Visuo-proprioceptive interactions during adaptation of the human reach

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Visuo-proprioceptive interactions during adaptation of the human reach. J Neurophysiol 111: 868 – 887, 2014. First published November 20, 2013; doi:10.1152/jn.00314.2012.—We examined whether visual and proprioceptive estimates of transient (mid-reach) target capture errors contribute to motor adaptation according to the probabilistic rules of information integration used for perception. Healthy adult humans grasped and moved a robotic handle between targets in the horizontal plane while the robot generated springlike loads that varied unpredictably from trial to trial. For some trials, a visual cursor faithfully tracked hand motion. In others, the handle’s position was locked and subjects viewed motion of a pointmass cursor driven by hand forces. In yet other trials, cursor feedback was dissociated from hand motion or altogether eliminated. We used time- and frequency-domain analyses to characterize how sensorimotor memories influence performance on subsequent reaches. When the senses were used separately, subjects were better at rejecting physical disturbances applied to the hand than virtual disturbances applied to the cursor. In part, this observation reflected differences in how participants used sensorimotor memories to adapt to perturbations when performance feedback was limited to only proprioceptive or visual information channels. When both vision and proprioception were available to guide movement, subjects processed memories in a manner indistinguishable from the vision-only condition, regardless of whether the cursor tracked the hand faithfully or whether we experimentally dissociated motions of the hand and cursor. This was true even though, on average, perceptual uncertainty in the proprioceptive estimation of movement extent exceeded that of visual estimation by just 47%. In contrast to perceptual tasks wherein vision and proprioception both contribute to an optimal estimate of limb state, our findings support a switched-input, multisensory model of predictive load compensation wherein visual feedback of transient performance errors overwhelmingly dominates proprioception in determining adaptive reach performance.

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1996; see also Dizio and Lackner 1995, 2000; Krakauer et al. 1999; Sainburg et al. 1995; Tong et al. 2002). For example, studies of subjects with large fiber sensory neuropathies have found that adaptive improvements in motor performance can occur to some extent without kinesthetic sense (Ghez et al. 1995; Sainburg et al. 1995; see also Lajoie et al. 1992), and so visual feedback of movement kinematics suffices to drive adaptive performance improvements. Similarly, studies involving the congenitally blind (Dizio and Lackner 2000) and studies involving sighted subjects deprived of visual feedback of motor performance (Franklin et al. 2007; Lackner and Dizio 1994; Scheidt et al. 2005; Shadmehr and Mussa-Ivaldi 1994) reveal that motor adaptation can occur when proprioceptive feedback alone drives adaptation. How does the central nervous system integrate information from the senses to drive motor command updating?

For multisensory perceptual tasks, such as estimating the size of a hand-held object (Ernst and Banks 2002), locating the position of the hand relative to the body (van Beers et al. 1999, 2002a) and assessing the geometry of hand path (Reuschel et al. 2010), sensory cue integration is well characterized as a maximum likelihood estimation (MLE) process wherein each sense $S_i$ contributes to a unified, multisensory estimate of state $S_{MS}$ in inverse proportion to the uncertainty $\sigma_i^2$ inherent to the individual estimates:

$$S_{MS} = \sum_i w_i S_i, \text{ with } w_i = \frac{\sigma_i^{-2}}{\sum_j \sigma_j^{-2}} \quad (1)$$

where $i$ and $j$ are indexes over the set of sensory information channels. The multisensory MLE estimate is optimal in that it has lower variance $\sigma_{MS}^2$ than that of any of the individual sensory estimates (Ghahramani 1997). In this way, the neural mechanisms that integrate sensory information for perception appear to use knowledge of the statistical properties of the cues to optimize the state estimate. In one report, van Beers and colleagues (2002b) provide preliminary experimental support for the idea that a similar optimization may govern visual and proprioceptive contributions to adaptive compensation for visuomotor perturbation.

However, accumulating neuropsychological, electrophysiological, and behavioral evidence suggests that the neural substrates of visual perception are distinct from those underlying the visual control of actions (Goodale and Milner 1992). More recently, an argument has been made that distinct neural pathways also contribute to the processing of somatosensory information (including proprioception) for perception and action (Dijkerman and de Haan 2007). It is possible therefore that the brain combines limb state estimates from the different senses differently for perception and for prediction/compensa-
tion of environmental loads. In one study (Scheidt et al. 2005), subjects made goal-directed reaches while holding a robotic handle that applied a velocity-dependent force field displacing the hand perpendicular to its intended trajectory. Subjects readily compensated for the perturbations when a visual cursor tracked the position of the moving hand accurately as well as when vision of the moving hand was completely blocked. Adaptive compensation was precluded, however, when cursor feedback was constrained to move in a straight line between the hand’s starting location and the target: a condition that eliminated visual feedback of trajectory errors during movement but did not eliminate cursor motion per se. Hand trajectories in this novel condition were explained using a control model that was sensitive to proprioceptive bias or “drift” in the estimation of initial limb state (cf., Wann and Ibrahim 1992), but was otherwise unadapted to the force field. Importantly, adaptation did not appear to be driven by a weighted combination of vision and proprioception as predicted by probabilistic models of sensorimotor integration. Instead, adaptation was overwhelmingly dominated by visual feedback. A similar result was reported by Pipereit and colleagues (2006) in a study that used vibration to degrade proprioception as subjects tried to adapt reaches to either a visuomotor rotation or a velocity-dependent force field. Vibration had little effect on rotation adaptation (where visual cursor motion deviated from the actual hand path), but it substantially impaired force field adaptation (where hand and cursor motion concurred). The authors concluded that proprioception’s contribution to adaptation was suppressed when it conflicted with visual feedback. In both studies, “visual capture” would not be predicted by optimization of visual and proprioceptive inputs based on their inherent precision as estimated during perception tasks (cf., van Beers et al. 2002a, 2002b).

Here, we used a planar robot, a simple virtual reality setup and systems identification techniques to characterize how visual and proprioceptive estimates of midmovement state contribute to motor adaptation and to determine whether they are combined according to probabilistic estimation rules like those used for perception. In particular, we sought to test directly whether proprioception and vision might interact in a manner inconsistent with these models, as suggested by recent experimental studies (Pipereit et al. 2006; Scheidt et al. 2005). Healthy human subjects grasped and moved the robot handle rapidly between spatial targets while the device generated springlike loads that varied unpredictably from one movement to the next. We used time-domain and trial-frequency analyses to characterize how sensorimotor memories of prior reach performance influence subsequent reaches when feedback is limited to vision or proprioception, or when visual and proprioceptive feedback are provided in combination. A control experiment characterized visual and proprioceptive uncertainty in midmovement state estimates while reaching against unpredictable springlike loads. We evaluated three feasible models of load prediction wherein the senses either cooperate or compete to predict and compensate for environmental loads. Only a switched-input multisensory model of load prediction is supported by the experimental findings. Portions of this study have been presented previously in abstract form (Judkins and Scheidt 2003; Scheidt 2004, 2013).

METHODS

Twenty-eight human subjects (aged 18 to 47 yr; 13 men, 15 women) provided written, informed consent to participate in this study. Experimental procedures were institutionally approved in accordance with the Declaration of Helsinki. All subjects were neurologically normal and had normal or corrected-to-normal vision. Subjects were seated in a high-backed chair, and a chest harness minimized trunk movement. Subjects held the handle of a horizontal planar robot with their right hand while the arm was supported against gravity (~85° abduction) using a lightweight, low-friction, chair-mounted arm support. Subjects’ wrists were splinted in a neutral position before testing to minimize wrist motion. Direct view of the arm was occluded by an opaque display screen mounted in the horizontal plane 1 cm above the plane of hand motion. A 16-bit data acquisition board (PCI-6031E; National Instruments, Austin, TX) sampled analog force and acceleration data from a load cell (85M35A-I40-A-200N12; JR3, Woodland, CA) mounted between the robot arm and its handle. Handle location was resolved within 0.038 mm using joint angular position data from two 17-bit, absolute angle encoders (A25SB17P180C06E1CN; Gurley Instruments, Troy, NY). Data collection and robot control were performed at 1,000 sample/s. We also recorded electromyographic activity from arm muscles; however, analysis of those signals was beyond the intended scope of this paper and is, therefore, deferred. Additional details of the robot’s design and control are described in Scheidt et al. (2010).

Primary Experiment

Twenty subjects participated in a primary testing session lasting ~90 min. The subject’s task was to manipulate the robot handle so as to move either the hand or a visual cursor representing the hand (i.e., a 0.5-cm-diameter disk) out-and-back from a central origin to one of two circular targets (1.0 cm diameter) projected onto the horizontal display screen (Fig. 1A). Targets and the hand’s origin were oriented such that movements away from the body (i.e., those toward the OUT target) started ~30 cm from the body and were directed radially along the midclavicular line on the subject’s right side. Movements toward the ACROSS target were directed along the subject’s azimuth to the left. We chose these target directions because previous studies have shown that the precision of visual and proprioceptive feedback varies across the radial and azimuth directions for perception of hand position (van Beers et al. 1998, 1999). In azimuth, vision is more precise than proprioception, whereas in the radial direction, the precision of proprioception is increased and that of vision decreased so that integration for perception relies more heavily on proprioception (van Beers et al. 2002a). Here we sought to test the direction-dependence of visuo-proprioceptive integration in a reaching task requiring adaptation to springlike loads.

In both movement directions, the origin and the targets were separated by 10 cm. Subjects were instructed to “move first to the target and then back to the origin in one smooth motion, reversing direction as accurately as possible within the target without pause.” Subjects were also instructed to achieve a peak hand speed of 0.5 m/s during movement. Graphical feedback was provided after each trial, indicating whether movement was too fast (>0.6 m/s), too slow (<0.4 m/s), or just right. The speed criterion was typically met if the target was acquired within 200–300 ms.

The robot’s motors partially compensated the manipulandum’s passive dynamics (Amans et al. 2002) and applied horizontal planar forces to the subject’s hand. Specifically, kinematic recordings were used to simulate, in real-time, a lightly-damped spring-mass system opposing handle motion:
Experimental Manipulations of Sensory Feedback and the Environmental Loads \( K^H \) and \( K^C \)

We sought to characterize how people combine visual and proprioceptive feedback of prior reach performance to enforce movement accuracy in the presence of unpredictable environmental loads. Subjects performed two blocks of out-and-back movements (>490 trials each). In one block, movements were all directed toward the OUT target while, in the other, movements were directed toward the ACROSS target. The intended target was displayed prior to each trial for a period of 1 s. The target disappeared and a tone sounded, cueing a goal-directed reach “out-and-back” to the remembered target location, which was to be acquired transiently midmovement. Each block included >10 trials performed in a “baseline” environment having relatively low stiffness (250 N/m) and continuous, veridical visual feedback. Subjects practiced until they indicated they were comfortable moving against the load. Practice was followed by four sets of 120 trials, each composed of 100 training trials (also called “test” trials) preceded and followed by 10 baseline trials. These baseline trials were included to “wash-out” adaptations that might occur during training. Subjects rested between sets.

