task. Participants watched either RH (n=19) or LH (n=24) videos of temporally occluded dart throws, across a control condition and three secondary task conditions: tone-monitoring, RH or LH force monitoring. These conditions were completed before and after physical practice throwing with the LH. Significantly greater improvement in prediction accuracy was shown post-practice for the LH- versus RH-video group. Consistent with previous work, effector-specific interference was shown, exclusive to the LH-video group. Only when doing the LH force monitoring task did the LH-video group show secondary task interference in prediction accuracy. These data support the idea that short-term physical practice resulted in the development of an effector-specific motor representation. The results are also consistent with other work in RH individuals (showing RH motor interference) and hence rule out the interpretation that these effector specific effects are due to the disruption of more generalized motor processes, thought to be lateralized to the left-hemisphere of the brain.

Keywords: motor simulation, anticipation, motor learning, handedness

1. Introduction

A large body of neurophysiological research has shown that cross-modal brain networks are activated when action-experienced individuals observe and/or make predictive judgements about another's actions that correspond with their own experiences (e.g., Calvo-Merino et al., 2005, 2006: Kim et al., 2011; Wimshurst et al., 2016; for reviews see Karlinsky et al., 2017; Smith, 2016; Yarrow et al., 2009). Despite significant evidence of such activation and what has been termed "action simulation" (Gallese & Goldman, 1998; Jeannerod, 2001), questions remain about the generalization of action experiences in informing perceptual judgements, particularly with respect to effector specificity and handedness effects in general. In the current study, we aimed to extend previous research showing effector-specific practice and interference effects in dart-throw prediction accuracy in right-hand dominant individuals (Mulligan et al., 2016a). Our specific aim was to test whether such effects were generalizable and linked specifically to action experiences by testing prediction accuracy of left-hand dominant individuals after physical practice with their left-arm. Prediction judgements were made for temporally occluded videos of dart-throws, which appeared to be made with either the same or opposite arm to that practiced. Our general aim was to evaluate the specificity of action-to-perception transfer and the functional role of the motor system in informing action prediction judgements.

There is considerable evidence that successfully predicting the outcome of another's actions partially relies on recruitment of the observer's motor system, or is at least augmented by its engagement (e.g., Abreu et al., 2012; Aglioti et al., 2008, Blakemore & Frith, 2005). Prediction accuracy is enhanced for individuals with motor-expertise in the observed action (e.g., Aglioti et al., 2008; Abreu et al., 2012; Cañal-Bruland et al., 2011; Mulligan et al., 2016a; Paolini et al., 2023; Wöllner & Cañal-Bruland, 2010) and after some short-term physical experience of the observed task (Mulligan et al., 2014; 2016b; Urgesi et al., 2012). One theoretical explanation for this motor-experience driven phenomenon is that action and perception are underpinned by a common sensorimotor code, which is developed through the coupling of actions with their sensory effects forming bidirectional linkages (James, 1890; Prinz, 1997). The underlying neurophysiological mechanism for what has been termed action simulation (Jeannerod, 2001), is the human mirror neuron system (Fadiga et al., 1995; Rizzolatti & Craighero, 2004), or what is more broadly termed the Action Observation Network (AON; Cross et al., 2009). This system or network is activated both broadly and specifically when actions are both performed and viewed (e.g., Decety & Grèzes, 1999; Hardwick et al., 2018; deVignemont & Haggard, 2008). One proposal is that social processes related to action prediction, such as action understanding, require a direct matching of an observed action to the observer’s experience-driven motor representation of that action (Rizzolatti et al., 2001). However, there are alternative action reconstruction accounts, whereby a top-down goal interpretation level precedes motor simulation, leading to what has been thought of more as emulation rather than imitative simulation of kinematic aspects of the action (e.g., Csibra, 2008; Grafton, 2009; Grush, 2004).

In sports, athletes often acquire an expertise which is isolated to one effector (e.g., in throwing darts, baseball pitching or cricket bowling). A well-established finding is that unilateral physical practice leads to lateralized neurophysiological activations in the contralateral hemisphere (Horenstein et al., 2009; Lorey et al., 2013; Scholz et al. 2000; Van Mier et al., 1998). Theoretically, by a strict common-coding perspective and related ideas of direct matching, observation of a learnt unilateral task should therefore result in the same somatotopic activation (i.e., action simulation) as physical execution. Indeed, evidence has been presented showing such somatotopic activations (e.g., Avenanti et al., 2007; Fadiga et al., 1995; Cavallo et al., 2012; Naish et al., 2016). Also congruent with these ideas, is evidence that recognition and prediction of one's own actions are enhanced compared to those of others, showing that similarity to our own action capabilities matters for prediction (e.g., Loula et al., 2005; Knoblich & Flach, 2001; Knoblich et al., 2002).

Neurophysiological evidence for effector-specific representations following observation-induced action simulations is rather mixed. In support of such effector specific representations, when watching both right- and left-handed grasping actions, the dominant arm of participants (either right or left) showed muscle specific activations in response to single pulse Transcranial Magnetic Stimulation (TMS; Sartori et al., 2013). Cabinio et al. (2010) also showed lateralized, effector specific responses when activation of the mirror neuron system was measured with fMRI, when individuals both watched and executed right and left-handed grasping actions. There was also greater muscle specific activation, rather than direction specific, in an effector (hand or foot), when observers watched actions that varied on these parameters and were either congruent or incongruent to the observer's own posture (Alaerts et al., 2009; see also Witt & Profitt, 2008; Paulus et al., 2009 for behavioral examples). Finally, in a basketball prediction task, the muscles that would be involved in the throw were activated via TMS in an effector-specific manner only among experienced individuals (Aglioti et al., 2008).

Such somatotopically mapped visuo-motor representations are thought to develop in a stepwise manner, with fMRI showing that movement information originates as a visual representation in the occipito-temporal cortex before goal-directed motor components are identified in the parietal cortex, which are then somatotopically mapped in the premotor cortex (Jastorff et al., 2010). Therefore, there may be multiple levels of representation. Indeed, in contrast to these “matched” effects, through TMS it was shown that observing a grasping action performed by different effectors (such as the foot or mouth), continued to activate the muscles of the hand that would typically be used to perform the grasp (Betti et al., 2019; see also Lorey et al., 2014). These data and those of others (e.g., Lorey et al., 2014; Borroni et al., 2008), support the idea that actions are represented at an action-goal level (e.g., Csibra, 2008), rather than an effector level, supporting the idea of an effector general representation. In this case, the (hand) muscles typically used to perform the action are activated regardless of what the observer sees.

