

RESEARCH ARTICLE | *Control of Movement*

Environmental consistency modulation of error sensitivity during motor adaptation is explicitly controlled

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Avraham G, Keizman M, Shmuelof L. Environmental consistency modulation of error sensitivity during motor adaptation is explicitly controlled. *J Neurophysiol* 123: 57–69, 2020. First published November 13, 2019; doi:10.1152/jn.00080.2019.—Motor adaptation, the adjustment of a motor output in face of changes in the environment, may operate at different rates. When human participants encounter repeated or consistent perturbations, their corrections for the experienced errors are larger compared with when the perturbations are new or inconsistent. Such modulations of error sensitivity were traditionally considered to be an implicit process that does not require attentional resources. In recent years, the implicit view of motor adaptation has been challenged by evidence showing a contribution of explicit strategies to learning. These findings raise a fundamental question regarding the nature of the error sensitivity modulation processes. We tested the effect of explicit control on error sensitivity in a series of experiments, in which participants controlled a screen cursor to virtual targets. We manipulated environmental consistency by presenting rotations in random (low consistency) or random walk (high consistency) sequences and illustrated that perturbation consistency affects the rate of adaptation, corroborating previous studies. When participants were instructed to ignore the cursor and move directly to the target, thus eliminating the contribution of explicit strategies, consistency-driven error sensitivity modulation was not detected. In addition, delaying the visual feedback, a manipulation that affects implicit learning, did not influence error sensitivity under consistent perturbations. These results suggest that increases of learning rate in consistent environments are attributable to an explicit rather than implicit process in sensorimotor adaptation.

NEW & NOTEWORTHY The consistency of an external perturbation modulates error sensitivity and the motor response. The roles of explicit and implicit processes in this modulation are unknown. We show that when humans are asked to ignore the perturbation, they do not show increased error sensitivity in consistent environments. When the implicit system is manipulated by delaying feedback, sensitivity to a consistent perturbation does not change. Overall, our results suggest that consistency affects adaptation mainly through explicit control.

consistency; explicit control; implicit adaptation; motor control; sensorimotor learning

INTRODUCTION

A fundamental principle in motor learning is modularity. Even simple motor learning behaviors, like adaptation, are driven by multiple learning processes (Smith et al. 2006). A striking behavioral account for such modularity was demonstrated by the existence of implicit and explicit processes during adaptation to visuomotor rotation, where participants change the movement direction of their hand to counteract a rotated cursor (Haith and Krakauer 2013; Mazzoni and Krakauer 2006; Taylor et al. 2014; Taylor and Ivry 2011). The implicit learning process refers to an automatic recalibration of the motor response to an experienced error, whereas the explicit learning process is the intentional update of aiming direction following a strategy to improve performance. These processes are also thought to be associated with different neural substrates; implicit learning depends on the cerebellum (Galea et al. 2011; Imamizu et al. 2000; Kim et al. 2015; Morehead et al. 2017; Schlerf et al. 2012; Taylor et al. 2010) whereas explicit learning is associated with cortical function (McDougle et al. 2016; Taylor and Ivry 2014) and the dopaminergic system (Leow et al. 2012).

Despite the accumulation of results supporting this modularity, the functional roles of the implicit and explicit processes, and the interaction between them during adaptation, are still largely unknown. It was proposed that each learning process is driven by a different error signal; the implicit process is driven by sensory prediction errors, the difference between the expected and the actual sensory feedback, and the explicit process is driven by target error, the difference between the target and the feedback (Mazzoni and Krakauer 2006; Reichenthal et al. 2016; Shmuelof et al. 2012a; Taylor and Ivry 2011). This idea can explain the parallel operation of these processes during the time course of visuomotor adaptation (Taylor et al. 2014). However, it does not explain secondary influences on learning, such as modulations of *error sensitivity*, the change in the reaction to errors, that were reported for different error magnitudes (Crisimagna-Hemming et al. 2010; Marko et al. 2012) and for different perturbation consistencies (Herzfeld et al. 2014).

Error sensitivity was shown to increase for small errors (Marko et al. 2012). However, this dependency is challenged

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by recent evidence showing invariance of the implicit process to error magnitude, i.e., that different errors lead to a constant and signed motor correction (Bond and Taylor 2015; Kim et al. 2018; Morehead et al. 2017). The apparent error-sized-dependent modulation of error sensitivity may therefore be an outcome of dividing the (fixed) correction by different error magnitudes.

Another contextual effect on error sensitivity is the consistency of the perturbation. Gonzalez Castro et al. (2014) and Herzfeld et al. (2014) have shown that humans adapt faster to perturbations that are consistent compared with perturbations that are random. Importantly, sensitivity to error in these studies was measured for probe trials in which the experienced error was similar across the different consistency conditions, thereby controlling for the concern that modulation of error sensitivity was merely a normalization artifact that reflects differences in error magnitudes. The effect of consistency on adaptation poses an important question regarding its underlying mechanism; on the one hand, the increased learning rate for the consistent errors could be a result of an implicit error-sensitivity modulation in the cerebellum (Hanajima et al. 2015; Herzfeld et al. 2014), or alternatively, consistency can increase the awareness of the participant to the perturbation and thereby enhance the involvement of strategies.

In a series of visuomotor rotation experiments, we take a close look at the interaction between awareness and perturbation's consistency. We report that the modulation of error sensitivity due to the consistency of the perturbation depends on explicit processes, and that manipulating implicit learning has no detectable effect on error sensitivity under consistent perturbations. Our results emphasize the crucial role of explicit control in sensorimotor learning, and provide further support for the limited contribution of context to implicit learning.

METHODS

Participants

Seventy-one healthy right-handed volunteers (aged 19–34 yr; 44 women) participated in three experiments: 18 in *experiment 1*, 31 in *experiment 2*, and 22 in *experiment 3*. All experiments were conducted after the participants signed an informed consent form approved by the Human Subjects Research Committee of Ben-Gurion University of the Negev, Be'er-Sheva, Israel.

Experimental Setup and Task

Participants sat facing a computer monitor (resolution: $1,280 \times 1,024$ pixels; dimensions: 37.7×30.1 cm), distant by ~ 1.5 meters, and controlled a screen cursor by making pointing movements with the fist through flexion-extension and pronation-supination of the right wrist (Krakauer et al. 2006; Shmuelof et al. 2012b). Their right forearm rested within a stabilization device that prevented its supination. The cursor location on the screen was mapped to the position of a retroreflective marker attached to the knuckle of the index finger; it was calibrated such that a 1-cm deviation of the marker caused a 3.2-cm deviation of the cursor. The marker position was recorded using three motion capture cameras (Qualisys, Göteborg, Sweden).

We conducted three experiments. In all experiments, participants were requested to move the cursor to the target by performing a wrist pointing movement (Fig. 1). The start location, depicted as a circle in the center of the screen, and a gray target, 1.2-cm diameter and distant by 6.3 cm from the start location, were both presented on the screen throughout the trial. Each trial was initiated with the appearance of an orange cursor, 0.6-cm diameter, simultaneously with a presentation of a tone, signaling the participants to move to a start location, which was colored in blue. If participants remained in the start location for 0.5 s, they received a "Go" cue: both cursor and start location turned black, marking the onset of a fast movement toward the target. In *experiments 1* and *3*, participants were requested to perform an out-and-back (slicing) movement with the goal of placing the reversal point on the target. In *experiment 2*, participants were instructed to perform a straight, center-out, movement and to slice through the target. Movement completion was determined online and was considered the last sample point before the movement reversal (*experiments 1* and *3*) or before the hand traveled the radial distance to the target (*experiment 2*). To eliminate online feedback corrections, the cursor disappeared as soon as it traveled a radial distance of 10% of the distance to the target. After some time delay from movement completion, participants received performance feedback: the black cursor reappeared at a location corresponding to the hand location at movement completion (with or without rotation) and the target changed color either to green for target hits, or to red for misses. In *experiments 1* and *2*, this feedback delay was fixed at 1,000 ms with respect to movement completion, whereas in *experiment 3*, the delay ranged between 600 and 2,500 ms (see *Experimental Protocol*). We considered a hit when the center of the cursor was distant by < 0.65 cm from the center of the target (i.e., when the cursor's center was inside the target). Participants could experience two types of trials: Contingent and Noncontingent (Error Clamp). In Contingent trials, the location of the feedback cursor was contingent on participants'

