Adaptation to sensory–motor reflex perturbations is blind to the source of errors

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In the study of visual–motor control, perhaps the most familiar findings involve adaptation to externally imposed movement errors. Theories of visual–motor adaptation based on optimal information processing suppose that the nervous system identifies the sources of errors to effect the most efficient adaptive response. We report two experiments using a novel perturbation based on stimulating a visually induced reflex in the reaching arm. Unlike adaptation to an external force, our method induces a perturbing reflex within the motor system itself, i.e., perturbing forces are self-generated. This novel method allows a test of the theory that error source information is used to generate an optimal adaptive response. If the self-generated source of the visually induced reflex perturbation is identified, the optimal response will be a reflex gain control. If the source is not identified, a compensatory force should be generated to counteract the reflex. Gain control is the optimal response to reflex perturbation, both because energy cost and movement errors are minimized. Energy is conserved because neither reflex-induced nor compensatory forces are generated. Precision is maximized because endpoint variance is proportional to force production. We find evidence against source-identified adaptation in both experiments, suggesting that sensory–motor information processing is not always optimal.

Keywords: visual–motor adaptation, movement planning, plasticity


Introduction

Adaptation is a fundamental feature of the neural control of visually guided movement, by which organisms maintain a predictable relationship between desired and actual movement outcome. Previous investigations of visual–motor adaptation have used a visual or motor perturbation (Held & Freedman, 1963; Lackner & Dizio, 1994; Optican & Miles, 1985; Shadmehr & Mussa-Ivaldi, 1994; von Helmholtz, 1909/1962), where an invariant outcome is maintained when compensatory muscle torques are produced to eliminate the effect of the perturbation. Regardless of whether that perturbation is produced by a force field or target displacement, adaptation in these contexts always consists of a change in motor plan. For example, for a force perturbation, typically after several perturbation trials, subjects produce a compensatory force that is the mirror image of the applied force, approximately restoring unperturbed (on-target) trajectories; such compensatory forces also lead to a negative aftereffect when the force is removed (Figure 1A). Instead, we apply perturbations via a visual–motor reflex induced by slow drift of a large-field visual stimulus. This “visual drift” perturbs an ongoing reach in the direction of the visual motion (the “manual following response” [MFR]; Saijo, Murakami, Nishida, & Gomi, 2005; Whitney, Westwood, & Goodale, 2003). Our experiments therefore have the unusual feature that perturbing forces are self-generated and disturb the results of an existing, effective movement plan. Adaptation to such a visual–motor reflex could proceed along the same lines, with both a compensatory force generated to counteract the reflex and a negative aftereffect once the visual drift is removed (Figure 1B). However, in this situation, a second viable compensatory response is possible: purely neural compensation via gain control mechanisms (e.g., Lacquinti & Soechting, 1984; Nashner, 1976). Reducing the gain of the perturbing visuomotor reflex would allow the original pre-exposure motor plan to continue to be used and, in addition, would produce no negative aftereffect when visual drift is removed (Figure 1C).

For the motor system, which is capable of both force-based and gain control-based adaptive responses, the method of adaptation exhibited in our experiments has important theoretical implications. Gain-based adaptation is the optimal adaptive response to a self-generated perturbation, both in the sense of minimizing energy costs and maximizing movement precision. Energy is conserved because reflex-induced forces cease to be generated. Movement precision is maximized because endpoint error variance is proportional to force production (Harris & Wolpert, 1998).
Figure 1. Hypothetical patterns of adaptation to perturbed reaches. (A) External force perturbation. The pre-exposure reach is a normal reach (here shown as straight, although typical reaches are gently curved). Initial force-perturbed reaches are pushed off course by an external force. After a dozen or so reaches, force-based adaptation occurs. This results from a mechanism that adds the mirror image of the applied forces to the reach plan as a compensatory response. When the perturbation is removed, the compensatory response causes the reach to be perturbed in the opposite direction (aftereffect). (B) When a visual–motor reflex perturbation is used in place of an external force, one possible strategy is to produce a compensatory force. This will again lead to an aftereffect when the MFR-generating visual drift is removed. (C) However, in the case of reflex perturbation, a second strategy is to turn down the gain of the visual–motor reflex itself. Because this adaptive response produces no motor response to visual motion (or its absence), no aftereffect occurs when visual drift is removed.
Gain-based adaptation is only possible when perturbations are internally generated (as in the movement reflex we employ). The motor system can switch between gain- and force-based adaptation only if it can infer the causes of motor errors (motor noise, external force perturbation, motor reflex, etc.). Based on modeling work (Berniker & Körding, 2008), it has been proposed that the motor system assigns credit for each motor error across potential causes, adapting optimally based on those causes. Here, we provide an experimental test of this theory in which gain-based adaptation is the efficient adaptive response when the credit assignment problem is correctly solved.