Test trials were performed in one of four different sensory feedback conditions. We provided simple forms of sensory feedback in three of the training conditions. In the “vision = proprioception” (VP) condition, the cursor was visible throughout each movement and tracked hand position faithfully. The stiffness of the hand’s physical spring constant \( K^H \) changed pseudorandomly from trial-to-trial (Fig. 1B, top) and was normally distributed with a mean of 480 ± 80 N/m (mean ± SD, here and elsewhere). The magnitude of environmental impedance remained constant for the duration of each movement and changed only between trials. As described below, deviations from the average load were used to probe how people use performance feedback from prior trials to update motor commands on subsequent trials. The physical spring constant also varied pseudorandomly from trial to trial in the “proprioception only” (P) condition. Here, the cursor disappeared at the onset of each trial (i.e., along with the target and tone), and subjects reached to the remembered target location. Subjects received no visual information of hand position during or after movement. In the “vision only” (V) condition, the robot arm was rigidly fixed at the starting location such that the subject’s hand could not move. Subjects “moved” against the virtual spring load \( K^C \) = 500 ± 90 N/m by applying forces to the handle. Although proprioception was not eliminated per se, task performance was independent of miniscule motions of the handle and other potential motion-related proprioceptive cues (Scheidt and Mah 2003) because the trial series of cursor spring stiffness \( K^C \) changed pseudorandomly from trial-to-trial (Fig. 1B, bottom). Each subject experienced the same pseudorandom sequences during training.
We also characterized adaptation in a more complex “sensory conflict” (SC) condition wherein the hand was free to move against loads determined by the sequence $K_i^H$, but the cursor was driven by forces generated against the handle in proportion to the sequence of virtual spring loads $K^C$. The two sequences $K_i^H$ and $K_i^C$ had negligible autocorrelations and cross-correlation values for $\leq 50$ trial lags. Because different springlike loads were applied to the hand and the simulated point mass cursor, the cursor did not represent hand motion faithfully. We included this condition to assess how the brain might resolve sensory conflict during adaptation, specifically by quantifying how the brain combines memories of visual and proprioceptive performance when updating motor commands from one trial to the next. The presentation order of sensory feedback conditions within each block and the order of the blocks themselves were counterbalanced across subjects.

**Control Experiment**

Twelve subjects participated in a single-session control experiment that quantified uncertainty in the visual and proprioceptive perception of endpoint state within the context of our target capture task. Four subjects had previously participated in the primary experiments. All subjects performed two blocks of 100 trials. Each trial consisted of two phases. In the first, subjects reached to the OUT target under the same experimental conditions and against the same unpredictable loads as described above for the V and P test blocks. In the second phase of each trial, we required subjects to indicate how far they had just reached (i.e., the location of the hand or cursor at movement reversal). The two control blocks differed in whether subjects controlled hand position or cursor position, the type of movement-related feedback provided during phase 1, and how subjects were to indicate the spatial location of the reversal point in phase 2. No visual feedback of the hand’s actual position was provided during phase 2 (the assessment phase) in either block.

In the P control block, a visual cursor tracked hand position faithfully for the first 30 reaches to allow subjects to calibrate reach extent to the visual target distance. For the remaining trials in this block, no visual cursor was provided, and all reaches were guided by proprioceptive feedback alone. In the V block, motion of the arm was precluded, and subjects moved the cursor out-and-back to the target according to Eq. 3.

In the second phase of each P trial, subjects were instructed to move their hand to the location where they perceived their most recent reach had reversed direction. They did so using the same hand that had moved against the spring-like load. Subjects were instructed to hold the hand steady at the desired location as they pressed a button (with their left hand) that recorded their assessment and initiated the next trial. The robot generated no resistance during this phase. In the second phase of each V trial, subjects indicated peak reach extent using a three-button response box. The buttons manipulated the location of a visual pointer (0.5-cm-diameter circle) that appeared 0.5 s after the end of movement at a random location (SD = 1 cm) centered on the target location. One button moved the marker away from the subject along the line of cursor motion, whereas a second button moved the marker toward the subject. The third button registered the assessment and initiated the subsequent trial. In both control blocks, subjects indicated peak movement extent using the same sensory modality that drove adaptation of the reach. The presentation order of the V and P blocks was counterbalanced across subjects. Throughout the entire experiment, subjects were encouraged to be as accurate as possible in indicating the peak extent of their reach, taking as much time as needed.

**Data Analysis**

**Movement kinematics.** We refer to motions of the hand and cursor both as “endpoint” motions. Endpoint trajectories were low-pass filtered prior to computing velocities using a second-order, zero-lag Butterworth filter with 20-Hz cutoff frequency. Velocities were filtered similarly before computing accelerations. We computed seven kinematic measures of task performance from the initial stroke of each out-and-back movement in the primary experiment using an automated algorithm within the MATLAB programming environment (The Mathworks, Natick, MA). Each measure was verified visually, and trials were excluded from analysis if: 1) the subject moved before the “go” signal; 2) the hand’s displacement profile was not smooth and exhibited more than one peak, suggesting presence of corrective submovements (cf., Fishbach et al. 2005; Milner 1992); or 3) total movement time out-and-back exceeded 0.8 s.

Movement onset occurred when the endpoint velocity (hand or cursor) first exceeded 0.05 m/s at the beginning of the trial. The endpoint’s starting point was its $x$-$y$ location 100 ms prior to movement onset. The peak acceleration point was defined as the $x$-$y$ location of the endpoint at the moment it reached peak tangential acceleration. The peak speed point was defined as the $x$-$y$ location of the endpoint at the moment it reached maximum speed. The reversal point was taken as the endpoint position at its maximum radial displacement from the starting position. Peak movement extent was the distance between the endpoint reversal location and the starting point. Extent error ($e$) was the difference between movement extent and the instructed 10-cm displacement. Where appropriate, these kinematic performance measures were computed separately for motions of the hand and cursor.

In the control experiment, we computed assessment error for each trial as the $y$-axis distance between the endpoint’s actual peak movement extent and the spatial location that the subject indicated as his or her reversal point. We quantified uncertainty in the visual and proprioceptive perception of peak (midreach) movement extent using the standard deviation (SD) of assessment errors from the last 60 trials in the V and P trial blocks, respectively.

**Adaptation modeling.** In our primary experiment, we used $e$ as the main measure of performance when characterizing how sensorimotor information is processed during motor adaptation. Because the perturbation sequences were uncorrelated from one trial to the next, history-dependent changes in performance error could not be due to the perturbations themselves, but rather must have originated from information filtering within the neuromotor controller. Previous studies of motor adaptation under simple feedback conditions (e.g., Scheidt et al. 2001; Scheidt and Stoeckmann 2007; Takahashi et al. 2001) have shown that this learning is well described by a family of limited-memory autoregressive models with external input:

$$e_i = \sum_{j=1}^{Q} a_i e_{i-j} + \sum_{g=0}^{R} b_{i-g} K_{i-g} + \epsilon_i$$

(4)

In the simple feedback conditions, $e_i$ is a state variable representing the $e$ for the hand (P and VP conditions) or the cursor (V condition) on trial $i$. $K_i$ corresponds to the hand’s spring constant during P and VP blocks, whereas it corresponds to the cursor’s spring constant during V blocks. In all cases, the $a_i$ and $b_i$ coefficients reflect the relative influence of prior errors and perturbation magnitudes on subsequent errors. The minimum numbers of memory terms needed to describe the evolution of trial-by-trial errors are represented by constants $Q$ and $R$. The family of model structures described by Eq. 4 can represent adaptive processes having very limited memory requirements (when constants $Q$ and $R$ are small), as well as processes having more complex dynamics (see APPENDIX).

For the SC condition, we assume that adaptation is linear in its inputs (cf., Scheidt et al. 2001) and extend the single-input, single-output memory-based model of Eq. 4 to accommodate two input perturbation sequences ($K^H_i$ and $K^C_i$) and two potential output sequences ($e^H_i$ and $e^C_i$):

$$e^H_i = \sum_{j=1}^{Q} a^H_{i-j} e^H_{i-j} + \sum_{g=0}^{R} b^H_{i-g} K^H_{i-g} + \epsilon^H_i$$

$$e^C_i = \sum_{j=1}^{Q} a^C_{i-j} e^C_{i-j} + \sum_{g=0}^{R} b^C_{i-g} K^C_{i-g} + \epsilon^C_i$$

(5a)
\[ e_i^* = \sum_{m=1}^{N} a_m^c e_i^c - m + \sum_{n=0}^{L} b_n^c K_{i-n} + \sum_{p=0}^{V} d_p^K H_{i-p} \]  

(5b)

In this multi-input, multi-output (MIMO) model, as, bs, and ds are coefficients reflecting the relative influence of prior trial errors and perturbation magnitudes on subsequent hand (H) and cursor (C) errors. Because we assume that movements were performed feedforward with respect to visual feedback, the summation index \( j \) starts from 1.

For each test block, we identified the most parsimonious model structure capturing adaptive performance changes. We first averaged movement error on a trial-by-trial basis across subjects within blocks of identical sensory feedback and movement direction. Given that the trial-series of movement errors observed in each block may be considered a stochastic realization of a motor response to the perturbation sequence, averaging across subjects reduces the effect of intersubject execution variability on the structure estimation procedure. For each of the average datasets, we removed the mean from the time series before using MATLAB’s systems identification toolbox (identify and arx commands) to fit model structures of moderate complexity (Q through V \( \leq 8 \)) to one-half of the [perturbation, error] time series data (the estimation dataset). We then evaluated the models’ abilities to predict the sequence of errors in the other half (the cross-validation dataset). We used the minimum descriptor length (MDL) criterion (Ljung 1999) to identify the structure most consistent with the information filtering manifest in the trial series of errors. Of all models considered, the MDL model is the one that minimizes a modified mean-square-error (MSE) function:

\[ \text{MSE}_{\text{MDL}} = \text{MSE} \left[ 1 + n \log(k)/k \right] \]  

(6)

where \( n \) is the total number of parameters in the model being considered, and \( k \) is the number of data points in the estimation set. The MDL criterion offers a compromise between model complexity and quality of fit to the data. After identifying the MDL model for each training condition, we refit that structure to each subject’s time series and report the individualized estimates of coefficients a, b, and d within each trial block. Importantly, systematic changes in model structure and/or coefficient values across the different feedback training conditions would reflect differences in how the subjects use visual and proprioceptive information to update motor commands for subsequent reaches.

**Frequency domain analysis of adaptation model performance.** A characteristic of real-world disturbances is that perturbing stimuli can disappear as suddenly as they appear. Because the ability of an adaptive system to reject disturbances often depends on the relative frequency of disturbances, we used frequency-domain analysis techniques to characterize each subject’s ability to reject perturbations that vary slowly vs. those that vary rapidly. As described in the Appendix, we use the z-transform (a generalization of the Fourier transform) to obtain a closed-form mathematical description of how errors evolve in response to arbitrary inputs (such as \( K^H \) and \( K^C \)). The resulting description, called a transfer function, is commonly expressed as the ratio of two polynomial functions of the variable \( z^{-1} \), which for our purposes is a “trial delay” operator. Of particular importance are the adaptation model parameters corresponding to the system transfer function zero and pole values (which are the roots of the transfer function numerator and denominator polynomials, respectively). Depending on the relative values of the transfer function zeros and poles, a system may exhibit a “high-pass” response typical of adaptive systems (wherein the effect of steady-state perturbations are minimized) or a “low-pass” response (wherein high-frequency inputs are attenuated). Readers unfamiliar with transfer function poles and zeros are encouraged to review the material included in the Appendix, which also describes relationships between time-domain, frequency-domain and state-space representations of motor adaptation.