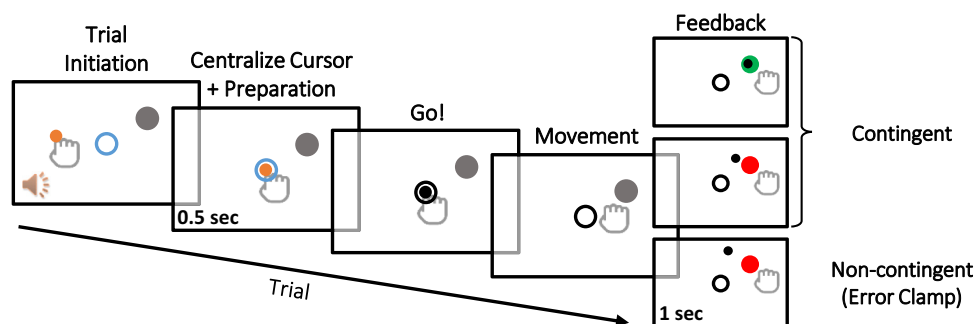


Fig. 1. Experimental task. Trial initiation was marked by the appearance of a cursor (orange dot) representing the location of the hand and a presentation of an auditory tone. Participants were requested to move the cursor to a start location (blue circle). Following 0.5 s in the start location, they received a "Go" cue (both cursor and start location turned black), signaling participants to move to the target (filled gray circle). The cursor was not presented during the movement. Trials ended with participants receiving performance feedback: a black dot reappeared at the location corresponding to movement completion and the target changed color either to green for target hits or to red for misses. In Contingent trials, the location of the feedback cursor was contingent on participants' movements. In Noncontingent (Error Clamp) trials, the cursor landed at the radius of the target in a predetermined position that was rotated by 15° clockwise or counterclockwise with respect to the target.

movements, either veridical or rotated (to the clockwise or counterclockwise direction) with respect to movement direction. In Error Clamp trials, the cursor landed in a position that was noncontingent on participants' movements; this position was rotated by 15° clockwise or counterclockwise with respect to the target, and in both cases, the cursor appeared at the radius of the target. The purpose of the Error Clamp trials was to measure error sensitivity for a constant error size.

Experimental Protocol

In all three experiments, participants did multiple experimental runs. Each run started with a baseline epoch with veridical visual feedback. This epoch was followed by an adaptation epoch in which the cursor was rotated with respect to the movement direction of the hand. Rotation magnitudes ranged from -30 to 30° in steps of 5° (negative and positive values represent counterclockwise and clockwise, respectively). Runs were different by the schedule of the presented rotations, and each run comprised of one of two types of conditions that varied by consistency: Random and Random Walk (see Fig. 2 for illustrations of each type). For the Random condition, the rotations were presented in a pseudorandom order and changed between successive trials, such that the consistency, measured by lag-1 autocorrelation (Gonzalez Castro et al. 2014), is small (Table 1). For the Random Walk condition, the rotations varied from trial to trial according to a random walk algorithm: for each successive trial, the rotation changed by 5° , either clockwise or counterclockwise. The resulting perturbation function of the Random Walk condition had higher consistency than the Random perturbation function (Table 1).

Most of the trials during the adaptation epoch were Contingent trials, and some trials were Error Clamp trials (see below for exact percentages in each experiment). For both the Random and the Random Walk conditions, the Error Clamp trials were only presented after contingent trials that constitutes of rotation size that was similar to the clamp size (15°), i.e., 10 – 20° .

Experiment 1. *Experiment 1* consisted of a single group of participants ($n = 18$). All participants did four experimental runs. In each run, they moved to a different target that was presented in one of four angular positions with respect to the abscissa: 45 , 135 , 225 , and 315° . Each run started with a baseline epoch of 12 trials, followed by the adaptation epoch that consisted of 120 trials. $\sim 17\%$ of the trials in the adaptation epoch (20 trials) were Error Clamp trials. During the adaptation epoch of two of the four runs, for which targets were separated by 180° from each other, participants experienced Random perturbation sequences, and during the other two runs, they experienced the Random Walk perturbation sequences [for each consistency condition, each participant experienced 2 of the 4 $R(1)$ values in the associated cells in Table 1]. The two conditions alternated in each experiment, and we counterbalanced the condition that was presented on the first run across participants. Across participants, all targets were associated with both conditions.

Experiment 2. *Experiment 2* consisted of two groups of participants. All participants did two experimental runs, moving to a single target, presented at 45° . In each run, the baseline epoch consisted of 20 trials, and the adaptation epoch consisted of 220 trials. Twenty trials in the adaptation epoch ($\sim 9\%$) were Error Clamp trials. Unlike in *experiment 1*, where Error Clamp trials could appear anytime during the adaptation epoch, here they were presented only after the second half of the run (after *trial 120*) to ensure that participants had sufficient exposure to the perturbations and their error sensitivity could be adjusted. During the adaptation epoch of one of the two runs, participants experienced the Random perturbation sequence, and during the other run, they experienced the Random Walk perturbation sequence. All participants experienced the same Random and Random Walk perturbation sequences (Table 1). The order of the conditions was counterbalanced across participants.

To examine the role of awareness in error sensitivity modulations, participants of one group (Ignore, $n = 15$) were briefed about the perturbation and were requested to ignore the cursor and to move their hand directly to the target. Participants of the other group (Counteract, $n = 16$) were not told about the rotation and were instructed to keep trying to hit the target with the cursor. Similar instructions were previously shown to enable distinguishing the contributions of implicit (Ignore group) and explicit (Counteract group) processes in sensorimotor learning (Morehead et al. 2017; Welch 1969).

Experiment 3. *Experiment 3* consisted of a single group of participants ($n = 22$). All participants did four experimental runs. In each run, they moved to a different target that was presented in one of four locations: 45 , 135 , 225 , and 315° . The order of the targets was the same for all participants. In each run, the baseline epoch consisted of 12 trials, and the adaptation epoch consisted of the 120 trials. Twenty trials in the adaptation epoch ($\sim 17\%$) were Error Clamp trials. During the adaptation epoch of each run, participants experienced a different Random Walk perturbation sequences (Table 1) and were requested to always try to hit the target with the cursor. Across participants, a given target location was always associated with the same perturbation sequence.

Across runs, we manipulated the implicit process by imposing different delays between the moment of movement reversal and the feedback presentation. Within each run, the delay was either constant at $1,000$ or $2,000$ ms, or varied randomly between 600 and $1,500$ ms or $1,600$ and $2,500$ ms in steps of 100 ms. All participants experienced all four types of delay schedules, but the order was randomized between participants. Across participants, all targets were associated with all delay schedules.

Data Analysis

The marker position (attached to the fist) was recorded throughout the experiment at 60 Hz. It was analyzed offline using a custom-written MATLAB code [The MathWorks, Natick, MA; Research Resource Identifier (RRID): SCR_001622]. As mentioned above, for *experiments 1* and *3*, movement completion was determined by the movement reversal. To measure the movement reversal of the marker, for each trial, we identified the first sample (i) in which the movement amplitude was smaller than the previous sample ($i - 1$). The movement reversal was defined as the location of the marker on sample $i - 1$. For *experiment 2*, movement completion was defined as the last sample the movement amplitude was smaller than the radial distance of the target. We defined the hand's movement angle (MA) as the angle between the imaginary lines connecting the movement origin to the movement completion location and to the target. We calculated the directional error (e_n) at trial n as the angular difference between the feedback and the target. For each error, we measured learning from error (LE) as the change in MA from the trial in which the error was experienced to the next trials:

$$LE_n = MA_{n+1} - A \cdot MA_n \quad (1)$$

where A represents the retention. The value of A (0.924) was based on an estimate of retention in visuomotor rotation experiments (Zarahn et al. 2008).

Error sensitivity (ES) was calculated as:

$$ES_n = LE_n / e_n \quad (2)$$

We calculated learning from error for all trials. Error sensitivity was obtained separately for all 15° Error Clamp trials and for contingent feedback trials in which the experienced absolute error was between 10 and 20° .

