Motor Learning by Observing

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Summary

Learning complex motor behaviors like riding a bicycle or swinging a golf club is based on acquiring neural representations of the mechanical requirements of movement (e.g., coordinating muscle forces to control the club). Here we provide evidence that mechanisms matching observation and action facilitate motor learning. Subjects who observed a video depicting another person learning to reach in a novel mechanical environment (imposed by a robot arm) performed better when later tested in the same environment than subjects who observed similar movements but no learning; moreover, subjects who observed learning of a different environment performed worse. We show that this effect is not based on conscious strategies but instead depends on the implicit engagement of neural systems for movement planning and control.

Introduction

The human motor system can generate accurate movements under widely varying mechanical conditions. For example, a skilled athlete can accurately throw a light baseball or a heavy football, even though the underlying muscle forces are very different. This important feature of the motor system is based on the acquisition of neural representations of the ways in which the environment's mechanical properties affect the motor system (Brashers-Krug et al., 1996; Conditt et al., 1997; Flanagan and Wing, 1997; Gandolfo et al., 2000; Gribble and Scott, 2002; Shadmehr and Mussa-Ivaldi, 1994). Each mechanical context may be associated with a neural representation of its properties, which is used to specify the patterns of control signals to muscles that are required to generate an accurate movement in that context (Haruno et al., 2001; Wolpert and Kawato, 1998).

Recent advances in the understanding of motor learning have been based on experiments using robotic devices to create novel mechanical environments, which typically involve the application of forces that perturb the limb during movement. After an initial phase in which movements are perturbed from their intended trajectory, they eventually return to normal despite the ongoing application of forces to the arm. This adaptation (known as motor learning) is thought to reflect the acquisition of a neural representation of the novel mechanical environment and its subsequent use by neural systems involved in limb control.

A powerful new idea in neuroscience links motor control with action observation. When we observe the actions of others, we activate the same neural circuitry responsible for planning and executing our own actions. For example, so-called "mirror neurons" in the premotor cortex are activated both when observing an action and when performing the same action (Gallese et al., 1996; Rizzolatti et al., 1996). Evidence for a mechanism linking observation and action has been demonstrated both in humans and nonhuman primates, in neurophysiological (Strafella and Paus, 2000; Watkins et al., 2003), brain-imaging (Buccino et al., 2001; Grafton et al., 1997; lacoboni et al., 1999), and eye-tracking studies (Flanagan and Johansson, 2003). It has been proposed that this mechanism forms the basis by which we understand the actions of others (Carey, 1996; Rizzolatti et al., 2001; Wilson et al., 2004): by mapping a representation of observed actions onto motor systems, observers gain knowledge of those actions by "internally" executing them. In a series of experiments, we test the intriguing possibility that such a system linking observation and action could facilitate motor learning.

It has been demonstrated that high-level information about the form of movements can be acquired by observing the actions of others. For example, rats can learn the spatial relationships in a Morris water maze by observing other rats engaged in the same task (e.g., see Petrosini et al., 2003, for review). Studies examining reaction times indicate that human observers can learn finger-tapping sequences by watching others (Kelly et al., 2003). These experiments and others like them (Heyes and Foster, 2002; Vinter and Perruchet, 2002) show that information about "what" movements to make (details used at the planning stage, e.g., movement direction) can be acquired visually based on observation. Here however, we address a new and fundamentally different question: can information specifying "how" to make movements at the level of motor execution (e.g., novel patterns of muscle forces) be conveyed through observation?

