State dependence of adaptation of force output following movement observation

Paul A. Wanda, Gang Li, and Kurt A. Thoroughman
Department of Biomedical Engineering, Washington University in Saint Louis, Saint Louis, Missouri

Submitted 27 April 2012; accepted in final form 6 June 2013

Wanda PA, Li G, Thoroughman KA. State dependence of adaptation of force output following movement observation. J Neurophysiol 110: 1246–1256, 2013. First published June 12, 2013; doi:10.1152/jn.00353.2012.—Humans readily learn to move through direct physical practice and by watching the movements of others. Some researchers have proposed that action observation can inform subsequent changes in control through the acquisition of a neural representation of the novel dynamics, but to date learning following observation has been described by kinematic metrics. Here we designed an experiment to consider the specificity of adaptation to novel dynamic perturbations at the level of force generation. We measured changes in temporal patterns of force output following either the performance or observation of movements perturbed by either position- or velocity-dependent dynamic environments to 1) establish whether previously described observational motor learning effects were attributable to changes in predictive limb control and 2) determine whether such adaptation reflected a learned dependence on limb states appropriate to the haptic environment. We found that subjects who observed perturbed movements produced significant compensatory changes in their lateral force output, despite never directly experiencing force perturbations firsthand while performing the motor task. The time series of observers’ adapted force outputs suggested that the state dependence of observed dynamics shapes adaptation. We conclude that the brain can transform observation of kinematics into state-dependent adaptation of reach dynamics.

motor control; force channels; action observation; human motor adaptation; haptic environments

PEOPLE CAN LEARN new motor skills through physical practice and by observing the movements of others. As our bodies fatigue, age, or suffer injury and as we interact with a changing environment, the dynamics of movement are altered and, as a result, constant motor adaptation is necessary to maintain performance. During physical practice of volitional movement, this adaptation is informed by sensory feedback, including vision and proprioception, and the predicted sensory outcomes inferred from neural motor commands (Shadmehr et al. 2010).

When observing the movements of others, people lack this full range of sensory feedback and neural activity associated with generating one’s own movement; any adaptive processes must be informed through vision alone. While visual information informs higher-level concepts that affect motor planning and goal selection, movement observation has been shown to induce formation of motor memories that bias evoked force outputs toward replicating the kinematics of the observed actions (Stefan et al. 2005) or aid in moving in novel environment dynamics (Mattar and Gribble 2005). Mattar and Gribble (2005) found that naive observers who watched another person performing a series of point-to-point reaching movements in an unknown dynamic environment performed better (or worse) than nonobserving control subjects when later experiencing and adapting to the same (or opposite) dynamic environment themselves. While subsequent studies replicated and expanded upon this effect (Brown et al. 2009, 2010), these studies queried learning by measuring changes in kinematic performance during exposure to dynamic perturbations, leaving unclear whether learning by observing builds knowledge of kinematics or dynamics.

In studies of motor control and learning, researchers have examined the adaptation of point-to-point reaching movements to various external loads including robot-generated force field environments. Initially, the unlearned dynamics of these novel body-object interactions cause movement errors. The neural representations of body and environment dynamics may be described as internal models (Kawato 1999), a flexible sensorimotor map. During physical practice, new mappings accounting for the novel external loads are learned, and movements become increasingly accurate (Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi 1994) as people incrementally modify their temporal patterns of muscular activation (Thoroughman and Shadmehr 1999) to compensate for the novel limb dynamics imposed by the environment. Through the careful design of psychophysical studies and models of learning, some have suggested that the acquisition and modification of internal models takes place through the training of a network of motor primitives whose activity depends on kinematic signals such as position and velocity (Sing et al. 2009; Thoroughman and Shadmehr 2000). Although adaptation has been typically quantified by kinematic performance metrics (Donchin et al. 2003; Hwang et al. 2003; Thoroughman and Taylor 2005), such as displacement errors during training or aftereffects during perturbation-absent washout periods or individual “catch” trials, kinematic metrics reveal the outcome of haptic learning rather than directly assaying the forces people generate.

Another assay, the force channel, or error clamp (Scheidt et al. 2000), directly reads out generated lateral forces and allows researchers to measure predictive force output (Hwang et al. 2006a; Sing et al. 2009; Smith et al. 2006; Wagner and Smith 2008; Wei et al. 2010). Sing et al. (2009) measured subjects’ force output when adapting to various state-dependent force field environments and found that force production progressed from an initial stereotyped joint dependence on kinematic limb states, such as position and velocity, to a stronger dependence on the perturbation-relevant limb state (i.e., velocity when adapting to a viscous force field) during training.
Here we asked whether previously described learning effects of prolonged movement observation (Mattar and Gribble 2005) could be attributed, at least in part, to changes in predictive generation of forces. We were especially motivated to determine whether visually sensed, kinematic information from observation was truly transformed into an adaptation of dynamic force output, which previous studies were not capable of showing. We designed an experimental paradigm that not only allowed us to evaluate the direction and magnitude of adaptation following observation but allowed us to consider the temporal pattern, or shape, of force output, by using force channel movements to probe adaptation as changes in lateral force output. By training subjects in either position-dependent or velocity-dependent force fields, we further tested whether changes in the temporal pattern of lateral forces differentially reflected the novel state-force mapping of the observed force field, as typically seen after physical practice.

