

Observed effector-independent motor learning by observing

Alexandra Williams^{1,3} and Paul L. Gribble^{1,2,3}

¹The Brain and Mind Institute, ²Department of Psychology, ³The University of Western Ontario, London, Ontario, Canada

Submitted 12 August 2011; accepted in final form 16 December 2011

Williams A, Gribble PL. Observed effector-independent motor learning by observing. *J Neurophysiol* 107: 1564–1570, 2012. First published December 21, 2011; doi:10.1152/jn.00748.2011.—A compelling idea in cognitive neuroscience links motor control and action observation. Recent work supports the idea that a link exists not just between action observation and action planning, but between observation and motor learning. Several studies support the idea that cortical regions that underlie active motor learning also play a role in motor learning by observing. The goal of the present study was to test whether motor learning by observing is effector dependent (as in active motor learning) or effector independent (as in studies of action observation and mirror neurons). Right-handed human subjects observed a video depicting another individual learning to reach to visual targets in a force field (FF). The video showed reaching in a clockwise FF (CWFF) or a counter-clockwise FF (CCWFF), and depicted an individual reaching with the right or left arm. After observation, all subjects were asked to reach in a CWFF, using their right arm. As in our prior studies, subjects who observed a CWFF prior to the CWFF test performed better than subjects who observed a CCWFF. We show here that this effect was seen both when observers watched others reach using their right arm, and when observers watched others learning to reach using the left arm. These results suggest that information about novel forces learned through observation is represented in an effector-independent coordinate frame, and are consistent with the idea that the brain links not only observation and movement, but motor learning as well, through abstract representations of actions.

human; observation; arm movement; force field; reaching

RECENT WORK IN COGNITIVE NEUROSCIENCE links action and observation (Fadiga et al. 1995; Rizzolatti et al. 1996). Brain regions involved in action planning are also recruited when observing actions of others (Caspers et al. 2010; Strafella and Paus 2000; van Schie et al. 2004). We recently established that novel forces may be learned by observing, likely through activation of motor systems for movement planning and control (Mattar and Gribble 2005). This suggests that a link exists not just between action observation and planning, but motor learning as well. Other studies support the idea that brain regions involved in motor learning are recruited when we observe actions of others (Brown et al. 2009; Malfait et al. 2010; Stefan et al. 2005).

Work on the neural basis of the observation-action link has focused on mirror neurons, first reported in the ventral premotor cortex of macaques. Cells show increased firing rates when monkeys observe an action performed by another individual, and when performing the same action themselves (di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1996). There is some evidence that mirror neurons encode actions in a relatively high-level, abstract representation. While mirror neuron activity typi-

cally depends on observed and performed actions sharing a goal (e.g., grasping an object), it is not necessarily dependent on effector specificity. In electrophysiological work in non-human primates, a subset of mirror neurons in area F5 were active both when the monkey grasped an object with the hand, and with the mouth (Gallese et al. 1996). In another study, mirror neurons in the same area (F5), which has been proposed as a monkey homolog of Broca's area in humans (Petrides et al. 2005), discharged both when a monkey performed an action and when it was presented with an acoustic stimulus associated with that action (Kohler et al. 2002). A similar pattern in humans has been observed in a temporo-parieto-premotor circuit using fMRI (Gazzola et al. 2006). These studies support the idea that mirror neurons link action and observation using abstract, effector-independent representations (Costantini et al. 2008).

In contrast, studies of motor learning show that information about novel forces is represented in an intrinsic, muscle-based coordinate system (Malfait et al. 2002; Shadmehr 2004), and that generalization of dynamics learning to adjacent movement directions is limited (Donchin et al. 2003; Gandolfo et al. 1996; Mattar and Ostry 2007; Thoroughman and Shadmehr 2000; Tremblay et al. 2008). While some instances of interlimb transfer have been reported (Crisicimagna-Hemminger et al. 2003; Sainburg and Wang 2002), once cognitive influences are removed, no interlimb transfer is observed for dynamics learning (Malfait and Ostry 2004).

Here we investigated observed effector dependence in motor learning by observing. Right-handed subjects observed videos depicting another individual reaching, using the right or left arm, in a novel force field (FF). After observing either a clockwise FF (CWFF) or counter-clockwise FF (CCWFF), subjects were asked to reach in a CWFF, using their right arm. As in our previous studies, subjects who observed a CWFF prior to the CWFF test performed better than subjects who observed a CCWFF. Here we show that this effect was seen both when subjects observed reaches depicted using the right arm, and also when observing FF learning depicted with the left arm. These results are consistent with the idea that the brain links observation and motor learning through abstract representations of actions.

METHODS

Participants. Sixty undergraduate students (mean age = 18.5 ± 1.0 yr) participated in the study. All subjects reported normal or corrected vision, and no known history of neurological or musculoskeletal problems. All participants were right-handed (Van Strien 2002). All participants were naïve to the apparatus and motor task. Subjects provided informed consent, and the study was approved and conducted in full compliance with the regulations set out by The University of Western Ontario Human Subjects Research Ethics Board.

Apparatus. Participants were seated with shoulder straps to minimize shoulder and torso translation during the experiment. The chair

Address for reprint requests and other correspondence: P. L. Gribble, The Brain and Mind Institute, Dept. of Psychology, The Univ. of Western Ontario, 1151 Richmond St., London, Ontario, Canada N6A 5B7 (e-mail: paul@gribblelab.org).