**Viable models of load prediction.** Although the transformation from motor output to performance is generally nonlinear, variations in reach performance are reasonably approximated as a linear function of load about an operating point established by the predicted load (cf., Scheidt et al. 2001, 2012; Scheidt and Stoeckmann 2007; Takahashi et al. 2001; see also Fig. 5, C and D, below):

\[ e_i = b_0(K_i - K^\text{predicted}) \]  

(7)

Performance error \( e_i \) therefore reflects errors in load prediction \( (K_i - K^\text{predicted}) \). As highlighted recently (Marko et al. 2012), accuracy of load prediction is important because a saturating function of prediction error appears to drive adaptation of reaching actions.

Recall that Eq. 4 provides a second equation for \( e_i \). Equating Eqs. 4 and 7 yields an estimate of the subject’s internal prediction of upcoming load based entirely on terms that can be estimated using visual and kinesthetic feedback \((e_{i-1 - o} \text{ and } K_{i-1 - o})\). For simplicity, consider the case where \( R = K_{i} \) and \( R = K_{i} \) in Eq. 4 both equal 1:

\[ K_i^{\text{predicted}} = \frac{-a_1}{b_0} e_{i-1} + \frac{-b_1}{b_0} K_{i-1} \]  

(8)

Load prediction can therefore be viewed as a memory integration process wherein a specific weighted sum of recent sensorimotor memories comprises the prediction. The number of memories (right-hand terms) depends on the structure of the adaptation model identified using Eq. 4. Because information about kinematic errors and perturbations can only be obtained via sensory feedback, Eq. 8 implies that the precision of load prediction \( (\sigma_{\text{load\ prediction}}) \) is determined in part by the precision of individual sensory transduction mechanisms (i.e., \( \sigma_V \) and \( \sigma_0 \)). We therefore designed our primary experiment to test whether visual and proprioceptive estimates of midmovement performance error combine optimally to drive adaptation according to the probabilistic estimation rules used for perception.

We consider three models of load prediction that span the range of possibilities wherein the senses jointly cooperate or individually compete to exclusively form the load prediction (Fig. 2). Because vision and proprioception both suffice to guide adaptation, estimation of reach errors for motor adaptation might be optimized in a MLE sense (Eq. 1) as previously found for perceptual tasks (Ernst and Banks 2002; Reuschel et al. 2010; van Beers et al. 1999). In the simplest model of multisensory motor adaptation (Fig. 2A; model 1), the senses work together (i.e., cooperate) to form a maximum likelihood estimate of error, which then combines with an estimate of the most recent load to yield a prediction of the pending load. In this unified, multisensory adaptation model, load predictions are composed using a set of computations that do not depend on which feedback modality or modality provides task-relevant feedback. Also in this model, MLE optimization occurs only during the multisensory estimation of endpoint state \( e_i^{\text{ME}} \). In a second cooperative model of adaptation (Fig. 2B), visual and proprioceptive state estimates drive separate modality-specific predictions that are subsequently combined to form an optimal prediction. This approach is cooperative in the sense that, by combining predictions in inverse proportion to their individual uncertainties, a multisensory prediction with lowest possible variability is obtained. When we manipulate \( K^H \) and \( K^C \) so that the unimodal predictions disagree, the multisensory prediction of model 2 should reflect a weighted contribution of the individual sensory predictions:

\[ K_i^{\text{predicted}} = w_V \left[ (a_c^V/b_0^V) e_{i-1} - (a_c^V/b_0^V) K_{i-1} \right] + w_P \left[ (a_c^P/b_0^P) e_{i-1} - (a_c^P/b_0^P) K_{i-1} \right] \]  

(9a)

As reviewed by van Beers (2002b), \( w_V \) typically ranges between 0.2 and 0.4 for most perception tasks, while \( w_P \) ranges between 0.6 and 0.8. We designed our control experiment to obtain estimates of \( w_V \) and \( w_P \) for the perception of endpoint state within the specific context of our target capture task. Note that, over the entire range of values reported by van Beers, model 2 predicts that memories of prior perturbations of both the hand and cursor should contribute to the multisensory prediction of environmental load, as should memories of
either case, the optimized weights may be influenced by one or more Ki state estimates to be optimized as per prior hand and cursor errors. This also holds true if we allow endpoint errors. In either case, the optimized weights may be determined by the inherent precision of the individual sensory estimates (van Beers et al. 1999), which vary strongly with movement direction for the perceptual task of limb position matching (van Beers et al. 2002b). If so, the optimal weights should differ systematically for movements to the OUT and ACROSS targets because vision is more precise (and should be weighted more heavily) than proprioception in estimating limb position in azimuth, whereas proprioception is more precise (and should be weighted more heavily) than vision for estimating limb position in depth (van Beers et al. 2002b). Finally, the brain might forego multisensory integration during load prediction and instead form separate predictions driven by vision and proprioception as in Fig. 2C (cf., Haruno et al. 2001). In this case, the separate predictions would compete to drive adaptation. If motor command updating were dominated by one sense or the other in the SC condition, only one endpoint (cursor or hand) should exhibit a “high pass” adaptive response. In this case, and as per Fig. 2C, load predictions for the adapted endpoint should not depend on memories associated with prior performances of the other endpoint and should not vary by movement direction.

Fig. 2. Viable models of feedforward control and multisensory load prediction. A: cooperative model wherein separate visual and proprioceptive estimates of state are maintained and used to form separate load predictions, which are then combined to form a prediction of the pending environmental load. B: cooperative model wherein separate visual and proprioceptive estimates of state are maintained and used to form separate load predictions, which then compete to determine behavior. See text for additional discussion and definition of terms.

**Statistical Hypothesis Testing**

Our primary experiment tested the null hypothesis that subjects use the same limited-memory strategy of adaptation, regardless of whether vision, proprioception, or both provide feedback during reaching. It did so by comparing adaptation model structures (Eqs. 4 and 5) and coefficient values across sensory feedback conditions and movement directions. Separate two-way, mixed model, repeated-measures analysis of covariance (ANCOVA) and subsequent post hoc t-tests evaluated whether model coefficients varied with sensory feedback condition (VP, V, and P) and/or movement direction (OUT and ACROSS) while controlling for small differences in the kinematics of endpoint motion observed in the different training conditions. Our control experiment estimated the magnitude of uncertainty in the visual and proprioceptive estimation of midmovement endpoint state within the context of our target capture task. Two-way, analysis of variance (ANOVA) evaluated whether the variability of assessment error varied across feedback conditions (V, P) and prior exposure to the primary experiment. Hypothesis testing was carried out in the Minitab computing environment (Minitab, State College, PA). Data values in the text are reported as means ± 1 SD. Error bars in figures represent ± 1 SE. Effects were considered statistically significant at the α = 0.05 level.

**RESULTS**

**Primary Experiment**

As shown for a representative subject’s VP hand paths out-and-back to the OUT target (Fig. 3), test trial movements were consistently smooth, and they reversed direction near the target within the desired time interval, despite considerable variability in environmental load. Load variability typically induced ≈3.5 cm of variation in peak movement extents. One subject did not wish to complete all of the training blocks in this experiment and was therefore excluded from analysis. For the remaining 19 subjects, we discarded only 1.3 ± 2.9% of trials due to motion in anticipation of the go cue, presence of corrective submovements, and/or excessive movement times.

Across subjects, only three training blocks had more than 10% sources of uncertainty. If the weights are influenced heavily by recent performance variability (Koerding and Wolpert 2004; see also Haswell and Scheidt 2006), they should be approximately equal in the SC condition because the imposed visual and mechanical perturbations were designed to induce similar amounts of variability in cursor and hand motions. Alternatively, the weights might be determined by the inherent precision of the individual sensory estimates (van Beers et al. 1999), which vary strongly with movement direction for the perceptual task of limb position matching (van Beers et al. 2002b). If so, the optimal weights should differ systematically for movements to the OUT and ACROSS targets because vision is more precise (and should be weighted more heavily) than proprioception in estimating limb position in azimuth, whereas proprioception is more precise (and should be weighted more heavily) than vision for estimating limb position in depth (van Beers et al. 2002b). Finally, the brain might forego multisensory integration during load prediction and instead form separate predictions driven by vision and proprioception as in Fig. 2C (cf., Haruno et al. 2001). In this case, the separate predictions would compete to drive adaptation. If motor command updating were dominated by one sense or the other in the SC condition, only one endpoint (cursor or hand) should exhibit a “high pass” adaptive response. In this case, and as per Fig. 2C, load predictions for the adapted endpoint should not depend on memories associated with prior performances of the other endpoint and should not vary by movement direction.

where $e^{MS}_{i-1}$ is the multisensory memory of target capture error. In either case, the optimized weights may be determined by the inherent precision of the individual sensory estimates (van Beers et al. 1999), which vary strongly with movement direction for the perceptual task of limb position matching (van Beers et al. 2002b). If so, the optimal weights should differ systematically for movements to the OUT and ACROSS targets because vision is more precise (and should be weighted more heavily) than proprioception in estimating limb position in azimuth, whereas proprioception is more precise (and should be weighted more heavily) than vision for estimating limb position in depth (van Beers et al. 2002b). Finally, the brain might forego multisensory integration during load prediction and instead form separate predictions driven by vision and proprioception as in Fig. 2C (cf., Haruno et al. 2001). In this case, the separate predictions would compete to drive adaptation. If motor command updating were dominated by one sense or the other in the SC condition, only one endpoint (cursor or hand) should exhibit a “high pass” adaptive response. In this case, and as per Fig. 2C, load predictions for the adapted endpoint should not depend on memories associated with prior performances of the other endpoint and should not vary by movement direction.

Statistical Hypothesis Testing

Our primary experiment tested the null hypothesis that subjects use

the same limited-memory strategy of adaptation, regardless of

whether vision, proprioception, or both provide feedback during

reaching. It did so by comparing adaptation model structures (Eqs. 4

and 5) and coefficient values across sensory feedback conditions and

movement directions. Separate two-way, mixed model, repeated-measures analysis of covariance (ANCOVA) and subsequent post hoc

t-tests evaluated whether model coefficients varied with sensory

feedback condition (VP, V, and P) and/or movement direction (OUT

and ACROSS) while controlling for small differences in the kinematics of endpoint motion observed in the different training conditions.

Our control experiment estimated the magnitude of uncertainty in the

visual and proprioceptive estimation of midmovement endpoint state

within the context of our target capture task. Two-way, analysis of

variance (ANOVA) evaluated whether the variability of assessment

error varied across feedback conditions (V, P) and prior exposure to

the primary experiment. Hypothesis testing was carried out in the

Minitab computing environment (Minitab, State College, PA). Data

values in the text are reported as means ± 1 SD. Error bars in figures

represent ± 1 SE. Effects were considered statistically significant at

the α = 0.05 level.

RESULTS

Primary Experiment

As shown for a representative subject’s VP hand paths out-and-back to the OUT target (Fig. 3), test trial movements were consistently smooth, and they reversed direction near the target within the desired time interval, despite considerable variability in environmental load. Load variability typically induced ≥3.5 cm of variation in peak movement extents. One subject did not wish to complete all of the training blocks in this experiment and was therefore excluded from analysis. For the remaining 19 subjects, we discarded only 1.3 ± 2.9% of trials due to motion in anticipation of the go cue, presence of corrective submovements, and/or excessive movement times. Across subjects, only three training blocks had more than 10%
discarded trials (one for subject 3 and two for subject 7). These blocks also were excluded from analysis.