MATERIALS AND METHODS

A total of 50 neurologically normal, right-handed human volunteers (20 men, 30 women), aged 18–38 yr, were recruited from the Washington University in St. Louis community to participate in a 1-h, single-day study. Subject handedness was evaluated with the Edinburgh inventory (Oldfield 1971). The experimental protocol was approved by the Washington University Hilltop Human Studies Committee. All subjects gave informed consent.

All subjects were trained to perform horizontal-plane reaching movements while holding the handle of a planar five-bar, two-link robotic manipulandum (Interactive Motion Technologies, Cambridge, MA) capable of generating torques at each joint. Customized software acquired data from position encoders and tachometers on the manipulandum and generated commands at a rate of 1 kHz. An illustration of the setup is provided in Fig. 1. An overhead LCD projector generated visual feedback, including the cursor, start location, and targets, during the reaching task and displayed movies for movement observation. The projected images were reflected and projected into the plane of reaching via a half-silvered mirror located above the reach workspace. Subjects were seated upright with their upper right arm supported by a sling such that their elbow flexed 90° with the hand holding the manipulandum handle at the start location. A lamp mounted below the mirror was on during active reaching, allowing subjects vision of their arm, but was off during observation.

Movement Task

Throughout the entirety of the task, subjects maintained their grip on the handle of the manipulandum. A yellow circular cursor indicated the veridical location of the manipulandum handle and the subject’s hand in the task workspace. Movement start location was indicated by a white-outlined circle fixed at the origin of a rectangular coordinate system centered over the workspace. Subjects waited with their hand at the start location until a circular target appeared at one of eight possible locations, evenly distributed on the circle 10 cm about the start location. Subjects were trained to move and stop on the target in the correct time to turn it green. To perform a successful reaching movement, subjects were required to stop on the target 750 ± 50 ms after initiating the movement. The target color changed to provide timing feedback: green, successful; red, early; blue, late. After completion of each movement, the manipulandum returned the handle and the subject’s hand and arm back to the starting location and posture.

Fig. 1. Apparatus, observation movie, and force channel. A: illustration of the experimental apparatus. Subjects were trained to grip the handle of a robotic manipulandum and perform reaching movements. Visual task feedback was displayed in the plane of reaching via an overhead projector and mirrors. B: still frame taken from a movie shown to Observation group subjects during the Learning block, showing an actor’s arm performing a reaching movement with visual feedback overlaid. C: illustration of force channel movement. The robotic manipulandum generated forces to cancel lateral forces produced by the subject, restricting the cursor along a straight-line path from the start location to the target location.
**Force Channel Trials**

During a force channel trial, subjects performed a reaching movement to the target as the robotic manipulandum implemented real-time forces on the handle as a stiff spring-damper system,

\[ F_l = -Kx_l - Bx_l \]  

where \( x_l \) and \( \dot{x}_l \) denoted the real-time position and velocity components of handle movement perpendicular to a straight-line vector pointing from the start location to the target location, with spring constant \( K = 6,000 \text{ N/m} \) and a damping constant \( B = 150 \text{ Ns/m} \) (Eq. 1). The time series of robot-generated clamp forces reflected a mirror image of the subjects’ predictive lateral force output. The forces reduced to millimeters the lateral deviation of the manipulandum handle from a straight-line trajectory from start location to the target.

**Learning block.** Movement group subjects performed 192 reaching movements in the presence of either a viscous (\( V_{\text{MOV}} \) group) or a stiff (\( S_{\text{MOV}} \) group) curl field, with forces \( F_x \) and \( F_y \),

\[
\begin{bmatrix}
F_x \\
F_y \\
\end{bmatrix} = 
K
\begin{bmatrix}
x \\
y \\
\end{bmatrix} 
+ 
B
\begin{bmatrix}
0 & 1 \\
-1 & 0 \\
\end{bmatrix}
\begin{bmatrix}
x \\
y \\
\end{bmatrix}
\]

(2)

where \( x \) and \( y \) were the current Cartesian hand position and \( \dot{x} \) and \( \dot{y} \) were the current Cartesian hand velocity and the origin of the Cartesian plane lay at the central start location. When exposed to the state-dependent force field, subjects need to produce compensatory forces that mirror the manipulandum-generated forces to move in a straight-line fashion. For the \( V_{\text{MOV}} \) group, the viscous gain \( B = 21 \text{ Ns/m} \) while the stiff gain \( K = \) 0 N/m for all perturbation trials; for the \( S_{\text{MOV}} \) group, \( K = 45 \text{ N/m} \) and \( B = 0 \text{ Ns/m} \). The viscous and stiff gains were selected to produce similar peak forces (~4.5 N) for typical movements made in each force field. All subjects were given a 3-min break from the movement task after the first 96 movements and then performed another 96 movements in the same force field condition.