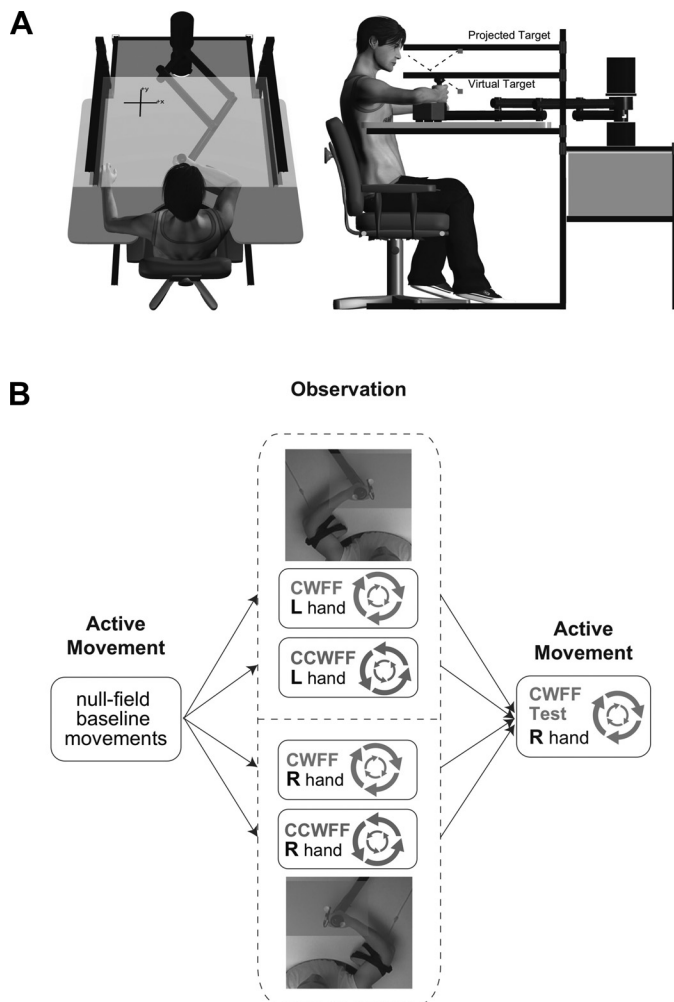


Fig. 1. Experimental design. *A*: subjects were seated while grasping the handle of an InMotion2 robot arm, and guided a cursor, projected onto a semi-silvered mirror, to virtual targets that appeared to float in the same plane as the hand. *B*: subjects first performed 96 reaching movements using their right arm in a null field (no forces). Subjects were then randomly assigned to 1 of 4 groups, who observed videos of another individual learning to reach either in a clockwise force field (CWFF) or a counter-clockwise force field (CCWFF), using their left (L) or right (R) arm. All subjects then performed 96 reaching movements using their right arm in a CWFF.

was positioned and secured in front of a horizontal tabletop surface such that the table was at the subject's chest height.

Subjects grasped the handle of an InMotion2 robot arm (Interactive Motion Technologies) with their right hand. Their arm was abducted at the shoulder and an air-sled was positioned under the proximal segment. The air-sled supported the arm against gravity, minimized friction with the tabletop, and restricted movement to a horizontal plane. Subjects could not see their arm but only a cursor representing the position of the robot handle.

During movement trials with the robot, visual targets were projected onto a horizontal semi-silvered mirror (107×75 cm) located above the arm. This arrangement produces the illusion that targets are floating in the same plane as the hand (Fig. 1*A*). Subjects were asked to reach quickly and accurately from a central start target (located at the subject's midline, 20 cm in front of the sternum, 20 mm in diameter) to 1 of 8 circular targets (24 mm in diameter) spaced equally around the circumference of a circle (10 cm radius). At the end of each reach, the target changed color to indicate to the subject whether their movement speed was slow, fast, or within the desired duration, which was 150–200 ms (time between leaving the start target and entering the end target).

The robot was programmed to apply novel FFs to the arm during reaching movements. Forces were applied in a direction perpendicular to the instantaneous direction of hand motion, with a magnitude proportional to the instantaneous tangential hand velocity. FFs were applied in either CW or CCW directions, perturbing limb movements and resulting in curved movement trajectories. Forces were generated according to the following equation

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = \begin{bmatrix} 0 & dk \\ -dk & 0 \end{bmatrix} \begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix}$$

where F_x and F_y represent robot-generated forces in the left-right and forward-backward directions, respectively; \dot{x} and \dot{y} represent hand velocities, $k = 25$ Ns/m, and $d = +1.0$ (CW) or -1.0 (CCW). At the start of each trial, forces applied by the robot were zero, and increased proportionally to increasing hand velocity such that maximal force corresponded to peak tangential hand velocity midway along the movement. Forces were controlled by custom software using the RT-Linux operating system running on a Pentium 4 CPU. Robot handle positions, velocities, and applied forces were sampled at 200 Hz and stored on a digital computer for analysis.

Experimental design. A total of 60 human participants were randomly assigned to one of four experimental groups ($n = 15$ each). Each group completed a similar sequence of tasks. First, all subjects performed an initial reaching task in a null FF (no forces) with their right arm. The purpose was to measure baseline levels of movement curvature. Next, subjects were asked to view one of four videos displaying a series of reaching movements made by another individual, either in a CWFF or CCWFF, and either using the right or left arm. Following observation, all subjects performed the reaching task again, this time in a CWFF using their right arm (Fig. 1*B*).

