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Brevity of haptic force perturbations induces heightened adaptive sensitivity

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Abstract

We have exposed human participants to both full-movement and pulsatile viscous force perturbations to study the effect of force duration on the incremental transformation of sensation into adaptation. Traditional views of movement biomechanics could suggest that pulsatile forces would largely be attenuated as stiffness and viscosity act as a natural low-pass filter. Sensory transduction, however, tends to react to changes in stimuli and therefore could underlie heightened sensitivity to briefer, pulsatile forces. Here, participants adapted within perturbation duration conditions in a manner proportionate to sensed force and positional errors. Across perturbation conditions, we found participants had greater adaptive sensitivity when experiencing pulsatile forces rather than full-movement forces. In a follow-up experiment, we employed error-clamped, force channel trials to determine changes in predictive force generation. We found that while participants learned to closely compensate for the amplitude and breadth of full-movement forces, they exhibited a persistent mismatch in amplitude and breadth between adapted motor output and experienced pulsatile forces. This mismatch could generate higher salience of error signals that contribute to heightened sensitivity to pulsatile forces.

Keywords

trial-by-trial learning; human motor adaptation; motor control; haptic environments; force channels

Introduction

Humans quickly and flexibly adapt their motor behavior in order to learn new movements and respond to new sensory information. This ability affords the conservation of motor capabilities despite both rapid and gradual changes in the physical means of their bodies, as imposed by fatigue, age, or injury, and challenges imposed by novel tasks and tools. Many researchers have explored properties of motor learning and adaptation by designing psychophysical experiments controlling the parameters of imposed external dynamics (Lackner and Dizio 1994; Goodbody and Wolpert 1998; Conditt et al. 1997; Brashers-Krug et al. 1996) and considering changes in motor memories over hundreds of movements. We and other researchers (Thoroughman and Shadmehr 2000; Scheidt et al. 2001; Donchin et al. 2003; Thoroughman and Taylor 2005; Cheng and Sabes 2007; Fine and Thoroughman 2007) have investigated trial-by-trial adaptation of humans to haptic, or force-feedback,

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environments, by altering environmental force across individual movements. To better achieve a motor goal in the presence of such perturbations, the nervous system generates a within-movement feedback response for immediate compensation and updates its predictive control of arm dynamics for future movements. With these experiments, we aim to better understand the neural computations underlying the ability of the brain to transform sensation of one movement into prediction for the next movement.

In a previous study (Fine and Thoroughman 2006), we trained subjects to perform arm reaching movements toward a single target, directly away from the body. A small subset of these movements was perturbed with short duration force pulses that pushed the hand to either the left or right with varying strengths. We found participants' adaptive responses were surprisingly insensitive to the magnitude of the force pulses. This insensitivity to very brief force pulses contrasted with a previous study in which other researchers had described a linear sensitivity in response to movement-long viscous forces that were applied in every movement and always pushed in the same direction (Scheidt et al. 2001). Since, we have explored the dependence of adaptive sensitivity on the frequency and directional bias of forces, finding that as full-movement forces are presented more frequently or with a strong directional bias, participants adapt in a more sloped, proportionate manner with respect to experienced movement error (Fine and Thoroughman 2007). Here we focus on the possible dependence of trial-by-trial haptic learning on the third major factor differing between our earlier study (2006) and Scheidt et al. (2001): the within-movement duration of forces.

The preponderance of haptic environments used in psychophysical motor control studies (Shadmehr and Mussa-Ivaldi 1994; Thoroughman and Shadmehr 2000; Scheidt et al. 2001) produced forces as functions of movement kinematics, such that forces were applied during the entire movement duration. Here, we considered the effect of perturbation duration on adaptation. We have two alternate hypotheses regarding the effect of force duration on adaptation. On one hand, movement biomechanics, including the equations of motion for a linked arm and the stiff-viscous properties of muscles and tendons (Winters 2000), tend to dampen short-lived perturbations, acting as a natural low-pass filter. Biomechanics would tend to minimize the effect of rapid pulses when compared to slower full-movement forces. On the other hand, sensory transduction tends to be sensitive to changes in input signals rather than the steady state values. Both vision (DeAngelis et al. 1995) and proprioception through spindles (Chen and Poppele 1978) responded strongly to changes in position; this velocity sensitivity acts more like a high-pass filter. If trial-by-trial adaptation were more strongly influenced by primary sensation than by the biomechanics of the body, the more rapid onset and resolution of pulsatile forces could generate a stronger adaptive response than full-movement forces.

Here, we trained participants to perform reaching movements while experiencing frequently presented, strongly directionally-biased viscous forces of varying durations; forces were present for 25%, 50%, 75%, or the entirety of a movement's length. Subsequently, we trained a second group of participants to perform a similar task, experiencing 25%-movement-duration and full-movement forces. Here, we employed force channel, or error-clamped, movement trials, a technique pioneered by Scheidt (Scheidt et al. 2000) and refined by others (Hwang et al. 2006; Smith et al. 2006; Wagner and Smith 2008; Sing et al. 2009), to assay the participants' predictive generation of hand force in the absence of error-induced, mid-movement feedback.

Methods

Thirty-two neurologically normal, right handed, adult human volunteers were recruited from the Washington University in St. Louis community and performed reaching movements

while gripping the handle of a planar five-bar, two-link robotic manipulandum (IMT, Inc., Cambridge, MA). Handedness was evaluated using the Edinburgh handedness inventory (Oldfield 1971). All protocols were approved by the Washington University Hilltop Human Studies Committee.