During the Learning block, observation group subjects did not perform reaching movements. Instead, they watched a movie of a naive actor performing 192 reaching movements with the viscous (\( V_{\text{OBS}} \) group) or stiff (\( S_{\text{OBS}} \) group) curl field conditions described above, respectively, with a 3-min break after watching the first 96 movements. During observation, subjects were instructed to remain motionless, holding the handle at the start location. They were not informed of the content of the movie and only instructed to watch it. The movie they watched was a combination of 1) a movie showing a birds-eye view of an actor’s right arm and hand holding the manipulandum and performing reaching movements and 2) a movie showing the actor’s hand cursor, start location, and target locations. The combined movie shown during observation was created with Adobe Premier Pro v7.0 software (Adobe Systems) by cropping, scaling, and overlaying the movies to closely match the typical visual feedback experience of a reaching movement trial.

**Testing block.** After the last trial of the Learning block, all groups of subjects immediately transitioned to the Testing block with no break and performed 24 force channel movement trials, 1 to each target location, pseudorandomly ordered within each bin of 8 trials.

The blocked experiment design of the present study was largely inspired by Mattar and Gribble (2005), with the intent of replicating their reported learning effect for the \( V_{\text{OBS}} \) group. However, this implementation does differ from their design in a key aspect in the Learning block. Subjects in the present study observed another person progressing from naive to experienced in the force field over the course of 192 reaching movements, with a break midway during observation, while in Mattar and Gribble (2005) observers twice watched the first 96 movements of a naive learner training in the force field. We altered this feature so that our movement and observation groups experienced parallel training; we cannot restart naive direct action training after 96 movements. Aside from this difference, the protocol experienced by the \( V_{\text{OBS}} \) group largely mimicked the conditions used for the viscous force field observation groups in the primary experimental results reported by Mattar and Gribble (2005).

**Observation Movie Actors**

Two observation movie actors [Viscous Observation actor (\( V_{\text{ACTOR}} \)), female, age 21; Stiff Observation actor (\( S_{\text{ACTOR}} \)), female, age 21] had no previous training on the motor task prior to the experiment and experienced the same task design as their respective Movement group. Actors were aware that their movements were being visually recorded by an overhead camera. Because of the constraints of using an overhead camera, these actors performed the task with visual feedback provided via a vertically mounted computer screen and peripheral vision of the arm unobstructed. Except for this difference in feedback...
presentation, each actor performed the same task as their respective Movement group subjects.

**Experiment 2**

After analysis of experiment 1, we recruited additional subjects for a second Stiff Observation group (S\textsubscript{Obs2}, n = 10). These subjects experienced a modified Learning block but otherwise identical experimental design as described for experiment 1. As previously noted, the design for experiment 1 deviated from that of Mattar and Gribble (2005), as subjects watched movies covering 192 movements instead of twice observing the same sequence of 96 movements. Here we hypothesized that by twice showing subjects movements depicted early and later training in the stiff force field, we might enhance the learning effect. Instead of observing the full course of training over 192 reaching movements as the original S\textsubscript{Obs} group, the S\textsubscript{Obs2} group twice watched the first 96 reaching movements of the stiff force field movie, with a 3-min break between viewings.

**Analyses**

To facilitate analyses across trials and subjects, we aligned all kinematic and force channel time series at peak speed. Force output was measured as the sign-flipped time series of lateral forces generated by the robot during force channel trials. Adaptation of force output (adapted lateral force profiles) was quantified as the change in lateral forces measured during the Testing block from the lateral forces measured during the Baseline block, averaged across 8-movement bins (1 movement to each target). By averaging across trials, we measured the overall adaptive effects of the Learning block and reduced the effect of trial-to-trial variability and noise. We calculated an adaptation metric for each subject by integrating the adapted lateral force profiles across time. For each subject, we modeled the degree to which their adapted lateral force output exhibited dependence on movement state by fitting the adapted lateral force profiles as a linear combination of weighted position and velocity signals (Sing et al. 2009),

\[ \hat{F}_L = \hat{K}_{xL} + \hat{B}_{\dot{x}L} \]  

where \( \hat{F}_L \) is the modeled time series of lateral forces, \( \hat{K} \) and \( \hat{B} \) are the modeled stiff and viscous gains, and \( x_L \) and \( \dot{x}_L \) are the parallel components of the Cartesian position and velocity signals. Although the implicit target duration was 750 ms, to include all data from all movements we centered kinematic and force output traces at peak hand speed and then included data 500 ms before and after the time of the peak.

To better express the magnitude of state-dependent adaptation, we normalized the modeled viscous and stiff gain parameters by dividing by the actual viscous gains \( B \) and \( K \) to yield the learned velocity dependence (\( \hat{B}/B \)) metric and learned position dependence (\( \hat{K}/K \)) metrics, respectively. A unity value would reflect a fully learned state, while a value of zero would reflect no learned state dependence. Model goodness of fit was measured with the variance accounted for (\( vaf \)) metric,

\[ vaf = 1 - \frac{\text{var(residual)}}{\text{var(data)}} \]

All analyses were performed with MATLAB (MathWorks, Natick, MA).