Endpoint trajectories had similar kinematics in all training blocks. Average displacements, velocities and accelerations of the hand (i.e., target width); vertical gray band, desired duration of the initial outward movement.

Fig. 3. Time series of hand displacements for all out-and-back movements made to the OUT target in the visual and proprioceptive feedback (VP) trial block from a representative subject. Horizontal gray band, desired movement extent (i.e., target width); vertical gray band, desired duration of the initial outward movement.

Endpoint trajectories had similar kinematics in all training blocks. Average displacements, velocities and accelerations of the hand (Fig. 4; d, v, a) overlapped in the VP and P conditions for both movement directions for the population as a whole. Cursor trajectories also overlapped in the VP and V cases. Two-way, mixed-model, repeated-measures ANOVA identified small differences in mean movement extent across training conditions and movement directions, despite instructions encouraging accuracy of target capture [condition: $F_{(2,89)} = 15.89, P < 0.0005$; direction: $F_{(2,85)} = 10.54, P = 0.002$]. In the OUT direction, mean endpoint motions were largest in the V condition ($13.2 \pm 2.4$ cm), followed by the P condition ($11.5 \pm 1.9$ cm) and smallest in the VP condition ($10.7 \pm 0.9$ cm). Mean endpoint motions to the ACROSS target were also larger in the V and P conditions ($11.3 \pm 1.0$ cm and $11.2 \pm 1.6$ cm, respectively) than in the VP condition ($10.6 \pm 0.8$ cm). These small differences in movement extent likely reflect systematic, modality-dependent bias in either the neural representation of endpoint state during movement or the representation of the goal (cf., Wann and Ibrahim 1992).

We also observed differences in the variability (standard deviation) of endpoint movement extent across training conditions [two-way repeated-measures ANOVA: $F_{(4,89)} = 145.56, P < 0.0005$]. Endpoint variability was larger in the V condition ($2.8 \pm 0.5$ cm) than in the P and VP conditions ($1.4 \pm 0.3$ cm and $1.1 \pm 0.3$ cm, respectively). By contrast, unperturbed execution variability (i.e., pretraining “baseline” movement extent variability) was virtually identical in the two movement directions, averaging $0.9 \pm 0.3$ cm across subjects. Post hoc Tukey $t$-tests found that hand variability in the SC training condition ($1.4 \pm 0.2$ cm) was greater than in the VP condition ($T = 3.23; P = 0.016$), whereas cursor variability in the SC condition ($2.4 \pm 0.2$ cm) was lower than in the V condition ($T = 4.86; P = 0.0001$), suggesting that subjects preferentially controlled cursor motion in the SC condition. In the analyses that follow, we control for feedback-dependent differences in movement kinematics by using the mean and standard deviation of test trial movement extent as cofactors in analyses of variance.

Fig. 4. Subject average endpoint trajectories under simple feedback conditions: vision only (V), proprioception only (P), and VP. Displacements ($d$), velocities ($v$) and accelerations ($a$) of the hand (left) and cursor (right) for movements made to the OUT ($A$) and ACROSS ($B$) targets are shown. Shading corresponds to $\pm 1$ SE of the across-subject average time-series from the V trials, which had greatest across-subject variability (i.e., the worst-case condition).
By design, motions of the hand (Eq. 2) and cursor (Eq. 3) were dominated by environmental inertia early in the movement and by environmental stiffness later on. Figure 5 presents, for a representative subject, average hand forces as a function of endpoint displacement for the hand (panel A) and cursor (panel B) from trials in the P and V blocks, respectively. The three curves in each panel are the average of 15 trials with the strongest, weakest and most moderate perturbation strengths. In both panels, the curves overlay another from movement onset until about the time of peak acceleration, but diverge from that time onward. Given that the neural delays associated with central “long-loop” responses to limb perturbations are relatively large (greater than \(\sim 50\) ms; cf., Pruszynski et al., 2008), moment-by-moment error feedback is not likely to have contributed to target capture performance in our task because appreciable errors do not arise until after the time of peak acceleration. Thus, due to the feedforward nature of these movements, the peak extent of reach scaled with load strength for both the hand and cursor. The relationship between peak displacement and load strength was approximately linear across all training conditions in both directions (OUT: Fig. 5C; ACROSS: Fig. 5D), justifying the use of linear systems techniques, and particularly Eq. 7, to analyze motor adaptation.

Adaptation Modeling–Simple Feedback Conditions

A single model structure (Eq. 10) was identified as the MDL model of choice in each of the simple sensory training conditions, regardless of movement direction. This structure accounted for 89% to 94% of the data variance in the cross-validation data sets and yet required retention of very few sensorimotor memories:

\[ e_i = a_1 e_{i-1} + b_0 K_i + b_1 K_{i-1} \]  

(10)

Other structure selection techniques were also evaluated (including Akaike’s Information Criterion choice) (Ljung 1999). However, the best improvement in data variance accounted for over the MDL choice was always small (<4% variance accounted for) at a cost of considerable model complexity (>4 additional memory terms). Figure 6 shows the representative case of P block movements to the OUT target, where the best-fit model requires eight additional memory terms (1 more perturbation memory and 7 more error memories).

Table 1 details the model coefficients obtained by refitting Eq. 10 to each individual subject’s time series in each training block. The \(z\)-transform of Eq. 10 is identical to that of a discrete-time filter, having an effective gain of \(b_0\) and a single pole and a single zero (with values \(a_1\) and \(-b_1/b_0\), respectively) (cf., APPENDIX). The system pole and zero suffice to describe how subjects use sensorimotor memories of perturbation and error to influence performance on subsequent trials. We note that in all cases, \(|a_1| < 1\), and thus the adaptive behaviors we observed were stable.

Model coefficients varied systematically across sensory feedback condition (Fig. 7, A–C) but not direction. Model parameter \(a_1\) (the adaptation model pole) quantifies the extent to which memories of prior performance errors influence subsequent reaches. Two-way, repeated-measures ANCOVA found a main effect of simple sensory feedback training condition on \(a_1\) [V, P, VP: \(F_{2,80} = 48.24, P < 0.0005\)], but no effect of movement direction [OUT, ACROSS: \(F_{1,86} = 0.62, P = 0.432\)] and no interaction between the two factors [\(F_{2,80} = 1.68, P = 0.193\)]. We observed no effect of either covariate (mean or SD of peak movement extent) on this parameter. After collapsing across directions, average \(a_1\)
values in the P condition (0.49 ± 0.12) were significantly larger than those in either the VP (0.19 ± 0.12) or V condition (0.21 ± 0.11) (T_{18} > 9.0 and P < 0.0005 in both cases), which did not differ from each other (T_{18} = 0.39, P = 0.92).

The effective transfer function gain $b_0$ quantifies the overall ability of subjects to reject perturbations in the different feedback conditions. (The parameter $b_0$ is analogous to the subject’s effective “compliance” with the perturbations, but should not be confused with the limb’s mechanical compliance). Two-way, repeated-measures ANCOVA found a main effect of simple sensory feedback training condition on $b_0$ [V, P, VP: $F_{(2,86)} = 311.78, P < 0.0005$], but no effect of movement direction [OUT, ACROSS: $F_{(1,86)} = 1.51, P = 0.222$]. We observed no effect of either covariate (mean or SD of peak movement extent) on this parameter. After collapsing across directions, average $b_0$ values in the V condition ($-2.06 ± 0.45 \times 10^{-4} \text{ m}^2/\text{N}$) were significantly larger in magnitude than those in either the P ($-0.94 ± 0.27 \times 10^{-4} \text{ m}^2/\text{N}$) or VP condition ($-0.81 ± 0.25 \times 10^{-4} \text{ m}^2/\text{N}$) ($T_{18} > 15.5$ and $P < 0.0005$ in both cases), which did not differ from each other ($T_{18} = 1.83, P = 0.17$).

A third two-way, repeated-measures ANCOVA revealed a main effect of training condition on the ratio $-b_1/b_0$ [$F_{(2,86)} = 8.35, P < 0.0005$], but no convincing effect of direction [$F_{(2,86)} = 3.79, P = 0.055$] and no interaction between the two factors [$F_{(2,86)} = 1.03, P = 0.363$]. The ratio $-b_1/b_0$ quantifies the relative influence of prior perturbations on performance. Again, we observed no effect of either covariate on this transfer function parameter. After collapsing across directions, average transfer function zero values in the P condition (0.92 ± 0.25) were significantly larger (i.e., closer to a value of 1.0) than those in either the VP (0.64 ± 0.24) or V condition (0.62 ± 0.17) ($T_{18} > 4.1$ and $P < 0.001$ in both cases), which did not differ from each other ($T_{18} = 0.31, P = 0.95$).

Differences in adaptation model coefficients imply differences in ability to compensate for perturbations when visual feedback was available vs. when it was absent. Frequency response functions estimated from the individual-subject adaptation models confirmed a differential ability to reject variable perturbations across the simple feedback training conditions (Fig. 7D). It is difficult to infer this information directly from the model coefficients themselves due to the nonlinear relationship between transfer function {pole, zero} values and the gain of the system function (APPENDIX). In Fig. 7D, we used the coefficients in Table 1 to obtain individualized response curves for each simple feedback training block, and then averaged the responses across subjects and directions within each condition. Each response curve was characteristic of a high-pass filter in that transfer function gain was lowest at low trial frequencies (as expected for adaptive responses that reduce the effect of biased load sequences like those we applied). Consistent with the trends observed in model parameter $b_0$, average response gain was lower in the P condition than during V training throughout the entire range of perturbation frequencies. Thus subjects were less effective in rejecting endpoint disturbances when vision alone drove the compensatory response vs. when proprioception provided meaningful performance feedback. Subjects were most effective at resisting perturbations when vision and proprioception provided consistent feedback of endpoint motion. This was particularly evident for midrange frequencies (e.g., at 0.1 oscillations per trial), where the VP curve was lower than both the V curve (paired t-test: $T_{18} = -14.18, P < 0.0005$) and the P curve ($T_{18} = -4.27, P = 0.004$).

We compared the influence of training condition on transfer function shape by aligning the transfer functions of Fig. 7D at the point of maximum gain (i.e., at a trial frequency of 0.5 oscillations/trial) (Fig. 7E). In effect, this operation discounts feedback-dependent differences in model parameter $b_0$. These offset-corrected transfer functions highlight differences in the frequency-dependency of perturbation rejection under the three simple training conditions. Similarity in transfer function {pole, zero} values in the V and VP conditions yielded similar −3-dB cutoff frequencies (~0.06 oscillations/trial) when visual feedback was present. When only proprioception was available, motor adaptation displayed a −3-dB cutoff frequency <0.02 oscillations per trial. That is, providing visual feedback enhances rejection of perturbations with higher trial frequencies (i.e., those between 0.02 and 0.06 oscillations/trial).

In summary, the overall load sensitivity in the VP condition was similar to that in the P training condition, reflecting similar $b_0$ values in the two cases. However, VP performance exceeded P performance at moderate trial frequencies due to visually-enhanced rejection of midfrequency perturbations resulting from similar processing of sensorimotor memories in the VP and V conditions. Because the model coefficients varied systematically across sensory feedback conditions, we conclude therefore that subjects did not use a unified multisensory prediction of load to compensate for the imposed environmental perturbations in our experiments (therefore rejecting Fig. 2A: model 1).
### Table 1. Model coefficients: V, P and VP conditions

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<th>VP</th>
</tr>
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<td>b0,a</td>
<td>-b1/b0</td>
<td>a1</td>
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<td>0.587</td>
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<tr>
<td>S11</td>
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<tr>
<td>S12</td>
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<td>Mean ±SD†</td>
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<td>0.050</td>
<td>-1.830</td>
<td>0.697</td>
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</table>

V, vision only; P, proprioception only; VP, consistent visual and proprioceptive feedback. *×10⁻⁴ m²/N. †Due to the nonlinear relationship between [pole, zero] values and the gain of the system function, it is possible to resolve erroneous conclusions when comparing frequency response functions estimated using population-averaged parameters. The preferred approach is to estimate individual responses before averaging across subjects (as in Fig 7).