We used an experimental paradigm in which a robotic device generated novel force environments that perturbed the trajectory of the limb during reaching movements (Shadmehr and Mussa-Ivaldi, 1994). Our goal was to determine whether observing another individual undergoing the process of motor learning could affect the subsequent performance of naive observers. We show that neural representations of novel environments can be acquired visually on the basis of observation, and further experiments indicate that this process is not dependent on the use of conscious strategies but instead is based on the implicit engagement of motor systems. These findings broaden the scope of theories linking observation and action by demonstrating that by watching another individual learning to move, observers

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Figure 1. Experimental Setup and Design (A) Subjects sat grasping the end of the robotic device, which they used to guide an on-screen cursor to targets (see inset). (B) All subjects first performed 96 movements in a null field (no force field). In a first experiment, subjects were then randomly assigned to one of three groups who observed CWFF learning, CCWFF learning, or who observed nothing. All subjects were then tested in a CWFF. Subsequent control studies are described in Results.

can learn not only what movements to make, but how to make them as well.

Results

Effects of Observing Motor Learning

Subjects (n = 12) who observed a video depicting another person learning a clockwise (CW) force field (FF) (see Experimental Procedures and Figure 1) performed significantly better when later tested in the same CWFF than control subjects (n = 12) who did not observe but rested for an equivalent amount of time (12 min). Moreover, another group of subjects (n = 12) who observed learning of a counterclockwise (CCW) FF performed worse than subjects who did not observe learning. Figure 2B shows examples of typical movement trajectories of subjects in each group as they first encountered the CWFF. Movement trajectories of subjects who observed CWFF learning before encountering the CWFF themselves were less curved than those of control subjects and subjects who first observed CCWFF learning.

Figure 3 shows mean learning curves for control subjects and subjects who observed CW or CCWFF learning. Performance on each movement trial was estimated by computing a measure of movement curvature known as perpendicular distance (see Experimental Procedures). All three groups of subjects reduced trajectory curvature over time. When subjects who observed CWFF learning first encountered the CWFF themselves, their movements were characterized by an average of 23% less curvature than control subjects who observed nothing (Figure 3B). In contrast, when

subjects who observed CCWFF learning first encountered the CWFF, their movements were characterized by an average of 18% more curvature than controls. Thus, while all subjects learned the CWFF, performance was significantly affected by having observed another person learning CW or CCW force fields.

Observation had immediate effects on subsequent motor performance (see Figure 4A). Significant differences were observed among mean curvature averaged over the first eight movements (one to each target) in each experimental condition (p < 0.001). Curvature for subjects who observed CWFF learning was significantly less than for control subjects (p < 0.05) and for subjects who observed CCWFF learning (p < 0.01). Conversely, curvature for subjects who observed CCWFF learning was significantly greater than for controls who observed nothing (p < 0.05).

It should be noted that the force fields used here were velocity dependent; thus, the magnitude of perturbing forces generated by the robot varied directly with the speed of arm movement. To rule out the possibility that the observed differences in movement curvature were due to differences in the magnitude of perturbing forces (due to differences in movement speed), we examined hand tangential velocity in each experimental group. No significant differences in peak hand tangential velocity (and hence the magnitude of perturbing forces) were observed between the control, CWFF, and CCWFF observation groups (p > 0.05).

To assess potential differences in the temporal characteristics of movement as a result of observation, we computed four additional measures: time to peak curvature, time to peak difference in curvature (relative to



Figure 2. Hand Trajectories

(A) Typical hand trajectories for movements to the eight targets in a NF (purple dashes) and initial exposure in the CWFF (solid blue lines).

(B) Representative hand trajectories for movements to one target for subjects when first tested in a CWFF, after first observing nothing (blue), CWFF learning (green), or CCWFF learning (red).

(C) Lateral displacement (X) plotted against time for the example trajectories shown in (B).

(D) Lateral displacements (X) plotted relative to the trajectory for the control group (blue) who observed nothing prior to being tested in the CWFF.

(E) Tangential velocity of the hand plotted against time for the example trajectories shown in (B).

the no observation group), time to peak hand tangential velocity, and total movement time. MANOVA was used to test for effects of viewing condition. No significant effects of viewing condition were present for any of the four measures (p > 0.05 in all cases).