**RESULTS**

**Kinematic Performance During Adaptation**

To verify that the hand trajectories viewed by Observation group subjects were representative of the positional hand trajectories generated by Movement group subjects, we compared the mean performance of the Movement group subjects and their respective actor shown in the observation movies. We calculated average full time course positional trajectories from reaching movements in the Learning block in 8-movement bins, for the Viscous Movement (VM\textsubscript{MOV}) and Stiff Movement (SM\textsubscript{MOV}) group means and the V\textsubscript{ACTOR} and S\textsubscript{ACTOR} movie actors. The average trajectory of movie actor movements shown in the observation movies qualitatively mimicked the mean trajectories of the Movement group subjects (Fig. 3).

We further examined the evolution of movement error, as quantified by perpendicular displacement (p.d.) at peak speed (Fig. 3C). We found no significant difference between the Viscous Movement group and the Viscous actor in movement error over the first six bins (unbalanced 2-way ANOVA, \( P > 0.5, F_{1.5} = 0.28 \)) and between the Stiff Movement group and the Stiff actor (unbalanced 2-way ANOVA, \( P > 0.8, F_{1.5} = 0.02 \)). We did find that the average p.d. at peak speed in the first movement bin was larger in magnitude for the Viscous Movement group than the Stiff Movement group (1-tailed, unpaired 2-sample t-test, \( P < 0.001 \)).

**Experiment 1: Viscous Movement and Viscous Observation Groups**

To establish a baseline level of force output, subjects reached to each target in force channels in the Baseline block, interspersed with null force field movements. We generated adapted lateral force profiles as the difference in lateral forces measured in force channels in the Testing block from baseline performance. As a metric of adaptation, we quantified the overall direction and magnitude of adaptation by integrating over the time series of adapted lateral forces, i.e., the area under the curve. Recall that the force fields were designed to push clockwise with respect to the subject’s direction of movement (Eq. 2). By convention, a positive integrated force indicated that the subject generally pushed more counterclockwise with respect to the target, compensatory for the force field, and a negative integrated lateral force clockwise, or in the same direction as the force field.

We found that after physical practice the VM\textsubscript{MOV} group subjects, who directly experienced the viscous force field, adapted their lateral force output to oppose the direction of the experienced or observed force field (Fig. 4A; integrated force mean with 95% confidence interval = 1.37 ± 0.18 Ns), with the adaptation metric significantly greater than zero (1-tailed t-test; \( P < 0.001 \)). The VO\textsubscript{Obs} group subjects, who observed the actor’s movements in the same viscous force field, had a smaller, but also significant, compensatory change in their lateral force output (Fig. 4B; 0.10 ± 0.05 Ns; 1-tailed t-test: \( P = 0.003 \)). Although differing in overall magnitude of the adaptive response (\( P < 0.001 \)), the temporal profiles, or shapes, of both the VM\textsubscript{MOV} and VO\textsubscript{Obs} responses were strikingly similar and reminiscent of a bell-shaped velocity profile.

The force field experienced by the VM\textsubscript{MOV} group subjects and the V\textsubscript{ACTOR} actor, whose movements were observed by the VO\textsubscript{Obs} group subjects, was viscous, or velocity dependent. Thus any learned dependence of the adapted force output on velocity would reflect stimulus-appropriate learning of the force field’s novel velocity-force mapping. Conversely, any dependence on position signals would indicate stimulus-inappropriate learn-
Experiment 1: Stiff Movement and Observation Groups

While both groups who were exposed to the viscous force field, either directly (VMOV) or visually (VOBS), adapted in a stimulus-appropriate, seemingly state-dependent manner, we did not find this to be the case for the first stiff force field observation group (S_OBS). Replicating the previously described analyses, we considered how subjects adapted to the stiff, or position-dependent, force field. We found that Stiff Movement (SMOV) group subjects also strongly compensated for the position-dependent curl field and their adapted lateral force profiles reflected learning of the novel position-force mapping (Fig. 5A). Calculating the adaptation (integrated force) metric for each subject, we found that the SMOV group subjects adapted with a significant compensatory response (mean ± 95% CI) of 2.16 ± 0.23 Ns (1-tailed t-test: P < 0.001). Fitting the state-dependent model to the adapted lateral force output for each subject, we found that the SMOV group subjects had a strong and significant dependence on positional signals and a much weaker, though significant, dependence on velocity signals: the mean model parameters with 95% confidence intervals were \( \hat{K} = 41.06 \pm 6.56 \) and \( \hat{B} = 1.55 \pm 0.53 \), corresponding to a stimulus-appropriate mean learned position dependence \((\hat{K}/\hat{K}^*)\) of 0.912 and stim-

Fig. 3. Hand trajectories averaged over 8-trial bins in the Learning block. For each force field type, the mean Movement group performance is compared to the respective actor performance viewed by Observation group subjects. Here, the first bin of movements (bin 1; 1–8, solid), the second bin (bin 2: 9–16, dashed), and the midtraining bin (bin 12; 89–96, dotted) are averaged and plotted. Mean kinematics were similar for each force field type. A: Viscous Movement (VMOV) group and the Viscous Observation actor (VACTOR). B: Stiff Movement (SMOV) group and the Stiff Observation actor (SACTOR). C: movement error across 8-trial bins. For the VMOV group subjects, movement error was quantified by the mean perpendicular displacement at peak speed for bins 1–12 [mean ± 95% confidence interval (CI)].