### Adaptation Modeling—SC Condition

The MDL models identified using data from the SC trial blocks retained the fundamental structure of Eq. 10 for both the hand and cursor output equations, although this structure was augmented in each case with the addition of a single cross-modal input term:

\[
\begin{align*}
    e_i^C &= a_i^C e_{i-1}^C + b_{0i}^C K_i^C + b_{1i}^C K_{i-1}^C + d_i^C K_i^H \\
    e_i^H &= a_i^H e_{i-1}^H + b_{0i}^H K_i^H + b_{1i}^H K_{i-1}^H + d_i^H K_{i-1}^C
\end{align*}
\]

(11a)

(11b)

For cursor errors \( e_i^C \), the additional term was an influence of the current-trial hand perturbation \( K_i^H \) (Table 2) that was a likely consequence of the limb’s intrinsic compliance. For hand errors \( e_i^H \), the additional term was a memory correlated with the prior cursor perturbation \( K_{i-1}^C \). These results facilitate a comparison of system function poles and zeros across training conditions because Eqs. 11a and 11b can be viewed as a MIMO system, wherein each output reflects the superposition of two uncorrelated inputs.

Like Eq. 10, the hand error model of Eq. 11b has a single pole and a single zero in the relationship between hand perturbations and errors. Transfer function zero locations in the SC training blocks (OUT: \(-0.01 \pm 0.57\); ACROSS: \(0.41 \pm 0.24\)) were smaller than those during P training (\(T_{18} < 4.93\) and \(P < 0.0001\) in both directions), indicating that prior hand perturbations influenced subsequent performance considerably less in the SC trials than in P trials. Pole values in the SC training blocks (OUT: \(0.39 \pm 0.11\); ACROSS: \(0.40 \pm 0.13\)) did not differ from values in P training blocks. By contrast, the cursor model of Eq. 11a, which also has a single pole and a single zero in the relationship between perturbation and error, had pole locations (OUT: \(0.16 \pm 0.10\); ACROSS: \(0.30 \pm 0.16\)) and zero locations (OUT: \(0.48 \pm 0.15\); ACROSS: \(0.56 \pm 0.13\)) that did not differ systematically from those obtained in the V feedback condition.

Figure 7F plots the average cursor and hand frequency response curves from the SC training blocks, with the average V and P curves from Fig. 7D replicated for comparison. Relative to the P conditions, introducing a sensory conflict reduced error attenuation at low perturbation frequencies for both the hand (SC-Hand) and the cursor (SC-Cursor) (paired t-tests: \(T_{18} > 5.43\), \(P < 0.0005\) in each case). In contrast, the SC transfer function gains at the lowest frequency did not differ from those in the V condition (paired t-tests: SC-Hand

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[1] *J Neurophysiol* • doi:10.1152/jn.00314.2012 • www.jn.org
vs. V: T_{18} = 1.78, P = 0.392), and, if anything, steady-state cursor performance was slightly worse than in the V condition (SC-Cursor vs. V: T_{18} = 3.02, P = 0.028). The frequency response curves of the cursor and hand diverged at higher perturbation frequencies, with only the cursor retaining a high-pass behavior indicative of an adaptive response. In contrast, the hand demonstrated a low-pass response very different from those seen in the P and VP cases. Thus subjects appeared to discount proprioceptive feedback altogether when solving the SC target capture task, even though the average physical load (500 N/m) was greater than the average physical perturbation (480 N/m), and even though visual and proprioceptive perception of inherent uncertainty of visual and proprioceptive perception was varied considerably. Across subjects, assessment error averaged 3.64 cm in the P block and 1.96 cm in the V block (panel D), assessment errors averaged 1.96 ± 1.04 cm. Across subjects, assessment error averaged −3.64 cm in the P blocks and −1.33 cm in the V blocks.

**Control Experiment**

As shown for a representative subject (Fig. 8), target capture movements in the control experiment were smooth, they reversed direction near the target within the desired time interval, and they exhibited considerable variability induced by the unpredictable loads (panel A: P trial block; panel B: V block). As shown for a representative trial in each feedback condition (black hand path profiles and white assessment squares), subjects tended to underestimate peak movement extent during assessment. For the P trial block (panel C), assessment error in the final 60 trials averaged −4.85 ± 1.28 cm. In the V block (panel D), assessment errors averaged −1.96 ± 1.04 cm. Across subjects, assessment error averaged −3.64 cm in the P blocks and −1.33 cm in the V blocks.

We estimated the expected contributions of vision and proprioceptive load prediction in the SC task (i.e., values for w_v and w_p in Eq. 9) if MLE had indeed been used to combine sensory information (i.e., Fig. 2B; model 2). We quantified the inherent uncertainty of visual and proprioceptive perception of
Table 2. Model coefficients: SC condition

<table>
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<tr>
<th>Subject No.</th>
<th>Direction</th>
<th>( a_i^t )</th>
<th>( b_i^t )</th>
<th>(-b_i^t/a_i^t )</th>
<th>( a_i^c )</th>
<th>( b_i^c )</th>
<th>(-b_i^c/a_i^c )</th>
<th>( d_i^c )</th>
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</thead>
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<td>S01</td>
<td>Out</td>
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<td>-0.659</td>
<td>0.387</td>
<td>0.301</td>
<td>0.263</td>
<td>-2.110</td>
<td>0.569</td>
</tr>
<tr>
<td></td>
<td>Across</td>
<td>0.382</td>
<td>-1.120</td>
<td>0.493</td>
<td>0.284</td>
<td>0.304</td>
<td>-2.130</td>
<td>0.512</td>
</tr>
<tr>
<td>S02</td>
<td>Out</td>
<td>0.278</td>
<td>-0.769</td>
<td>-0.319</td>
<td>0.650</td>
<td>0.081</td>
<td>-1.810</td>
<td>0.519</td>
</tr>
<tr>
<td></td>
<td>Across</td>
<td>0.322</td>
<td>-1.409</td>
<td>0.522</td>
<td>0.312</td>
<td>0.211</td>
<td>-1.800</td>
<td>0.449</td>
</tr>
<tr>
<td>S03</td>
<td>Out</td>
<td>0.293</td>
<td>-0.986</td>
<td>-0.196</td>
<td>0.646</td>
<td>0.072</td>
<td>-2.080</td>
<td>0.399</td>
</tr>
<tr>
<td></td>
<td>Across</td>
<td>0.208</td>
<td>-0.921</td>
<td>0.516</td>
<td>0.275</td>
<td>0.096</td>
<td>-1.920</td>
<td>0.243</td>
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<tr>
<td>S04</td>
<td>Out</td>
<td>0.429</td>
<td>-0.810</td>
<td>0.309</td>
<td>0.542</td>
<td>0.320</td>
<td>-1.680</td>
<td>0.732</td>
</tr>
<tr>
<td></td>
<td>Across</td>
<td>0.588</td>
<td>-0.930</td>
<td>0.545</td>
<td>0.285</td>
<td>0.561</td>
<td>-1.570</td>
<td>0.745</td>
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<tr>
<td>S06</td>
<td>Out</td>
<td>0.408</td>
<td>-0.820</td>
<td>0.521</td>
<td>0.327</td>
<td>0.230</td>
<td>-2.040</td>
<td>0.462</td>
</tr>
<tr>
<td></td>
<td>Across</td>
<td>0.497</td>
<td>-1.020</td>
<td>0.751</td>
<td>0.354</td>
<td>0.466</td>
<td>-1.680</td>
<td>0.696</td>
</tr>
<tr>
<td>S07</td>
<td>Out</td>
<td>0.360</td>
<td>-0.150</td>
<td>-2.073</td>
<td>0.195</td>
<td>0.034</td>
<td>-1.770</td>
<td>0.305</td>
</tr>
<tr>
<td></td>
<td>Across</td>
<td>0.294</td>
<td>-1.150</td>
<td>-0.099</td>
<td>0.597</td>
<td>0.051</td>
<td>-1.840</td>
<td>0.576</td>
</tr>
<tr>
<td>S08</td>
<td>Out</td>
<td>0.407</td>
<td>-1.303</td>
<td>0.101</td>
<td>0.783</td>
<td>0.226</td>
<td>-2.028</td>
<td>0.696</td>
</tr>
<tr>
<td></td>
<td>Across</td>
<td>0.348</td>
<td>-0.718</td>
<td>0.302</td>
<td>0.364</td>
<td>0.168</td>
<td>-2.180</td>
<td>0.382</td>
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<tr>
<td>S09</td>
<td>Out</td>
<td>0.679</td>
<td>-1.370</td>
<td>0.578</td>
<td>0.169</td>
<td>0.411</td>
<td>-2.274</td>
<td>0.535</td>
</tr>
<tr>
<td></td>
<td>Across</td>
<td>0.309</td>
<td>-0.886</td>
<td>0.556</td>
<td>0.306</td>
<td>0.283</td>
<td>-2.370</td>
<td>0.406</td>
</tr>
<tr>
<td>S10</td>
<td>Out</td>
<td>0.394</td>
<td>-1.360</td>
<td>0.383</td>
<td>0.255</td>
<td>0.265</td>
<td>-1.990</td>
<td>0.416</td>
</tr>
<tr>
<td></td>
<td>Across</td>
<td>0.487</td>
<td>-0.729</td>
<td>0.171</td>
<td>0.125</td>
<td>0.163</td>
<td>-1.850</td>
<td>0.440</td>
</tr>
<tr>
<td>S11</td>
<td>Out</td>
<td>0.321</td>
<td>-1.080</td>
<td>0.237</td>
<td>0.743</td>
<td>0.242</td>
<td>-1.810</td>
<td>0.674</td>
</tr>
<tr>
<td></td>
<td>Across</td>
<td>0.213</td>
<td>-0.833</td>
<td>0.046</td>
<td>0.055</td>
<td>0.080</td>
<td>-2.450</td>
<td>0.155</td>
</tr>
<tr>
<td>S12</td>
<td>Out</td>
<td>0.518</td>
<td>-0.711</td>
<td>0.612</td>
<td>0.085</td>
<td>0.356</td>
<td>-1.960</td>
<td>0.462</td>
</tr>
<tr>
<td></td>
<td>Across</td>
<td>0.379</td>
<td>-0.859</td>
<td>-0.399</td>
<td>0.771</td>
<td>0.059</td>
<td>-2.250</td>
<td>0.524</td>
</tr>
<tr>
<td>S13</td>
<td>Out</td>
<td>0.425</td>
<td>-0.814</td>
<td>0.207</td>
<td>0.709</td>
<td>0.159</td>
<td>-2.100</td>
<td>0.548</td>
</tr>
<tr>
<td></td>
<td>Across</td>
<td>0.324</td>
<td>-0.623</td>
<td>0.069</td>
<td>0.341</td>
<td>0.063</td>
<td>-1.950</td>
<td>0.278</td>
</tr>
<tr>
<td>S14</td>
<td>Out</td>
<td>0.592</td>
<td>-0.961</td>
<td>0.860</td>
<td>0.199</td>
<td>0.694</td>
<td>-2.060</td>
<td>0.757</td>
</tr>
<tr>
<td></td>
<td>Across</td>
<td>0.565</td>
<td>-0.921</td>
<td>0.490</td>
<td>0.567</td>
<td>0.371</td>
<td>-2.100</td>
<td>0.714</td>
</tr>
<tr>
<td>S15</td>
<td>Out</td>
<td>0.385</td>
<td>-1.010</td>
<td>0.351</td>
<td>0.417</td>
<td>0.298</td>
<td>-1.760</td>
<td>0.608</td>
</tr>
<tr>
<td></td>
<td>Across</td>
<td>0.300</td>
<td>-0.864</td>
<td>0.172</td>
<td>0.542</td>
<td>0.222</td>
<td>-1.630</td>
<td>0.718</td>
</tr>
<tr>
<td>S16</td>
<td>Out</td>
<td>0.215</td>
<td>-1.580</td>
<td>0.147</td>
<td>0.798</td>
<td>0.072</td>
<td>-1.790</td>
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<tr>
<td></td>
<td>Across</td>
<td>0.434</td>
<td>-0.597</td>
<td>0.007</td>
<td>0.541</td>
<td>0.090</td>
<td>-2.020</td>
<td>0.438</td>
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<tr>
<td>S17</td>
<td>Out</td>
<td>0.275</td>
<td>-0.966</td>
<td>0.322</td>
<td>0.584</td>
<td>0.211</td>
<td>-1.910</td>
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</tr>
<tr>
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<td>Across</td>
<td>0.508</td>
<td>-0.740</td>
<td>0.166</td>
<td>0.519</td>
<td>0.169</td>
<td>-1.480</td>
<td>0.524</td>
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<tr>
<td>S18</td>
<td>Out</td>
<td>0.404</td>
<td>-1.600</td>
<td>0.406</td>
<td>0.138</td>
<td>0.421</td>
<td>-1.870</td>
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</tr>
<tr>
<td></td>
<td>Across</td>
<td>0.512</td>
<td>-0.561</td>
<td>-0.053</td>
<td>0.285</td>
<td>0.111</td>
<td>-1.880</td>
<td>0.402</td>
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<tr>
<td>S19</td>
<td>Out</td>
<td>0.474</td>
<td>-0.844</td>
<td>0.648</td>
<td>0.247</td>
<td>0.349</td>
<td>-1.750</td>
<td>0.541</td>
</tr>
<tr>
<td></td>
<td>Across</td>
<td>0.443</td>
<td>-0.795</td>
<td>-0.205</td>
<td>0.601</td>
<td>0.212</td>
<td>-1.990</td>
<td>0.583</td>
</tr>
<tr>
<td>S20</td>
<td>Out</td>
<td>0.304</td>
<td>-0.987</td>
<td>-0.069</td>
<td>0.441</td>
<td>0.125</td>
<td>-2.000</td>
<td>0.422</td>
</tr>
<tr>
<td></td>
<td>Across</td>
<td>0.394 ± 0.106</td>
<td>-0.762 ± 0.211</td>
<td>-0.008 ± 0.573</td>
<td>0.447 ± 0.184</td>
<td>0.160 ± 0.101</td>
<td>-1.973 ± 0.249</td>
<td>0.480 ± 0.152</td>
</tr>
<tr>
<td>Mean ± SD†</td>
<td>Out</td>
<td>0.400 ± 0.129</td>
<td>-1.080 ± 0.204</td>
<td>0.408 ± 0.241</td>
<td>0.394 ± 0.231</td>
<td>0.302 ± 0.159</td>
<td>-1.911 ± 0.176</td>
<td>0.557 ± 0.132</td>
</tr>
</tbody>
</table>
ories as used in the V condition. The adaptation model pole and zero values were similar to those in the V condition, whether the visual cursor tracked the hand faithfully (the VP case), or whether we experimentally dissociated motions of the hand and cursor (the SC training condition) (Fig. 7, A and C). The variances of hand and cursor motions were similar in the SC condition. Moreover, the inherent uncertainties of proprioceptive and visual perception of midmovement endpoint state were of comparable magnitudes (e.g., Fig. 8, C and D). Therefore, the influence of visual and proprioceptive memories on motor performance should have had comparable magnitudes in the SC condition, if subjects had used maximum-likelihood load prediction to drive adaptation, as predicted by adaptation models 1 and 2 (Fig. 2). Likewise, if prediction were determined by an MLE process driven by unequal and direction-dependent weightings of the two senses (van Beers et al. 2002b), load prediction should have been influenced by memories of both hand and cursor performance variables in a direction-dependent manner. Neither of these predictions was supported by our data. Instead, subjects resolved visuo-proprioceptive conflict by reducing the variability of visual performance errors at the expense of elevated hand variability. Only the cursor (not hand) displayed a trial-frequency response curve characteristic of an adaptive system. Cursor performance reflected predictions based exclusively on visual performance memories. Taken together, these results do not support sensorimotor adaptation models wherein vision and proprioception both contribute to an estimate of endpoint state at midreach, but instead support a switched-input model whereby vision overwhelmingly dominates memory-based load prediction.