Previous experimental work has provided only ambiguous evidence concerning this question. One might predict a lack of gain-based adaptation based on the work of Saijo et al. (2005), who show that the MFR is present over repeated reaches, or Aivar, Brenner, and Smeets (2008), who demonstrate that an inefficient trajectory correction occurs repeatedly. However, neither experiment was designed to test this theory, and consequently, they report only average data that give no indication of whether the sizes of these effects diminish over trials. In addition, the movement tasks they used do not strictly require that subjects correct their reflex-induced errors (Aivar et al., 2008; Saijo et al., 2005). On the other hand, source identification might be predicted from the many reports of reflex gain control, including instances where gain control mechanisms appear to be sensitive to the movement context (e.g., Das, Dell’Osso, & Leigh, 1999; Pruszynski, Kurtzer, & Scott, 2011). However, this does not necessarily imply that such effects, though optimal, are a general component of sensory-motor adaptation. We report two experiments to directly test the source identification theory of Berniker and Körding (2008). The first distinguishes between gain- and force-based adaptation by examining the aftereffect of adaptation to a predictable reflex perturbation of visually guided reaches and shows that the optimal gain-based adaptive strategy is not used. The second provides an independent test of the presence of gain-based adaptation by measuring the response to an unpredictable reflex perturbation. The second experiment also allows us to examine the possible role of impedance control mechanisms and of a possible mixture of gain- and force-based adaptation to these reflex perturbations. The results of both experiments clearly indicate that gain-based adaptation, although optimal in this context, is not used.

### Methods

### Subjects

Eight naive subjects participated in two experiments. Subjects were asked to complete two sessions, over 2 days (one session for rightward-perturbed reaches and one for leftward-perturbed reaches during the predictable drift experiment, order randomized across subjects).

### Apparatus

Subjects were seated in a dimly lit room 42.5 cm away from a frontoparallel transparent polycarbonate screen mounted flush to the front of a 21” computer monitor (Sony Multiscan G500, 1920 × 1440 pixels, 60 Hz). Reach trajectories were recorded using a Northern Digital Optotrak 3D motion capture system with two 3-camera heads located above left and above right of the subject. Subjects wore a ring that was slid over the distal joint of the right index finger that held the 6 infrared emitting diodes (IREDs) used to track the fingertip (for further details, see Hudson, Tassinari, & Landy, 2010 and Supplemental methods section in the Supplementary materials).

### Stimuli

Subjects attempted to touch targets on a computer screen, represented visually as a circle within a circle \((r_{\text{inner}} = 4\, \text{mm}, r_{\text{outer}} = 25\, \text{mm})\). Target locations were chosen randomly and uniformly within a vertically oriented rectangle on the screen \((20 \times 50\, \text{mm})\); the dimensions were chosen to give the appearance of a range of target locations, while restricting the horizontal range of actual target locations (and therefore maintained similar reach biomechanics). Points were awarded to maintain motivation. Hits on the target earned subjects one or three points (outer or inner circle, respectively). Missing the target earned no points, and too slow reaches were repeated.

### Procedure

There were two sessions of data collection that took place on separate days, scheduled at least 1 week apart. Two experiments were completed in each session. The predictable drift experiment differed on the 2 days only in the direction of the drift (rightward vs. leftward). The unpredictable drift experiment was identical in the two sessions. Note that to avoid any contaminating effects from having adapted to a single direction of visual drift during the unpredictable drift experiment, the unpredictable drift experiment was always performed first during a session.