Notably, differences in effector-specific activations among right and left-handed individuals in response to observation have been shown (Rocca et al., 2008; Sartori et al., 2014). For example, Sartori et al. (2014) showed that patterns of cortical activation during observation of familiar movements for left-handers differed to that of right-hand dominant individuals. Right-hand dominant individuals showed hand activations in a manner corresponding to the desired response (matching or performing an opposite hand complementary action). Left-hand dominant individuals did not show this response-specific effect, but instead showed left-hand activations regardless of the potential response. The authors proposed these effects to be driven by more bilaterally spread brain functions in left-handers, potentially due to a functional difference in the organization of motor and pre-motor areas. However, in a behavioural action prediction task, where left and right-hand dominant handball athletes watched and made predictions about the type and direction of throws made in handball, no handedness related differences were shown (Loffing & Hagemann, 2020). Right-handed throws were generally easier to predict than left-handed throws; thought to be a result of the increased perceptual experience for all athletes in playing against right-hand dominant players (and hence throws). One of the issues in this cross-sectional research, however, is that the visual-motor experiences of the players have not been controlled and as such perceptual experiences can dominate motor-based processes (Urgesi et al., 2012; Tomeo et al., 2013).

Through short-term motor learning studies, it is possible to study the influence of a particular type of experience on action prediction processes. For example, Mulligan et al. (2016b) showed that short-term practice of a right-handed throwing action led to improvements in action predictions of this same throwing action for right-hand dominant individuals. Moreover, only for participants who had physical practice (not visual only), did a right-handed force monitoring task, incongruent with the observed action, interfere with prediction accuracy. Interestingly, this interference effect was not present when the same motor task was performed with the untrained left hand, suggesting that action simulation mechanisms were somehow disrupted when the same effector which would be involved in the observed action was activated (Witt & Profitt, 2008; Paulus et al., 2009; see also Ambrosini et al., 2012). One concern regarding such conclusions about this effector-specific interference, which could reflect lateralized simulation processes, is that this interference in right-handed observers could also be due to the interference of cortical motor-related functions in the left hemisphere. There is research, broadly consistent with what has been termed the left-hemisphere-dominance hypothesis, supporting the role of the left hemisphere in motor planning and related processes (e.g., Taylor & Heilman, 1980; Johnson-Frey et al., 2005; Frey, 2008; Janssen et al., 2011). If left-handed individuals also show a lateralization for motor-related processes associated with planning in the left-hemisphere (Frey, 2008; Janssen et al., 2011), then we would be able to dissociate motor interference effects, which are thought to be due to somatotopic simulation, from interference effects due to motor-related processes thought to be prioritized in the left hemisphere.

In this study, we tested prediction accuracy in novice left-handed individuals after physical practice in a dart throwing task. Our aim was to evaluate action-to-perception transfer and the effector-specific nature of associated action representations that develop from physical practice and later support action prediction. Similar to previous research where short-term action experiences led to evidence of motor-based "simulation" processes underlying action prediction accuracy in right hand dominant individuals (e.g., Mulligan & Hodges, 2014; Mulligan et al. 2016a, 2016b), left-handed participants made predictions whilst concurrently performing effector-specific interference tasks. In addition to only testing and training left-hand dominant individuals, a key difference in the current paradigm to that of previous studies (i.e., Mulligan & Hodges, 2014; Mulligan et al. 2016a,b), was that participants were allocated to watch either a right-handed (RH) throw before and after practice or a somatotopically matched left-handed (LH) throw. Therefore, one group would see effector-incongruent video clips of the practiced task (i.e., RH veridically filmed videos), while the other group would only see effector-congruent videos (i.e., RH-videos flipped in the horizontal axis to appear left-handed).

We hypothesized that the LH-video group's prediction accuracy (i.e., perceptual judgements) would improve more than that of the RH-video group following physical practice, even though both groups would essentially receive the same practice experiences and see the "same" videos (the LH-video being the non-veridical one). Moreover, if simulation is somatotopically mapped, performing a motor interference task with the LH, but not the RH, would interfere with predictions for the LH-video group after practice. In addition to prediction accuracy, we also measured confidence in predictions to help give some additional insight into awareness of action-prediction ability following practice (e.g., Jackson & Mogan, 2007). We expected confidence to be higher for the LH- versus RH-video group at post-test as a result of observing effector-congruent videos that matched their physical practice experience.

2. Methods

We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. No part of the study procedures was pre-registered prior to the research being conducted

2.1. Participants

Forty-five novice left-handed males (18-50 years) with reported normal or corrected-to-normal vision were initially tested. Participants were randomly allocated to either a right-hand video group (RH-video group; *n* = 21) or a left-hand video group (LH-video group; *n* = 24). Due to some error in randomization to groups and data from two participants that we were unable to retrieve, we ended up with unequal ns/group. Two participants from the RH-video group were excluded due to E-prime software issues and inability to access the data files. We did not conduct a power analysis initially, but planned to test a minimum of *n*=20/group based on prior work in this area and novelty of the participants (left-handed), with new between group comparisons based on video perspective (veridical RH or flipped, LH). A sample size analysis, based on previous work with RH participants, yielded an estimate of N =16 participants. This calculation was based on a repeated measures ANOVA, within-between interaction function, with $\alpha = .05$, $ß = .95$, $f = .50$ (as determined from an effect size for a 3-way interaction by Mulligan et al., 2016b; G*Power v3, Faul et al., 2007). All participants provided written informed consent before participation and ethics was approved by the Behavioural Research Ethics' Board of the University of British Columbia.

2.2. Apparatus

Methods were generally based on those adopted in previous studies (e.g., Mulligan & Hodges, 2014; Mulligan et al., 2016a, b). A standard dartboard, 451mm in diameter, was placed at 1.73m height from the floor to the bullseye. All wiring was removed from the dartboard. The dartboard was divided equally into three sections by two horizontal lines demarked with thin string, in order to denote the top, middle, and bottom sections. The throwing line was standardized at 2.37m from the dartboard. Video clips were integrated into E-prime 2.0 and relayed via a computer (HP ProBook 4530s) onto a projector screen (Cineplex Pro, IN, USA). This set-up projected an approximate life-size video, as seen by participants from a distance of ~4m. A force plate (JR3 Inc, Woodland, CA, USA) used during the two motor interference task conditions, was positioned at a height of 87cm on a strong metal post, at this 4m distance from the video screen next to where the participant would stand when making predictions (to the right of the throwing line; for an image of the set up for right-hand videos see Mulligan et al., 2016a, Fig 2). The placement of the screen was adjusted to be seen from the left or right of the post/standing position of the participant, depending on the video shown. For all right-hand videos, the screen was to the right of the participant. For left-hand videos, the screen was shifted more to the left for the first ten participants that were tested, so it would appear that the dart was moving away from the participant (see Fig. 1). However, as a result of a change in personnel, the screen did not get moved for the last fourteen participants in this group.