Sensory Perception vs. Sensorimotor Control

There is disagreement between the results we have described and those reported by van Beers and colleagues (2002b), wherein people adapted reaching movements in a direction-dependent manner consistent with MLE integration of visual and proprioceptive feedback. In that study, subjects responded to brief (i.e., very limited) exposures to horizontal shear or scaling distortions of visual feedback that were applied gradually over the first 10 out of 12 movements made to a set of four targets. Only three movements were made to each target. Because the amount of adaptive change in reaches to visual and proprioceptive targets varied with the type of visual distortion experienced during training, the authors concluded that MLE integration was supported. In contrast, participants in our experiments were subjected to perturbations that varied dramatically from one trial to the next within blocks of 100
movements made to a single target. It is certainly possible that differences in the amount of exposure and/or in the statistics of the perturbation sequences (Burge et al. 2008) encouraged different forms of compensation in the two studies.

For example, there is considerable evidence indicating that the proprioceptive sense of limb position can drift relative to the visual representation of endpoint state (Paillard and Brouchon 1968; Scheidt et al. 2005; Wann and Ibrahim 1992), and that this bias develops rapidly, within seconds of visual occlusion (Paillard and Brouchon 1968; see Smeets et al. 2006 for an alternate interpretation of drift). In van Beers’ study, subjects were provided visual feedback of hand position to bring it to the starting position in preparation for each reach. This was done with the specific intent to minimize proprioceptive drift. In contrast, we did not provide veridical feedback during the SC testing block, which likely encouraged the development of bias in the proprioceptive representation of endpoint state (cf., Scheidt et al. 2005). Because the MLE model of Eq. 1 is optimal only under the assumption that sensory estimates are corrupted by zero-mean Gaussian noise, development of drift between proprioceptive and visual estimates of endpoint state would invalidate the optimality of that approach. Instead, allowing one sense to dictate behavior would facilitate optimization of performance for one endpoint (hand or cursor) at the expense of the other.

Another explanation is also plausible. Psychophysical evidence supports the idea that compensatory responses to perturbation involve both conscious “strategic perceptual-motor” responses and subconscious sensorimotor adaptations (Redding and Wallace 1993, 1996; see also Welch et al. 1974). These responses are dissociable in that sensorimotor adaptations can occur “implicitly” without subject awareness (Carine et al. 2007; Hatada et al. 2006; Klassen et al. 2005), they can occur “automatically” (Magescas and Prablanc 2006) in response to discrepancy between intended and realized task performance (Tseng et al. 2007) and can even occur at the expense of cognitive (explicit) strategies that fully compensate for the effects of perturbation (Mazzoni and Krakauer 2006). For example, if subjects are informed that cursor motion will be rotated 45° about the unseen hand’s starting point when reaching and that they should counter-rotate their aim by the same amount so that the cursor captures the target, they are unable to maintain implicit control and instead make increasingly large targeting errors with practice (Mazzoni and Krakauer 2006). Observations that strategic perceptual-motor responses arise and decay more quickly than subconscious adaptations (Carine et al. 2007; see also Redding and Wallace 1993, 2002) and are influenced differentially by concurrent performance of mental arithmetic (a distractor task) (Redding et al. 1992) further support the hypothesis that the two compensatory mechanisms reflect learning in separate neural pathways. Despite the fact that van Beers’ subjects reported that they did not notice the relatively rapid increase in perturbation strength over just a few trials per target, they nevertheless may have employed some strategic perceptual-motor compensation wherein visual and proprioceptive perceptions of hand position were combined in an optimal manner to drive the observed response. In contrast, several subjects in the present study spontaneously remarked that they thought their task unlearnable, even though they all used memories of prior perturbations and errors in an attempt to predict the imposed loads. Random perturbation in our study may have discouraged perceptual-motor compensations, thereby unmasking an implicit, switched-input multisensory prediction mechanism. Future studies should carefully consider the extent to which observed adaptations result from cognitive compensations (including postural and/or aim adjustments), sensory adaptations (including multisensory alignments), the adaptation of motor coordination patterns intended to achieve the desired task objectives (cf., Redding et al. 1992), as well as factors that drive the dominance of one sensory modality over another for prediction.

The Interpretation of Adaptation Model Parameters

The APPENDIX describes fundamental relationships between time-domain, frequency-domain and state space representations of memory-based adaptation. The three representations are complementary in that each provides unique insight into how the brain adapts motor commands to stabilize performance about some desired value. State space and time-domain analyses are parametric and yield different perspectives on how sensorimotor memories are used to counter environmental perturbation. State space analysis has been employed effectively to identify limits of generalization of adaptation (i.e., tuning curves) as a function of movement direction, velocity and extent for physical and visuomotor perturbations (Donchin et al. 2003; Hwang et al. 2003; Krakauer et al. 2000; Liu et al. 2011; Thoroughman and Shadmehr 2000). State space analysis also provides a means of evaluating the overall stability of adaptation. Time domain analyses reveal explicitly how sensorimotor memories can give rise to predictive behavior (Eq. 9; see also Scheidt et al. 2012). Prediction is one of the most useful things a mind can do (Minsky 1985) as it facilitates planning and execution of actions that will achieve desired outcomes without resorting to trial and error. Because there exist multiple equivalent state- and time-domain representations of any given system (differing in their definition of state; cf., Eqs. 11 vs. A15), one is free to choose a representation to use as a tool for interpreting performance changes. As a result, the definition of state is arbitrary, and one should be circumspect when interpreting models that depend on any particular definition of state. In contrast, the frequency-domain representation is nonparametric and yields the same frequency response function for all equivalent model structures and parameter sets. The frequency response characterizes how well adaptive systems reject disturbances, spanning the range from very low frequency, steady-state perturbations to high frequency, erratic perturbations. As demonstrated in the APPENDIX, small changes in the weights of memory-based adjustments to motor commands can have profound effect on both the long-term (steady-state) and short-term (high-frequency) resistance to perturbation (cf., Fig. 9, C and D).