Participants were trained to perform point-to-point reaching movements in the horizontal plane. The task was to reach with the right arm, while gripping the manipulandum handle, and move a cursor representing hand position from a start location to a target location. Participants were seated in a chair in a darkened room and positioned such that their elbow flexed 90° at the start position. To constrain the arm into the horizontal reaching plane, a ceiling-mounted sling supported the participant's upper arm. An opaque table located above the reaching space occluded vision of the participant's arm. Visual feedback, including cursors, start location, targets, and task-specific feedback, was displayed on a vertically mounted LCD monitor. Kinematic movement data was acquired in real-time by position encoders, tachometers, and an accelerometer. Custom software sampled data and generated commands at a rate of 200 Hz (experiment 1) and 1 kHz (experiment 2); the increased frequency of data sampling and force generation in experiment 2 was necessary for improved accuracy of force channel generation (described below).

The start location was placed at the origin of a rectangular coordinate system centered over the workspace and with a principal axis (referred to as the y-axis) aligned with the participant's right shoulder and parallel to the body's sagittal plane. A single target location was located 10 cm from the start location. Participants were instructed to attempt each movement in a single continuous motion. To complete a movement correctly, participants were instructed to stop on the target within a specific time range: 500 ms for Experiment 1, 750 ms for Experiment 2. The target changed color to indicate timing feedback: red if early to the target, blue if late, and green if on time. After completion of each movement, any trial-specific force perturbations were removed and the robot generated a steady force towards the center target, to return the handle and participant's hand to the start location.

Experiment 1

Twenty-four participants trained for 5 days; each day, participants made 4 sets of 180 reaching movements. Participants rested for 3 minutes between sets. During the first day, participants trained without the robot generating any force. On each of Days 2 through 5, participants experienced viscous forces of a 25%, 50%, 75%, or full-movement duration. Here, duration is defined as a proportion of the straight-line path from the start location to the target location. Participants experienced a single duration condition per day, and the day-to-day presentation of factors was shuffled across participants to counterbalance for across-day effects.

The viscous forces were generated as

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = h(y)B_i \begin{bmatrix} 0 & 1 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix} \quad (1)$$

where y is the Cartesian component of position (parallel to a straight line connecting the start and target locations), and $\dot{x}$ and $\dot{y}$ are the Cartesian components of velocity. Forces were experienced in 80% of movement trials, with the viscous gain in movement i (B_i , Eqn. 1) pseudo-randomly drawn from a distribution strongly biased to the left ($B = [0, -6, -12, -18, -24, -30, -36]$ Ns/m). We limited the duration of the force via a windowing function $h(y)$:

$$h(y) = 1 - \left(\frac{1}{1 + e^{-a(y - 0.05 - \frac{c}{2})}} + \frac{1}{1 + e^{a(y - 0.05 + \frac{c}{2})}} \right) \quad (2)$$

The parameter a ($= 333$) controlled the shape of the perturbation; it was chosen to generate a Gaussian-shaped profile. The window had 3 different widths (Fig. 1, inset), set by c ($= [0.025 \ 0.050 \ 0.075]$ m), which limited forces to the central 25%, 50%, or 75% of a movement. For the full-movement, 100% duration condition, the windowing function in Eqn. 1 is assigned a constant value ($h(y) = 1$).

Experiment 2

Eight participants trained for 3 days; each day, participants made 4 sets of 180 movements. During the first day, participants experienced the baseline condition, reaching in the absence of perturbing forces on 80% of movement trials and under the force channel condition (see section below) on 20% of trials, pseudo-randomly distributed. During Days 2 and 3, participants experienced either a leftward, 25% duration perturbation or a rightward, full-movement perturbation. Participants experienced a single duration condition within a day, and duration conditions were shuffled across subjects to counterbalance cross-day effects. The viscous gains were drawn from a strongly biased distribution of gains ($B = [-6, -12, -18, -24, -30, -36]$ Ns/m) for the 25% duration condition and ($B = [6, 12, 18, 24, 30, 36]$ Ns/m) for the 100% duration condition. Perturbation characteristics were the same as described for Experiment 1 (Eqns. 1 and 2). Participants made reaching movements in the presence of perturbing forces on 80% of trials and in the force channel condition on 20% of trials, pseudorandomly distributed.

Force channel movements

During Experiment 2, we used force channel trials to measure participants' lateral force output produced during reaches. The robotic manipulandum generated forces to constrain the handle along a straight-line path from the start location to the target location, implemented as a stiff spring-damper system,

$$F_x = -Kx - B\dot{x} \quad (3)$$

where x and $\dot{x}$ denote 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 a spring constant K of 6 kN/m and a damping constant B of 150 Ns/m. Maximum subject hand deviation from a straight line to the target was limited to less than a millimeter during a typical force channel trial. By design, the force perturbations experienced by participants pushed in the direction perpendicular to the straight-line trajectory from start to the target. Since force channel trials effectively eliminated within-movement displacements, and thus feedback control, the measured lateral forces should be representative of a predictive compensation resulting from previous experience.

In Experiment 1, we found our participants moved with a mean peak speed of around 0.42 m/s, which was faster than the peak speed usually achieved to move in environments with constant force field strength. Our variable force field strength requires feedback control to successfully reach the target in the desired movement time of 500ms, throughout the course of the task (Fig. 2). Previous researchers reported that they trained participants to move with peak speed ranging from 0.3–0.35 m/s in a force channel of similar stiffness and damping parameters (Wagner and Smith, 2008). By increasing the time-to-target to 750 ms in Experiment 2, we trained participants to move with a mean peak speed of 0.33 m/s for this

motor task, so we could use established stiffness and viscosity parameters for the force channel.