2.3. Experimental Stimuli

Video stimuli were recorded using a Cannon HV20 camera (30fps, 33ms/frame). These videos depicted an intermediately skilled, right-handed male, aiming for the horizontal and vertical centre of one of the three sections on the dartboard (1 = “top”, 2 = “middle” and 3 = “bottom”). Videos were filmed from the side-on, third-person perspective, perpendicular to the throwing lane. This angle provided a clear view of both the kinematics of model and the trajectory of the dart. Three video clips showing successful throws to each section were selected where the thrower had landed the dart in the horizontal and vertical centre of the dart board. These nine videos were edited at three different occlusion points (OPs) using Adobe Premiere Pro. The three OPs were dart release (~ 0 ms), one frame later (+ 33 ms), and two frames after dart release (+ 66 ms). This editing resulted in 27 audio-less stimuli to be used in each condition for the action-prediction test. Depending on group, videos were either shown in the original, veridical perspective (i.e., right-handed throwing) or the videos were transformed in the horizontal axis to appear as though the actor was now throwing left-handed (see Figure 1). Participants in the LH-video group were not told that the video was edited to appear left-handed. Within each condition and across participants, videos were delivered in a random order.

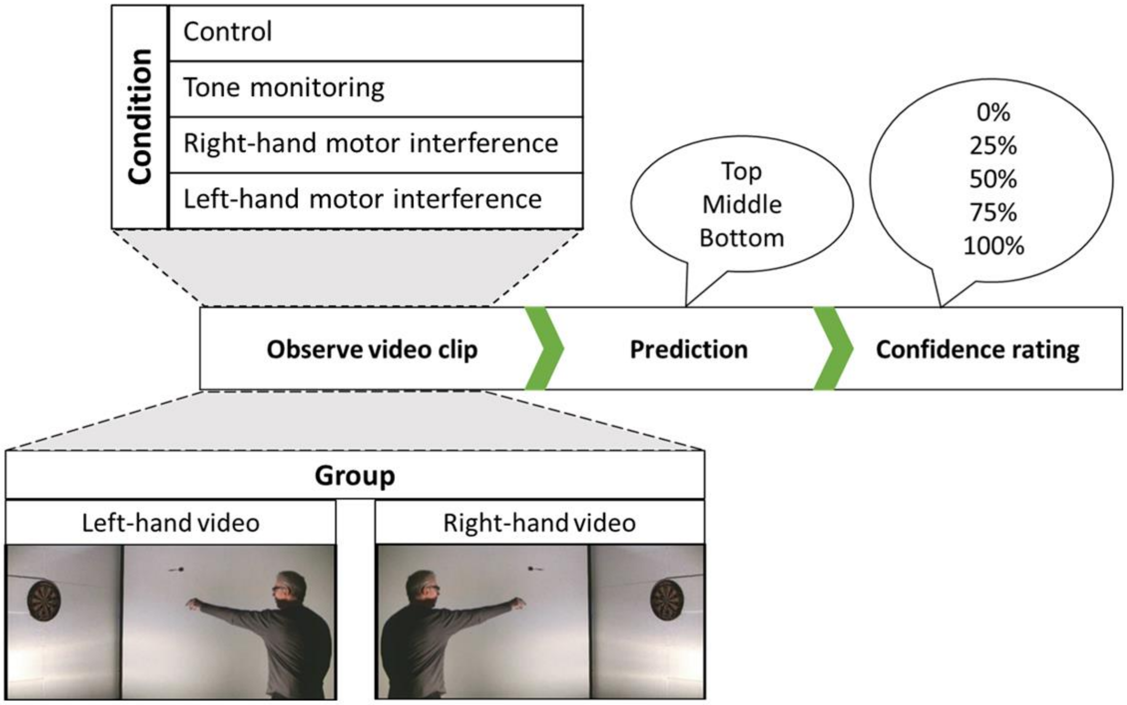

Figure 1. Typical trial structure for action prediction trials pre and post physical practice. Dependent on group, participants first saw a video of either a right-handed throw or what appeared to be a left-handed throw, occluded at or just after dart release. Immediately after the video, participants verbally reported where they believed the dart landed and then they gave their confidence in the prediction.

2.4. Procedure

Participants attended a single testing session which comprised three phases; pre-test, physical practice and post-test. On arrival, participants provided written informed consent before completing the Edinburgh Handedness Inventory (Oldfield, 1971). For the Inventory, scores of less than negative 40 or greater than +40 represented left- or right-hand dominance, respectively. After confirming hand dominance (LH-video group, *M* = -66.4, *SD* = 27.7; RH-video group, *M* = -70.9, *SD* = 28.7), participants completed the pre-test prediction test under the four conditions (control, tone monitoring, right-hand motor interference task, left-hand motor interference task). All trials involved watching temporally occluded video clips of an intermediately skilled actor throwing darts at the dartboard. As illustrated in Figure 1, participants were asked to predict where the dart would land (top, middle or bottom). These conditions were delivered in a random order across participants. The order of these conditions was consistent across pre- and post-test within each participant. All conditions were completed while standing adjacent to a metal post with a force plate attached. This post was angled 45-degrees off the centre of the projector screen where videos were presented. After making each prediction, an instruction screen appeared asking for confidence in their prediction, from 0-4, that corresponded to 0-100% confidence, in increments of 25%.

Participants completed the prediction pre and post-tests under four conditions. There were three secondary task conditions in addition to a no secondary task control condition. The control condition involved observing occluded video clips and reporting the landing area of the dart before reporting confidence in their choice, as described above. There were two motor interference tasks (left- and right-handed motor interference), where participants did an isometric force monitoring task whilst watching the video. Participants stood adjacent to the post with a force plate attached. They were asked to apply a small force (20% of max. voluntary contraction/MVC) to the plate with a closed fist, with their left or right hand, whilst their arm was fully extended by their side. This isometric hold through a straight/locked arm was anatomically incongruent to the watched elbow extension required to throw the dart. Before each of the motor interference task conditions, participants completed three 4 s trials, where they were encouraged to produce a MVC with either hand. From these MVC trials an average was generated and the relatively low force of 20% MVC was calculated. There were then three further practice trials to ensure that the participant could maintain ~20% MVC for ~4 s. During familiarization, participants were coached to maintain a rigid posture (i.e., not to lean towards the force sensor) and only to apply force through their arm. At the beginning of the right- and left-handed motor interference task trials, participants were prompted to begin applying force with the respective arm before the video appeared and not to stop until the instruction screen appeared after the video. Throughout each trial the experimenter received real-time feedback of the participants' force and provided verbal feedback when needed to keep the participant within this approximate 20% zone (feedback was never provided when the video was being shown). This task was completed for each arm in separate 27 trial blocks.

We included a fourth attention control condition, where participants were required to monitor a tone when watching the videos and determine whether the tone changed in pitch (i.e., tone monitoring condition). This condition served as an attention control for the two motor interference tasks, where force monitoring was required. Changes in pitch occurred randomly on approximately one third of trials (9 trials). Before this task, participants had experienced one trial with the tone change to confirm they could identify the stimuli. Audio files used for the tone-monitoring secondary task were created using Audacity Inc. software, v2.0.2 (Boston, MA, USA). The control tone that was heard on all trials, played at a 250 Hz pitch and the randomly interspersed high tone, played at a 440 Hz pitch. This tone change was integrated into 9 out of 27 trials for this condition.