To rule out the possibility that subjects covertly moved their arm or activated arm muscles during observation, we conducted a control experiment in which we recorded muscle activation patterns first during 96 movements in a null field (NF) and then during passive observation of the video depicting 96 trials of CWFF learning. Surface electrodes were used to record muscle activation patterns from four shoulder and elbow muscles (see Experimental Procedures).

For recordings made while subjects performed movements in a NF, typical biphasic and triphasic patterns of agonist and antagonist muscle activity were seen in all four muscles and for all eight movement directions. Two-factor repeated measures MANOVA and Tukey post hoc tests were used to test for differences between mean EMG as a function of movement direction, across three time windows: a baseline, agonist, and antagonist window (see Experimental Procedures). Significant differences between mean EMG in baseline



Figure 3. Learning Curves

Mean learning curves for subjects when tested in a CWFF after first observing CWFF learning (green), CCWFF learning (red), or no observation (blue). (A) The curvature of hand trajectories is plotted against movement number. Each data point represents the average of eight movements. Vertical bars indicate 1 SEM. (B) Learning curves for the CWFF and CCWFF observation groups are plotted relative to the control group (horizontal dashed line at zero) and are expressed as a proportion of curvature for the first mean in the no observation group. Vertical bars indicate one SEM.

versus agonist and antagonist windows were seen in all eight movement directions for pectoralis and deltoid (p < 0.01) and in six out of eight movement directions for biceps and triceps (p < 0.01). The particular pattern of differences depended on movement direction (Hasan and Karst, 1989; Karst and Hasan, 1991). For recordings made during passive observation, no visibly detectable muscle activation patterns were seen for any subject during any point in the observation session. Nevertheless, to quantitatively test for the possibility of muscle activations, we again used MANOVA to test differences between baseline and agonist and baseline and antagonist EMG as a function of target direction. No significant differences were detected between baseline EMG and agonist or antagonist EMG for any muscle or any target direction (p > 0.05 in all cases).

It is possible that the effects of observing CW and CCWFF learning on subsequent performance may have been due in part to some nonspecific effect of observing curved hand motions rather than the observation of motor learning itself. To rule this out, we tested another





(A) Mean trajectory curvature averaged over the first eight movements in the CWFF for subjects who first observed CWFF learning (CW), CCWFF learning (CCW), or no observation (no OBS). Vertical bars indicate one SEM. *p < 0.05; **p < 0.01.

(B) Effect of observation expressed as the decrease in curvature relative to the control group who observed nothing for subjects who observed movements in a random FF (Random), for subjects who observed CWFF learning (CW), for subjects who observed CWFF learning while performing a distraction task (Distraction Task), and while performing rhythmic arm movements (Motor Engagement). Vertical bars indicate one SEM. *p < 0.05.

group of subjects (n = 12) who observed an individual attempting to learn a randomly varying FF. The FF presented by the robot was randomly varied from trial to trial between a CW, CCW, or null field. Thus, subjects who observed an individual attempting to learn the random FF were exposed to the same kinds of hand motions as in the original CW or CCW FF conditions, but did not observe the progressive and systematic decrease in movement curvature over time typically associated with motor learning. Figure 4B shows the performance of subjects who observed a random FF, averaged over the first eight trials when first exposed to the CWFF. Performance is plotted as the decrease in curvature relative to controls who observed nothing-thus, values near zero indicate little benefit of observation, while large values indicate a large benefit of observation (a large decrease in curvature). The decrease in curvature for subjects who observed the random FF was not significantly different than zero (p > 0.05). This indicates that performance in a CWFF was not influenced by the observation of a random FF. For comparison, the significant decrease in curvature as a result of observing CWFF learning is plotted on the same scale (p < 0.01).