Training dot

To aid participants in learning to time their movements correctly and to reduce natural motor variance during the task, participants were asked to mimic a “training dot”. The dot began moving as the human hand initiated movement; it moved from the start location to the target with appropriate timing (Fine and Thoroughman 2006). For both experiments, while training on the baseline task (Day 1), the training dot was visible during 100%, 75%, 50%, and 25% of trials during sets 1–4 respectively. On subsequent days, the dot was visible on 20% of trials.

Performance metrics

We reduced the full time series of position to perpendicular displacement (p.d.) at 7 cm, just after mid-movement. Here, we may also refer to p.d. at 7 cm as “p.d.” or “movement error”. The timing of this metric was appropriate to capture error induced by even the briefest (mid-movement) pulsatile force and to capture adaptation in the following movement.

We defined adaptation as the change in movement error across a given trial (i.e. how is performance on movement $n + 1$ affected by movement n). We calculated adaptation as full adaptive trajectories using p.d. across all time points and as a scalar adaptation metric using p.d. at 7 cm. First, if a movement was made in the presence of a perturbation, the p.d. for that trial was mean-corrected by subtracting the mean p.d. of all movements made with the same perturbation gain. We then calculated adaptation for each movement n by subtracting the mean-corrected p.d. of the previous movement ($n - 1$) from the mean-corrected p.d. of the following movement ($n + 1$). For each gain, we calculated average adaptation by averaging across all replicates of the particular gain. Every three-consecutive trial triplet was included in this analysis.

State-space analysis

We used our previously published state-space model (Eqn. 4, Fine and Thoroughman 2007) to analyze the sensitivity to error across the different gain and duration conditions:

$$\begin{aligned} y_n &= D(B_n - \hat{B}_n) \\ \hat{B}_{n+1} &= A\hat{B}_n + \vec{S} \cdot \vec{P}_n \end{aligned} \quad (4)$$

The output of the model, the movement error y_n , matched the difference between the perpendicular displacement (p.d. at 7 cm) and the average null-field movement, calculated by averaging the last 50 movements on Day 1. Note that in experiment 2, data from force channel trials was not included in this model. The modeled error depended on a compliance parameter D , which transforms the prediction error $B_n - \hat{B}_n$, the difference between the actual gain B_n and the modeled estimated gain $\hat{B}_n$ into a positional error. As modeled here, the parameter D does not represent a true compliance. Rather than converting force into a displacement, it transforms a (difference in) viscous gain into a displacement error.

The modeled estimate was a function of the previous estimate, weighted by a scalar coefficient A , and a sensitivity vector $\vec{S}$ ($[1 \times 7]$, Experiment 1; $[1 \times 6]$, Experiment 2), which parameterized how adaptation depended on the gain of the perturbation. Each element of the sensitivity vector corresponded to one of the viscous gains ($B = [0, -6, -12, -18, -24, -30, -36]$, where $B = 0$ represents a non-force trial, experiment 1; $B = [-6, -12, -18, -24, -30, -36]$, experiment 2). If a participant were completely insensitive to a viscous gain, then the corresponding element of the sensitivity vector would equal zero. If all force gains led to

equal updates in prediction, each element of the sensitivity vector would be equal. Note that each element of the sensitivity function is separately parameterized in this model, allowing the flexibility for an overall nonlinear shape, if needed. The vector $\vec{p}$ was designed so only a single element of the sensitivity vector contributed to the update of the estimate. An element of $\vec{p}$ equaled 1 when the corresponding perturbation was applied; elements equaled 0 otherwise.

The shape of the sensitivity vector was quantified using a slope metric, derived from a linear fit of the vector elements plotted versus viscous gain, impulse, or p.d. We calculated impulse (force integrated over time) to consider sensitivity with respect to overall force, as narrowing the positional window (Equation 2) lessened overall force with the same viscous gain. We used the Gauss-Jordan method to optimize for D , A , and S that minimized the squared-difference between predicted and actual participant performance.

Force channel trial analysis

For our analysis, we first calculated a baseline lateral force profile by averaging the lateral forces produced during the last 10 force channel trials of Day 1. We then subtracted the baseline force profile from the lateral force profiles for individual force channel trial on the following days. Additionally, for each trial, we also generated a so-called “ideal” force profile using the movement's position and velocity time-series and Eqns. 1 and 2 with a viscous gain (B_j) of 21 Ns/m, the average experienced gain. This “ideal” profile represented the forces that would have been necessary for the participant to compensate for an average-strength perturbation were one present on that trial.

For each force channel trial, we calculated the breadth metric as the width (in units of time) of the force profile measured across at half-maximum amplitude. To assess the quality of participants' steady-state adaptive compensation, we then averaged the breadth metric across the final 72 force channel trials. We compared this average breadth metric of participants' adapted force profiles to the breadth of an “ideal” compensative force profile.

Statistical Significance

In testing significance in three-trial triplets, we used standard t-test and one-way within-subjects ANOVA with Tukey-Kramer method for multiple comparisons. When using t-tests to ascertain changes in slope, we subtracted slopes within participants and compared the difference across participants. In testing significance in our state-space model, we used standard bootstrap methods with replacement (Efron and Tibshirani 1998). When bootstrapping, we randomly drew a participant from the participant pool, replaced that participant, then drew again. We repeated this draw for the original number of participants, then averaged the positional data across the resampled population of participants. We used the Gauss-Jordan method to optimize for D , A , and S that minimized the squared-difference between the predicted and resampled data; using S , we calculated the slope for the sensitivity function. We repeated this process 1000 times, and the distribution of metrics was sorted across all 1000 samples to determine p values and confidence intervals. A p value of less than 0.05 was considered significant. The bootstrap method calculates a distribution of the mean behavior and does not permit calculations of sums of squares. An ANOVA-style multiple comparison is therefore not possible with bootstrapping, so we present uncorrected pair-wise p values.