Null field baseline movements. All subjects first performed 12 blocks of 8 reaching movements (96 total), from the start position to each of 8 targets, and back to the start position, with their right arm, in a null FF (no forces imposed by the robot). The target order within each block of 8 movements was pseudo-randomized. Subjects were instructed to look down at the semi-silvered mirror, and guide the cursor (indicating their hand position) toward the targets. Subjects were asked to move quickly and accurately from the start position to the target, landing on the target without moving through it, and to maintain a desired movement duration (150–200 ms).

Observation. The videos shown during the action observation segment of the experiment depicted a top-down view of another individual's left or right arm, and the workspace within which reaching movements were made (Fig. 1*B*). The image of a cursor was superimposed over the position of the robot handle, and the images of the targets were superimposed over the workspace. The videos showed a right-handed individual learning to reach to targets while grasping the robot arm, using either the left or right arm, and in either a CWFF or CCWFF. The video depicting left-arm movements was produced by flipping, as a mirror image, the video of the right-handed subject reaching with the right arm. The videos depicted subjects completing 12 blocks of 8 reaching movements (96 total). The target order within each block of 8 movements was pseudo-randomized. The recordings were made using a Canon GL2 digital video camera and edited with Final Cut Pro 4 software (Apple). The duration of each recording was about 6 min.

Each subject group viewed a different video (Fig. 1*B*). One group watched another individual learning to reach in a CWFF with the right arm. A second group observed another individual reaching in the same FF, but with the left arm. Two other groups were tested, who observed an opposite CCW FF, one with the right arm and the second with the left arm.

To ensure that subjects were paying attention throughout each video, subjects were instructed to verbally report to the experimenter the color of the target at the end of each observed movement. Recall that on each movement trial, target color was changed based on the

speed of each movement (red/green/blue for fast/slow/correct, respectively). Mean error rate across this attentional control task was 4%.

CW FF test. After observation, all subjects were tested for active movement in a CW FF, using their right arm. Subjects completed 12 blocks of 8 movements (96 total). Procedures and instructions to the subjects in this test were identical to those in the initial null field baseline movements (see above) except for the presence of the FF. Subjects were not informed in advance about the presence of forces, but were instructed, as before, to reach quickly and accurately to each target.

Measures and statistics. Performance on each of the 96 reaching movement trials was assessed on a trial by trial basis using custom software written in MATLAB (The Mathworks). Performance on each trial was based on hand trajectory curvature, which was characterized by calculating the maximum perpendicular deviation of the hand path from a straight-line segment linking the start and end positions of movement (Brashers-Krug et al. 1996; Malfait et al. 2002; Thoroughman and Shadmehr 1999). Scores for each movement were averaged across bins of eight movements. Differences between means across groups were assessed using analysis of variance and Tukey post hoc tests.

RESULTS

A three-factor mixed-design analysis of variance was carried out to assess differences in mean movement curvature as a function of movement block (12 levels, repeated-measures factor), observed FF (CWFF vs. CCWFF, between-groups factor), and observed limb (left vs. right, between-groups factor). A main effect of movement block was observed [$F(11,616) = 25.1, P < 0.0001$], indicating that all subjects reduced movement curvature over the course of the CWFF movement test. The only other statistically reliable effect was an interaction between observed FF and movement block [$F(11,616) = 2.6, P < 0.005$]. This suggests that, as in our previous work (Brown et al. 2009, 2010; Mattar and Gribble 2005), the pattern of decrease in movement curvature during the CWFF movement test depended on the FF that was previously observed (CW vs. CCW).

Figure 2 gives peak movement curvature in the final CWFF movement test, as a function of movement trial, for subjects who previously observed another individual reaching in a CWFF (both left and right arm) and for subjects who observed a CCWFF. Movement curvature is initially high, and over the course of training, curvature decreases. Differences are seen early in learning (the first block of 8 movements in particular) that depend on what subjects observed prior to the CWFF movement test. Subjects who observed another individual reaching in a CWFF performed better (lower movement curvature) in the CWFF movement test than subjects who observed a CCWFF ($P < 0.01$ for the first block).

In our previous work on motor learning by observing, we have shown, using a series of different control conditions, that the differential effects of observing a CW vs. CCWFF on subsequent movements are a result of both facilitatory effects of CWFF observation and detrimental effects of CCWFF observation (Brown et al. 2009, 2010; Mattar and Gribble 2005). In the present paper, the focus is on effector independence and left vs. right arm observation, and so, for the sake of brevity, we have not repeated the groups that have been repeatedly documented in previous studies such as no-observation or observation of a randomly varying FF.