Learning from error functions (or sensitivity functions) was obtained by sorting errors experienced in each condition for each

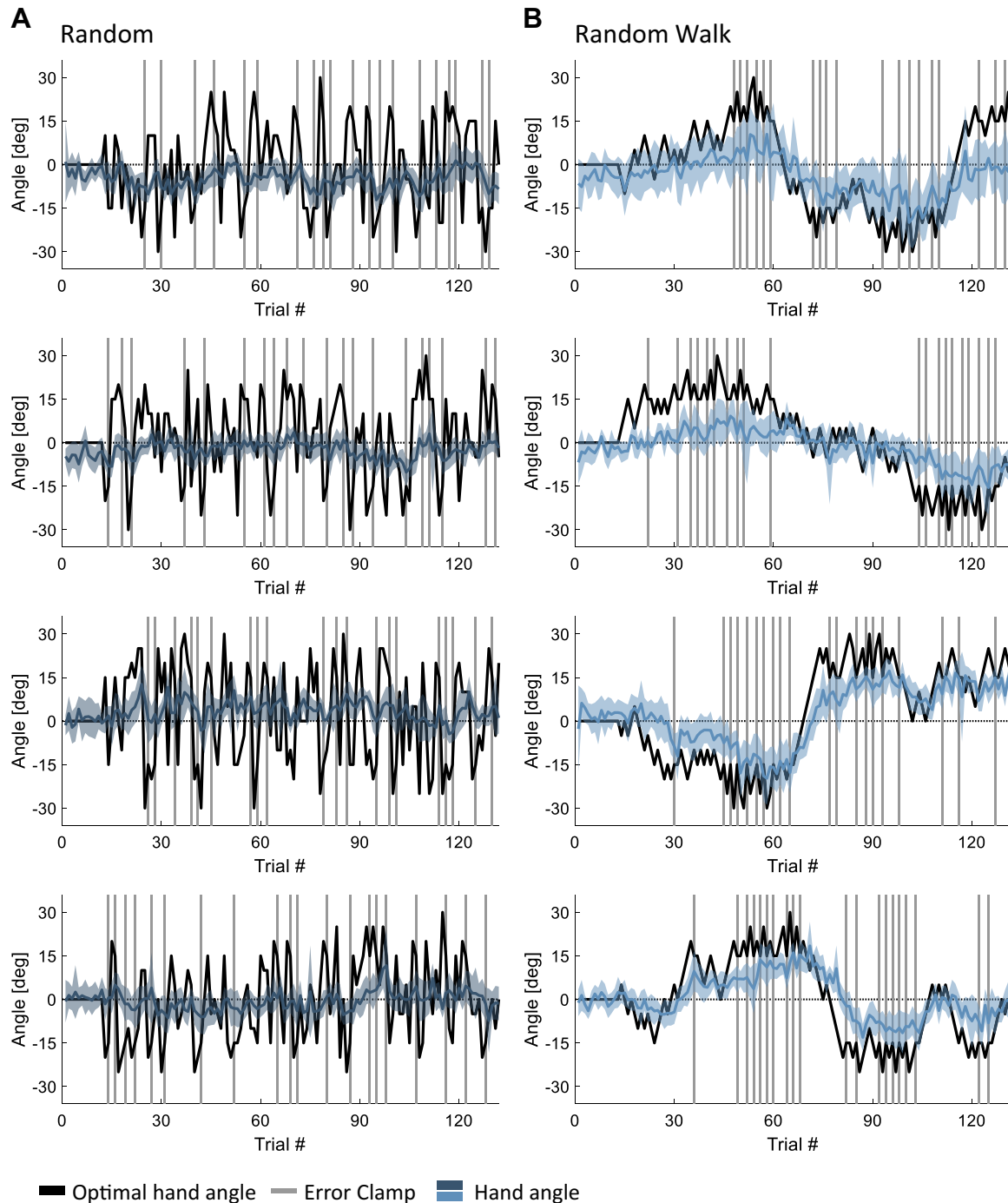


Fig. 2. *Experiment 1*: hand angle during Random and Random Walk sequences of visuomotor rotation. *A* and *B*: time courses of the optimal hand angle (black lines) for counteracting the applied rotation and actual hand angle (colored lines) during Random (*A*, dark blue) and Random Walk (*B*, light blue) perturbation sequences. Each plot represents the results from a different perturbation sequence. Vertical gray lines represent Error Clamp trials. Shading represents 95% confidence interval.

participant based on magnitude, binning them to 10 bins, and averaging the experienced errors and the trial-by-trial change in hand angle within each bin. Then, we calculated the between-participant means \pm SE of the experienced errors and the change in hand angle for each bin.

We quantified the learning from error by fitting a linear function to the change in hand angle with respect to the error size on each trial (not to the binned average) for each participant and condition. We used the slope of the fitted linear function as a measure for learning from error across all of the experienced error magnitudes. Since

typically there is a negative relationship between the directions of the error and the trial-by-trial change in hand angle, we multiplied the slope by -1 such that higher values represent higher sensitivity. We will refer to this measure as “negative slope.”

To verify that retention alone cannot account for the observed consistency effects on error sensitivity, we examined the relationship between trial-by-trial change in hand angle and the actual hand angle (motor state) at each trial. For each participant and condition, we fitted a linear function to the motor state versus error size relationship and calculated the slope of these functions (similar to analysis described

Table 1. Lag-1 autocorrelation [$R(1)$] values

	Random	Random Walk
Experiment 1	0.25, 0.27, 0.18, 0.26	0.91, 0.91, 0.92, 0.91
Experiment 2	0.04	0.93
Experiment 3		0.91, 0.92, 0.89, 0.93

A single value represents the $R(1)$ of a perturbation schedule in a single run, i.e., the correlation coefficient between the rotation magnitudes in 2 successive trials. All values within each cell represent all possible runs in an experiment.

above for the learning from error functions, except here we used the original slope and not the opposite value). Next, for each of the motor state and learning from error measures, we calculated the difference between the slopes of the Random Walk and Random conditions and examined the correlation between them across participants.

We measured reaction time and movement time offline. For all experiments, the reaction time was calculated as the time between the Go cue and the moment the cursor traveled a radial distance of 10% of the distance to the target (movement initiation). Movement time was considered the time between movement initiation and movement completion (at movement reversal in experiments 1 and 3 or at the radial distance of the target in experiment 2). For experiments 1 and 3, we also measured the return time from movement completion to the first moment the hand's radial velocity was <5% of the maximum radial velocity at the returning phase of the out-and-back movement.

Statistical Analysis

Statistical analyses were performed using custom-written MATLAB functions, the MATLAB Statistics Toolbox, and IBM SPSS (RRID: SCR_002865). We used the Lilliefors test to determine whether our measurements were distributed normally (Lilliefors 1967). In the repeated-measures ANOVA models, we used Mauchly's test to examine whether the assumption of sphericity was met. For the factors that were statistically significant, we performed planned comparisons and corrected for familywise error using the Bonferroni correction. We denote the Bonferroni-corrected P values as P_B .

The statistical analyses for all three experiments were done on the following measures: 1) the slope of the learning from error function, 2) mean error sensitivity across 10–20° error trials and 3) all 15° Error Clamp trials, 4) median reaction time, 5) median movement time, and 6) median return time (experiments 1 and 3), calculated separately for each participant and each condition.

To examine the influence of consistency on each of the above measures in experiment 1, for each participant, we pulled together the data from two runs of the same consistency condition (Random and Random Walk) and calculated each participant's measures for each consistency condition. We used a two-tail paired-sample t test to examine whether the difference in each measure between the Random and the Random Walk conditions is statistically significant.

To examine the effects of explicit strategies on each measure in environments with different levels of consistency in experiment 2, we calculated the above measures for each consistency condition. For each measure, we fitted a two-way mixed-effect ANOVA model, with the measure as the dependent variable, one between-participants independent factor (Strategy: 2 levels, Ignore and Counteract), and one within-participant independent factor (Consistency: 2 levels, Random and Random Walk).

To examine the effects of delayed feedback (modulation of implicit adaptation) on each measure, we calculated each participant's measures for each delay condition. For each measure, we fitted a one-way repeated-measures ANOVA model, with the measure as the dependent variable and one within-participant independent factor (Delay: 4 levels, 600–1,500, 1,000, 1,600–2,500, and 2,000 ms).

Throughout this paper, statistical significance was set at the $P < 0.05$ threshold.