**All reaches.** The order of events during a reach is shown in Figure 2A. All reaches began at the same location on the tabletop and ended by touching the computer monitor. Reaches were required to reach the screen within 500 ms of movement onset. At the halfway point of the reach, a
vertical sinewave grating (which replaced the target stimulus at movement onset) began to drift leftward, rightward, or remained stationary. When the fingertip reached the screen, the grating disappeared and was replaced with the same target stimulus that preceded the grating to allow a comparison of target and fingertip position. Both the fingertip endpoint and a running total of points were displayed on-screen at reach completion.

Figure 2. Adaptation to predictable reflex perturbations. (A) Sequence of events within a reach. When the fingertip was at the start position ($t_1$), the target appeared on-screen. At reach onset ($t_2$), the entire display was filled by a sinewave grating that (during "drift trials") began to move leftward or rightward when the hand was halfway to the screen ($t_3$). When the screen was touched ($t_4$), the target reappeared and feedback was given. (B) Sequence of drift speeds across a session. Blue: drift trials; gray: stationary trials. (C) Reach endpoints. Initial unperturbed reaches (a; gray) are on target. Initial reflex-perturbed reaches during exposure to visual field drift (b; blue) are deviated, showing the initial effectiveness of the reflex perturbation. Later perturbed reaches (c) are nearly on target indicating compensation. Initial unperturbed post-exposure reaches (d; gray) are, on average, deviated in a pattern consistent with an adaptation-induced movement aftereffect. Note that the first post-exposure data point includes catch trials. The first 12 data points following drift onset or offset are single reaches; other data points are averages of 8 successive reaches. All data points are differences between endpoints from rightward- and leftward-drift sessions averaged over 8 subjects. Average error bars ($\pm 1 \ SE$ at each reach number, averaged across reaches) for all perturbed (blue) and all unperturbed (gray) reaches are shown at the end of the data plot. Dashed lines indicate the best-fitting exponential to exposure and post-exposure reaches.
Predictable drift experiment. Subjects first completed 8–12 reaches to targets when there was no visual drift, to allow them practice with unperturbed reaches before baseline (unperturbed) performance in the experiment was measured. These reaches were not analyzed. Following this short practice set, there were three phases of the experiment: pre-exposure (no drift), exposure (consistent drift), and post-exposure (no drift). Initially, there were 24 pre-exposure reaches to targets with a stationary grating. There were then 156 reaches to targets during which the grating drifted consistently left or right on all trials. During the second half of this exposure phase, six no-drift “catch trials” were interspersed unexpectedly. Catch trials were always separated by at least 7 reaches, and the final catch trial occurred at least 9 trials prior to the end of the exposure phase. Following the exposure phase, there were 52 post-exposure (no-drift) reaches. Catch trials were used to increase the reliability of the first of the 52 post-exposure measurements and were averaged with that reach trajectory. The transition from pre-exposure to exposure to post-exposure reaches was not signaled in any way. If a timeout occurred at the transition from the pre-exposure to exposure or from exposure to post-exposure phases of this experiment, the trial could not be rerun, and the subject was not notified that a timeout occurred (this occurred twice during the experiment; removal of these data would not affect any of our conclusions).

After each reach, reverse-direction visual motion was presented that matched the duration and speed of MFR-producing drift from the preceding reach. Reverse motion was used to counteract the buildup of a motion aftereffect from repeated exposure to unidirectional drift during predictable drift reaches. Reverse drift proceeded as follows: The fingertip returned to the start position and remained at that location throughout. A tone then indicated that a small white circle near the screen center should be fixated. Following a 50-ms pause, the grating began to drift. Within the final 100 ms of opposite direction drift, a letter (a, s, d, or f) flashed for 50 ms within the fixation circle. Subjects reported the letter by keypress. To ensure fixation was maintained and the grating motion seen, this sequence was repeated for incorrect responses. Repetition could only serve to reduce overall visual adaptation to motion in the perturbing direction and, therefore, work against any explanation of the results in terms of visual effects (see Purely visual effects do not explain the results section in the Supplementary materials for details).