After completing the pre-test prediction tasks, participants physically practiced throwing darts. The goal of the practice phase was for participants to successfully throw darts at specific areas of the dartboard (top, middle or bottom), aiming for the centre of the section in horizontal and vertical coordinates. Participants completed 135 dart throws, throwing forty-five darts to each section in a pre-determined random order. Five darts were provided at a time and the experimenter verbally specified which target to aim for (e.g., sections 1, 3, 3, 2, 1 etc). Twenty-seven different 5-target sequences were generated using the random number generator in Microsoft Excel, with the constraint that there were equal attempts at each section. The order of the generated sequences was identical for all participants. The experimenter recorded the section where the dart landed to provide a measure of accuracy during practice.

2.5. Data analysis

No part of the study analyses was pre-registered prior to the research being conducted. Data were analyzed using linear mixed-effects (LME) or fixed-effect linear regression models (without random-effects, where datasets did not involve repeated measures) in R (R core team, 2022). All outputs from each analysis are given in Supplementary Materials. LME models were systematically built, first establishing a participant based, random-effect structure, before adding fixed-effects. Random-effects accounted for variability between participants and models were compared to establish whether the responses varied differently across time points (i.e., random slopes). Fixed-effects, were added individually before determining whether interactions between factors improved the model fit. Model comparisons were conducted using likelihood ratio tests with the Akaike information criterion (Akaike, 1974) indicating the best model fit, while still addressing primary hypotheses. Post hoc tests were conducted using the emmeans package with Bonferroni adjustments applied (Lenth, 2019), whereas for all other tests, $p < .05$ denoted statistical significance.

2.5.1. Action prediction accuracy and confidence ratings

Each participant had a percentage accuracy and confidence score for each condition, based on the percentage of 27 trials. Group (RH-video, LH-video) and time (pre-test, post-test) factors were sum contrast coded, allowing for the interpretation of effects in the same way as a typical ANOVA (Brehm & Alday, 2022; Schad et al., 2020). Secondary-task Condition (control, tone monitoring, right-hand motor interference, left-hand motor interference) was Helmert contrast coded based on orthogonal pre-planned comparisons, driven by our major hypotheses (bypassing the need for post-hoc comparisons). The first contrast compared the control condition to all other secondary task conditions (i.e., tone monitoring and right- and left-handed motor interference tasks), allowing conclusions about the effects of the secondary tasks broadly. For the second contrast, the tone-monitoring condition was compared to the two motor interference task conditions (i.e., right- and left-handed motor interference), to determine whether the motor tasks interfered with more than just general attention. For the final contrast, the left- and right-hand motor interference conditions were compared, to allow determination as to somatotopically-based effector interference. The occlusion point factor was also Helmert contrast coded with ~0 ms (early) being first compared to later (i.e., mid and later) occlusion points and the second contrast allowing comparisons between these later occlusion points.

2.5.2. Physical practice

Each block (27) of five dart throws were scored from 1 to 5 based on outcome success. The number of successful throws per block were analyzed using an LME model so we could assess improvements across time. Group and Block were included as fixed effects. Group was again sum contrast coded (RH-video, LH-video) and the twenty-seven blocks were treated as a continuous variable.

2.5.3. Exploratory analysis on the relationship between throwing practice improvement and prediction accuracy improvement

To determine whether improvements in throwing accuracy during practice were related to improvements in the action prediction post-test, we conducted a fixed-effect linear regression on the change scores for each participant between pre- and post-test prediction accuracy and blocks 1 and 27 of their throwing accuracy. We did not include the left-hand motor interference condition in calculation of prediction accuracy change scores due to the hypothesized interference effects during this condition. The regression analysis included group (sum coded) and practice change score, as well as their interaction; with the dependent variable being pre-post prediction accuracy change score. Pearson correlations were calculated to represent these relationships.

3. Results

3.1. Action prediction accuracy

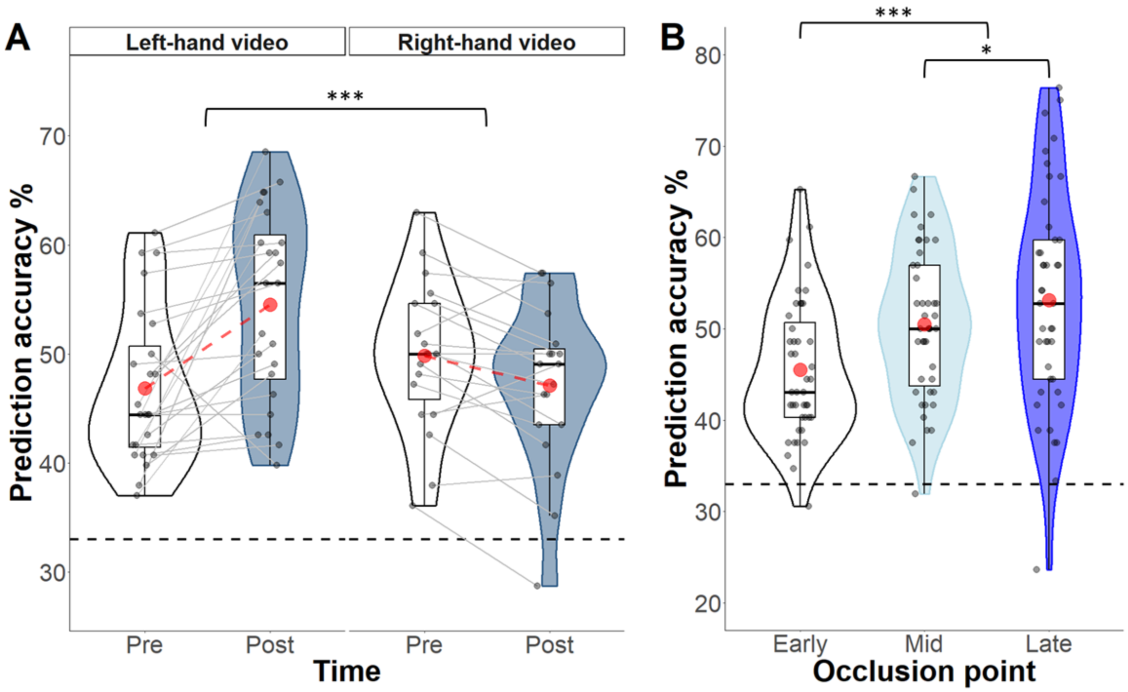

Figure 2. Panel A - Mean percentage accuracy scores for groups (Left-hand video, Right-hand video) across time (pre-test, post-test). Panel B – Mean percentage accuracy across occlusion point (early, mid, late). Red dots within boxplots represent group means. Grey individual data points depict participant means with grey thin lines across the pre and post-test illustrating

individual change over time. The dashed line intercepting on the y-axis shows chance at 33%. * = $p < .05$, *** = $p < .001$.