RESULTS

Experiment 1: Consistency of the Perturbation Increases Error Sensitivity

A group of participants ($n = 18$) experienced both Random and Random Walk schedules of visuomotor rotations on different experimental runs (Fig. 2). During the Random condition, the rotations were presented in a pseudorandom order, changing between successive trials, such that the consistency, measured by lag-1 autocorrelation (Gonzalez Castro et al. 2014), is small [mean $R(1) = \sim 0.24$, see METHODS for further details]. During the Random Walk condition, the rotations varied from trial to trial according to a random walk algorithm, resulting a perturbation function with higher consistency [mean $R(1) = \sim 0.91$] than the Random perturbation function.

The time courses of the mean hand angle (Fig. 2) suggests that participants adapted to some degree to both the Random and Random Walk perturbation; this is evident by the gradual change in hand angle in the direction of the optimal performance, and it is more pronounced in Random Walk (Fig. 2B) than in the Random perturbation sequences (Fig. 2A).

During the Random Walk condition, participants showed higher sensitivity to errors than during the Random condition. We examined the trial-by-trial change in hand angle as a function of the error size across the entire range of the experienced errors for all Contingent-feedback trials (learning from error, Fig. 3A). This analysis reveals that the negative slope of the learning from error function for the Random Walk ([mean 95% confidence interval], 0.277, [0.201 0.354]) schedule is higher than for the Random perturbation 0.181, [0.150 0.210] [$t(17) = 3.20$, $P = 0.005$, Fig. 3B], suggesting that participants apply bigger corrections for the experienced error during the former than the latter condition. Additionally, participants experienced smaller errors during Random Walk than during Random conditions. The projections of the curves on the abscissa (Fig. 3A) indicate that the errors experienced during the Random Walk condition have a narrower distribution than the errors experienced during the Random condition (as a result of the increased error sensitivity and the consistent perturbation schedule that allowed for a gradual reduction in error size).

To measure error sensitivity, we normalized the change in hand angle by the error size. We first did this analysis for Error Clamp trials (trials in which the feedback cursor was presented 15° away from the target, irrespective of the performance of the participant). There was a significant increase in error sensitivity from the Random (0.025, [−0.017 0.066]) to the Random Walk (0.104, [0.049 0.15]) condition [$t(17) = 2.61$, $P = 0.018$]. We note that the results from the Error Clamp trials should be treated with caution. The Error Clamp trials were presented within the sequence of changing perturbations in which there is some adaptation. Thus we did not control for the magnitude of sensory prediction error in these trials. Furthermore, the Error Clamp trials were presented in both consistency conditions after perturbation of similar size. Therefore, the sensory prediction error should typically be smaller than the experienced error magnitude in these trials. As error sensitivity is the quotient between the motor correction and the sensory prediction error, its estimation based on the experienced error magnitude underestimates error sensitivity. To address this limitation, we

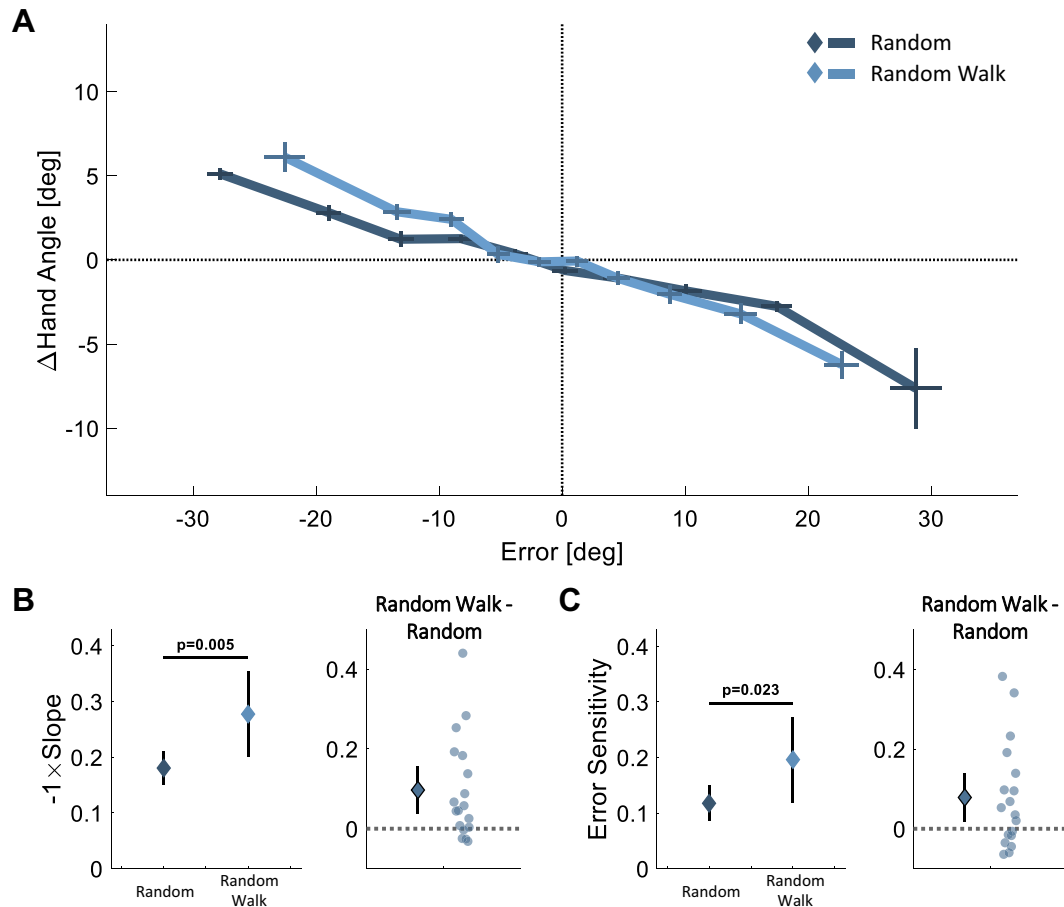


Fig. 3. *Experiment 1*: error sensitivity is higher for Random Walk than for Random sequences of visuomotor rotation. *A*: mean change in hand angle as a function of the experienced error for the Random (dark blue) and Random Walk (light blue) perturbation sequences. The trials were binned by error size for each participant. The centers of the crosses represent the mean hand angle for the mean error of each bin, and the vertical and horizontal lines of the crosses represent between-participant standard error. The aspect ratio does not reflect the true proportions of the axes to highlight the difference between the conditions. *B* and *C*: between-participants mean negative slope for the functions in *A* (*B*) and mean error sensitivity computed for $10\text{--}20^\circ$ error trials (*C*) for each perturbation sequence (*left*) and the within-participants Random Walk-Random difference for each measure (*right*). Error bars represent 95% confidence interval. Colored dots represent data of individual participants.

computed error sensitivity for all the Contingent-feedback trials in which the experienced error size was within a range of $10\text{--}20^\circ$. We chose to focus on large errors within this range since it incorporates the largest errors experienced in both consistency conditions of all groups (including *experiments 2* and *3*) and to avoid inflation of the error sensitivity estimate due to a division by small errors. This analysis also revealed a significantly higher error sensitivity in the Random Walk (0.196, [0.119 0.273]) than in the Random (0.118, [0.085 0.150]) condition [$t(17) = 2.51$, $P = 0.023$, Fig. 3C]. These results are in agreement with the previous reports that sensitivity to errors in sensorimotor tasks is higher as the consistency in the environment increases (Gonzalez Castro et al. 2014; Herzfeld et al. 2014).

As described in Eq. 1, the estimation of error sensitivity is computed as the change in motor state [movement angle (MA)] between two consecutive trials (n and $n + 1$), while taking into account trial-by-trial retention (the A term), divided by the experienced error magnitude on the first trial in the pair (e_n). Although we used a retention rate that has been previously reported in the literature for visuomotor rotation experiments (Zarahn et al. 2008), other retention values could influence the estimation of error sensitivity.

For example, low retention decreases the contribution of MA_n to the calculation of error sensitivity. This can either cause an overestimation of error sensitivity when MA_n and e_n have opposite signs (the error is in the opposite direction of the movement angle), or an underestimation when they have the same sign. To address this concern, we tested whether differences in motor states between the consistency conditions can potentially explain the differences in the change in hand angle. We fitted linear functions to the relationship between the MA_n and e_n for each consistency condition, extracted the slopes of these functions, and computed for each participant the difference between the slopes of the Random Walk and Random conditions. We did not find a significant correlation between the within-participant differences in the slopes of the motor state and change in hand angle functions ($r = 0.254$, $P = 0.308$), suggesting that by itself, retention cannot account for the consistency effects on error sensitivity.