To consider the degree to which adapted lateral force outputs reflected state-dependent dynamics, we regressed the time series of adapted lateral force outputs, averaged over the first eight Testing block trials, on the averaged position and velocity time series (Eq. 3). As expected, the VMOV group subjects adapted their lateral force outputs with a strong stimulus-appropriate velocity dependence and negligible stimulus-dependent position dependence. The mean model parameters with 95% confidence intervals across subjects were \( \hat{K} = -0.52 \pm 1.86 \) and \( \hat{B} = 13.76 \pm 1.31 \). We normalized the mean velocity-dependent model parameter \( \hat{B} \) by the actual force field gain \( \hat{B} = 21 \) Ns/m, calculating a mean stimulus-appropriate learned velocity dependence \((\hat{B}/\hat{B})\) of 0.665 (Fig. 4C). Although the force field was not position dependent, we also normalized the mean model parameter \( \hat{K} \) by the “equivalent” stiffness gain of \( \hat{K}^* = 45 \) N/m to calculate an equivalent mean learned position dependence \((\hat{K}/\hat{K}^*)\) of \(-0.012\); recall that the VMOV group subjects did not experience position-dependent forces. Goodness of fit across subjects was measured as variance accounted for or \( vaf \) (w/95% CI) of 0.91 ± 0.02. When fitting the model to the VMOV group subject average data, the \( vaf \) was 0.93. We additionally calculated the contributions of each state-dependent parameter to the overall fit, finding a partial position \( vaf < 0.01 \) and a partial velocity \( vaf \) of 0.93, demonstrating that the velocity-dependent component of the model largely contributed to the overall quality of the fit.

Applying the same analysis to the VOBS group subjects, we found that their adapted lateral force outputs also had a significant velocity dependence and negligible position dependence, with mean model stiffness and viscosity parameters across subjects of \( \hat{K} = -0.95 \pm 1.03 \) and \( \hat{B} = 1.35 \pm 0.64 \). Goodness of fit \((\hat{vaf})\) across subjects was 0.30 ± 0.13. For the VOBS group subjects, we calculated a mean learned velocity dependence \((\hat{B}/\hat{B})\) of 0.064 (Fig. 4D), which was \(-9.6\%\) of the mean velocity dependence for the VMOV group subjects. The equivalent mean learned position dependence \((\hat{K}/\hat{K}^*)\) was \(-0.021\). Fitting the model to average data across all VOBS group subjects, the model fit \((\hat{vaf})\) was 0.71. As before, we calculated the contributions of each state-dependent parameter to the overall fit, finding a partial position \( vaf \) of 0.09 and a partial velocity \( vaf \) of 0.57, again finding that the velocity-dependent component of the model largely explained the quality of fit.
The inappropriately equivalent mean learned velocity dependence \( \frac{\hat{K}}{K} \) of 0.074 (Fig. 5C). Goodness of fit \( (vaf) \) across subjects was 0.97 ± 0.01. Again fitting the model to the average data, we calculated a \( vaf \) of 0.99, a partial position \( vaf \) of 0.99, and a partial velocity \( vaf \) of 0.02, finding that the position-dependent component largely contributed to the overall fit. Overall, our analysis for the SMOV group subjects found a strongly stimulus-appropriate, position-dependent adaptation of force output, as expected.

Unlike the other three groups, the Stiff Observation (S OBS) group subjects did not significantly adapt to compensate for the observed force field (Fig. 5B), with integrated force metric of 0.01 ± 0.13 Ns (2-tailed \( t \)-test: \( P = 0.874 \)). Applying the state-dependent model to force outputs of each subject within the \( S_{OBS} \) group, the stiff and viscous parameters (mean ± 95% CIM) were \( \hat{K} = -0.15 \pm 1.88 \) (mean \( \hat{K}/K \) of -0.003) and \( \hat{B} = 0.35 \pm 0.65 \) (mean \( \hat{B}/B^* \) of 0.017) (Fig. 5D), with \( vaf \) across subjects of 0.25 ± 0.12. Although the model accounted for some variance in the force trace within subjects, the high variability of the stiff and viscous parameter values indicated a lack of consistency across subjects. When fitting the model to average data across all group subjects, the goodness of fit was 0.24, with a partial position \( vaf \) of -0.03 and a partial velocity \( vaf \) of 0.27, exhibiting negligible dependence on stimulus-appropriate positional signals.

**Experiment 2: Modified Stiff Force Field Observation Protocol (S OBS,2) Group**

We designed experiment 1 so that action and observation subjects experienced parallel training (Fig. 2). This protocol, however, deviated from foundational work (Mattar and Gribble 2005) within which observational subjects watched two cycles of 96 movements of training. We saw no consistency in the adapted force outputs and state dependence in the \( S_{OBS} \) group of experiment 1, so we designed experiment 2 to replicate more directly the foundational work that provided double exposure to erroneous and learned behavior.