Prediction accuracy data were analyzed using a LME model with Group (RH-video, LH-video), Time (pre-test, post-test), secondary-task Condition and Occlusion point as fixed effects. As above, Helmert contrast coding was applied to Condition (i = control vs other; ii = tone vs LH and RH motor tasks; and iii = LH vs RH motor tasks) and Occlusion point (i = early vs other; ii = mid vs later). Model comparisons determined that a model including the three-way interaction between the fixed-effects of Group, Time and Condition, with an independent fixed-effect of occlusion point, was the best model estimate. As Occlusion point did not interact with other fixed effects (and we had no hypotheses pertaining to an interaction), this factor was included separately.

The LME model analysis yielded a significant main effect of Time ($\beta = -1.23$, $p = .031$), which was superseded by a Group X Time interaction, $\beta = -2.59$, $p < .001$ (see supplementary materials for all LME outputs). As illustrated in Figure 2, and in line with our hypotheses, prediction accuracy for the LH-video group improved from pre- to post-test, which was confirmed by post hoc comparisons ($p = .003$). There was no significant increase for the RH-video group, with a surprising trend across participants for a decrease in accuracy over time.

With respect to secondary-task condition effects; the contrast between the two motor interference tasks was significant ($\beta = 3.45$, $p = .006$), with lower prediction accuracy for the left- vs. right-hand motor interference task. Consistent with effector-specific predictions, there was also a significant interaction between Group, Time and the two motor interference tasks, $\beta = -3.12$, $p = .013$, as illustrated in Figure 3. For the LH-video group, prediction accuracy increased (across pre and post-tests) for the right-hand motor interference task but not for the left-hand motor task. This was not the case for the RH-video group, where accuracy did not differ or showed a small decrease for both motor interference task conditions across time. Follow-up post hoc analysis of this 3-way interaction further confirmed a group difference to be present when isolating this comparison to the post-test. The LH-video group showed significantly greater differences between right-handed and left-handed motor interference conditions compared to the RH-video group (p = .008).

For other contrasts, the difference between the tone monitoring and motor interference conditions to rule out general attention effects, was evidenced by two-way interactions with Group (β = 2.67, p = .014) and with Time (β = -2.16, p = .048). For the LH-video group, prediction accuracy was higher for the tone monitoring than for the motor interference tasks, while the opposite was true for the RH-video group. Predictions were also more accurate for the tone task than for the motor interference tasks at post-test. With respect to occlusion point, as expected, prediction accuracy was significantly higher for the mid and late occlusion points compared to the early point (β = -6.31, p < .001; Figure 2b) and higher for late compared to the mid occlusion point (β = -2.62, p = .016). There were no other statistically significant effects.

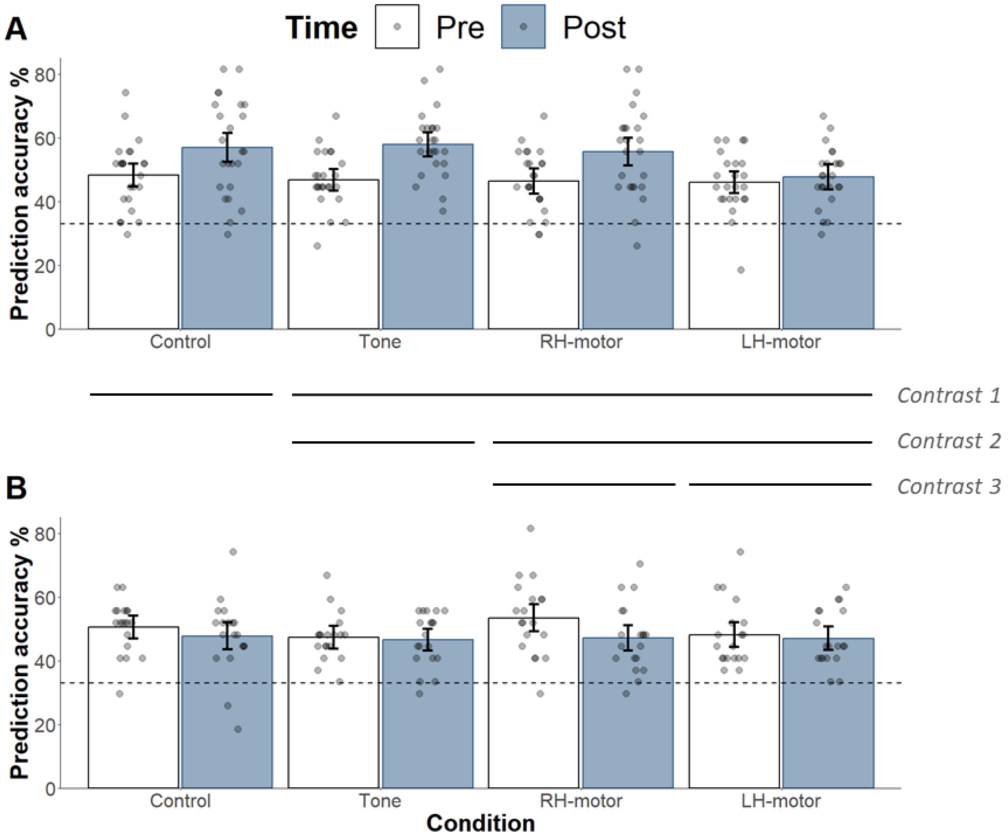

Figure 3. Mean pre-post differences in prediction accuracy (%) for the Left-hand video group (Panel A) and the Right-hand video group (Panel B) for each condition. Grey datapoints represent participant means. Error bars depict 95% confidence intervals and the dashed line intercepting on the y-axis represents chance (33%). Note, the condition labels refer to the "tone"-monitoring condition and the right hand (RH) and left hand (LH) "motor" interference tasks. We have included horizontal lines showing where pre-planned contrasts were made across the secondary-task conditions (see labels in Panel A). The condition preceding each vertical line was compared to all subsequent conditions (to the right of the line).