The perturbation consistency did not influence any timing aspects of the movement. We did not find significant changes in reaction time, movement time, and return time between the Random and the Random Walk conditions (Table 2).

Table 2. *Experiment 1: timing analysis*

	Random		Random Walk		<i>t</i> (17) (Random Walk-Random)	<i>P</i>
	Mean	95% CI	Mean	95% CI		
Reaction time, s	0.400	[0.374,0.427]	0.402	[0.380,0.423]	0.24	0.814
Movement time, s	0.317	[0.305,0.400]	0.305	[0.224,0.387]	-1.02	0.324
Return time, s	0.331	[0.291,0.372]	0.310	[0.279,0.342]	-1.70	0.107

Mean and 95% confidence interval of reaction time, movement time and return time for each of the Random and Random Walk conditions. For each measure, the *t* (with the degrees of freedom in parenthesis) and *P* values represent the results of a paired *t* test that examines the difference between the Random Walk and Random conditions.

Experiment 2: Increased Error Sensitivity in Consistent Environments Depends on Explicit Strategies

The higher sensitivity to errors for the Random Walk condition with respect to the Random condition in *experiment 1* could have been driven by implicit changes in responses to the errors, by a modulation of explicit control strategies, or both. We examined these possibilities in *experiment 2*.

Two groups of participants performed the same visuomotor task as in *experiment 1*. Both groups experienced both Random [$R(1) = 0.04$] and Random Walk [$R(1) = 0.93$] perturbation schedules in different experimental runs. To examine the role

of awareness in error sensitivity modulations, participants in the Ignore group ($n = 15$) were requested to ignore the feedback and to move their hand directly to the target, whereas participants in the Counteract group ($n = 16$) were instructed to keep trying to reach the target with the cursor.

Error sensitivity was the highest when participants were counteracting for the Random Walk perturbation schedule. This is demonstrated by the analysis of the trial-by-trial change in hand angle across all experienced error magnitudes in Contingent-feedback trials (Fig. 4A). The negative slopes of the learning from error functions were significantly higher in

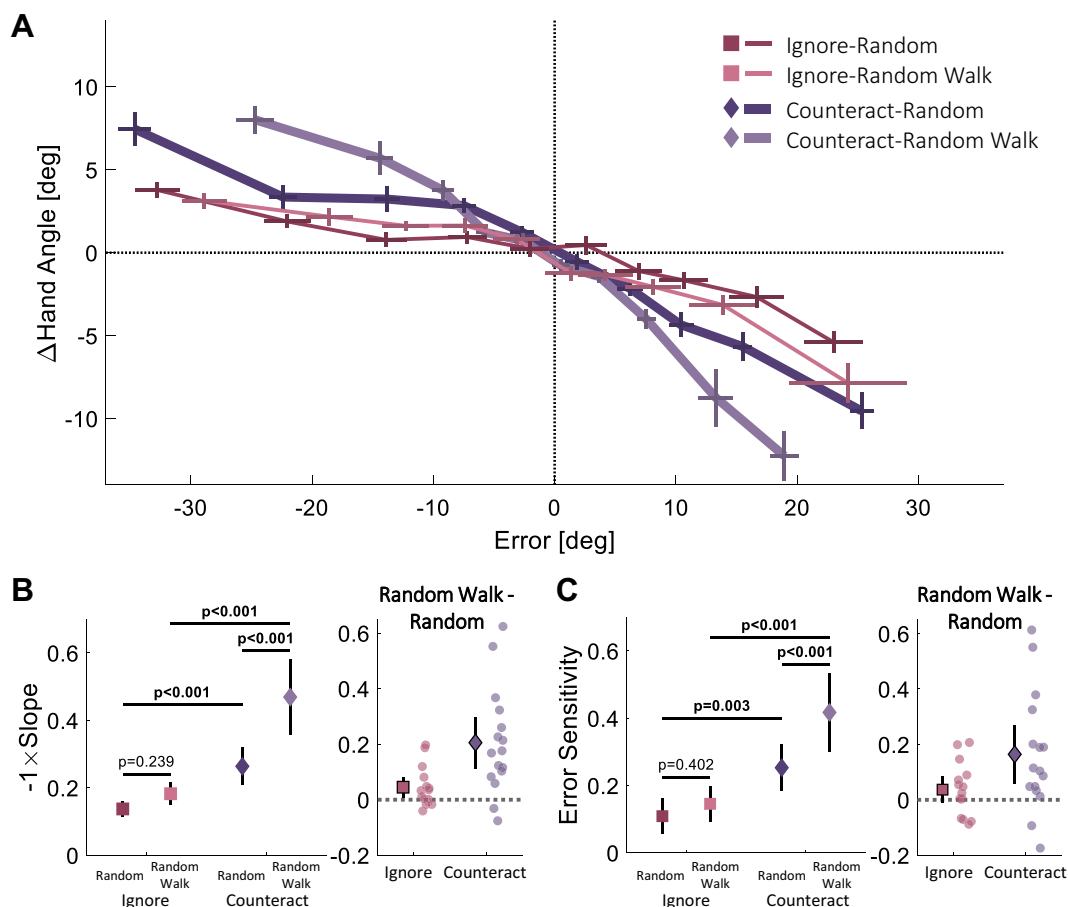


Fig. 4. *Experiment 2*: error sensitivity is higher for Random Walk than for Random sequences of visuomotor rotation when participants counteract rather than ignore the perturbations. *A*: mean change in hand angle as a function of the experienced error for the Ignore (thin pink lines) and Counteract (thick purple lines) groups for the Random (dark colors) and Random Walk (light colors) perturbation sequences. The trials were binned by error size for each participant. The centers of the crosses represent the mean hand angle for the mean error of each bin, and the vertical and horizontal lines of the crosses represent between-participant standard error. *B* and *C*: between-participants mean negative slopes for the functions in *A* (*B*) and mean error sensitivity computed for 10–20° error trials (*C*) for each perturbation sequence (*left*) and the within-participants Random Walk-Random difference for each measure (*right*). Error bars represent 95% confidence interval. Colored dots represent data of individual participants. Significant *P* values are bolded.

the Counteract (0.366, [0.308 0.425]) than in the Ignore group (0.160, [0.100 0.220]) [Strategy main effect: $F(1,29) = 25.36$, $P = 2.30 \times 10^{-5}$], suggesting that the Ignore manipulation attenuated error corrections. Similar to *experiment 1*, the participants showed increased negative slope when faced with the Random Walk (0.326, [0.263 0.388]) compared with the Random condition schedule (0.201, [0.168 0.233]) [Consistency main effect: $F(1,29) = 23.05$, $P = 4.40 \times 10^{-4}$]. Most importantly, the difference between the groups increased when they experienced Random Walk compared with Random perturbation schedules [Strategy-Consistency interaction effect: $F(1,29) = 9.45$, $P = 0.005$, Fig. 4B]. While the negative slopes of learning from error functions of the Ignore group are comparable between the Random (0.137, [0.091 0.184]) and Random Walk (0.183, [0.093 0.272]) conditions ($P_B = 0.239$), the learning from error function of the Counteract-Random Walk condition has a larger negative slope (0.469, [0.382 0.556]) than that of the Counteract-Random function (0.264, [0.219 0.308], $P_B = 4.00 \times 10^{-6}$). Furthermore, the abscissa projection of the learning from error function of the Counteract-Random Walk condition is narrower than all other functions (Fig. 4A), indicating that during this condition, participants experienced the smallest distribution of errors.

Statistical analyses of error sensitivity in the 10–20° error trials (Fig. 4C) revealed a significantly higher error sensitivity in the Counteract (0.335, [0.266 0.404]) than in the Ignore group (0.127, [0.056 0.198]) [Strategy main effect: $F(1,29) = 18.46$, $P = 1.80 \times 10^{-4}$] and for the Random Walk (0.281, [0.213 0.350]) than for the Random (0.181, [0.135 0.227]) condition [Consistency main effect: $F(1,29) = 11.18$, $P = 0.002$]. We also found an interaction effect between strategy and consistency influences on error sensitivity modulation in the 10–20° error trials [Strategy-Consistency interaction effect: $F(1,29) = 4.50$, $P = 0.043$]. While the Ignore group did not exhibit any significant change in error sensitivity between the Random (0.109, [0.043 0.175]) and Random Walk (0.146, [0.047 0.244]) conditions ($P_B = 0.402$), the Counteract group had a significantly higher error sensitivity during the Random Walk (0.417, [0.322 0.512]) than during the Random (0.253, [0.189 0.317]) condition ($P_B = 4.90 \times 10^{-4}$).