Unpredictable drift experiment. Subjects completed 180 reaches to targets. Reaches were exactly as before, except that each reach might include grating drift to the left, right, or no drift (1/3 each, ordered unpredictably). Intertrial reverse drift was not needed in this experiment to control for an asymmetry of seen motion because leftward and rightward drift were presented equally often.

Data collection

Before each experimental session, Optotrak measurements were calibrated by having subjects (fitted with IREDs) touch their right index finger (pointing finger) to a metal calibration nub located to the right of the screen while the Optotrak recorded the locations of the 6 IREDs on the finger. During each reach, we recorded the 3D positions of all IREDs at 200 Hz and converted them into an estimate of fingertip location (see Supplemental methods section in the Supplementary materials for details).

Data analysis

Raw reach trajectories were transformed from Optotrak coordinates into screen-centered coordinates (Hudson, Maloney, & Landy, 2008). Data were transformed to a right-handed coordinate system whose origin was at the screen center, with positive axes oriented rightward (x⁺), forward (y⁺), and upward (z⁺) relative to the frontal screen. Transformed trajectories were then filtered: First, outliers were removed using a 5-point median filter, and then trajectories were smoothed using a 5th-order low-pass Chebyshev filter with stopband attenuation of 30 dB and cutoff at half the Nyquist frequency (i.e., at 100 Hz).

We model each subject’s leftward-minus-rightward-drift endpoint data during the exposure and post-exposure periods of the predictable drift experiment using separate exponential decay models, \( d_s(t) = Ae^{-at} + o + e_i(t) \), each having amplitude (\( A \)), decay (\( a \)), and offset (\( o \)) parameters in the presence of additive Gaussian noise \( [e_i(t) ~ N(0, \sigma_i)] \) and a time index that ran from \( t = 0 \) to 1 less than the length of the exposure or post-exposure period. The initial effect of exposure or after termination of exposure is \( \Delta = A + o \). Note the subscript, \( s \), indicating noise variance is a subject-specific parameter; each corresponding to one of \( N \) subjects’ data sets from the full experiment, \( D = \{d_1(t), d_2(t), ..., d_N(t)\} \). We assume that all subjects share common values of \( A, a, \) and \( o \). See Supplemental methods section in the Supplementary materials for details of these model fits.

Note that while averaging helps suppress the visual appearance of noise and highlight the visual appearance of an underlying signal and is therefore used for plotting, all model fits are based on individual trials from individual subjects, not on data averages across trials or subjects. However, \( t \)-tests, which are normally used to test for the presence of a nonzero initial perturbation and aftereffect and are also included here, are computed from data averages and ignore differences in noise variance between subjects (unlike the calculation of the posterior distribution \( p(\Delta|D) \) used to compute error bounds on model parameters; see Supplemental methods section in the Supplementary materials). For this reason, we prefer the
Results

Predictable drift experiment

We investigated the response of the central nervous system (CNS) to predictable, reflexive perturbation. The MFR perturbation used a large visual stimulus that began to drift at the halfway point of a rapid reach to a target (Figure 2A). In the predictable drift experiment, we presented an initial series of unperturbed reaches followed by a number of perturbed reaches sufficient to allow errors to be detected and corrected and, finally, a second series of unperturbed reaches during which the presence and character of any aftereffect could be assessed (Figure 2B).

For the perturbed reaches, the drift was always rightward in one experimental session and leftward in another (see Methods section).

Average differences between reach endpoints during leftward and rightward predictable drift experiments are shown in Figure 2C. At the beginning of consistent drift, reaches were significantly biased due to the MFR (the average of differences between the first perturbed reach during leftward- and rightward-drift sessions across subjects was $7.37 \text{ mm}$, $t(7) = 4.5$, $p_{1\text{-tail}} < 0.01$). Within the next five to eight trials, adaptation brought reaches nearly back on target. Thus, adaptation to this reflex perturbation displays a similar time course to adaptation to a force field (e.g., Lackner & DiZio, 2005). Note that adaptation to forces imposed on reaches by holding a robotic manipulandum has a different time course (e.g., Shadmehr & Mussa-Ivaldi, 1994), possibly due to differences in learning the dynamics of the arm vs. those of a held object or tool.