Results

Experiment 1: changing the duration of forces

To determine how the duration of exposure to perturbing forces might influence the trial-by-trial adaptive response, we trained participants to perform reaching movements while gripping the handle of a robotic arm that generated unidirectional viscous forces. The duration of the perturbations was enforced by a windowing function centered over the midpoint of the reaching movement (5cm from the start location along a straight-line trajectory to the target). Durations experienced were 25%, 50%, 75%, and 100% of the movement length. Perturbing forces were experienced during 80% of reaching trials; the remaining 20% of trials were experienced in the absence of forces.

Within each duration condition, the overall magnitude of perturbing forces scaled proportionally with the viscous gain. By qualitative assessment, we found that the peak strengths of the forces, at constant gain, varied only slightly as duration increased (25% to 100%). The force perturbations exhibited a characteristic shape and approximately evenly-distributed maximum forces centered at mid-movement (Fig. 1). For each of the duration conditions, we plotted subject hand movement trajectories for each replicate of a particular perturbation gain, averaged across all participants (Fig. 2). As the duration of force perturbations increased, participants produced larger magnitude perpendicular displacements for the same perturbation gains, due to the greater total amount of force experienced.

As described in Methods (subsection: Performance metrics), we analyzed adaptation by quantifying changes in perpendicular displacement across single trials. We averaged across all replicates of each particular gain to estimate the adapted response. When considering the full time course of adaptation, we saw that as duration increased there was a qualitatively similar response to each viscosity (Fig. 3). Specifically, the two extreme duration conditions (25% and 100%) showed a surprising similarity in responses despite the very different experienced perturbations (Fig. 1) and corresponding hand trajectories (Fig. 2). To better consider differences in adaptation, we repeated our analysis using a scalar measure of change in perpendicular displacement (p.d.) at 7 cm and quantified the responses by the slopes of the linear fits of this metric.

First, we considered the relationship between adaptive response and the controlled experimental variable of experienced viscosity. For each duration condition, we quantified the adaptive strategy via a slope metric, calculated via a linear fit with the quality of fits assessed using R^2 . We found that the relationship between adapted response and viscous gain changed as duration increased (Fig. 4A), differing significantly only between the 25% and 100% durations (ANOVA with Tukey-Kramer, $p < 0.05$). In general, the slope trended to increase in magnitude with increasing duration: 25%, -0.0058 ± 0.0015 cm/(Ns/m); 50%, -0.0065 ± 0.0020 ; 75%, -0.0094 ± 0.0035 ; 100%, -0.0098 ± 0.0029 , slopes with 95% CI of mean, increasing significantly between the 25% to 100% duration condition (t-test, $p = 0.02$). All other differences in slopes across duration conditions were not significant (ANOVA with Tukey-Kramer, $p > 0.05$). The R^2 values for the fits as duration increased were 0.99, 0.95, 0.95, and 0.97.

Recall that due to the interaction between the viscous gain and the windowing function controlling for duration (Eqns. 1 and 2); the same viscous gain resulted in a different force impulse for each duration condition (Fig. 1). To compensate for this difference, we also considered adaptation with respect to the average experienced force impulse (or integrated force over time) of the robot-generated force profiles (Fig. 4B), which was a more honest representation of actually experienced dynamics than viscosity alone. Contrary to the previous analysis with respect to viscosity, we found that the slope of adaptation versus

impulse trended to decrease in magnitude as duration increased: 25%, -0.2347 ± 0.059 cm/(Ns); 50%, -0.1296 ± 0.040 ; 75%, -0.1240 ± 0.046 ; 100%, -0.0965 ± 0.028 ; however, while there were decreases in slope across all conditions, we found a significant difference only between slopes for the 25% condition vs the 50%, 75%, and 100% conditions (ANOVA with Tukey-Kramer, $p < 0.05$; t-test, $p = 0.001$, < 0.001 , < 0.001). The R^2 values for the fits of adaptation vs impulse for the 25%, 50%, 75%, and 100% duration conditions were 0.99, 0.95, 0.95, and 0.97.

Finally, we considered the relationship between adaptive response and experienced positional displacements, recalling again that due to differences in force impulse across durations, participants experienced a broadening range of hand trajectories (Fig. 2). Here, we considered adaptation with respect to the average experienced p.d. for each viscous gain (Fig. 4C). As with force impulse, the slope of adaptive response versus average p.d. trended to decrease in magnitude as duration increased: 25%, -0.1377 ± 0.035 unitless; 50%, -0.0854 ± 0.026 ; 75%, -0.0893 ± 0.033 ; 100%, -0.0801 ± 0.023 . Again, there was a significant difference in the slopes between the 25% condition and the 50%, 75%, and 100% conditions (ANOVA with Tukey-Kramer, $p < 0.05$; t-test, $p = 0.007$, 0.009 , and 0.006 respectively), while the slopes for the 50%, 75%, and 100% conditions were statistically identical (ANOVA with Tukey-Kramer, $p > 0.05$). Here, the R^2 values for the fits of adaptation for the 25%, 50%, 75%, and 100% duration conditions were 0.99, 0.96, 0.95, and 0.97.