Despite the influence of the Error Clamp trials in underestimating error sensitivity, statistical analysis of error sensitivity for these trials revealed a similar picture. While there was no significant main effect of Consistency {Random: 0.051, [0.001 0.101], Random Walk: 0.147, [0.057 0.237], $F(1,29) = 3.91$, $P = 0.057$ }, we found a significant main effect of Strategy {Ignore: 0.023, [−0.054 0.099], Counteract: 0.175, [0.101

0.249], $F(1,29) = 8.57$, $P = 0.007$] and Strategy-Consistency interaction effect [$F(1,29) = 5.97$, $P = 0.021$], with a significant increase in error sensitivity with increasing consistency in the Counteract group (Random: 0.068, [−0.001 0.137], Random Walk: 0.282, [0.157 0.407], $P_B = 0.004$) and not in the Ignore group (Random: 0.034, [−0.037 0.105], Random Walk: 0.012, [−0.118 0.141], $P_B = 0.749$). Overall, these results suggest that the increase in error sensitivity in consistent environments depends on the use of an explicit strategy.

Ignoring the visual feedback under the different consistency conditions did not influence any timing aspects of the movement. We did not find significant main effects of both Strategy and Consistency and no significant Strategy-Consistency interaction effects on reaction time and movement time (Table 3).

Experiment 3: Modulations of Feedback Delay Does Not Influence Error Sensitivity

The observed enhancement of error sensitivity in the Random Walk condition in the Counteract group in *experiment 2* is in line with the idea that the use of explicit strategies is required for modulating error sensitivity in consistent environments. In addition, the absence of difference in error sensitivity between the consistency conditions in the Ignore group suggests that implicit processes do not contribute to increases in error sensitivity in changing, yet highly consistent, environments such as the Random Walk perturbations. We examined this conclusion in *experiment 3*.

One group of participants ($n = 22$) experienced Random Walk perturbation schedules across different experimental runs [$R(1) = -0.91$]. The participants were requested to always try to hit the target with the cursor. Across runs, we manipulated the implicit process by imposing different delays between the movement and the feedback. Delayed feedback was previously shown to attenuate adaptation (Kitazawa et al. 1995) through implicit processes (Brudner et al. 2016; Parvin et al. 2018). The magnitudes of the delays ranged between 600 and 2,500 ms. Within each run, the delay was either constant (1,000 or 2,000 ms) or variable (600–1,500 ms or 1,600–2,500 ms). If implicit adaptation contributes to the increased error sensitivity observed when deliberately counteracting the rotation in the Random Walk perturbation schedule, we expected a lower sensitivity to errors for higher delays.

The delay of the feedback did not affect error sensitivity. During all four delay conditions, participants exhibited similar learning from error functions (Fig. 5A) that had comparable negative slopes [Fig. 5B, 600–1,500 ms: 0.346, [0.265 0.430], 1,000 ms: 0.390, [0.311 0.469], 1,600–2,500 ms: 0.410, [0.319

Table 3. *Experiment 2: timing analysis*

	Ignore				Counteract				Strategy Main		Consistency Main		Interaction	
	Random		Random Walk		Random		Random Walk		$F(1,29)$	P	$F(1,29)$	P	$F(1,29)$	P
	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI						
Reaction														
time, s	0.464	[0.406,0.522]	0.476	[0.421,0.531]	0.473	[0.417,0.528]	0.460	[0.407,0.513]	0.02	0.905	0.001	0.980	0.48	0.496
Movement														
time, s	0.111	[0.085,0.136]	0.115	[0.092,0.138]	0.124	[0.099,0.149]	0.120	[0.097,0.142]	0.34	0.565	0.0004	0.985	0.75	0.394

Mean and 95% confidence interval of reaction time and movement time for each of the Random and Random Walk conditions in each of the Ignore and Counteract groups. For each measure, we present the F (with the degrees of freedom in parenthesis) and P values for each of the main effects (Strategy and Consistency) and for the Strategy-Consistency interaction effect.

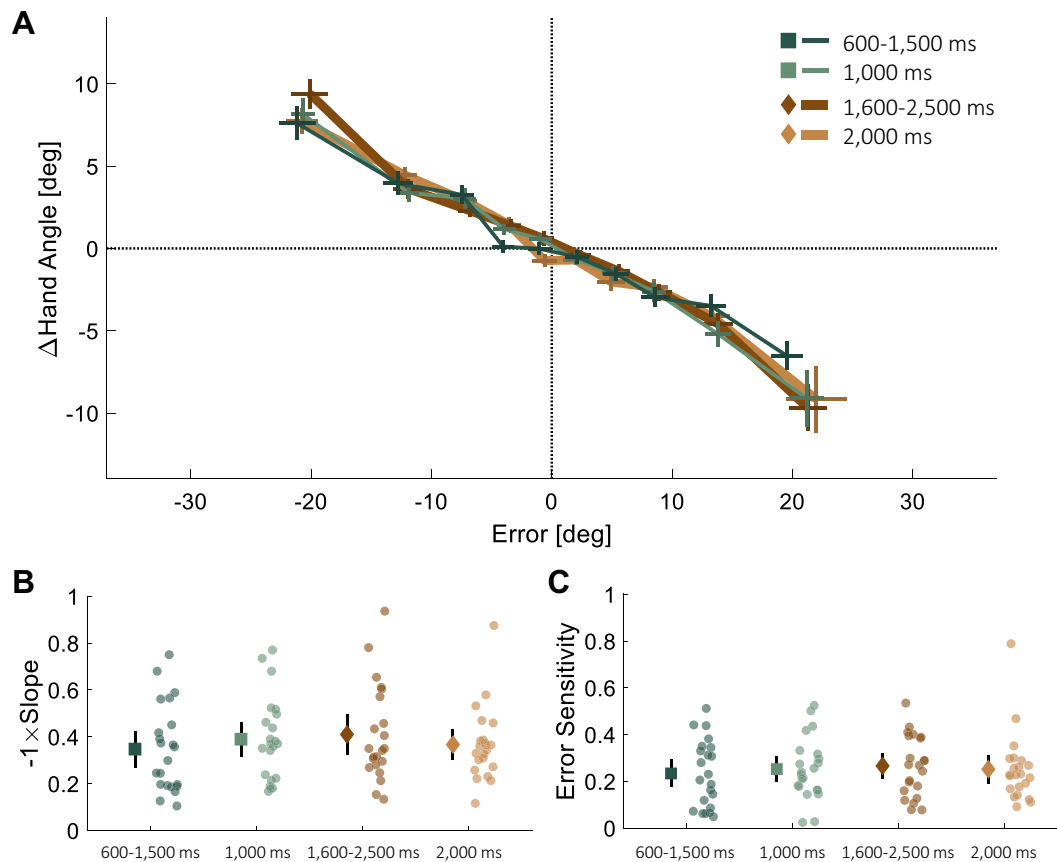


Fig. 5. *Experiment 3*: error sensitivity for Random Walk is comparable between different magnitudes of feedback delays. *A*: mean change in hand angle as a function of the experienced error for feedback delays of 600–1,500 ms (thin dark green line), 1,000 ms (thin light green line), 1,600–2,500 ms (thick dark brown line), and 2,000 ms (thick light brown line). The trials were binned by error size for each participant. The centers of the crosses represent the mean hand angle for the mean error of each bin, and the vertical and horizontal lines of the crosses represent between-participant SE. *B* and *C*: between-participants mean negative slope for the functions in *A* (*B*) and mean error sensitivity computed for 10–20° error trials (*C*) for each delay condition. Error bars represent 95% confidence interval. Colored dots represent data of individual participants.