When the perturbation was removed, a negative aftereffect was clearly evident (average differences of first post-exposure and catch trial errors during leftward- vs. rightward-drift sessions was $3.95 \text{ mm}$, $t(7) = 3.5$, $p_{1\text{-tail}} < 0.01$), demonstrating that compensatory forces had been used to counteract predictable reflex perturbations. Note also that there was no significant difference between initial error and aftereffect magnitudes, $t(7) = 1.6$, $p_{2\text{-tail}} > 0.1$. Movement endpoint variance was also affected by the MFR. Figure S1 shows that MFR onset coincided with an immediate and roughly constant 30% increase in endpoint standard deviation. Endpoint noise quickly returned to baseline levels once perturbation ceased.

Reaches were constrained to be completed within 500 ms following reach initiation, with visual drift onset occurring as the fingertip crossed the halfway point (spatially in the y-dimension) of the reach. On average, reaches were completed within $423 \ [367 \ 448]$ ms and $415 \ [348 \ 459]$ ms during the predictable and unpredictable drift experiments, respectively (ranges correspond to the shortest interval encompassing 95% of the histogram of all reach times). The fingertip passed the halfway point of the reach with $196 \ [139 \ 244]$ ms and $203 \ [141 \ 248]$ ms remaining before the screen was touched. In our data, latency to the MFR-induced trajectory perturbation was just over 150 ms, slightly longer than that reported by Saijo et al. (2005). Compensation for this trajectory perturbation takes an additional 80–100 ms (Saijo et al., 2005), i.e., compensation could only begin approx. 250 ms after visual drift onset (see Timing of movement perturbation onset section in the Supplementary materials). Only 1.9% and 2.1% of the second half of reaches extended beyond 250 ms after drift onset. No conclusions are changed by excluding these reaches.

Model fits. Estimates of initial exposure and aftereffect rightward-minus-leftward-drift endpoints were $\Delta = 7.28 \ [4.4 \ 10.2]$ and $\Delta = 4.35 \ [2.4 \ 6.4]$ mm, respectively (ranges correspond to the shortest interval encompassing 95% of the posterior distribution $p(\Delta | D)$; see Methods). These ranges show that the initial effect of MFR perturbation and negative aftereffect are different from 0 but not different from one another (in the sense of the logic of a statistical test, where >0.05 of the probability mass of the two distributions is overlapping). Decay parameter fits were $\alpha = 0.44 \ [0.21 \ 0.94]$ and $\alpha = 0.17 \ [0.1 \ 0.37]$ during the exposure and post-exposure phases of the experiment, respectively. Offset parameter fits were $\sigma = 0.68 \ [0.46 \ 0.91]$ and $\sigma = 0.22 \ [-0.29 \ 0.74]$ during exposure and post-exposure periods, respectively. A positive offset parameter whose range does not include 0 during exposure suggests that a portion of the perturbation was uncompensated; this is common during adaptation to large perturbations (e.g., Criscimagna-Hemminger, Bastian, & Shadmehr, 2010).

Trajectories. Figure 3 plots average reach trajectories as the difference between leftward- and rightward-drift-session reaches, highlighting responses to the perturbation. Initial unperturbed reaches show no significant differences between the two sessions (Figure 3A). Once visual drift is initiated (exposure phase), the first few reaches display reflex perturbation in the last moments of the reach (Figure 3B shows an average over the first three reaches across subjects). Later predictable drift reaches display compensation, with error bars overlapping zero (Figure 3C). Reach trajectories leading to the aftereffect observed in Figure 2C can be seen in Figure 3D (average of the first three post-exposure and catch trials). After-effect deviations occurred at nearly the same distance from the target as the original reflex perturbation and are roughly the mirror image of the reflex perturbation observed during initial perturbed reaches (Figure 3B).
This is precisely what one would predict if observers used a counteracting force (Figure 1A) to adapt to this reflex perturbation.

We note that subjects were aware of the effect of visual drift on reach trajectories, as initial deviations were large enough to be felt. Indeed, several subjects spontaneously commented on this after first experiencing the drift perturbation and/or aftereffect.