Here, our analyses focused primarily on the time- and frequency-domain representations, as both are necessary for interpreting the experimental results. In the SC training condition, visual and proprioceptive feedback were forced to be in conflict, and we found the relationship between cursor errors and $K^C$ to be indistinguishable from that observed with V training. Remarkably, transfer function pole and zero values relating hand errors and recent perturbations in the VP condition also were indistinguishable from those observed during V training. (Recall that cursor motion tracked the hand faithfully...
in the VP condition and so cursor error was equivalent to hand error just as the sequence $K^E$ was equivalent to $K^C$ in that case.) Functionally however, rejection of low-frequency disturbance in the VP case was similar to that observed during P training without vision. The contrasting time- and frequency-domain results in the VP condition can be reconciled if we note that model parameter $b_0$ modulates the overall gain of the transfer function (see Eq. A5; cf., Fig. 8D, compare traces d and f). Whereas $b_0$ was low in the absence of visual feedback, and, when visual and proprioceptive feedback concurred, $b_0$ rose dramatically when subjects were compelled (V condition) or induced (SC condition) to rely solely on visually-guided adaptation. The observed variations in $b_0$ do not likely arise from an increase in limb muscle coactivity and an increase in limb impedance whenever feedback uncertainty increases. If that were the case, limb compliance should have been least (and hand error variability lowest) in the SC condition wherein we perturbed both the hand and the cursor randomly. Instead, hand variability increased (and thus hand compliance increased) in the SC condition relative to the VP case, further supporting the conclusion that subjects largely discounted proprioceptive feedback in the presence of substantial multisensory conflict.

Korenberg and Ghahramani (2002) proposed that motor learning can be viewed as the formation of a mapping from $n$ sensations $S(t)$ onto motor output $O(t)$: $O(t) = \sum w_i S_i(t)$. According to this view, the adaptive system models its environment by identifying a set of weights ($w$ values) that yield desired behaviors. As we have shown (Fig. 6), memories of sensations play a particularly important role in motor learning because they can be used to compose an explicit prediction of a pending load (Eq. 9). Prediction contributes to the formation of feedforward motor commands and the restoration of desired behavior (or, equivalently, a desired sensation), despite environmental disturbance. As such, we regard prediction as the output of an “internal model” of the limb’s mechanical environment, a model that is instantiated by the weights applied to sensorimotor memories.

It has recently been suggested that the brain adapts motor behaviors differently when errors are caused by factors within the body or by disturbances in the extrinsic world (Berniker and Koerding 2008). According to one model (Wei and Koerding 2009), adaptive trajectory corrections are approximately proportional to the size of prior disturbances when errors are small (less than ~2 cm) and likely of intrinsic origin (e.g., sensory transduction noise and motor execution variability). For errors larger than 2 cm (and thus unlikely to result from intrinsic variability), the adaptive response flattens in a sublinear manner (see also Marko et al. 2012). In our SC training condition, participants frequently experienced conflicting hand and cursor errors, and both would be considered “large” by the definition of Wei and Koerding. Because cursor error variability exceeded that of the hand, subjects could have devalued visual errors as irrelevant environmental noise during reaching, emphasizing proprioceptive feedback so as to bring the hand (not cursor) to its remembered target location as in the P and VP conditions. They did not do so in the SC condition and instead discounted proprioceptive memories of prior perturbations, especially in the OUT direction, thereby bringing the “proprioceptive zero” location close to the origin of the complex $z$-plane, resulting in visual domination of adaptive performance. This result makes sense if we consider that the subjects may have interpreted the task as requiring visual rather than physical target capture. If so, visual perturbations would be most task-relevant, whereas physical perturbations and hand trajectory errors could be considered “irrelevant” noise unworthy of compensation. Based on this logic, one could propose a task-based version of the Wei and Kording model, wherein trajectory compensations are initiated when errors are relevant to task execution but ignored when errors are irrelevant (cf., Latash et al. 2002; Scholz and Schoner 1999; Todorov and Jordan 2002). Indeed, a previous study has shown that, when a deterministic viscous curl field is applied to the hand, adaptation is precluded when cursor feedback is manipulated to minimize visual trajectory errors (Scheidt et al. 2005). Such behavior is not consistent with adaptation models wherein the senses jointly contribute to an optimal state estimate (e.g., Fig. 2A) or load prediction (Fig. 2B) (see also Denève et al. 2007).

On the Nature of Reaching

One might question whether it is fair to interpret what subjects did in our V task as “reaching.” The arm itself did not move, but subjects applied isometric forces to a hand-held tool to control displacement of the point-mass visual cursor. As emphasized by Gordon and Ghez (Ghez and Gordon 1987; Gordon and Ghez 1984), targeted isometric force impulses share with displacements many of the same challenges of neuromuscular control. In both cases, preprogramming of action is necessary to overcome the low-pass filtering action of the musculoskeletal system, which distorts and delays the effects of central commands (Ghez and Gordon 1987). Control of rapidly rising force trajectories requires precisely timed and coordinated actions in sets of opposing muscles (Ghez and Gordon 1987; Gordon and Ghez 1984) similar to the triphasic pattern seen in rapid voluntary limb displacements (Hallett et al. 1975; Scheidt et al. 2011). Moreover, reaching does not generally require the hand itself to acquire the spatial goal, because it is possible to extend one’s reach using a pole, rake or other tool. Depending on the mechanical properties of the tool (e.g., its stiffness and inertia), the trajectory of the tool tip can differ greatly from that of the hand, and yet the reach objective may be readily attained (cf., Dingwell et al. 2002). Indeed, a primary objective of brain-machine interface research is the development of tools and algorithms that will allow the brain to control reaching and grasping actions of robotic arms in the absence of limb movement (Carmena et al. 2003). It is highly unlikely that our subjects had adopted unique reach and nonreach solutions to the target capture task because they combined sensorimotor memories similarly when predicting pending loads in the V, VP and the SC (cursor) training conditions, despite the fact that the arm was clearly moving in the later two cases, but not in the first. We believe it reasonable therefore to conclude that subjects were in fact reaching, even in the isometric V training condition.

Limitations and Future Directions

Disagreement between our observations of visual capture during the VP and SC test blocks and the predictions of maximum-likelihood models of motor adaptation, wherein ~37% of the predicted load should have been driven by proprioceptive estimates of endpoint state, suggests either that our subjects were performing suboptimally, or that one or more
of the fundamental assumptions underlying the maximum likelihood models were violated. As noted above, MLE assumes that sensory noises are Gaussian-distributed with zero mean, but proprioceptive sensation is thought to “drift” in the absence of frequent visual recalibration (Wann and Ibrahim 1992; see also Scheidt et al. 2005). Developing a means to quantify visual and proprioceptive uncertainty and bias as they contribute to the subconscious control of movement, rather than the conscious perception of endpoint state as done here, would facilitate an understanding of which task features might promote MLE for action and which preclude it. However, our observation of visual capture of memory-based adaptation in the VP condition (Fig. 7E) implies that proprioceptive drift, which is precluded by veridical visual feedback in this case, is not the sole factor contributing to failure of MLE models in our experiments.

Another limitation of this study is the fact that all of the targeted movements were nominally 10 cm in length, and thus changes in movement extent were highly correlated with variations in hand force. It may be possible to disambiguate the contributions of sensory feedback sources related to hand force (or joint torque) from those related more explicitly to movement kinematics in a future study by varying intended movement extent in a manner uncorrelated with variations in load stiffness. Another limitation stems from the fact that kinematic errors arose only after the time of peak acceleration, which limited the subject’s ability to use online feedback to compensate for performance errors that occurred midmovement. Recent experimental studies have found that the brain likely implements separate feedforward controllers governing the initial reach trajectory and the limb’s final stabilized posture (Ghez et al. 2007; Humphrey and Reed 1983; Sainburg et al. 1999; Scheidt and Ghez 2007; Scheidt et al. 2011; Wang and Sainburg 2005). Again, it may be possible to test the proposed independence of the different control actions by monitoring and modeling responses to uncorrelated sequences of perturbations that are judiciously timed to favor adaptation of the initial movement vector (cf., Krakauer et al. 2000; Pine et al. 1996) or the final stabilized limb posture (Scheidt and Ghez 2007). Finally, we have only considered models of sensorimotor adaptation that use scalar estimates of sensorimotor state, whereas the brain likely has access to a richer, time-dependent representation of limb state (but see Fine and Thoroughman 2006). Future studies should continue efforts to understand how the time history of motor commands within each movement is adjusted based on performance errors on prior trials (cf., Sing et al. 2009).

The results we described have implications for the rehabilitation of neuromotor injury (e.g., stroke). If the different senses yield separate but complementary estimates of state, and if these estimates contribute to separate predictions of environmental load (as suggested in Fig. 2C), then damage to one adaptive pathway might be mitigated by sensory substitution training that promotes reliance on residual sensorimotor pathways (cf., Bach-y-Rita et al. 1969; Bach-y-Rita and Kercel 2003; Chen et al. 2006; Ghez et al. 2000). If, however, damage extends to mechanisms that mediate switching between competing information streams (cf., Haruno et al. 2001; Wolpert et al. 1998) then viable predictions formed by intact pathways (cf., Haruno et al. 2001; Wolpert et al. 2003; Chen et al. 2006; Ghez et al. 2000). If, however, damage extends to mechanisms that mediate switching between competing information streams (cf., Haruno et al. 2001; Wolpert et al. 2003; Chen et al. 2006; Ghez et al. 2000). If, however, damage extends to mechanisms that mediate switching between competing information streams (cf., Haruno et al. 2001; Wolpert et al. 2003; Chen et al. 2006; Ghez et al. 2000). If, however, damage extends to mechanisms that mediate switching between competing information streams (cf., Haruno et al. 2001; Wolpert et al. 2003; Chen et al. 2006; Ghez et al. 2000).

The focus of our study is motor adaptation, a process by which the brain can learn to recover some desired performance after the onset of an environmental disturbance. A characteristic of real-world disturbances is that they are often unpredictable: perturbing stimuli can disappear as suddenly and unexpectedly as they appear. Because the ability of an adaptive system to reject disturbances can vary depending on how frequently the disturbances appear and disappear, it is natural to apply frequency domain analysis techniques to characterize motor adaptation. This appendix motivates that analytic approach.

Motor adaptation can be characterized as a discrete-time process that transforms sensorimotor memories obtained during one iteration of a movement into motor commands that compensate perturbations on subsequent movement attempts (Donchin et al. 2003; Scheidt et al. 2001; Thoroughman and Shadmehr 2000). Each attempt (or trial) gives rise to a sample of sensory information from which task performance can be assessed and motor commands updated. Because sensorimotor memories must be retained at least until the next trial is initiated, adaptive responses to environmental perturbation have an inherent sampling interval of one trial. When arm movements are suddenly exposed to novel environmental dynamics, people gradually recover their original desired hand path kinematics within several trials (Shadmehr and Mussa-Ivaldi 1994), and thus adaptation demonstrates a nontrivial dynamic response to perturbation. Previous studies have found that kinematic performance errors $e_n$ on any given trial $n$ can be predicted with high fidelity solely from the field strength on that trial ($K_n$) and from the field strength and error exhibited on the previous trial ($K_{n-1}$ and $e_{n-1}$, respectively) (Scheidt et al. 2001; Takahashi et al. 2001):

$$ e_n = a_1 e_{n-1} + b_0 K_n + b_1 K_{n-1} $$

Equation A1 describes an autoregressive model of the trial-by-trial evolution of performance errors because the output $e_n$ depends on a prior version of itself (i.e., $e_{n-1}$). Computer simulations (Scheidt et al. 2001) demonstrate that this model can capture salient features of human motor adaptation, including the gradual recovery of desired performance and transient catch trial errors described by Thoroughman and Shadmehr (2000), as well as an inability to learn and/or unlearnable stability such as may occur in certain disease conditions (cf., Shabbott et al. 2013).