0.501], 2,000 ms: 0.367, [0.298 0.436], Delay main effect: $F(3,63) = 0.82$, $P = 0.487$). In addition, we did not find statistically significant differences in error sensitivity for either 10–20° error trials [Fig. 5C, 600–1,500 ms: 0.234, [0.170 0.297], 1,000 ms: 0.252, [0.194 0.311], 1,600–2,500 ms: 0.266, [0.209 0.323], 2,000 ms: 0.252, [0.186 0.317], Delay main effect: $F(3,63) = 0.40$, $P = 0.750$] or 15° Error Clamp {600–1,500 ms: 0.186, [0.111 0.261], 1,000 ms: 0.159, [0.090 0.229], 1,600–2,500 ms: 0.148, [0.079 0.216], 2,000 ms: 0.132, [0.067 0.198], Delay main effect: $F(3,63) = 0.66$, $P = 0.570$ }. These results suggest that under random walk perturbation, suppression of the implicit process by increasing feedback delay does not affect error sensitivity and therefore provide support for the central contribution of explicit control to

enhanced error sensitivity in consistent environments (but see DISCUSSION).

The delayed feedback did not influence any timing aspects of the movement. We did not find a significant Delay effect on reaction times, movement times, and return times (Table 4).

DISCUSSION

Environmental consistency is considered to be an important factor in sensorimotor learning (Burge et al. 2008). We corroborated this here by demonstrating that sensitivity to errors is higher when experiencing random walk sequences of visuomotor perturbations compared with random sequences. Nevertheless, we show that consistency by itself is not a sufficient condition for increasing learning rates. When instructed to

Table 4. *Experiment 3*: timing analysis

	600–1,500 ms		1,000 ms		1,600–2,500 ms		2,000 ms		Delay Main	
	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI	$F(3,63)$	P
Reaction time, s	0.429	[0.403,0.456]	0.441	[0.411,0.472]	0.455	[0.421,0.488]	0.448	[0.410,0.486]	1.94	0.133
Movement time, s	0.327	[0.259,0.395]	0.356	[0.288,0.425]	0.360	[0.295,0.425]	0.377	[0.301,0.453]	2.12	0.107
Return time, s	0.394	[0.333,0.454]	0.412	[0.352,0.471]	0.406	[0.348,0.464]	0.463	[0.382,0.543]	2.67	0.055

Mean and 95% confidence interval (CI) of reaction time, movement time, and return time for each of the delayed feedback conditions. For each measure, we present the F (with the degrees of freedom in parenthesis) and P values for the main effect of Delay.

ignore the perturbations, a manipulation that suppresses explicit processes and thereby reveals the contribution of implicit learning processes (Mazzoni and Krakauer 2006; Morehead et al. 2017), our participants did not exhibit an increase in error sensitivity in a consistent environment. Furthermore, variation of the delay of the feedback, a manipulation that typically influences implicit adaptation, yielded comparable levels of sensitivity to errors under random walk conditions, supporting the contribution of explicit learning processes to adaptation in consistent environments. Overall, our results suggest that the sensorimotor system increases error sensitivity in consistent environments mainly due to the contribution of explicit strategies rather than by influencing the rate by which internal models are implicitly updated.

Previous examinations of consistency effects on sensorimotor learning largely ignored the roles of conscious awareness of the perturbations. This is likely a reflection of the historic view that motor learning is entirely implicit, an assumption that was based on reports that gradually increasing perturbations (implicit) produce comparable, and sometimes stronger, aftereffects (Kagerer et al. 1997) and retention (Klassen et al. 2005) than abrupt perturbations (implicit and explicit). Studies that specifically examined changes in error sensitivity that are due to perturbation consistency have modeled these changes using a single-rate state space model, which implies that a single process governs adaptation (Gonzalez Castro et al. 2014; Herzfeld et al. 2014). The hidden assumption behind this approach is that the modulation of error sensitivity under such conditions is implicit (McDougle et al. 2015). Nevertheless, recent evidence illustrated that the learning from error function of the explicit learning process to different magnitudes of visuomotor rotations is influenced by environmental consistency (Hutter and Taylor 2018). Interestingly, the observed effect was nonmonotonic: sensitivity increased from inconsistent to low-consistent perturbations but decreased as consistency increased farther. Importantly, the learning from error in Hutter and Taylor (2018), was examined as a function of the perturbation size rather than the experienced visual error. The distribution of the latter varies between different levels of consistency, which may explain the nonmonotonicity behavior of the sensitivity function.

The main studies that examined consistency effects on error sensitivity used force field perturbations (Gonzalez Castro et al. 2014; Herzfeld et al. 2014). While it is difficult to isolate the contribution of explicit strategies to the compensation for force feedback, previous results with this paradigm may address another central question in motor learning: do the environmental manipulations affect the sensitivity to error directly, or elicit other explicit strategies, such as a recall of a previous successful action? Gonzalez Castro et al. (2014) showed that if participants are suddenly exposed to a perturbation that is opposite to the trained perturbations, they react to it in the same way that they reacted to the trained perturbations; i.e., they apply a negative and inappropriate correction. This behavior reflects an involvement of a process other than error sensitivity modulation, such as a recall of previous correct responses (Haith and Krakauer 2014). Our results support that notion by showing that consistency effects are mediated by explicit control.

Which strategy underlies the faster adaptation to consistent perturbations? A recent study provided evidence for distinct

cognitive strategies during sensorimotor learning of visuomotor rotation: a recall of stimulus-response contingencies and parametric computation of error correction (McDougle and Taylor 2019). The former relates to a fast process that utilizes memories of acquired associations between stimuli and responses, whereas the latter is a process that computes the aiming direction by means of mental rotation based on the experienced target error (Taylor and Ivry 2011). We speculate that in the context of a constantly changing perturbations, the consistency in the random walk condition may enhance the mental rotation strategy of the participants. Possibly, a prolonged practice with a consistent perturbation would enable a caching process of stimulus response associations (Huberdeau et al. 2019) mediated by an increase in movement repetitions (Huang et al. 2011; Mawase et al. 2018).

The link between error sensitivity and explicit sensorimotor learning is also studied in the context of savings, i.e., the faster learning upon reexposure to the same perturbation. Herzfeld et al. (2014) explained savings as a change in error sensitivity in face of an error that was previously encountered. More recently, savings was explained as a retrieval of an explicit aiming strategy that was previously associated with a better performance (Haith et al. 2015; Morehead et al. 2015). Interestingly, despite previous evidence of the necessary role of both error-driven adaptation and repetitions of successful movements in inducing savings (Huang et al. 2011), Leow et al. challenged this view, suggesting that the experience of previously encountered errors is sufficient (Leow et al. 2019) as long as the perturbation is adequately stable (Leow et al. 2016). Our results are in line with this idea and suggest that savings is a product of enhanced sensitivity to an error that was processed explicitly due to the experience of consistent perturbations. Thus savings can be viewed as an exemplar for more general phenomena of error correction facilitations that are driven by strategic processes. This conjecture also leads to the prediction that the neural substrates of savings that are localized to the motor cortex (Landi et al. 2011; Li et al. 2001) and basal ganglia circuits (Leow et al. 2012; Ruitenberg et al. 2018) will also be involved in the increased corrections for consistent perturbations. Nonetheless, savings and reaction to consistency may differ in terms of the processes that underlie their formation; while savings possibly depends on encoding of successful reactions to distinct errors (Huang et al. 2011; Huberdeau et al. 2015), consistency detection requires a continuous estimation of the ability to reduce external errors (Baddeley et al. 2003; Gonzalez Castro et al. 2014).

The current study supplements the growing body of literature that emphasizes the important contribution of explicit strategies to sensorimotor learning. Whereas the implicit process is highly rigid, the explicit process can be flexibly tuned to task demands, e.g., by scaling the correction to the error size (Bond and Taylor 2015), and as mentioned above, by adjusting the reactions according to previous experience (Haith et al. 2015; Huberdeau et al. 2017; Morehead et al. 2015). Furthermore, age-related declines in motor learning were recently shown to be associated with both behavioral and neural changes in the explicit memory system (Vandevorde and Orban de Xivry 2018; Wolpe et al. 2018). Here we show that the interaction between environmental consistency and motor learning is related to the modulations of explicit strategies rather than to the modulation of implicit adaptation.