**Unpredictable drift experiment**

In this experiment, subjects made a series of rapid reaches to a target, but the visual stimulus either drifted leftward, rightward, or remained stationary randomly from trial to trial. Reach endpoints do not change over the course of the 180 unpredictable drift reaches (Figure 4; in t-tests, the slopes of leftward- and rightward-drift reach endpoints are not significantly different from 0, p > 0.1), indicating that errors due to the MFR perturbation are not compensated under these conditions.

Because there were many repetitions of uncorrected perturbations in the unpredictable drift experiment, we were able to measure the timing of the MFR relative to the onset of visual drift to verify that online corrections did not affect reach endpoints in the predictable drift experiment. Leftward-perturbed and rightward-perturbed trajectories deviate from one another starting at over 150 ms following drift onset (Figure S2). This is consistent with earlier reports (Saijo et al., 2005) of the timing of trajectory deviations due to the MFR. Since online correction for MFR perturbation requires approx. 250 ms following drift onset, we conclude that online correction could not have affected our results.

**Discussion**

We have described two experiments involving a reflex perturbation that, as predicted for an optimal adaptive mechanism utilizing source identification (Berniker & Körding, 2008), could be compensated purely neurally and independently of the motor torques used to control the arm. We found no evidence for this optimal reflex gain control strategy in either experiment (and can exclude interpretations of the results based on impedance control, online corrections, and purely visual motion adaptation—see Supplemental discussion section in the Supplementary materials). Instead, compensation for our internally...
generated, reflex-based perturbation was produced by balancing reflex-induced torques with increases in antagonistic muscular activation; thus in the case of adaptation to the MFR, the response is not energy efficient and behaves in a manner that is inconsistent with theories of optimal sensory–motor adaptation (Berniker & Körding, 2008; Burge, Ernst, & Banks, 2008).

Of course, balanced increases in antagonistic muscular activation, termed impedance control, are a common feature of motor control in the face of perturbation, particularly when complex dynamic perturbations are incompletely modeled by the CNS (Tomii, Gouko, & Ito, 2008) or when dynamic instability or noise is present (Burdet et al., 2006; Franklin et al., 2007). In addition, based on the aftereffects observed and the increased endpoint variance of exposure phase reaches, we assume that adaptation consisted of balancing the visually induced reflex torques with pre-planned compensatory torques (but see Supplemental discussion section in the Supplementary materials for a possible alternative). So why is it surprising to find an “impedance-like” element in the current results? Recall the unusual feature of the current experiment that no external force perturbed the arm. Because perturbing forces were internally generated, any adaptive forces (tending to return reach trajectories to normal) generated during exposure to visual drift (as measured by the aftereffects they produced) would be formally identical to co-contraction (i.e., self-generated opposing muscle torques that increase joint stiffness). Although we did not measure muscle activations (e.g., EMG measurements), the timing of the MFR effect (Figure 3B) and adaptation aftereffect (Figure 3D) were identical, suggesting that opposing muscle activations did indeed occur. Force-based adaptation, which would logically have increased the impedance of the arm during exposure to visual drift in our first experiment due to co-contraction, would, in this circumstance, be an energy-suboptimal solution to the problem. Note, however, that observed responses to the imposed perturbation in these experiments could not properly be called “impedance control,” because arm impedance was clearly not the variable controlled during adaptation; only half of the impedance-generating motor command was pre-planned, as demonstrated by aftereffects observed following exposure during the predictable drift experiment. Impedance control has been modeled as a minimum energy response to task constraints (Franklin, So, Kawato, & Milner, 2004). Here, we observe an unnecessary escalation of force production, with opposing patterns of force used to counteract self-generated perturbing forces, rather than the energy-conservative reduction of those perturbing forces that would have been produced via gain-based adaptation. Whereas our predictable drift experiment was designed to assess the possibility of gain-based adaptation by examining the aftereffect period, our unpredictable drift experiment assessed this possibility by examining reaches during exposure to perturbing drift. In this experiment, it was impossible to generate mirror-image forces to compensate for gain-based perturbation. That is, we used an unpredictable pattern of visual–motor perturbation similar to that used in studies of the effect of visual noise on closed-loop error correction (Franklin et al., 2007) and the internal representation of motor noise during reach planning (Hudson et al., 2010). Because the presence and direction of visual motion was unpredictable, a force compensation mechanism that added the mirror image of the average self-generated perturbing force in response to the drift (Scheidt, Dingwell, & Mussa-Ivaldi, 2001; Scheidt & Ghez, 2007) would produce no compensatory response and no reduction of endpoint perturbation. Instead, a reduction in MFR-induced error over the course of exposure would have provided evidence of gain-based adaptation. We find no such reduction, again suggesting that gain-based adaptation was not implemented.