Zero adaptation was located around the 18 Ns/m viscous gain (Fig. 4A), which was the average experienced viscous gain. Participants generated a mean force, however, that was somewhat below the mean experienced force strength, as reported in Scheidt et al. (2001). In Fig. 2, the birds-eye average trace for the 18 Ns/m viscous gain deviated leftwards from a straight-line trajectory. This has been also noted in a previous study using a similar distribution of force gains (Fine and Thoroughman 2007). As a result, when plotting the average adaptation versus the average p.d. at 7cm for each viscous gain, zero adaptation was not at zero displacement, but at a slightly negative (or leftwards) displacement (Fig. 4C).

Experiment 1: state-space analysis

Our previous analysis considered adaptation across single trials (n) by comparing the previous ($n - 1$) and subsequent ($n + 1$) trials. We corrected for mean displacements produced by the robot-generated forces, but additionally, each previous movement ($n - 1$) was influenced by another preceding perturbed movement ($n - 2$); this additional complexity was ignored in our estimation of adaptation. Instead, we quantified the trial-by-trial evolution of adaptation using state-space analysis, described in Methods (Equation 4). The quality of the state-space fits by R^2 were 0.97, 0.98, 0.99, and 0.99 as duration increased.

To more completely relate error sensitivity to experienced dynamics and kinematics, we plotted the sensitivity function versus force impulse (Fig. 5A) and average p.d. (Fig. 5B), rather than viscous gain, as discussed in the previous subsection. In both comparisons, we found that as duration decreased, participants became increasingly sensitive to the respective signal. The slope of the fits increased as the duration of the perturbation decreased: versus impulse: 25%, -5.20 ± 1.87 (Ns/m)/(Ns); 50%, -1.77 ± 0.89 ; 75%, -1.13 ± 0.39 ; 100%, -0.82 ± 0.24 ; versus p.d.: 25%, -3.06 ± 1.12 (Ns/m)/cm; 50%, -1.17 ± 0.59 ; 75%, -0.82 ± 0.29 ; 100%, -0.68 ± 0.21 . For parameter S versus impulse, the difference in slopes for the 25% duration condition compared to all other conditions was significant (bootstrap, $p < 0.001$), as well as between the 50% and 100% condition (bootstrap, $p = 0.047$) and 75% and 100% condition (bootstrap, $p = 0.046$). The difference in slopes between the 50% and 75%

duration condition was not significant (bootstrap, $p = 0.062$). The R^2 for the linear fits were 0.98, 0.94, 0.91, and 0.93, as duration increased.

When plotting sensitivity parameter S versus movement error, the 25% duration condition had a significantly larger slope than all other duration conditions (bootstrap, $p < 0.001$). The slope also decreased, but not significantly, between the 50% and 75% duration conditions, the 50% and 100% conditions, and the 75% and 100% conditions (bootstrap, $p = 0.081$, 0.053, and 0.155, respectively). Quality of the linear fits by were 0.98, 0.94, 0.92, and 0.94, as duration increased.

Experiment 1: state-space parameters

The modeled compliance D increased with increasing duration: 25%, $41.5 \times 10^{-3} \pm 2.5 \times 10^{-3}$ cm/(Ns/m); 50%, $75.3 \times 10^{-3} \pm 5.1 \times 10^{-3}$; 75%, $103.4 \times 10^{-3} \pm 10.0 \times 10^{-3}$; 100%, $121.2 \times 10^{-3} \pm 10.6 \times 10^{-3}$ (all changes significant, $p < 0.001$). The unitless coefficient A did not change across durations: 25%, 0.728 ± 0.119 ; 50%, 0.735 ± 0.161 ; 75%, 0.781 ± 0.054 ; 100%, 0.780 ± 0.058 (for all, $p > 0.05$). Note that in Fig. 1, we saw that for the same viscous gain, participants experienced increasing amounts of total force as duration increased. Consequently, the average displacement for the same viscous gain increased across durations as well (Fig. 2). Therefore, the increasing value of modeled compliance accounts for this increase in total experienced force, and associated movement error, as duration increases.

To consider the contribution of parameters A and S , independent of the contribution of the compliance and viscous gain component of the model, we performed a model fit of the residual data after subtracting the effect of viscosity by holding compliance parameter D constant at the best-fit values from the original model. These partial fits had R^2 as duration increased of 0.51, 0.45, 0.60, and 0.58, significant by a permutation test ($p < 0.001$).

Our display of state space analysis sensitivity (Fig. 5) mapped positional error into the parameter S , which quantified how each perpendicular displacement updated the expectation of viscosity. This is appropriate given the formalism of the state space model, but does compare computational elements with different units (Ns/m vs. cm). The state space model maps the expectation of viscosity into positional error via the compliance parameter D ; since the force duration is shorter for pulses, this parameter is likewise smaller for briefer force presentation. An alternative way to display this data would have been to multiply each sensitivity S by the appropriate D . This mapping of displacement into displacement would still generate significant differences dependent on force duration, with 25% duration having the steepest slope (0.12) and 100% duration the shallowest (0.066), now with unitless slopes.

Experiment 2: replicated results of Experiment 1

In Experiment 2, we found that the peak amplitude of the force, at constant gain, did not appreciably change with the duration of the perturbation. Forces in Experiment 2 were generally lower in amplitude than in Experiment 1 due to the longer time-to-target and slower associated movement speeds but were similar in shape and relative breadth. Movement trajectories increased in perpendicular displacement as viscous gain increased as in Experiment 1.