3.2. Confidence ratings

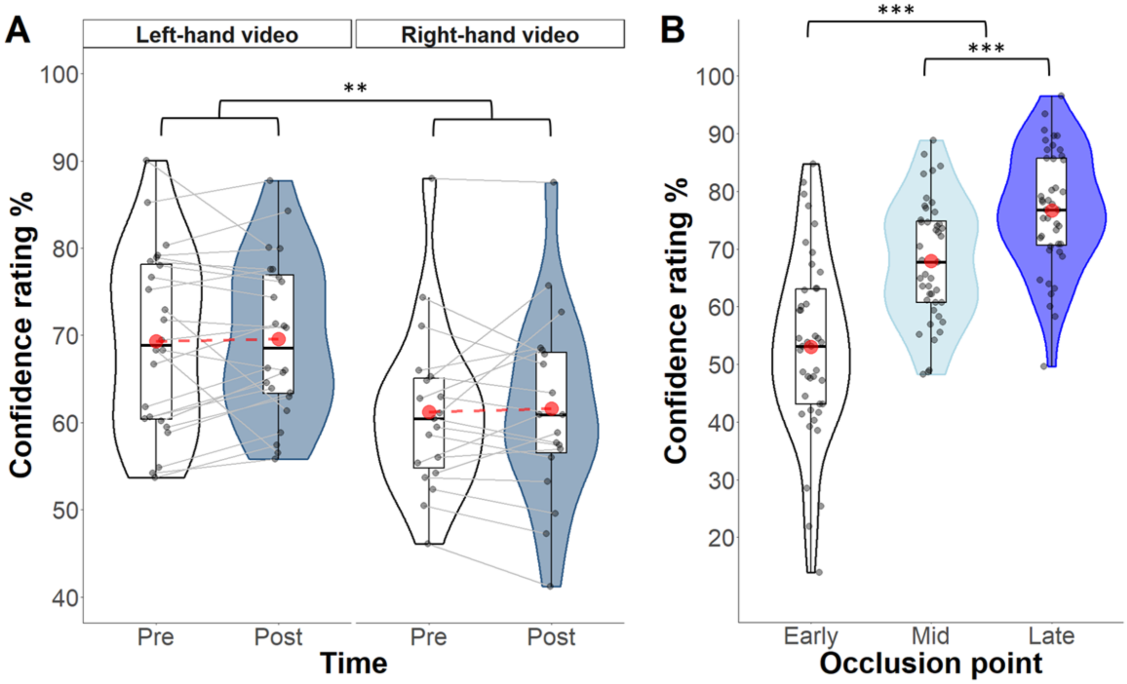

Figure 4. Panel A – Mean confidence % scores for groups (Left-hand video, Right-hand video) across time (pre-test, post-test). Panel B – Mean percentage accuracy across occlusion point (early, mid, late). Red dots within boxplots represent group means. Grey individual data points depict participant means with grey thin lines depicting individual change over time. ** = *p* < .01, *** = *p* < .001.

The LME model for the percentage confidence data again included fixed effects of Group, Time point, secondary-task Condition and Occlusion point. All fixed effects used the same contrast coding schemes as used for the prediction accuracy analysis. Based on model fit, similar to the action prediction data, Occlusion point did not interact with other fixed-effects. Therefore, only the three-way interaction between Group, Time and secondary-task Condition was included in the model, with the separate factor of Occlusion point.

As shown in Figure 4, panel A, the LH-video group had significantly more confidence in their predictions than the RH-video group ($\beta = 8.11$, $p = .007$). There was no effect of time ($\beta = -2.49$, $p = .16$) nor any effect of Condition or significant interactions (*ps* > .05). As would be expected based on the amount of information presented in the video, participants were significantly less confident when responding to earlier occluded videos than later occluded videos (β = -19.25, $p < .001$) and less confident for mid-occlusion trials than late-occlusion trials (β = -8.80, $p < .001$).

3.3. Physical practice

Practice data were analysed using an LME model, which included the fixed effects of Group and practice Block as well as their interaction. Both groups improved with practice, evidenced by a significant Block effect (β = .02, $p < .001$), as illustrated in Figure 5A. There were no group main effects or interactions.

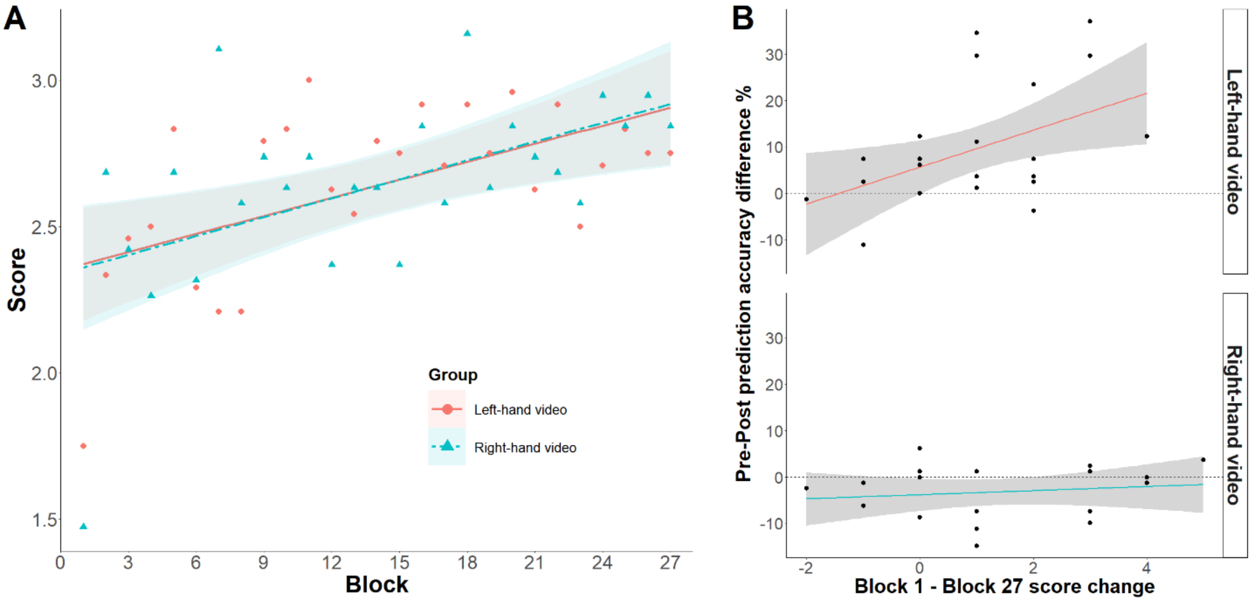

Figure 5. Panel A – Mean number of successful throws (out of 5) for each group across practice blocks. Data points represent group means for blocks and bands around lines represent 95% confidence intervals. Panel B – Scatterplots illustrating the correlations between the prediction accuracy change scores across the pre to post-test and practice change scores between block 1 and 27. Data are shown for the LH-video group (top) and RH-video group (bottom). Note that the left-handed motor interference condition was omitted when prediction accuracy change scores were calculated to represent un-interfered prediction scores.

3.4 Exploratory analysis on the relationship between throwing practice improvement and prediction accuracy improvement

A fixed-effect linear regression was conducted to determine the relationship between change in throwing accuracy (across blocks) and change in prediction accuracy pre-to-post practice. We also included the fixed effect of group and the interaction of practice change score as predictors in the model. We have plotted two graphs in Figure 5, panel B for the LH-video (top) and RH-video (bottom) groups; showing difference in the pre-post prediction accuracy (excluding the left-handed motor task) as a function of change scores in dart-throwing accuracy. The LH-video group showed a medium-to-large positive correlation ($r = .47$, $p = .02$); whereas the RH-video group showed a small, but non-significant correlation ($r = .15$, $p = .54$). The fixed-effect linear regression supported these group differences in terms of a main effect of group ($\beta = 4.75$, $p < .01$) and interaction between Group and practice change score ($\beta = 1.77$, $p = .047$). The change in accuracy between the first and final practice block was a significant predictor of improved prediction accuracy for the LH-video group only.