Role of Conscious Strategies

We used a distractor paradigm to assess the extent to which the effect of observation on subsequent motor performance depends on conscious strategy formation. A separate group of subjects (n = 12) was asked to perform an arithmetic addition task while simultaneously observing learning of a CWFF. Beside each of the movement targets in the video depicting CWFF learning, a number between 1 and 8 appeared as the subject in the video began to move. The task for the observer was to add the current number to the number from the previous movement and verbally indicate the sum to the experimenter. Subjects were not required to monitor the speed of observed movements (unlike in the original experiment). Thus, the distractor task involved both an arithmetic operation and a load on working memory. The task was designed in such a way as to be easy enough to perform while still observing the motor learning depicted in the videos, but challenging enough that subjects required attention and cognitive effort to complete the task. This task is similar to those that frequently appear in the cognitive literature in divided-attention paradigms (Baddeley, 2003; Tulving and Craik, 2000). The proportion of errors during the arithmetic/memory task ranged across subjects to a maximum of 8.9% (mean = 2.1%, SD = 1.5%).

After observing CWFF learning and simultaneously performing the distractor task, subjects were exposed to the CWFF. Subjects in the distractor group showed the same benefit from observing CWFF learning as subjects in the original experiment. Figure 4B plots the decrease in curvature for the subjects in the distractor group relative to the control subjects who observed nothing, averaged over the first eight movements when first exposed to the CWFF. The decrease in curvature for the distractor group (expressed as a proportion of the curvature in the control group who did not observe anything, mean = $21.4\% \pm 4.9\%$) was not significantly different from that of the original group of subjects who observed CWFF learning (p > 0.05). Thus, the distraction task did not reduce the beneficial effect of observing CWFF learning on subsequent performance in a CWFF

To further assess the extent to which the effect of observing motor learning may have been due to the conscious formation of movement strategies, we interviewed subjects after the end of exposure to the CWFF. We asked subjects in the CW, CCW, and random observation groups the following question: "were the forces you felt when you were moving the robot the same as the forces that were shown in the video?" The number of correct responses (14 correct responses out of 36) was not significantly different than what would be expected if subjects were randomly guessing (χ^2 analysis, p > 0.05). Subjects were not aware of how the forces they experienced in the CWFF related to the forces depicted in the CW or CCWFF recordings. Thus, although motor performance of subjects in the CWFF was significantly affected by the observation of CW and CCWFF learning, this effect was not based on conscious strategies (e.g., "I should try to push to the left").

Role of Motor Systems

We used a paradigm involving the performance of unrelated arm movements to assess the extent to which the effect of observation is based on the activation of systems for motor control. A group of subjects (n = 12) was instructed to slowly move their arm in a circular motion while observing another person learning a CWFF. To eliminate any systematic bias due to the direction of circular motions, subjects were instructed by the experimenter to alternate movements between CW and CCW directions once, halfway through the observation session. After observation, subjects were tested in the CWFF. The beneficial effect of observing CWFF learning was significantly reduced for subjects in this "motor engagement" group. Figure 4B shows the mean reduction in curvature for the motor engagement group plotted beside the mean reduction in curvature for the original CWFF observation group and the attentional distraction group. For subjects who moved their arm while observing CWFF learning, the reduction in movement curvature when first exposed to the CWFF (mean reduction = $10.4\% \pm 4.6\%$) was significantly less than for subjects who did not move their arm (p < 0.05). The reduction in curvature was still significantly greater than zero (p < 0.05), indicating that although the magnitude of the beneficial effect was reduced, subjects still received some benefit from observing CWFF learning.

To control for the possibility that the observed decrease in performance in the CWFF may have resulted from factors related to moving one's arm in a circular pattern (e.g., fatigue or unintended motor learning), we tested an additional group (n = 12) who were asked to perform the same motions for 12 min prior to being tested in a CWFF. This group did not observe anything during these 12 min but only performed the circular arm movements. These subjects performed no differently when tested in the CWFF than controls who did not perform circular arm movements. Mean curvature during the first eight movements was not significantly different than for control subjects (p > 0.05). Thus, the performance of circular arm movements on its own had no effect on subsequent performance in a CWFF.