The $z$-transform $Z[-]$, a generalization of the Fourier transform, is commonly used to analyze the dynamic responses of discrete-time systems (cf., Oppenheim and Schafer 1989):

$$ Z[x[n]] = \sum_{n=-\infty}^{\infty} x[n] z^{-n} = X(z) $$

where $z$ is a complex variable $z = r e^{i\omega}$. Note that when $z$ is constrained to have unit magnitude (i.e., $|z| = 1$), the $z$-transform corresponds to the Fourier transform, with $\omega$ being the angle between a vector from the origin to a point $z$ on the unit circle and the real axis of the complex $z$-plane (Fig. 9A).

If we let $X(z)$ denote the $z$-transform of $x[n]$, then we may use the time-shifting property of the $z$-transform (cf., Oppenheim and Schafer 1989):

$$ X(z) = \sum_{n=-\infty}^{\infty} x[n] z^{-n} = Z[x[n]] $$

where $z$ is a complex variable $z = r e^{i\omega}$. Note that when $z$ is constrained to have unit magnitude (i.e., $|z| = 1$), the $z$-transform corresponds to the Fourier transform, with $\omega$ being the angle between a vector from the origin to a point $z$ on the unit circle and the real axis of the complex $z$-plane (Fig. 9A).
Fig. 9. Frequency-domain analysis of memory-based motor adaptation (APPENDIX). A: the unit circle in the complex z-plane as used to analyze the frequency response of sensorimotor adaptation in this paper. Transfer function zeros are represented as open circles, and poles as x’s. Trial frequency \( \omega \) is the angle between the real axis of the complex z-plane and a vector pointing from the origin to a point \( z \) on the unit circle. B: transfer function response gain vs. trial frequency (units: trial\(^{-1}\)) for a representative “high-pass” system with a pole at \( z = 0.31 \) and a zero at \( z = 0.84 \) (solid line) and a representative “low-pass” system with a pole at \( z = 0.84 \) and a zero at \( z = 0.31 \) (dashed line). The horizontal dotted line indicates a gain of \(-3\) dB. Pole-zero plot (C) for the analysis of sensitivity of the frequency response function (FRF) to variations in zero location. The thick line is the response for a system with a pole at 0.3 and a zero at 0.8 with a gain of 1.0. The dashed line is the response for a system with a pole at 0.3 and a zero at 0.8 with a gain of 1.707 (+3 dB), showing that modification of the transfer function gain \( b_0 \) shifts the entire FRF vertically. Im, imaginary; Re, real.

1989) to obtain the z-transform of \( x[n - 1] \) (i.e., the memory of \( x[n] \) retained for 1 trial):

\[
Z\{x[n - 1]\} = X(z)z^{-1}
\]

where the term \( z^{-1} \) is the time delay operator. The z-transform of Eq. A1, therefore, can be written:

\[
E(z) = a_0 z^{-1} E(z) + b_0 K(z) + b_1 z^{-1} K(z)\]

from which we derive the system transfer function of Eq. A1:

\[
H(z) = \frac{E(z)}{K(z)} = \frac{(b_0 + b_1 z^{-1})}{(1 - a_0 z^{-1})} = \frac{\left[ z - \left(\frac{-b_1}{b_0}\right) \right]}{(z - a_1)}
\]

This function provides a closed-form description of how the system output \( E(z) \) responds to an arbitrary input \( K(z) \). For example, the system’s steady-state response can be obtained by analyzing the system function when \( z = 1 \) (i.e., \( z \) is on the unit circle with \( \omega = 0 \)). If \( K_\omega \) is a nonzero value that does not change from trial to trial (i.e., the trial frequency \( \omega = 0 \)), the steady-state response gain is \( H(z) = b_0 (1 + b_1/b_0)/(1 - a_1) \). If \( b_1/b_0 = -1 \), then \( H(z) = 0 \) when \( \omega = 0 \), corresponding to ideal steady-state compensation for the perturbation. The value \(-b_1/b_0\) is referred to as a “zero” of the system function \( H(z) \), and zeros are represented on the z-plane as open circles (Fig. 9A). If instead \( a_1 \) approaches the value 1, the system’s response to steady-state perturbations will approach infinity (an unstable adaptive response). The value \( a_1 \) is referred to as a “pole” of the system function \( H(z) \), and each pole is represented by an “x” on the z-plane (Fig. 9A).

It is helpful to consider that for system functions having a single pole and a single zero, the magnitude of the response at any specific perturbation frequency \( \omega_p \) may be determined graphically as the ratio of lengths of two vectors: the first being from the system zero located at \(-b_1/b_0\) to a point \( z_p \) on the unit circle (the zero vector) and the second from the system pole \( a_1 \) to \( z_p \) (the pole vector). To determine the system’s frequency response at all perturbation frequencies, we evaluate this ratio along the unit circle from \( \omega = 0 \) (the steady-state or “dc” condition) to \( \omega = \omega_{\text{max}} \) where \( \omega_{\text{max}} \) is 0.5 trial\(^{-1}\) or one-half the sample rate of 1 sample per trial.

When the system pole and zero are oriented as shown in Fig. 9A (gray symbols), the corresponding frequency response is shown in Fig. 9B (solid trace). In this case, high-frequency inputs are passed through to the output, whereas the influence of low-frequency input signals is attenuated (reduced) in the output. This type of response is a “high-pass filter” response and is typical of adaptive systems where effects of steady-state perturbations are to be minimized. If instead the pole and zero locations were switched, the corresponding frequency response would be as shown in Fig. 9B (dashed trace). In that case, low-frequency inputs are passed on to the output, whereas high-frequency inputs are attenuated (a low-pass response). By convention, the frequency at which the response function gain has fallen 3 dB from its peak value is regarded as the filter’s cutoff frequency. Systematic variation in the system zero location (Fig. 9C) leads to systematic changes in the system’s frequency response function (Fig. 9D). Changing the value \( b_0 \) adjusts the overall gain of the response (Fig. 9D, compare traces d and f).

Adaptive systems with more complex dynamics. This analytic approach is easily extended to systems with more complex dynamics, such as those having both fast and slow adaptive responses (Smith et al. 2006; Lee and Schweighofer 2009). Consider a case wherein the response to a step application of perturbation (\( K u_p \)) is the sum of two real exponential functions of trial number \( n \):

\[
e_n = 0.75^a K u_a + 0.92^b K u_a
\]

The first exponential (i.e., 0.75\(^a\)) reflects a “fast” component of learning with a time constant of about 3 trials, while the second
exponential (0.92) reflects a “slow” component with a time constant of about 12 trials (cf., Smith et al. 2006). Using Eq. A2 and the familiar formula for the sum of terms of a geometric series, we obtain the $z$-transform of Eq. A6 as:

$$E(z) = \frac{1}{K(z)} \left[ \frac{1}{1 - 0.75 z^{-1}} \right] + \frac{1}{(1 - 0.92 z^{-1})} = \frac{2(1 - 0.84 z^{-1})}{(1 - 0.75 z^{-1})(1 - 0.92 z^{-1})} \quad (A7)$$

Note that the system function of Eq. A7 corresponds to a difference equation in the form of Eq. A1 having only one additional memory term corresponding to $e_{n-2}$:

$$e_a = 1.67 e_{n-1} - 0.69 e_{n-2} + 2.0 K_a - 1.67 K_{n-1} \quad (A8)$$

Note also that when Eq. A7 is rewritten in pole-zero form, we see that the new system has two poles and two zeros:

$$E(z) = \frac{2z(1 - 0.84 z^{-1})}{(z - 0.75)(z - 0.84)} \quad (A9)$$

The poles are located at $z = 0.75$ and $z = 0.92$ in the complex plane, and the zeros are located at $z = 0.84$ and the origin.

Adaptive systems with multiple inputs and multiple outputs. This analysis also extends to systems with more than one input and one output, as exemplified in the adaptation model of Eqs. 5a and 5b. To the extent that linear models suffice to describe adaptive motor behavior in people, performance must conform to the rule of superposition, which states that the combined response to separate signals applied simultaneously to the two inputs is equal to the sum of the responses obtained when each signal is applied alone. Superposition implies that model coefficients obtained via separate application of the two input perturbation sequences should equal those obtained when the perturbations are applied simultaneously. This prediction is tested by the SC condition of our experiments.

A state-space representation of the MIMO adaptation model. Equations 11a and 11b and Table 2 provide a MIMO model of the trial-by-trial evolution of performance errors obtained by applying systems identification analysis to human reach data. We convert Eq. 11 into state space form:

$$X_{i+1} = AX_i + BU_i \quad (A10)$$

by defining the input vector $U_i = [K_{iC}, K_{iH}]^T$ and the state vector $X_i = [x_iC, x_iH]^T$, where $T$ is the transpose operator, and the states are taken to be a weighted combination of all current-trial sensory information:

$$x_iC = e_iC - b_0K_{iC} - d_0K_{iH} \quad (A11a)$$

and

$$x_iH = e_iH - b_0K_{iH} \quad (A11b)$$

Invoking the time delay operator $z^{-1}$, we obtain:

$$x_iC = z^{-1}[a_1C e_iC + b_1C K_{iC}] \quad (A12)$$

$$x_iH = z^{-1}[a_1H e_iH + b_1H K_{iH} + d_1H K_{iC}] \quad (A12)$$

Substituting Eq. A11 for $e_iC$ and $e_iH$ in Eq. A12 yields:

$$z x_iC = a_1C (x_{i-1}C + b_0K_{iC} + d_0K_{iH}) + b_1C K_{iC} \quad (A13a)$$

or, equivalently

$$x_{i+1} = a_1C (x_{i-1}C + b_0K_{iC} + d_0K_{iH}) + b_1C K_{iC} \quad (A14a)$$

Rearranging Eqs. A11 and A14 yields a MIMO state space model:

$$[x_{i+1}C, x_{i+1}H] = \begin{bmatrix} a_1C & 0 \\ 0 & a_1H \end{bmatrix} [x_iC, x_iH] + \begin{bmatrix} a_1B_0 + b_1C & a_1D_0 \\ d_1H b_0 + b_1H & d_1H + d_1H \end{bmatrix} \begin{bmatrix} K_{iC} \\ K_{iH} \end{bmatrix}$$

where the output vector is $Y_i = [e_iC, e_iH]$, and the parameter matrices are arranged in the form of Eq. A10:

$$A = \begin{bmatrix} a_1C & 0 \\ 0 & a_1H \end{bmatrix}, B = \begin{bmatrix} a_1B_0 + b_1C \\ d_1H b_0 + b_1H \end{bmatrix}, C = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}, \text{ and } D = \begin{bmatrix} b_0 & d_0 \\ 0 & b_0 \end{bmatrix}$$

Asymptotic stability of sensorimotor adaptation is assured if the eigenvalues of the system $A - AI = 0$ all lie within the unit circle (i.e., $|\lambda| < 1$), otherwise the adaptive system is unstable for $i \to \infty$.

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

Author Contributions

Author contributions: T.N.J. and R.A.S. performed experiments; T.N.J. and R.A.S. analyzed data; T.N.J. and R.A.S. interpreted results of experiments; R.A.S. drafted manuscript; R.A.S. conception and design of research; R.A.S. approved final version of manuscript.

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