4. Discussion

We investigated effector-specific representations underlying action prediction processes in left-handed individuals. Prediction accuracy was hypothesised to improve after practice, but in a manner dependent on what the observer was seeing. Effector compatible stimuli (i.e., LH-video) would yield improvements in prediction accuracy more than would be seen when watching throws made with the right arm (i.e., RH-video group). This prediction was made, despite the fact that both groups saw the “same” video, with the difference being that the RH video was mirror-reversed to appear like the throws were being made with the left-hand for one group. Although both groups predicted above chance at pre-test (and at this time point, groups were considered equivalent[1]), left-hand physical practice throwing only benefitted prediction accuracy for the LH-video group. Moreover, there were no differences in throwing accuracy between the two groups during practice and both groups improved in dart throwing across blocks. This experience-driven facilitation of successful predictions has previously been documented for RH individuals in this same paradigm (Mulligan et al., 2014; 2016a,b) and through other tasks (Abreu et al., 2012; Aglioti et al., 2008; Hohmann et al., 2011) and modalities (e.g., auditory; Murgia et al., 2017). However, here we have now shown an effector-specific congruency effect supporting action-to-perception transfer. Only when the physically trained arm was somatotopically compatible to the observed effector did improvements in prediction accuracy manifest. This result suggests that motor-based representations underpinning action predictions are developed in an effector-specific manner following short-term practice.

4.1. Physical experience enhances action predictions, but only when stimuli are congruent to the practiced effector

Improvements in prediction accuracy were shown as a product of short-term physical practice when the practiced and observed effectors were somatotopically matched, as previously reported in RH individuals (Mulligan et al. 2014, 2016b). This time, the improvements were for left-handed individuals practicing with their left-hand and watching left-handed stimuli. Not only did these left-hand dominant individuals show the same effect as right-handed individuals, but here we also showed that the improvements in action prediction were stimuli dependent. The asymmetries in post-practice predictions between the LH-video and RH-video group suggests that motor-based representations that are developed with practice are effector specific and that any simulation-type mechanisms that are thought to be engaged in action prediction (and benefit action prediction) are specific to the hand and stimuli being observed and predicted. Moreover, improvements in throwing accuracy for the LH-video group only, were also correlated at an individual level with improvements in action prediction. These data are in line with the common coding hypothesis (Prinz, 1990) and a direct-matching account of action simulation (Rizzolatti et al., 2001; Gallese et al., 2004), where a particular effector that is repeatedly paired with a particular outcome can aid future predictions based solely on observation of another's action. One hypothesis is that this is achieved through a direct resonance of the action and effector in the brain in a somatotopically mapped fashion (Avenanti et al., 2007; Fadiga et al., 1995; Cavallo et al., 2012; Naish et al., 2016). It is also possible that the recognition of visual input affording predictions does not need to involve action simulation or that the prediction itself precedes simulation (Csibra, 2008). However, there is additional data from this study, as discussed next, that speaks in favour of action simulation underpinning action prediction.

4.2. Interference effects from performing a motor task were effector specific

Performing a motor interference task only interfered with prediction accuracy when it was performed with the left-hand (not the right-hand) and this was specific to the LH-video group post-practice. This latter result speaks to how the predictions were made and the functional role of the motor system and presumably simulation-type processes in these predictions. In previous work, a right-hand motor interference task during observation (in right-handed individuals watching a right-handed thrower) reduced prediction accuracy for skilled dart-throwers and for individuals with short-term physical, but not observational practice (Mulligan et al., 2014, 2016b). There is also evidence that such posture incongruent secondary motor tasks can interfere in other simulation reliant processes (e.g., Tausche et al., 2010; Stevens, 2005; Guilbert et al., 2021). The idea is that such incongruent actions interfere with the motor program that would be needed to covertly simulate the observed action. In our case, observers were performing isometric holds through a constantly extended arm, by actively pressing against a force gauge with their hands in a fist and arms straight at their sides, thus performing an action opposite to the elbow extension motion of a dart throw. Thus, postures and tasks which occupy the motor system in an action-incongruent manner, interfere with the simulation process and subsequently the accuracy of predictions (Mulligan & Hodges, 2019; see also Unenaka et al., 2018).

An alternative explanation for right-hand motor interference effects in previous work was that the RH motor interference task disrupted general motor processes that may be exclusive to the left hemisphere, such as those related to planning (e.g., Johnson-Frey et al., 2005; Frey, 2008; Janssen et al., 2011). Because left-handed individuals showed the same effector-specific effect and not interference from a right-hand motor interference task, our data speak against this alternative left-hemisphere dominance explanation. Rather, these data add confirmatory evidence for the action simulation hypothesis, whereby the motor system needs to be 'available' (unoccupied) for accuracy advantages to be shown.

When performing either motor interference task (right- or left-handed), there may have been down-stream cortical effects, beyond those initially assumed within this design. An additional consideration and consequence associated with the performance of unimanual actions is interhemispheric inhibition (IHI). The motor cortex that is ipsilateral to the hand performing the action (in our case an isometric contraction), has been shown to receive brief, inhibitory cortical projections from the controlling contralateral hemisphere (e.g., Nuara et al., 2023; Perez & Cohen, 2009; Vallido et al., 2023). As such, when performing the left-hand force task, there may have also been some "silencing" of the opposite hemisphere, which could have contributed to interference effects. Without neurophysiological measures, perhaps through paired-pulse

TMS, we are unable to make any strong conclusions about such processes. It is possible that temporal measures of prediction might also be more sensitive to any cross-hemisphere inhibitory effects.

4.3. Are left-handed individuals responding in a way that is similar to right-handed individuals?

There is evidence in the sport expertise literature that the outcomes of left-handed actions are more difficult to predict than right-handed actions (Hagemann et al., 2009; Loffing et al., 2012; Loffing & Hagemann, 2020), with the rationale that individuals are typically less exposed to left-handed actions (i.e., a visual familiarity effect). Indeed, LH-dominant individuals only make up an estimated 10.6% of the general population (Papadatou-Pastou et al., 2020); however, this estimation is greater in some sports (Hagemann et al., 2009). Nevertheless, we did not find evidence here indicating any advantages for the more familiar RH-video, which if this was the case, may already have been apparent at pre-test. To draw more concrete conclusions regarding these potential biases would require testing individuals who play darts regularly and hence may have been exposed to watching more right-handed throws (c.f., Loffing & Hagemann, 2020).