Discussion

Here we have shown that by observing another individual learning to move accurately in a novel mechanical environment, observers move more accurately themselves. Subjects can acquire neural representations of novel force environments on the basis of visual information. Further, while motor learning by observing does not depend on conscious awareness of the observer, the tendency for an unrelated movement task to significantly reduce the ability of subjects to learn by observing indicates that the implicit engagement of motor systems is required.

Other work has shown that information used in planning movement can be acquired via observation. These studies have demonstrated that kinematic (spatio-temporal) information specifying figural aspects of movement (e.g., "what" movements to make) can be conveyed visually (Heyes and Foster, 2002; Kelly et al., 2003; Vinter and Perruchet, 2002). The present results are quite different and represent experimental evidence that observers can extract information used at the level of motor execution (e.g., "how" to make movements) on the basis of observation. By observing another individual learning to move accurately in a novel force environment, the observer was able to form a neural representation of the environment's mechanical properties, which was subsequently put to use in controlling movements in the CWFF.

Performance in the CWFF varied depending on what subjects had previously observed. Observation of a CWFF facilitated later performance in the same CWFF, while observation of a CCWFF disrupted performance in the CWFF. These findings are consistent with the idea that, as a result of observation, subjects were able to predict the influence of the observed FF on the arm. Acquired representations of the FFs, rather than nonspecific strategies (e.g., muscle co-contraction) governed movement.

The finding that subjects can learn something useful about novel force environments on the basis of observation is remarkable, given the complex relationship between movement kinematics and associated timevarying neural control signals to muscles. As a subject observes another person moving in a novel force environment (e.g., a CWFF), the only information directly available to the observer is visual in nature and specifies kinematic aspects of movement. In order for an observer to learn something about a novel mechanical environment, the nervous system must first assume that any deviations from a typical straight-line hand trajectory (Morasso, 1981) represent movement errors. On the basis of these errors, the motor system must then construct a representation of the perturbing forces that resulted in the observed hand trajectory. This would require an implicit model of the mechanical characteristics (e.g., stiffness) of the limb and its predicted response to external forces. Finally, in order to benefit from this learning, the motor system must determine the changes in neural control signals to muscles that would be required in order to oppose the predicted perturbing forces. Information about movement kinematics, acquired from visual information alone, must be transformed into a representation of forces and subsequently the required changes to neural control signals for movement. It is likely that the neural bases of motor learning by observing share the same substrates that have been described for sensorimotor transformations in overt voluntary movement (Cohen and Andersen, 2002; Kakei et al., 2003; Kalaska et al., 1997; Snyder, 2000).

We used a distraction task to determine the role of explicit, conscious strategies in motor learning by observing. Our findings indicate that observers can benefit from observation even when attentional systems are engaged by a distractor task, suggesting that these systems are not critical for motor learning by observing. While it could be argued that attentional or cognitive systems are indeed involved and that our distraction task simply failed to engage these systems to an adequate extent, this seems unlikely. Our subjects committed errors on the distraction task (see Results), indicat-

ing that it was challenging and required effort to complete. Error rates indicated that subjects were not ignoring the distraction task and simply attending to the motor aspects of the video recording. Another possibility is that, as an arithmetic task, the distractor only engaged mathematical and working memory systems, leaving other attentional mechanisms free to form conscious, explicit strategies. We interviewed subjects following testing in the CWFF to determine whether they used strategies during observation. Subjects could not correctly identify whether the FF observed was the same or different than the FF experienced (see Results), suggesting that subjects did not use explicit strategies to guide their performance. This lack of a dependence on explicit strategies has an intriguing implication, namely that motor learning by observing may occur unbeknownst to the subject.

In contrast, motor learning by observing was compromised when the motor system was engaged with an unrelated movement task. The beneficial effect of observing motor learning was reduced in subjects who performed rhythmic arm movements during observation (see Results). This suggests that motor systems are involved in acquiring neural representations of novel environments during observation. Recent findings indicate that observation of movement activates motor areas involved in producing the same movement (see Rizzolatti et al., 2001, for review). Our results suggest that the ability of visual information to drive motor learning through systems linking observation and action is significantly diminished when motor systems are occupied by the generation of unrelated movements.