We repeated the adaptation analysis results from experiment 1. Here, we present comparisons of adaptation and modeled sensitivity to average experienced displacements. The slope of adaptation with respect to movement error (average p.d.) was found to decrease in magnitude as perturbation duration increased (Fig. 6A). However, for this experiment, the difference in slopes of adaptation with respect to movement error between the 25% and

100% duration conditions was not found to be statistically significant (t-test, $p = 0.083$); quality of the linear fits were 0.95 (25% duration) and 0.91 (100% duration).

We also replicated the state-space analysis from Experiment 1. We plotted the elements of the sensitivity vector $\mathcal{S}$ against the average movement error for each corresponding gain, performing a linear fit for each vector (Fig. 6B). As before, we compared the slopes of the linear fits for each duration condition (25%, 2.09 ± 1.59 (Ns/m)/cm; 100%, 0.75 ± 0.38). We found that the slope significantly decreased in magnitude as the duration of the force perturbations increased (bootstrap, $p = 0.009$); quality of fits was 0.97 (25%) and 0.88 (100%). This steeper slope in error sensitivity for the 25% condition implied a greater sensitivity to movement errors; the modeled error sensitivity for the 25% condition covered a range comparable to that of the full-movement condition, with a much smaller range of experienced errors.

As in Experiment 1, the modeled compliance D (25%, $60.6 \times 10^{-3} \pm 4.0 \times 10^{-3}$ cm/(Ns/m); 100%, $170.0 \times 10^{-3} \pm 31.0 \times 10^{-3}$ cm/(Ns/m)) increased as duration increased from 25% to 100% (bootstrap, $p < 0.001$); the unitless coefficient A (25%, 0.774 ± 0.144 ; 100%, 0.723 ± 0.068) did not significantly change across duration conditions (bootstrap, $p > 0.05$).

Experiment 2: force channel movement analysis

Comparison of late-training lateral force profiles to an “ideal” lateral force profile found that participants adapted their force output more broadly and with lower peak magnitude than the experienced 25% duration perturbations (Fig. 6C). When adapting to the full-movement force perturbations, the overall shape and magnitude of participants’ adapted lateral force profiles were more similar to the “ideal” compensatory force profile (Fig. 6D). Note that for ease of qualitative comparison, we inverted the y-axis of the 100% duration lateral forces (from a negative, leftward compensation to positive, rightward compensation).

To compare adaptation to the different durations of experienced force perturbations, we compared the breadth of participants lateral force profiles as measured on force channel trials (Fig. 6, inset). We assessed differences in the steady-state characteristics of participants’ lateral force profiles by first calculating the breadth metric, as described in the Methods, for each participant averaged over the last 72 force channel trials. We found that the average force profile breadth differed significantly between the 25% and 100% duration conditions (t-test, $p < 0.0002$). We then compared the average breadth for each duration condition to an “ideal” profile breadth, representing the lateral forces necessary to compensate for an average-gain perturbation. We found the difference between the breadth of the participants’ lateral force profiles and “ideal” force profiles to be not significant for the full-movement duration condition (t-test, $p = 0.94$). However, for the 25% duration condition, the participant and “ideal” breadths differed significantly (t-test, $p < 0.0001$). These results suggest that at the steady state, participants developed a perturbation-appropriate compensation for the experienced full-movement forces, but not the 25% duration forces.

Discussion

We used trial-by-trial analysis and system identification to determine how human participants modified their adaptive strategy when experiencing force perturbations of different durations, ranging from transient force pulses to full-movement forces. We found that as force duration decreased, participants became increasingly sensitive with respect to the experienced force impulse and resulting positional errors. This was surprising: in the shortest duration condition (25% window), participants experienced less overall integrated force and thus lower magnitude errors, yet were more sensitive to dynamic and kinematic

(position) signals than when experiencing more total force and larger trajectory errors in the longer duration conditions.

A consensus of models of neural adaptation consist of a linear neural network, in which driving signals project divergently onto input neurons whose tuning functions span the signal space (Rumelhart et al. 1986; Kawato et al. 1987; Poggio and Bizzi 2004). The input neurons then project through adaptable weights to output neurons, which sum their inputs to generate outputs of the overall network. The simplest learning rule, the delta rule (Widrow and Hoff 1960; Pouget and Snyder 2000), generates adaptive steps that are proportional to the error of the generated output. In seeking a behavioral analog to that proportionality, here we observed that briefer force perturbations induced, per unit of viscosity, smaller impulses and smaller displacements of the hand than perturbations of longer duration. The adaptation to pulses, however, was robust, and the human adaptive sensitivity to impulse and displacement error was actually larger for brief pulses. This heightened sensitivity suggests that human adaptive response to forces of varying duration cannot be explained by simple proportional response to error.

A more nuanced learning rule adjusts the strength of adaptation by a gradient: the derivative of output error with respect to the weight connecting the input to output neurons (Pouget and Snyder 2000). Indeed, although a commonly used delta rule holds the learning rate constant, the full delta rule scales adaptation by this gradient (Widrow and Hoff 1960). The gradient space, however, is determined by the mathematical details of the neurons generating the control signal, not by the details of the perturbations generated by the movement environment. Our interpretation of gradient descent is therefore that the real magnitude of impulse and displacement error, dependent on the magnitude of weights, should be independent of perturbation type; therefore our observed changes in sensitivity cannot be explained by traditional consideration of the gradient of the error space. If these neural network models are relevant to human motor adaptation, perhaps the natural scale of tuning can be rapidly changed by the details of the environment, which would make our observed behaviors consistent with gradient descent. These rapid changes, while consistent with results from our own laboratory, challenge the concept that the rules of adaptation should remain fixed while learning in the short term.