Figure 3 gives mean movement curvature in the first block of eight movements, for subjects in all four groups: CCWFF-R,

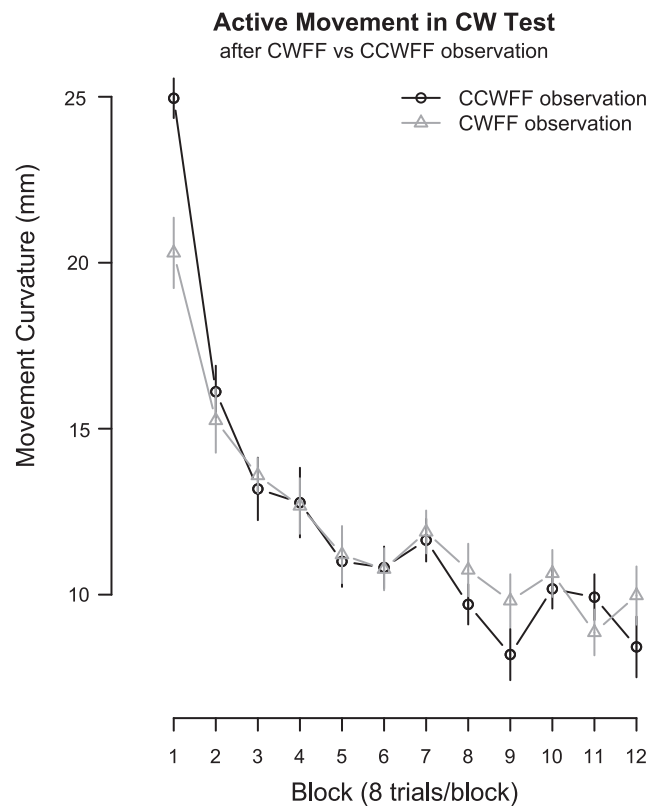


Fig. 2. Effect of FF observation on mean movement curvature in the CWFF movement test. Mean movement curvature is shown as a function of movement trial, averaged over 8-trial bins. Subjects who observed another individual learning to reach in a CCWFF prior to the CWFF movement test (circles) perform worse than subjects who observed a CWFF (triangles).

CCWFF-L, CWFF-R, and CWFF-L. It can be seen that when subjects observed FF learning depicted using the right arm, movement curvature in the CWFF movement test was greater (performance was poorer) for subjects that had previously observed reaching movements in a CCWFF compared with those who observed reaching in a CWFF ($P < 0.01$). The same effect can be seen for left arm observation, namely poorer performance for CCWFF observation than for CWFF observation ($P < 0.01$).

Moreover, in the analysis of variance, the main effect of observed limb (left vs. right) was not statistically reliable [$F(1,56) = 1.5, P > 0.23$]. In addition, no interaction effects containing the observed limb factor were statistically reliable ($P > 0.20$ in all cases). This suggests that the limb depicted in the observed videos (left vs. right limb) did not affect performance in the CWFF movement test over any of the 12 blocks examined.

Figure 4 gives peak movement curvature averaged over bins of eight movements, for subjects that observed left vs. right arm reaching. It can be seen that while all subjects reduce movement curvature over the course of the CWFF movement test, there are no statistically reliable differences between subjects that observed another individual reaching with their left vs. right limb ($P > 0.20$ in all cases). The absence of statistically reliable differences between left vs. right observation was likely not due to low power; as described above, for both left and right arm observation, we were able to detect differences in performance due to

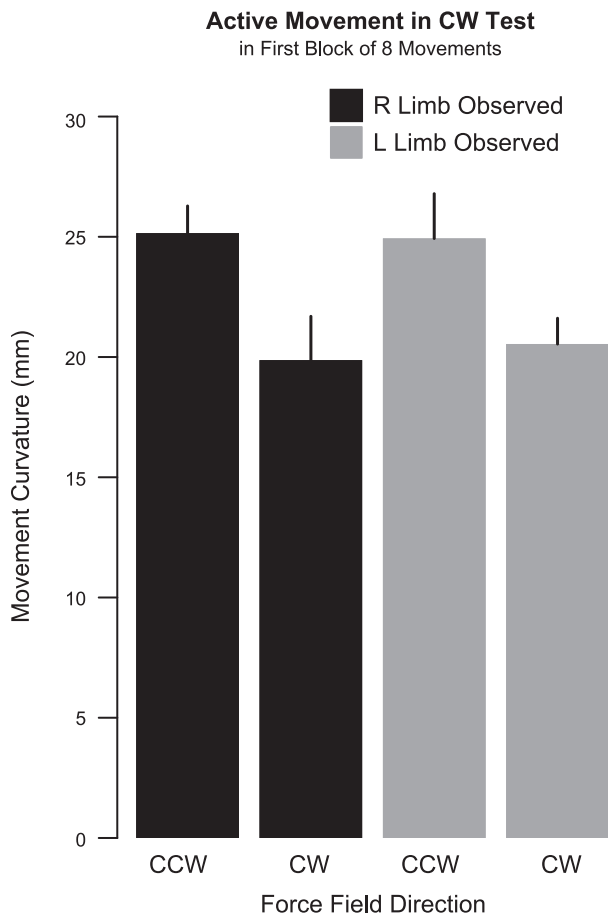


Fig. 3. Effect of observed FF and limb on movement curvature in the first 8-movement block of the CWFF movement test. Curvature varied with observed FF (CWFF vs. CCWFF) both when observing FF learning depicted using the left arm and the right arm.

CCWFF vs. CWFF observation. For completeness, Fig. 5, A and B, shows learning curves for all four groups.

Taken together, these results suggest that while performance in the CWFF movement test was determined by whether subjects had previously observed another individual reaching in a CWFF vs. CCWFF, their performance did not depend on whether they observed another person reaching with the left vs. right arm. The same detrimental effect of observing CCWFF learning (compared with the beneficial effect of observing CWFF learning prior to a CWFF test) was seen both when subjects observed FF learning depicting the right arm, and also when depicting FF learning with the left arm.