---

**Fig. 4.** Adapted force output for viscous force field groups and model fits. A and B: adapted lateral force profiles with shaded 95% CIs across subjects, with state-dependent model fits overlaid. Adapted profiles are calculated as the difference between the Testing block profile and the Baseline block profile, averaged over the first 8 force channel movements of the Testing block (1 to each target). The \( V_{MOV} \) group (A) and Viscous Observation \( (V_{OBS}) \) group (B) mean profiles both showed significant changes from baseline. B, inset: single trial force trace (gray) and mean force trace (black) for an individual \( V_{OBS} \) subject (subject 3). Subject had normalized parameter values of 0.01 \( (\hat{K}/K^*) \) and 0.10 \( (\hat{B}/B) \). C and D: respective bar plots show the normalized mean model state-dependent parameter values with 95% CI across subjects (C, \( V_{MOV}, n = 10; \) D, \( V_{OBS}, n = 10 \)).
We trained an additional 10 (SOBS,2) subjects on a modified observation task, in which the Training block twice showed the first 96 movements performed by the SACTOR movie actor. Unlike the previous SOBS group subjects, we found that the SOBS,2 group subjects, who experienced this modified protocol, produced a compensatory adaptive response (Fig. 6A) with integrated force of 0.24 ± 0.07 Ns (1-tailed t-test: P < 0.001).

As before, we fit the state-dependent model to adapted force outputs for individual subjects in the SOBS,2 group. The mean modeled stiffness and viscosity with 95% confidence intervals were \( \hat{K} = 3.27 \pm 0.84 \) and \( \hat{B} = 0.86 \pm 0.33 \), with \( \text{vaf} = 0.31 \pm 0.17 \). We calculated the mean learned position dependence \( (\hat{K}/\bar{K}) \) of 0.073 and the equivalent mean learned velocity dependence \( (\hat{B}/\bar{B}^*) \) of 0.041 (Fig. 6B), suggesting both a learned position dependence and velocity dependence. Fitting the model to data averaged across all group subjects, the \( \text{vaf} \) was 0.86, with a partial position \( \text{vaf} \) of 0.71 and a partial velocity \( \text{vaf} \) of 0.23, indicating that >80% of the variance accounted for within the force channel could be attributed to the time series of position.

**DISCUSSION**

Observation of Perturbed Reaches Induced Adaptive Changes in Reach Dynamics

The goal of this study was to determine whether movement observation alone informed the observers of novel environment dynamics at the level of force output and whether observation-driven adaptation of force output was demonstrably dependent on stimulus-specific movement state. Our hypothesis is that haptic learning via observation generates force outputs whose timing approximates forces experienced by the observed actor. This clarification identifies the adaptive system under study. The input is visual, so we characterize kinematics of actor trajectories early and late in training. The system under study, however, is learning of force outputs; the central contribution of our study is a characterization of forces generated by subjects who learn about forces only via observation rather than via direct experience. Previous studies found that observers reached more accurately after observation of another person reaching in a novel haptic environment (Brown et al. 2010;
The results demonstrated by Gribble and colleagues demonstrate that after watching the actor subjects move in the force field in a slightly more learned fashion. Here we explore additional details of what subjects can learn through observation. The Gribble results show that, as assessed by partial execution and force generation.

Mattar and Gribble (2005) and suggested this learning effect to be due to the acquisition of a neural representation of the haptic environment. However, a similar study of observational learning in which visual feedback was perturbed described a similar adaptive advantage after observation but absent the aftereffects that are the hallmark of changes in predictive control (Ong and Hodges 2010). Previous haptic studies probed learning by measuring the displacement of positional traces as subjects moved in the force field after observation, an indirect measure of force output that reflected both feedforward and feedback changes. Here we presented an experimental design that probed learning with an error-clamped force channel and isolated changes in feedforward force output in observers who never moved in the haptic environment at any point of training, eliminating the influence of testing in the perturbing environment itself. The measured change in lateral force generation reflected subjects’ estimation of necessary dynamics to successfully perform a reaching movement after their movement or observational training. Additionally, we trained subjects in different dynamic environments to consider how adaptation depended on movement state. Our results for the subjects who directly experienced viscous and stiff force fields replicated previous descriptions of force output adaptation (Sing et al. 2009; Wagner and Smith 2008) in terms of magnitude and state-dependent profile. Furthermore, our results showed that after observation of another person performing reaching movements perturbed in the direction perpendicular to the hand by velocity- or position-dependent forces, observers exerted compensatory lateral forces that reflected that state dependence (although more fully for velocity than for position dependence). This modest, but significant, change in predictive force output is congruent with the initial reductions in movement curvature reported previously by others (Mattar and Gribble 2005) and suggests that these previously reported performance gains were due to a feedforward adaptation at the level of execution and force generation.