We argued in the Introduction that only a system that modeled the source of the error would be capable of adapting via force-based and gain-based mechanisms, as the situation requires. This is important for optimal Bayesian models of adaptation, because the optimal solution in this circumstance requires not only that the nervous system learn the probability structure associated with possible errors (Hudson, Maloney, & Landy, 2007) but also that it identify the source of those errors. Only if the internal source of perturbing forces had been identified could the energy-optimal gain-based adaptive response be employed (i.e., gain-based adaptation would be useless in the face of an external perturbing force). The fact that we observed force-based adaptation to the imposed reflex perturbation suggests that either the source was not identified or that information about the source was not used in computing an adaptive response, which is inconsistent with the predictions of a recent Bayes-optimal motor adaptation model (Berniker & Körding, 2008).

There are two reasons that a system might fail to exhibit source identification-based adaptation: either the source of perturbations is not identified or information regarding the sources of perturbations is not used to formulate an adaptive response. In line with the idea that information regarding the source of MFR-induced errors, while available, was not used in generating the adaptive response, it is possible that the current results reflect disconnection of visuomotor reflex arcs (responsible for the MFR) and circuits responsible for motor adaptation. However, consider the neural circuit likely responsible for disconnection of visuomotor reflex arcs (responsible for the MFR). It clearly originates in ventral visual motion areas such as MT+ (Amano, Kimura, Nishida, Takeda, & Gomi, 2009), which have relatively direct connections via pontine nuclei to the cerebellum (Glickstein & Doron, 2008), and then directly or indirectly via ventral thalamic nuclei to primary motor cortex, where the MFR is likely initiated. This circuit appears perfectly situated for adaptive modulation of reflexive MFR gain not only due to its cerebellar involvement but also because interneuronal networks in M1 are thought to modulate anticipatory
reflex gain in response to changing task and environmental dynamics (Kimura, Haggard, & Gomi, 2006). From these considerations, it appears more likely that the internal source of our MFR-induced errors was not identified rather than that it was identified but not used for adaptation. Consistent with this view, we note that under conditions not involving adaptation, several recent experiments show evidence of “intelligent” reflex modulation depending on environmental and task conditions (Krutky, Ravichandran, Trumbower, & Perreault, 2008; Pruszynski et al., 2011), that is, some reflexes evidently can be modulated by environmental and task conditions.

If the observed reliance on force-based adaptation in these experiments does not result from limitations of neural connectivity, then the alternative is that they tell us something about general principles of motor adaptation and planning. If so, these experiments call into question notions of planning optimality involving source identification, energy expenditure (Alexander, 1997), and output (endpoint) variance (Bays & Wolpert, 2007; Körding & Wolpert, 2004) as general principles guiding the selection of motor plans. As outlined above, there would be substantial energy savings and, in addition, a reduction in (signal-dependent) endpoint variance (Harris & Wolpert, 1998; also see Figure S1), by implementing the Bayes-optimal (i.e., source-identified; Berniker & Körding, 2008) gain-based adaptation strategy in these experiments. We suggest, therefore, that our results provide a new constraint on theories of motor planning, particularly those that depend on an energy-use (e.g., Alexander, 1997; Miyamoto, Nakano, Wolpert, & Kawato, 2004; Nishii & Tanai, 2009; Todorov & Jordan, 2002), motor signal strength (e.g., Harris & Wolpert, 1998), or source identification (Berniker & Körding, 2008) component.

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