Control tests. The forces imposed on the limb by the robot were directly proportional to the velocity of hand movement. Thus the possibility exists that differences in movement curvature that arose in the CWFF movement test may have arisen because of differences in movement speed (and hence the magnitude of perturbing forces applied by the robot). To test this possibility, we measured peak tangential hand velocity on each movement trial for each of the four subject groups. We found no statistically reliable differences in peak tangential velocity as a function of subject group ($P > 0.1$ in all cases). Thus differences in performance in the CWFF test may be attributed to the effects of observation and not to differences in movement speed.

In the analyses described above, movements were averaged over bins of eight trials. To ensure that our results were not dependent on the particular choice of bin size, we repeated our analyses by averaging trials over bins of 4, 6, and 12 movements. In all cases the overall results were the same as for those described above for a bin size of eight trials, that is, performance on the CWFF test depended on whether subjects observed CCWFF or CWFF learning, and this effect was seen both for observation of the left and right arm ($P < 0.05$ in all cases).

Finally, one possible reason why we did not observe statistically reliable differences depending on observed effector, is that we did not have adequate statistical power to detect such effects. To address this possibility, we carried out a statistical power analysis in which we computed the power we have, given the characteristics of our data (number of subjects per group, observed within-group variance, etc.) to detect differences between groups as large as the mean differences we observed between CWFF and CCWFF groups (4.8 mm in the first block). The results of this analysis show that statistical power is 0.92, which is considered very high (Cohen 1988). We do not believe the absence of statistically reliable differences between observed effectors is due to low statistical power.

DISCUSSION

The goal of this study was to better understand the nature of motor learning by observing by testing whether information

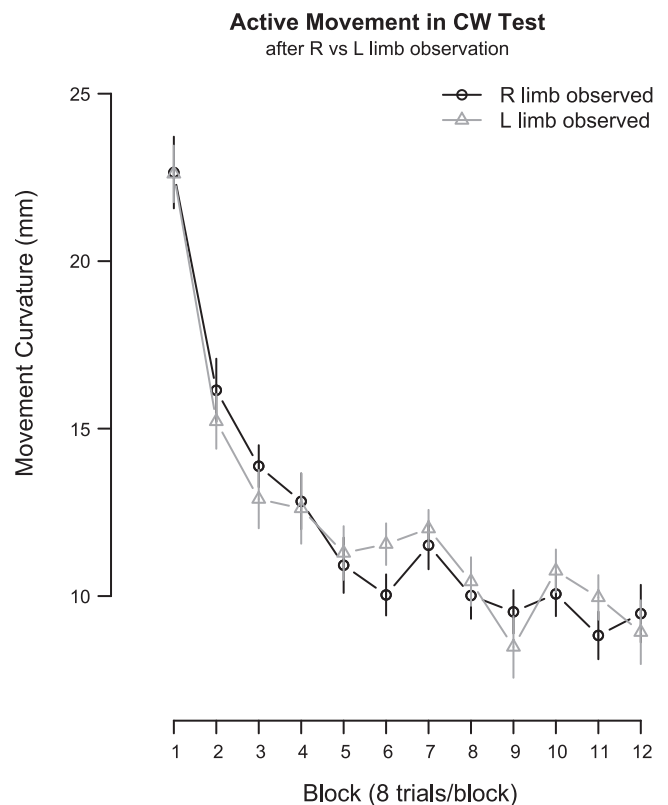


Fig. 4. Effect of limb observation on mean movement curvature in the CWFF movement test. Mean movement curvature is shown as a function of movement trial, averaged over 8-trial bins. No statistically reliable differences are seen for subjects who observed another individual learning to reach in a FF using their right arm (circles) compared with those who observed the left arm (triangles).