The results demonstrated by Gribble and colleagues demonstrate that after watching the actor subjects move in the force field in a slightly more learned fashion. Here we explore additional details of what subjects can learn through observation. The Gribble results show that, as assessed by partial (~15%) reduction of error in reaching, subjects predict that they will need to alter their motor output. We ask whether this prediction is relatively coarse or relatively fine. With a coarse prediction subjects could make a movement that corrects for the direction of movement, e.g., if a clockwise force field was learned, the subject could move more in the counterclockwise direction. With a finer prediction the subject could counter the temporal details of the forces. Subjects could match the state dependence of the observed forces, e.g., whether forces depended on hand position or on hand velocity. The latter prediction would suggest that adaptation moved beyond a directional sense (“move more clockwise or counterclockwise”) into a calculation of an appropriate time series of forces. To assess the difference between these two possibilities, we needed the force channel to measure force output throughout the entirety of the movement. We found force generation of the same scale as the Gribble kinematic improvement and with appropriate state dependence.

We found that subjects who observed movements perturbed by a velocity-dependent force field adapted their force output with a temporal profile well-described by a learned scaling of velocity signals, and, similarly, position-dependent force field observers’ outputs had an increased dependence on positional signals. That observation-driven adaptation reflected the acquisition of a similar stimulus-specific dependence suggested the engagement of feedforward learning mechanisms transforming the visual information acquired during observation into adaptation of reach dynamics. Models explaining force adaptation as expressions of motor primitives dependent on effector position and/or velocity (Hwang et al. 2003; Sing et al. 2009; Thoroughman and Shadmehr 2000) are reflective of the tuning properties of motor neurons (Ashe and Georgopoulos 1994; Moran and Schwartz 1999; Wang et al. 2007) and proprioceptive sensors such as muscle spindle fibers (Prochazka 1999). Observation seems to engage similar neural mechanisms that can encode dynamics in terms of limb states.

In human psychophysics, external dynamic loads appear to be learned with respect to intrinsic parameters such as limb state rather than extrinsic variables such as time or external coordinate systems (Conditt et al. 1997; Shadmehr and Mussa-Ivaldi 1994). Generally, visual signals are associated with motor.
planning, while proprioceptive signals are associated with the computation of joint- and muscle-based motor commands (Sober and Sabes 2003); here, however, visually captured information was transformed into an appropriate muscle-based force output. The force channel clamps trajectories, providing a full time series of human-generated force throughout the reach. Smith and colleagues (Sing et al. 2009; Wagner and Smith 2008) have built novel insight into timings, and putative state dependencies, of learned forces. We find a parallel to voltage clamping instructive. No real-life experiment is perfect, so there are certainly voltage fluctuations within a clamp. The control of the membrane is sufficient, however, to record a reliable time series of current. Similarly, here we clamp the horizontal component of trajectory not to provide a perfect minimization of displacement but to record a trace of the generated force. The force channel traces after movement in the fields demonstrate the reliability and appropriateness of this clamp; when subjects push into the wall with a strong force in these trials, there is not generation of strong vibration but rather a stable recording of the force via the trajectory clamp.

Proprioception alone may drive updates in feedforward predictions of dynamics and adaptation to haptic environments (DiZio and Lackner 2000; Krakauer et al. 1999; Scheidt et al. 2005; Tong et al. 2002). This seems appropriate since learned dynamics have been shown to be strongly represented in intrinsic-frame, joint coordinates (Shadmehr and Mussa-Ivaldi 1994). Interestingly, studies of deafferented patients suffering from several impaired or unreliable proprioception have found that visual information could be used both to improve the feedforward control and accuracy of unperturbed reaching movements (Ghez et al. 1995) and, recently, to adapt to a haptic environment (Sarlegna et al. 2010). Although deafferented subjects still strongly differ from observers in that they have access to self-generated motor plans, descending motor commands, and other movement-related signals among other aspects, the above studies suggest that visual signals can at least partially compensate for the absence of proprioception in motor control and learning. Our subjects, through observation, paralleled computations made by deafferented patients within which visual signals triggered computations typically ascribed to proprioception.

Repeated Observation of Early Perturbed Movements Induced Stronger Effect

The observed trajectories have sizeable error only in the earliest stages of training; error is smaller and decreases even more quickly in the position-dependent environment (Fig. 3). The complete set of 192 observed trials, therefore, contains observed error only in the first few bins. The delay between this initial learning and eventual force clamping likely underlies the small amplitude of the force trace, although our measured effect is of the same scale as the improvement measured in the Gribble work. Furthermore, we found that the Viscous Movement group mean adapted more slowly compared with the Stiff Movement group mean: the exponential decay rate of error differed between the two groups, with the viscous group decay rate of 0.36 and the stiff group decay rate of 0.96 (or a half-life of 1.9 bins vs. 0.7 bins). The quick decay of the stiff error indeed likely necessitates the repeated viewing to induce a noticeable force trace. The most direct test of our hypothesis, then, is comparison of traces after observation of velocity- and position-dependent forces. The shapes of the traces clearly differ and significantly depend on the state dependence of the observed dynamics, providing novel insight into the specificity of forces learned through observation.