In previous literature, there has been evidence that left-handed individuals show differences from right-handed individuals in how observed actions are represented. Sartori et al. (2013, 2014) showed through measures of muscle activation that left-handers simulate observed right-handed actions, with their left limb, which was different to right-handed participants who showed muscle specific activations in the right limb. The encoding and translation of information to the dominant left-hand was explained through more bilaterally spread brain activations, which maybe inherent to left-handed individuals (Cabinio et al., 2010). However, in our study, there was no evidence of this translation of information across effectors, at least at a behavioural level.

Future studies are needed to compare across left and right-hand dominant individuals within the same study for stronger conclusions to be made about handedness-related effects; which was not the primary aim here.

In some recent work on action predictions in sport-experts, Loffing and Hagemann (2020) showed that action predictions were independent of the participant's handedness (and supposedly trained effector) in handball penalty throws. As such, they argued against the idea that effector-specific representations were developed with practice. However, handball is a sport that involves both hands for catching and throwing and flexibility in being able to throw with both hands is likely a skill that is developed over time and might dissipate any effector-specific advantages in action predictions. In a recent study with baseball athletes (Besler et al., in preparation), we also failed to show effector-specific effects in action prediction accuracy when right-hand dominant skilled pitchers made discriminatory predictions about pitch type across left and right-hand thrown pitches. However, there was evidence of effector-specificity in a small sample of left-handed pitchers. Clearly additional work is needed to untangle these handedness/effector-specific effects. In TMS work involving recordings of different muscles across different effectors in sport experts, evidence for muscle-specific facilitation effects were quite strong when comparing hands and feet in goalkeepers versus penalty takers in soccer (Tomeo et al., 2013) and wrist versus finger muscles in free-throw shooting in basketball players versus fans (Aglioti et al., 2008). It may be that behavioural effects of such specificity are harder to show because it is difficult to uncouple the visual and motor experiences of experienced athletes and/or that perceptual experiences associated with visual kinematic cues dominate motor-acquired representations (Abernethy et al., 2008).

There is evidence that the perspective and angle which demonstrations are presented impacts on evidence for action simulation. Alaerts et al. (2009) used TMS to study action observation in RH individuals and they manipulated both the perspective of the observed limb as well as the congruency of the observer's and actor's limb positions. The third-person perspective led to the greatest cortical activation in MEPs when actions were observed from a specular (mirrored) orientation than an anatomical (first-person) arrangement, indicative of greater AON engagement. Loffing and Hagemann (2020) also showed videos in a mirrored arrangement (i.e., the actor facing the observer), but because athletes differed in hand dominance, some actions were spatially compatible while others were anatomically compatible (making strong conclusions about effector-specific and handedness effects difficult).

In our study, videos were filmed from a side-on, third-person perspective, prioritizing anatomical/spatially mapped aspects of the dart-throwing task. Therefore, differences across studies in terms of effector specificity or handedness effects, may be a result of the spatial or anatomical matched perspective with which stimuli are shown. Although the perspective was always the same across video conditions in our experiment, there was a change in screen position for the first ten participants in the LH-video group only (as a result of a miscommunication across experimenters). This meant that the dart was coming towards participants, rather than going away from participants, for the latter tested participants (although the dart board was always shown in the video to maintain perspective). To determine whether this change in screen position impacted the results, we compared the means for the first ten participants to the last fourteen in a LME analysis involving group, time and condition. There was more improvement for the first ten participants (M = 13.52%) than the later participants (M= 3.44%). There was no overall effect of group (*p*=.32), but there was a difference across group in the post-test, for the control condition only (*p*<.01). As such, although the trends remained towards improvement for participants in the LH-video group, it may be the case that the size of this effect was underestimated, if this small difference in screen placement impacted LH-video congruency effects.

One final point concerning left-right stimuli related differences is with respect to perceptions of confidence. We expected that the LH-video group would report higher confidence at post-test in response to observing the same effector as the one practiced. Surprisingly, the increased confidence for the LH-video group was not mediated by practice experiences, but rather was immediate. This enhanced perception of prediction ability, despite behavioural evidence to the contrary, shows that ability perceptions are also biased towards the dominant limb (even when we do not have the action experiences to facilitate these predictions).

5. Future directions

In future work, there is a need to test both left and right-handed individuals within the same study and potentially to use a repeated measures design to better isolate effector-specific effects. In initial pilot testing, it appeared that switching between watching left and right-handed throws decreased accuracy on the prediction task, not least because of the number of conditions that were necessary to run. This was one of the reasons we ran the current experiment as a between-groups' design. However, there would be some benefits of running such a study with experienced participants for both the right and left-hand, where lengthy pre- and post-testing procedures would not be needed. Moreover, there would be some interest in determining whether these short-term experiences come to dominate more general handedness tendencies when it comes to prediction accuracy (such as right-hand dominant individuals practicing with their non-dominant left hand). As above, some neurophysiological testing of cortical excitation/inhibition through TMS would also be useful in determining mechanisms underlying improvements in prediction accuracy for certain types of stimuli.

6. Conclusions

Here we have evidence of effector specificity in action predictions as a function of physical practice for LH dominant individuals. After short-term practice, only videos that depicted throwing actions in an effector compatible way improved prediction accuracy. In support of action-simulation processes being involved in improved action-prediction, a motor interference task impeded prediction accuracy, but only when it was performed with the left-hand, that is the effector that was practiced and would be involved in the action being observed. Collectively these findings support the proposal that motor experience contributes to action prediction processes and that these contributions are effector specific.

Acknowledgements

We would like to acknowledge the University of Münster in Germany for academically supporting an international research visit of author MK (supervised by Dr Karen Zentgraf), to come to Canada to conduct initial work on this project.

Data statement

Data, analysis code and the stimuli used in this research are openly available at: https://osf.io/savuw/?view_only=b7c51e702f87488ab03c5aa0ccbebf5d.

Funding sources

This research was supported by funding from the Natural Sciences and Engineering Research Council of Canada (NSERC) in the form of a Discovery grant awarded to NJH.

Declaration of competing interest

The authors declare that they have no conflict of interest.

Author contributions

Matthew W. Scott: Data curation; Formal analysis; Writing - Original Draft; Writing - Review & Editing; Visualization; Supervision. **Desmond Mulligan:** Conceptualization; Investigation, Methodology; Writing - Review & Editing; Software and Supervision. **Mareike Kuhne:** Investigation; Writing – Original Draft. **Megan Zhu:** Investigation; Formal analysis. **Minghao Ma:** Investigation; Formal analysis; Writing - Original Draft. **Nicola J. Hodges:** Conceptualization; Methodology; Writing - Original Draft; Writing - Review & Editing; Supervision; Funding acquisition.

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Footnotes

1. An equivalence test was conducted on group pre-test data using the TOSTER package in R. With equivalence bounds set at ± 5%, this test indicated no significant differences, $t(41) = -0.43$, $p = 0.33$.