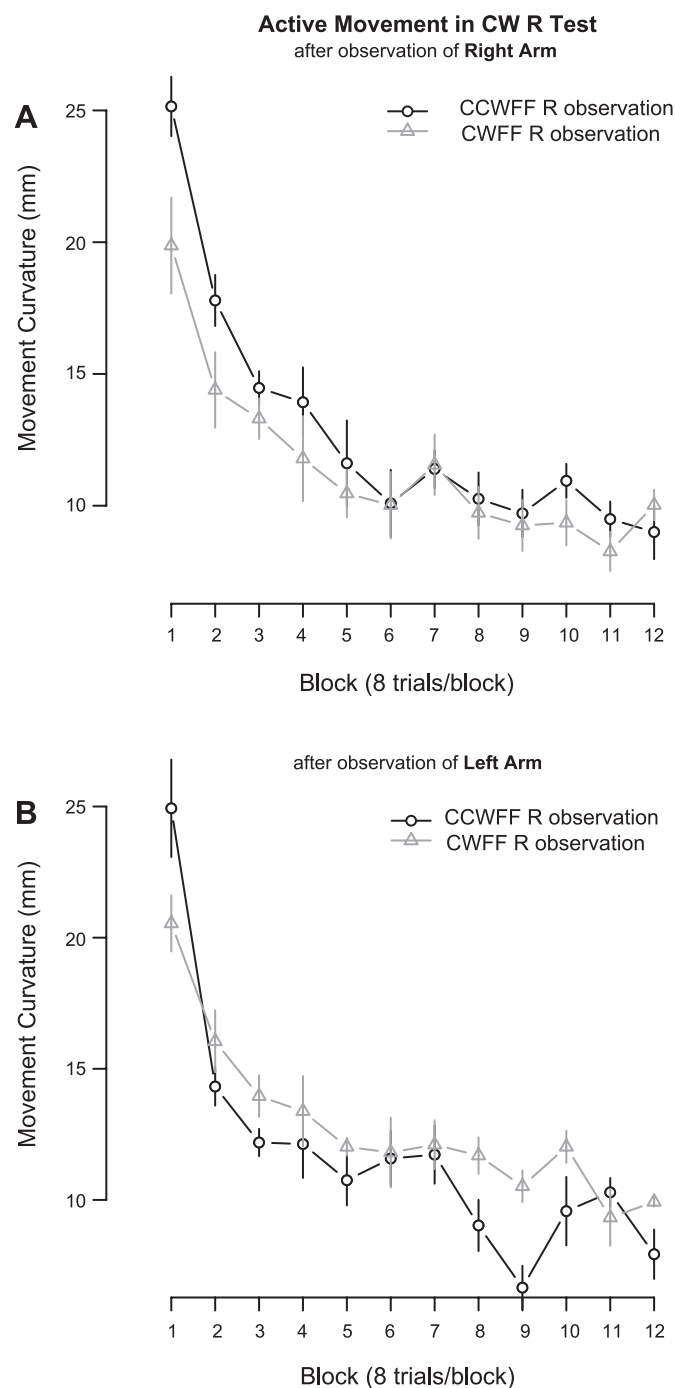


Fig. 5. Effect of limb observation on mean movement curvature after observation of right arm (A) and left arm (B). Mean movement curvature is shown as a function of movement trial, averaged over 8-trial bins.

about novel forces learned by observation is effector specific. When subjects observed another individual learning to reach in a CCWFF, their performance on the subsequent CWFF test was impaired relative to subjects who observed a CWFF. This pattern of results recapitulates our earlier findings in which we demonstrated that the effects of observing a CW vs. CCWFF on subsequent movements are a result of both beneficial effects of CWFF observation and detrimental effects of CCWFF observation (Brown et al. 2009, 2010; Mattar and Gribble 2005).

In addition, our present results support the idea that motor learning by observing is observed effector independent. The effects of observation, namely the difference in performance after observing a CCWFF vs. a CWFF, were present both when observers watched others learning to reach in a FF using their right and their left arm. These results are consistent with the idea that the brain links action and observation in an abstract, effector-independent coordinate frame (Costantini et al. 2008).

Previous investigations of effector specificity in active FF learning have produced mixed findings. Work on motor learning shows that novel dynamics are represented in intrinsic, muscle-based coordinate frames (Malfait et al. 2002; Shadmehr 2004). Another well-documented feature of dynamics learning is that generalization (for example, to other movement directions) is rather limited (Donchin et al. 2003; Gandolfo et al. 1996; Mattar and Ostry 2007; Thoroughman and Shadmehr 2000; Tremblay et al. 2008). There have been some reports of limited interlimb transfer of dynamics learning (Crisicimagna-Hemminger et al. 2003; Sainburg and Wang 2002). However, other work suggests that cases such as these may be based on a cognitive strategy that emerges as a result of the sudden introduction of load. Malfait and Ostry (2004) showed that once these cognitive factors are removed from the task, for example, by introducing the perturbing FF gradually, so that subjects are not aware of the perturbation (but they still learn to compensate for it), no interlimb transfer is observed.

In the present study, the FF present in the videos was introduced suddenly, and so the observed effector independence seen here may be due to cognitive influences associated with the sudden introduction to load. Although it would be desirable to tease apart cognitive effects by manipulating the introduction of load, as in studies of active motor learning, this would not be informative in this case. If observers were presented with videos depicting a load introduced so gradually that movement errors were imperceptible, the observer would not be exposed to any visual information about movement errors due to the underlying FF, and so presumably no learning by observing would take place. While in the current study the observers were given a task to ensure that they were paying attention to each movement (reporting the color of each target), it is not possible in the context of the current experimental design to assess what specific components of the video, in particular, are more or less responsible for the motor learning by observing effect. For example, it may be that by attending only to the motion of the cursor (and not the limb), similar effects would be seen. In this case the specific effector depicted in the video would of course be inconsequential. Future work is planned to explore the specific features of the observed task that best promote motor learning by observing.

The present findings in concert with other recent studies are consistent with the idea that learning by observing, and the neural substrate of the observation-execution matching system, is organized to represent the goal of the learned motor task, rather than the specific effector used during learning itself. Costantini et al. (2008) have observed facilitation of an observed motor task, originally performed with the arm, for the arm as well as the foot. The present study differs from this previous work in several important ways. First, in the Costantini et al. (2008) study, subjects were presented with visual depictions of meaningful and meaningless tasks; in the present study, observers were presented with a visual depiction of another subject executing the same arm movement task that the observer was to

perform. In the Costantini et al. (2008) study, the observer's task (their response) was to press a button after making a conscious judgment about whether the depicted action was meaningful or meaningless. In the present study, the observer was not asked to consciously interpret the actions they observed. Moreover, their task, which was completed after observation was over, was to perform a goal-directed reaching movement. In the Costantini et al. (2008) study, the observer's task was to press a response button. The results of the present study are in agreement with the basic findings of the study reported by Costantini et al. (2008), and, in light of the myriad methodological and task differences, extend the scope of the findings in important ways.