Although we induced position-dependent force generation in the second Stiff Observation group, there is lingering state inappropriate velocity dependence, unlike the clearer single dependence in the Viscous Observation group. Sing and colleagues established a default mode of early learning of position- or velocity-dependent forces, within which predicted forces depended on both states. Sing and colleagues further demonstrated through single-trial learning that exposure to stiff forces induced a more mixed dependence of position and velocity in human force output, whereas exposure to viscous forces induced force output more clearly dependent on velocity than position. Our present finding that observed stiff forces induce a more mixed dependence confirms the Sing et al. result and suggests that humans can likely individuate velocity dependence of environmental forces than position dependence.

A functional imaging study by Malfait et al. (2010) and a behavioral study by Brown et al. (2010) have implicated trajectory curvature of observed reaching movements as a relevant error signal for the adaptive process. In our study, the stronger adaptive effect of the \( S_{OBS,2} \) group coincided with the doubled presentation of the more highly curved trajectories from early training and supports the theory that an error signal related to curvature was driving adaptation. Others have suggested that visually sensed perturbation information can lead to awareness and the formation of weaker explicit internal models as opposed to strong gains in implicit knowledge depending on proprioceptive feedback (Hwang et al. 2006b). Although Mattar and Gribble (2005) included a distractor to control for explicit strategic learning effects and attention in their experimental design and found no difference in learning effect, Hwang et al. (2006b) hypothesized that top-down attentional effects driven by vision could modulate the tuning of the bases underlying subsequent implicit learning. Although in our present study observers did not directly train in force fields after observation, it is also possible that the observation of additional curved or a greater variety of deviated trajectories resulted in increased salience and attention paid during observation, amplifying some other learning signals derived from observation.

Neural Correlates of Learning by Observing

In nonhuman primates, passive observation of goal-directed movements is known to activate a subset of premotor and motor neurons known as mirror neurons (Dushmanova and Donoghue 2010; Gallese et al. 1996; Rizzolatti et al. 1996; Tkach et al. 2007). Furthermore, mirrorlike neurons (Mukamel et al. 2010) and mirrorlike facilitation of motor cortex (Fadiga et al. 1995; Stefan et al. 2005) have been described in humans, although the properties of mirror neurons in humans have not been characterized nearly to the degree as in nonhuman primates (Turella et al. 2009). The characterization of mirror neurons and the mirror system, to date, has relied on broad validations at the behavioral level; hand movements either generated or observed induced similar levels of neural activity. Here we introduced a finer-grained assay: the acquisition of
particular environmental force dependence, indicative of specific learning of dynamics. Our results pose a deeper question of mirrorlike dependence: does neurophysiological or imaged activity reflect broad recognition and understanding or precise motoric computation? This distinction could identify putative colocalized processing of observed and generated coordinates and transformations, not just the existence of an effector trajectory. Recent efforts have suggested human motor cortical involvement by interfering with the consolidation of observation-driven learning with repetitive transcranial magnetic stimulation (rTMS) (Brown et al. 2009) and by identifying similar BOLD activation in motor and cerebellar neural areas (Malfait et al. 2010) as during active reach adaptation (Diedrichsen et al. 2005). Although the roles of a potential human mirror neuron system in motor learning, imitation, and other visuo-motor behaviors are not fully understood, this system could underlie a common neural substrate for learning by observing and learning by doing.

In stroke rehabilitation, physical therapy aims to encourage plasticity and reorganization of damaged neural motor circuits, often through intensive, massed physical practice (Patton et al. 2006). Severe deficits in the ability to produce controlled volitional movement can make standard practice-based approaches very challenging (Garrison et al. 2010). Thus action observation represents an attractive avenue to engage motor regions in impaired patients without requiring active generation of movement (Pomeroy et al. 2005) and, hopefully, to rebuild motor function (Ertelt et al. 2007). Here we provided realistic specificity and impact to this hope, by demonstrating that observation of movement trajectories can train the brain to alter its output of forces, at the level of muscle activity, and with appropriate state dependence.

ACKNOWLEDGMENTS

We thank D. N. Tomov for technical expertise.

GRANTS

This work was supported by National Institute of Child Health and Human Development Grant R01 HD-055851. P. A. Wanda was also supported by National Science Foundation IGERT 0548890 through the Cognitive, Computational, Systems Neuroscience Pathway at Washington University in St. Louis.

DISCLOSURES

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

AUTHOR CONTRIBUTIONS

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

REFERENCES

Pomeroy VM, Clark CA, Miller JS, Baron JC, Markus HS, Tallis RC. The potential for utilizing the “mirror neuron system” to enhance recovery of the severely affected upper limb early after stroke: a review and hypothesis. Neurorehabil Neural Repair 19: 4–13, 2005.

J Neurophysiol • doi:10.1152/jn.00353.2012 • www.jn.org

Downloaded from http://jn.physiology.org/ by 10.220.33.1 on April 8, 2017


---

*J Neurophysiol* 10.1152/jn.00353.2012 • www.jn.org