Previously, researchers found human subjects responded to movement-long viscous forces that were applied in every movement and always pushed in the same direction by adapting in a manner proportionate to sensed error (Scheidt et al. 2001). Later, we found that human participants adopted a categorical adaptive strategy when experiencing infrequently-presented, directionally-unbiased, 70 ms viscous force pulses (Fine and Thoroughman 2006); after experiencing a force pulse, participants adapted to oppose the direction of perturbation in a manner insensitive to the magnitude of force and associated motor errors. By systematically altering two of the three properties of the perturbations where the 2006 study differed from the 2001 study, specifically the perturbation likelihood and directional bias, we induced participants to transition between proportionate and categorical adaptive strategies (Fine and Thoroughman 2007); prior to our current study, force duration was the remaining unexplored parameter that differed across these aforementioned studies. In light of our current findings, we conclude that the previously observed insensitivity to the size of perturbed errors reflected reductions in error sensitivity due to the low likelihood and lack of directional bias of the perturbations, which outweighed any increases in error sensitivity resulting from the shortened duration of the pulses.

Wei and Kording (2009) have observed saturation and nonlinearities in adaptive responses when quantifying adaptation over wide ranges of error values or other measures of experience or feedback. Here, we find that our analysis suggests a very first-order response.

We report R^2 values ranging from 0.95 to 0.99 for our linear fits in the adaptation analysis and R^2 values > 0.9 for the state-space model fits, suggesting that the linear, $y=mx+b$, approach well-captured the meaningful parts of the adaptation.

We began our study with two alternate hypotheses predicting how pulsatile forces would induce sensorimotor adaptation. The time course of pulsatile forces rises and falls from its peak more quickly than viscous forces; pulses therefore have more prominent high-frequency components and less prominent low-frequency components. Assuming linear transform of perturbing hand force into perturbed position and velocity, higher-frequency force components will generate higher-frequency components of perturbation kinematics. Stiff and viscous feedback (Shadmehr and Mussa-Ivaldi 1994) transform the unexpected components of perturbation into corrective forces. The totality of skeletal and muscle mechanics, plus reflexes produced by spindle and Golgi tendon organ sensation, generates a low-pass filter between kinematic perturbation and torque response (van der Helm and Rozendaal 2000). Biomechanical filtering, therefore, acts to minimize the relevance of force pulses with high-frequency content.

Sensory processing, however, tends to emphasize changes in stimuli over constant components. Of particular relevance to sensorimotor adaptation are sensitivities within vision (DeAngelis et al. 1995) and proprioception (Chen and Poppele 1978, McMahon) to rapid changes in stimuli. We see here a heightened sensitivity to pulses, suggesting that in response to forces of varying duration, sensory transduction likely plays a more dominant role in determining adaptive strength than does biomechanical filtering.

To gain a better understanding of the specific changes in reach dynamics underlying the adaptive responses, we performed our second experiment using the force channel technique to examine changes in predictive control resulting from short (25%) and full-movement (100%) duration forces. The force channel constrained lateral errors during reaches to nearly zero, which largely suppressed the within-movement feedback response for those trials. Thus, the forces generated by the manipulandum to constrain the handle are considered to represent participants' predictive lateral compensation for perturbations. A so-called ideal force profile exhibiting accurate learning of previously experienced force perturbations would resemble a mirror-image of the forces that would have been present were the movement a typical perturbation trial (Smith et al. 2006); such an ideal force profile can be readily calculated from the position and velocity data time series of the clamped trial and the perturbation function. As the participants in our study experienced perturbations with viscous gains pseudorandomly drawn from an even distribution, we reasonably expected them to adapt to around the average perturbation gain, as seen previously (Scheidt et al. 2001). At the steady state, the breadth of lateral force profiles for the full-movement condition closely matched that of an average-gain ideal force profile. However, the breadth of force profiles produced for the short-duration condition differed greatly from an ideal profile. Here, participants generated consistently broader lateral forces and matched neither the onset or offset timing of the experienced force pulses.

Although a viscous force field is considered a novel movement environment, it has been shown that participants do readily adapt to these perturbing forces, returning to a near-baseline level of performance (Shadmehr and Mussa-Ivaldi 1994; Thoroughman and Shadmehr 2000; Scheidt et al. 2001). This adaptation may take place through a learned velocity-dependence of the perturbations (Sing et al. 2009) and appropriate changes in reach dynamics. Whether using the velocity signal or a similarly shaped function, the nervous system could compute an estimate of the perturbing forces over the entire movement time series by simply multiplying the signal by some constant value, learned over training. Due to the positional windowing of the 25% duration perturbation condition, there might be a much

less ecological state-dependence of the experienced environmental dynamics across the movement time-series. In this case, the experienced pulsatile perturbations are poorly characterized by learned state-dependence and a simple signal multiplication. This may be evidenced by the mismatch between the steady-state force profiles and ideal force profiles calculated from the experienced pulse function.

We considered how this persistent temporal mismatch between predicted dynamics and experienced forces might be related to the changes in adaptive sensitivity seen in Experiment 1. While our previous analyses based on kinematic metrics supported a hypothesis that primary sensation's high-pass preferences might outweigh low-pass filtering effects due to the body's natural biomechanics, our consideration of reach dynamics suggests another possible factor: sensitivity to force pulses may have been influenced by attentional effects as explained by Bayesian surprise (Itti and Baldi 2009).