Similarly, Rijntjes et al. (1999) found that the same regions of the premotor cortex are activated when identical signature tasks are performed with either the dominant hand or ipsilateral foot. Therefore, while there is likely somatotopic organization in the observation-execution matching system, different effectors may access the same neural substrate when performing similar motor tasks with similar goals. The representations of observed actions appear to be coded based on extrinsic coordinates and action goals, such that learning is generally independent of the effector being used (Costantini et al. 2008). Information in extrinsic coordinates is most readily available when viewing an action, whereas information about joint angles, muscle lengths, and dynamics presumably must be inferred. The current results may be linked to the common coding hypothesis (De Maeght and Prinz 2004; Prinz 1984), which proposes that perceptual and motor representations are linked by a common shared representation. Seeing an event activates the action associated with that event, and performing an action activates the associated perceptual event.

Much focus has been placed on the function and organization of the observation-execution matching system, and some research has argued that mirror neurons play a significant role in this system in humans (Aziz-Zadeh and Ivry 2009; Buccino et al. 2001; Decety et al. 1997; Gallese et al. 1996; Rizzolatti et al. 1996; Umiltà et al. 2001). While in some cases mirror neurons appear to code for specific effectors (Buccino et al. 2001), in other cases mirror neuron activity is not necessarily dependent on effector specificity but seems to depend on observed and performed actions sharing a common goal (Gallese et al. 1996). These and several other studies support the idea that the mirror system encodes actions using relatively high-level, effector-independent representations of action (Costantini et al. 2008; Gazzola et al. 2006; Kohler et al. 2002). Electrophysiological studies of reaching in non-human primates may provide a neural basis for effector-independent observational learning. Several studies support the idea that neurons in a number of motor regions of the brain implicated in observation and the mirror system, including primary, premotor cortices and supplementary motor areas, are also involved in coding bimanual movements (Donchin et al. 1998, 2002; Rokni et al. 2003). Studies using fMRI in humans implicate the mirror neuron system in observation learning and identify commonalities in the neural substrates for physical and observational learning (Calvo-Merino et al. 2005; Cross et al. 2009).

In summary, we have demonstrated that motor learning by observing occurs for FF learning both when viewing active motor learning depicted using the left or right arm. Motor learning by observing depends on the characteristics of observed FFs, and these effects were seen when subjects observed others learning to reach with both their left or right arm.

These results are consistent with the idea that the observation-execution matching system represents actions using abstract, effector-independent representations.

ACKNOWLEDGMENTS

The authors thank Jeremy Wong for helpful comments and Dinant Kistemaker for helpful comments and for providing images of the experimental apparatus.

GRANTS

This research was supported by grants from the Natural Sciences and Engineering Research Council of Canada and the Canadian Institutes of Health Research.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: A.W. and P.L.G. conception and design of research; A.W. performed experiments; A.W. and P.L.G. analyzed data; A.W. and P.L.G. interpreted results of experiments; A.W. and P.L.G. prepared figures; A.W. and P.L.G. drafted manuscript; A.W. and P.L.G. edited and revised manuscript; A.W. and P.L.G. approved final version of manuscript.

REFERENCES

- Aziz-Zadeh L, Ivry RB. The human mirror neuron system and embodied representations. *Adv Exp Med Biol* 629: 355–376, 2009.
- Brashers-Krug T, Shadmehr R, Bizzi E. Consolidation in human motor memory. *Nature* 382: 252–255, 1996.
- Brown LE, Wilson ET, Gribble PL. Repetitive transcranial magnetic stimulation to the primary motor cortex interferes with motor learning by observing. *J Cogn Neurosci* 21: 1013–1022, 2009.
- Brown LE, Wilson ET, Obhi SS, Gribble PL. Effect of trial order and error magnitude on motor learning by observing. *J Neurophysiol* 104: 1409–1416, 2010.
- Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, Seitz RJ, Zilles K, Rizzolatti G, Freund HJ. Action observation activates premotor and parietal areas in a somatotopic manner: an fmri study. *Eur J Neurosci* 13: 400–404, 2001.
- Calvo-Merino B, Glaser DE, Grèzes J, Passingham RE, Haggard P. Action observation and acquired motor skills: an fmri study with expert dancers. *Cereb Cortex* 15: 1243–1249, 2005.
- Caspers S, Zilles K, Laird A, Eickhoff S. A meta-analysis of action observation and imitation in the human brain. *Neuroimage* 50: 1148–1167, 2010.
- Cohen J. *Statistical power analysis for the behavioral sciences*. Hillsdale, NJ: Lawrence Erlbaum, 1988.
- Costantini M, Committeri G, Galati G. Effector- and target-independent representation of observed actions: evidence from incidental repetition priming. *Exp Brain Res* 188: 341–351, 2008.
- Crisimagna-Hemminger SE, Donchin O, Gazzaniga MS, Shadmehr R. Learned dynamics of reaching movements generalize from dominant to nondominant arm. *J Neurophysiol* 89: 168–176, 2003.
- Cross ES, Kraemer DJ, Hamilton AF, Kelley WM, Grafton ST. Sensitivity of the action observation network to physical and observational learning. *Cereb Cortex* 19: 315–326, 2009.
- De Maeght S, Prinz W. Action induction through action observation. *Psychol Res* 68: 97–114, 2004.
- Decety J, Grèzes J, Costes N, Perani D, Jeannerod M, Procyk E, Grassi F, Fazio F. Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain* 120: 1763–1777, 1997.
- di Pellegrino G, Fadiga L, Fogassi L, Gallese V, Rizzolatti G. Understanding motor events: a neurophysiological study. *Exp Brain Res* 91: 176–180, 1992.
- Donchin O, Francis JT, Shadmehr R. Quantifying generalization from trial-by-trial behavior of adaptive systems that learn with basis functions: theory and experiments in human motor control. *J Neurosci* 23: 9032–9045, 2003.