It should be noted that not all observed motor behavior leads to motor learning in observers. We have shown here that observing an individual experiencing a randomly varying mechanical environment does not affect the subsequent performance of observers. For motor learning by observing to occur, the observer must presumably be exposed to systematic movement errors so that a representation of perturbing forces may be developed. Indeed, recent work has shown that motor cortical areas are activated when subjects observe movement error (van Schie et al., 2004). Presumably, observing the actions of skilled individuals (after learning has already occurred) would not lead to motor learning in the observer.

It is important to consider what specific information may be required for motor learning by observing. Presumably, consistent information about the nature of perturbing forces is required. In the present study, subjects observing CWFF and CCWFF learning were exposed to consistent CW or CCW movement errors that gradually decreased over time. Whether motor learning by observing depends on exposure to a gradual decrease in movement error over time cannot be addressed in the present study. However, it seems likely that observers would still benefit from exposure to systematic movement errors that do not decrease over time.

While performance in the CWFF clearly benefited from the prior observation of CWFF learning, subjects in the present study were not able to fully learn how to move accurately in the CWFF solely from observation. Additional experience performing movements in the CWFF was required to further reduce movement curvature. Nevertheless, considerable changes in performance were seen as a result of observation. Subjects who observed CWFF learning gained a significant advantage over control subjects who did not. Similarly, subjects who observed CCWFF learning experienced a significant and longer-lasting disadvantage compared to control subjects.

In summary, we have shown that motor learning occurs in the absence of overt movement by observing the actions of others. The human motor system incorporates the experiences of others in building the motor repertoire of the individual.

Experimental Procedures

Subjects

84 subjects (mean age 21.02 \pm 0.39 SE, 40 males) participated in the experiments described here. All subjects provided informed consent to procedures that complied with guidelines set out by the University of Western Ontario's Research Ethics Board. All subjects were right-hand dominant for writing, had normal or corrected vision and reported no neurological or musculo-skeletal impairments.

Robotic Device

Subjects used the InMotion2 robotic device (Interactive Motion Technologies) to guide an on-screen cursor to a series of visual targets presented using a system of mirrors and an LCD projector (see Figure 1A). Subjects sat in front of a custom-designed tabletop surface with their right arm supported by a padded air-sled, which was connected to a compressed air source to provide virtually frictionless motion and supported the arm against gravity. The level of the chair was adjusted so that the shoulder was abducted 90° from the sagittal plane.

Visual targets were presented to the subject using a semi-silvered mirror placed between the arm and a back-projection screen (see Figure 1A). Targets thus appeared to "float" in the same plane as the hand. A total of 8 movement targets were used, placed equally around the circumference of a circle. Targets were 24 mm in diameter and were located 10 cm away from a central start location (see Figure 1). Subjects were instructed to move quickly and accurately to targets in a single continuous motion. Movement speed was controlled by providing subjects with feedback on a trial-totrial basis. The color of the target changed to blue (correct speed), green (too slow) or red (too fast) according to the measured movement speed on each trial. Desired movement duration was 375 ms.

The robot was programmed to alter the dynamics of limb motion by applying forces ("force fields", FF) to a subject's arm during reaching movements to targets. Forces were velocity dependent and were applied in a clockwise (CW) or counterclockwise (CCW) direction according to the following equation:

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = \begin{bmatrix} 0 & dk \\ -dk & 0 \end{bmatrix} \begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix}$$
(1)

where F_x and F_y are robot-generated forces in the left/right and forward/backward direction, respectively, \dot{x} and \dot{y} are hand velocities, k = 20 Ns/m, and d = +1.0 (CW) or -1.0 (CCW). Thus, forces applied by the robot were zero at movement start and movement end and reached a maximum at peak hand tangential velocity. Across subjects, the mean peak force applied to the arm was 4.9 N (SD = 0.9 N).