Itti and Baldi's formalism of surprise considers sensory experiences that are particularly salient to be more surprising, and thus, more attractive to attention; here, saliency is a measure of how unexpected an experience is based upon prior beliefs. We have previously found that changes in attention during movement affect the transformation of errors into predictive control (Taylor and Thoroughman 2007). Here, there was an inability of the motor system to predict and/or generate a temporally matched compensatory response for the force pulses. By generating unnecessary compensatory actions preceding and following the pulses, the within-movement sensory experience unexpectedly became more complex than when predictive compensation more closely matched the full-movement perturbations. This unexpected complexity of experience could in turn cause increased attention, and sensitivity, to pulsatile movements. In the unwindowed viscous environment, the greater predictability of force onset, offset, and amplitude of full-movement forces might have demanded less attention and resulted in a reduced sensitivity.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Fig. 1.

Experiment 1. Subjects performed reaching movements from a fixed start location to a single target. Following an initial day of reaching in the absence of perturbing forces, subjects experienced robot-generated forces during reaches. Each colored trace represents the average experienced force profile for each viscous gain, for the 25% (A), 50% (B), 75% (C), and 100% (D) duration conditions. Subjects experienced a single duration condition within each day of training. During each reach, the viscous gain of the force perturbation was drawn from a strongly biased, leftward distribution, $[B = (0, -6, -12, -18, -24, -30, -36) \text{ Ns/m}]$. No force perturbation was present during reaches performed with 0 Ns/m gain (not pictured). (Inset) The windowing function was described in Eqn. 2. The window was dependent upon the displacement along the Cartesian y-axis towards the target. The shape of the window enforced the 25% (solid line), 50% (dashed line), and 75% (dotted line) force durations, centered about mid-movement (5 cm to the target). The function was set to a constant value 1.0 across all displacements for the 100% duration condition.

Fig. 2. Experiment 1. Each colored trace represents the average full-movement hand trajectory for each viscous gain, across all replicates and participants, for the 25% (A), 50% (B), 75% (C), and 100% (D) duration conditions.

Fig. 3.

Experiment 1. Adaptation across movement (n) for each specific viscous gain is calculated by subtraction of preceding ($n-1$) trajectories from subsequent ($n+1$) trajectories, mean-corrected. Each trace represents the full trajectory of adaptation across movements for each viscous gain, averaged across all replicates and participants, for the 25% (A), 50% (B), 75% (C), and 100% (D) duration conditions.

Fig. 4.

Experiment 1. The average adaptation across each viscous gain, for each duration condition. On average, participants adapted to the right (y-axis, positive) after the strongest leftward forces and adapted to the left (y-axis, negative) after the weakest leftward forces. When plotted versus viscous gain (A), the slope of a linear fit of adaptation (colored lines) increased in magnitude as duration increased. An x-axis plotting viscosity, however, failed to account for differences in impulse (Fig. 2) and positional displacements (Fig. 3), determined by the interaction between windowing function and viscous gain (Eqns. 1 and 2). In contrast, when plotted against the force impulse, or integrated force, (B) and average p.d.

at 7 cm (C) experienced for each of seven viscous gains, the slope of adaptation decreased in magnitude as duration increased.

Fig. 5.

Experiment 1. The trial-by-trial response was fit by a state-space model of data averaged across all participants. Elements of the sensitivity vector were plotted against the force impulse, or integrated force, (A) and average p.d. at 7 cm (B) for each of the seven viscous gains, for each duration condition. When plotted against either, the slope of fits of sensitivity (colored lines) decreased in magnitude as duration increased.

Fig. 6.

Experiment 2. Subjects performed reaching movements in the 25% and 100% duration conditions. During each reach, the viscous gain of the force perturbation was drawn from a strongly biased distribution [$B = \pm(6, 12, 18, 24, 30, 36)$ Ns/m] on 80% of trials; subjects moved in a force channel on 20% of trials. (A) The average adaptation metric for each of six viscous gains, for both duration conditions (triangle, 25% duration; square, 100% duration), was plotted against the average p.d. at 7 cm. The slope of the linear fits (colored lines) decreased in magnitude as duration increased at near-significance (t-test, $p = 0.083$). Note that for comparison, the positional metrics resulting from rightward full-movement forces were "flipped" across the y-axis. (B) The trial-by-trial response was quantified by a state-

space model of data averaged across all participants. Elements of the sensitivity vector were plotted against the average movement error for each corresponding viscous gain. The slope of the linear fit decreased in magnitude as duration increased (bootstrap, $p = 0.009$). For comparison, the positional metrics for the 100% condition were flipped across the y-axis. Average lateral force profiles from force channel trials for the 25% duration (C) and full-movement duration (D) conditions. For visual comparison, forces were plotted with the same directionality. The mean, steady-state force profiles (black, solid) were plotted versus a mean “ideal” force profile (black, dotted); mean profiles were calculated over the last 72 force channel trials. (Inset, bar plot) Mean force breadth metrics were plotted with standard deviations. Actual and ideal steady-state breadth metrics were calculated over the last 72 force channel trials for each subject, then averaged across subjects. The difference between actual steady-state breadth metrics for each duration condition was significantly different from zero (t-test, $p < 0.0002$). For the 25% duration condition, the difference between the actual breadth and ideal breadth was also significant (t-test, $p < 0.00001$). There was no significant difference between the actual and ideal breadths for the full-movement duration condition (t-test, $p = 0.94$).