- Donchin O, Gribova A, Steinberg O, Bergman H, Vaadia E.** Primary motor cortex is involved in bimanual coordination. *Nature* 395: 274–278, 1998.
- Donchin O, Gribova A, Steinberg O, Mitz AR, Bergman H, Vaadia E.** Single-unit activity related to bimanual arm movements in the primary and supplementary motor cortices. *J Neurophysiol* 88: 3498–3517, 2002.
- Fadiga L, Fogassi L, Pavesi G, Rizzolatti G.** Motor facilitation during action observation: a magnetic stimulation study. *J Neurophysiol* 73: 2608–2611, 1995.
- Gallese V, Fadiga L, Fogassi L, Rizzolatti G.** Action recognition in the premotor cortex. *Brain* 119: 593–609, 1996.
- Gandolfo F, Mussa-Ivaldi FA, Bizzi E.** Motor learning by field approximation. *Proc Natl Acad Sci USA* 93: 3843–3846, 1996.
- Gazzola V, Aziz-Zadeh L, Keysers C.** Empathy and the somatotopic auditory mirror system in humans. *Curr Biol* 16: 1824–1829, 2006.
- Kohler E, Keysers C, Umiltà MA, Fogassi L, Gallese V, Rizzolatti G.** Hearing sounds, understanding actions: action representation in mirror neurons. *Science* 297: 846–848, 2002.
- Malfait N, Ostry DJ.** Is interlimb transfer of force-field adaptation a cognitive response to the sudden introduction of load? *J Neurosci* 24: 8084–8089, 2004.
- Malfait N, Shiller DM, Ostry DJ.** Transfer of motor learning across arm configurations. *J Neurosci* 22: 9656–9660, 2002.
- Malfait N, Valyear KF, Culham JC, Anton JL, Brown LE, Gribble PL.** fMRI activation during observation of others' reach errors. *J Cogn Neurosci* 22: 1493–1503, 2010.
- Mattar AAG, Gribble PL.** Motor learning by observing. *Neuron* 46: 153–160, 2005.
- Mattar AAG, Ostry DJ.** Modifiability of generalization in dynamics learning. *J Neurophysiol* 98: 3321–3329, 2007.
- Petrides M, Cadoret G, Mackey S.** Orofacial somatomotor responses in the macaque monkey homologue of Broca's area. *Nature* 435: 1235–1238, 2005.
- Prinz W.** Modes of linkage between perception and action, edited by Prinz W and Sanders AF. Cognition and motor processes. Berlin, Heidelberg: Springer, pp. 185–193.
- Rijntjes M, Dettmers C, Büchel C, Kiebel S, Frackowiak RS, Weiller C.** A blueprint for movement: functional and anatomical representations in the human motor system. *J Neurosci* 19: 8043–8048, 1999.
- Rizzolatti G, Fadiga L, Gallese V, Fogassi L.** Premotor cortex and the recognition of motor actions. *Brain Res Cogn Brain Res* 3: 131–141, 1996.
- Rokni U, Steinberg O, Vaadia E, Sompolinsky H.** Cortical representation of bimanual movements. *J Neurosci* 23: 11577–11586, 2003.
- Sainburg RL, Wang J.** Interlimb transfer of visuomotor rotations: independence of direction and final position information. *Exp Brain Res* 145: 437–447, 2002.
- Shadmehr R.** Generalization as a behavioral window to the neural mechanisms of learning internal models. *Hum Mov Sci* 23: 543–568, 2004.
- Stefan K, Cohen LG, Duque J, Mazzocchio R, Celnik P, Sawaki L, Ungerleider L, Classen J.** Formation of a motor memory by action observation. *J Neurosci* 25: 9339–9346, 2005.
- Strafella AP, Paus T.** Modulation of cortical excitability during action observation: a transcranial magnetic stimulation study. *Neuroreport* 11: 2289–2292, 2000.
- Thoroughman KA, Shadmehr R.** Electromyographic correlates of learning an internal model of reaching movements. *J Neurosci* 19: 8573–8588, 1999.
- Thoroughman KA, Shadmehr R.** Learning of action through adaptive combination of motor primitives. *Nature* 407: 742–747, 2000.
- Tremblay S, Houle G, Ostry DJ.** Specificity of speech motor learning. *J Neurosci* 28: 2426–2434, 2008.
- Umiltà MA, Kohler E, Gallese V, Fogassi L, Fadiga L, Keysers C, Rizzolatti G.** I know what you are doing. A neurophysiological study. *Neuron* 31: 155–165, 2001.
- van Schie HT, Mars RB, Coles MGH, Bekkering H.** Modulation of activity in medial frontal and motor cortices during error observation. *Nat Neurosci* 7: 549–554, 2004.
- Van Strien J.** The dutch handedness questionnaire. Technical report, Department of Psychology, Erasmus University Rotterdam, 2002.