Robot forces were controlled using custom software routines written in C and Tcl programming languages and run within the RT Linux operating system on a Pentium 4 CPU. Robot positions, velocities, and applied forces were sampled at 200 Hz and stored on a digital computer for offline analysis.

Video Recordings

Video recordings provided subjects with a top-down view of another individual's right arm and the workspace within which movements to targets were made. Superimposed on the image of the arm were the visual targets and a cursor representing the position of the hand (see Figure 1B). Recordings were made using a digital video camera and were edited using Final Cut Pro 4 software (Apple Computer). Each recording was approximately 6 min in duration and demonstrated a series of 96 movements. Subjects were shown the appropriate video twice.

The recordings depicted an individual moving to targets as the robot applied perturbing forces to the arm. In the CWFF recording, forces were the same as those later experienced by the observer; in the CCWFF recording, the forces were applied in the opposite direction. These recordings showed the progression from highly perturbed to straight movements typically associated with motor learning (e.g., Figure 3A).

The random FF recording showed an individual interacting with the robotic device as it generated randomly varying perturbing forces. Subjects of course were not able to learn such an environment (Takahashi et al., 2001). Thus, the video demonstrated motions that were similar to those in the CW and CCWFF recordings but which lacked the progression from perturbed to straight movements associated with motor learning.

In the video used in the distraction condition, a digit from 1 through 8 was superimposed onto the CWFF recording at each target location. Subjects were asked to sum the digits indicated by successive movements (current + previous) and to indicate the result verbally to the experimenter.

Instructions to Subjects

Subjects were asked to use the robotic device to guide a cursor to targets. Following their initial familiarization with the task (96 movements with no forces applied, see Figure 1B), subjects were asked to observe a video recording of another individual performing a similar task. No mention was made of the CW, CCW, or random FFs depicted in the recordings. To ensure that subjects paid attention to the video recordings, we asked them to monitor the depicted movements and report to the experimenter when movements made by the subject in the video were too fast or slow (this was indicated by the targets changing color). Subjects were highly accurate in this regard (mean score > 98% correct). During observation, subjects were instructed to let go of the robot handle and to rest their arm on the tabletop surface. Following observation, subjects were again asked to guide the cursor to targets. Subjects were not warned that the robot would apply a CWFF. At the completion of the experiment, subjects were questioned with respect to their awareness of the FFs observed and experienced.

EMG Recordings

Electromyographic signals (EMG) were recorded from biceps long head, triceps lateral head, pectoralis clavicular head, and posterior deltoid using surface electrodes (Delsys). Signals were sampled at 1000 Hz, band-pass filtered between 30-300 Hz, and rectified prior to analysis. Mean EMG was computed during three windows timealigned to movement onset in the NF movements and time-aligned to the onset of each movement in the video depicting CWFF learning. An initial 200 ms baseline window beginning 300 ms prior to movement onset was used to characterize baseline levels of EMG. An agonist window beginning 100 ms prior to movement onset and ending 100 ms after movement onset was used to characterize phasic agonist muscle activation associated with movement acceleration. An antagonist window beginning 150 ms after movement onset and lasting 200 ms was used to characterize antagonist muscle activity associated with movement deceleration. Five subjects were tested in the control study.

Measures and Statistics

Performance on each movement trial when subjects were tested in the CWFF was quantified using a measure of movement curvature defined as the maximum perpendicular deviation from a line segment linking movement start position and the target's location (Malfait et al., 2002; Shadmehr and Brashers-Krug, 1997; Thoroughman and Shadmehr, 1999). Other similar measures such as angular error and path length yielded qualitatively similar results. Individual scores were collapsed across bins of eight movements, and differences between group means were tested using multivariate analyses of variance (MANOVAs) and Tukey post hoc tests. Data analyses were carried out using custom software routines written using Matlab (The Mathworks).

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