Error clamp trials were previously used to probe changes of sensorimotor representations in face of dynamic (Avraham et al. 2017; Scheidt et al. 2000) and kinematic (Morehead et al. 2017; Shmuelof et al. 2012a) perturbations. In our design, each experimental run consisted of multiple error clamp trials with 15° error size, aiming to provide sufficient recurrences for calculating error sensitivity for a constant error. However, in some of our experiments, analysis of the error clamp trials yielded no, or reduced, change in error sensitivity. As mentioned above, we suggest that this result can be explained by the fact that the error clamp trials in our design were presented within the perturbation sequence, and participants received them when they were in an adapted state. This causes underestimation in the calculation of error sensitivity based on the sudden, noncontingent and erroneous feedback presented farther away from the target. Therefore, we also examined error sensitivity for trials in which the experienced error was similar in size to the error experienced during error clamp trials (10–20°). These analyses revealed that error sensitivity was indeed modulated in all our conditions (e.g., Figs. 3C and 4C). Importantly, the analyses of the error clamp trials show that error sensitivity is the largest under consistent environments and an instruction to counteract the errors, and thus they are in line with the main conclusion of this study.

The finding that our delay manipulation did not affect the performance under the Random Walk conditions (*experiment 3*) was unexpected. First, it may be that the delay manipulation did not modulate the implicit adaptation. Although we used values that have been previously reported to attenuate implicit adaptation (Parvin et al. 2018; Schween and Hegele 2017), other studies have shown influences of larger delays (Brudner et al. 2016; Kitazawa et al. 1995). Possibly, under a changing perturbation, the delays were not long enough to modulate the implicit adaptation. Alternatively, it may be that implicit adaptation was already weak and that the lack of sensitivity modulations in *experiment 3* is due to a floor effect: We used end point feedback to avoid feedback correction during the movement, which results in smaller adaptation than continuous feedback (Taylor et al. 2014), and all our experiments included some baseline delay. Therefore, the nonzero change in hand angle that was observed in the Ignore group (*experiment 2*), which is driven by a process that is probably also active in *experiment 3*, may represent an implicit component that is immune to delays. Such a component could be driven by target error (Kim et al. 2019; Leow et al. 2018; Reichenthal et al. 2016) rather than the delayed sensory prediction error. Lastly, it is possible that the higher delays did attenuate implicit adaptation but that the explicit process compensated for it. This interpretation is consistent with a recent study that illustrated such an explicit compensation for constant visuomotor rotation under delayed feedback (Brudner et al. 2016). This explanation strengthens our claim that the explicit process significantly contributes to adaptation in consistent, yet changing, environments.

Overall, our results could not completely rule out the possibility that at least some consistency-driven modulations of error sensitivity are due to the implicit process. Although not significant, there is a tendency for increased sensitivity in the Ignore group when experiencing the more consistent condition (Fig. 4). This might stem from the possibility that participants sometimes do not comply with the instructions to ignore the

feedback and that this tendency reflects leaking of explicit effects. In general, the absence of clear effects in this group could be due to noise in the experimental design. This is directly linked to the possibility mentioned above that the observed implicit behavior is only a fraction of the total implicit process. Future studies are needed to examine the influence of perturbation consistency on error sensitivity modulations using manipulations that engage the implicit process in isolation from explicit strategies in a cleaner fashion, e.g., using task-irrelevant clamped feedback (Morehead et al. 2017), or by limiting preparation time (Haith et al. 2015).

The association between consistency and explicit strategies is mediated by the detection of the consistency. Consistency estimation requires monitoring both the perceived errors and the reaction to these errors, but could also be approximated by memorizing the history of error magnitudes alone (by either averaging recent errors or monitoring their trial-by-trial changes). The use of explicit strategies may contribute to the consistency estimation process by increasing the awareness to the error (Johnson et al. 2002), enhancing the notion of agency (Parvin et al. 2018), or facilitating the generation of memories for the experienced errors (Morehead et al. 2015). Understanding the benefits and the driving signals of explicit learning strategies is essential for improving motor learning in general and, specifically, could improve the outcomes of rehabilitative treatments.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

G.A., M.K., and L.S. conceived and designed research; G.A. and M.K. performed experiments; G.A. and M.K. analyzed data; G.A., M.K., and L.S. interpreted results of experiments; G.A. prepared figures; G.A. and L.S. drafted manuscript; G.A. and L.S. edited and revised manuscript; G.A., M.K., and L.S. approved final version of manuscript.

REFERENCES

- Avraham G, Mawase F, Karniel A, Shmuelof L, Donchin O, Mussa-Ivaldi FA, Nisky I. Representing delayed force feedback as a combination of current and delayed states. *J Neurophysiol* 118: 2110–2131, 2017. doi:10.1152/jn.00347.2017.
- Baddeley RJ, Ingram HA, Miall RC. System identification applied to a visuomotor task: near-optimal human performance in a noisy changing task. *J Neurosci* 23: 3066–3075, 2003. doi:10.1523/JNEUROSCI.23-07-03066.2003.

- Bond KM, Taylor JA.** Flexible explicit but rigid implicit learning in a visuomotor adaptation task. *J Neurophysiol* 113: 3836–3849, 2015. doi:10.1152/jn.00009.2015.
- Brudner SN, Kethidi N, Graepner D, Ivry RB, Taylor JA.** Delayed feedback during sensorimotor learning selectively disrupts adaptation but not strategy use. *J Neurophysiol* 115: 1499–1511, 2016. doi:10.1152/jn.00066.2015.
- Burge J, Ernst MO, Banks MS.** The statistical determinants of adaptation rate in human reaching. *J Vis* 8: 20, 2008. doi:10.1167/8.4.20.
- Criscimagna-Hemminger SE, Bastian AJ, Shadmehr R.** Size of error affects cerebellar contributions to motor learning. *J Neurophysiol* 103: 2275–2284, 2010. doi:10.1152/jn.00822.2009.
- Galea JM, Vazquez A, Pasricha N, Orban de Xivry JJ, Celnik P.** Dissociating the roles of the cerebellum and motor cortex during adaptive learning: the motor cortex retains what the cerebellum learns. *Cereb Cortex* 21: 1761–1770, 2011. doi:10.1093/cercor/bhq246.
- Gonzalez Castro LN, Hadjiosif AM, Hemphill MA, Smith MA.** Environmental consistency determines the rate of motor adaptation. *Curr Biol* 24: 1050–1061, 2014. doi:10.1016/j.cub.2014.03.049.
- Haith AM, Huberdeau DM, Krakauer JW.** The influence of movement preparation time on the expression of visuomotor learning and savings. *J Neurosci* 35: 5109–5117, 2015. doi:10.1523/JNEUROSCI.3869-14.2015.
- Haith AM, Krakauer JW.** Model-based and model-free mechanisms of human motor learning. In: *Progress in Motor Control: Neural, Computational and Dynamic Approaches*, edited by Richardson MJ, Riley MA, Shockey K. New York: Springer, 2013, p. 1–21. doi:10.1007/978-1-4614-5465-6_1.
- Haith AM, Krakauer JW.** Motor learning: the great rate debate. *Curr Biol* 24: R386–R388, 2014. doi:10.1016/j.cub.2014.03.077.
- Hanajima R, Shadmehr R, Ohminami S, Tsutsumi R, Shirota Y, Shimizu T, Tanaka N, Terao Y, Tsuji S, Ugawa Y, Uchimura M, Inoue M, Kitazawa S.** Modulation of error-sensitivity during a prism adaptation task in people with cerebellar degeneration. *J Neurophysiol* 114: 2460–2471, 2015. doi:10.1152/jn.00145.2015.
- Herzfeld DJ, Vaswani PA, Marko MK, Shadmehr R.** A memory of errors in sensorimotor learning. *Science* 345: 1349–1353, 2014. doi:10.1126/science.1253138.
- Huang VS, Haith A, Mazzoni P, Krakauer JW.** Rethinking motor learning and savings in adaptation paradigms: model-free memory for successful actions combines with internal models. *Neuron* 70: 787–801, 2011. doi:10.1016/j.neuron.2011.04.012.
- Huberdeau DM, Haith AM, Krakauer JW.** Formation of a long-term memory for visuomotor adaptation following only a few trials of practice. *J Neurophysiol* 114: 969–977, 2015. doi:10.1152/jn.00369.2015.
- Huberdeau DM, Krakauer JW, Haith AM.** Practice induces a qualitative change in the memory representation for visuomotor learning (Preprint) *bioRxiv*, 2017. doi:10.1101/226415.
- Huberdeau DM, Krakauer JW, Haith AM.** Practice induces a qualitative change in the memory representation for visuomotor learning. *J Neurophysiol* 122: 1050–1059, 2019. doi:10.1152/jn.00830.2018.
- Hutter SA, Taylor JA.** Relative sensitivity of explicit reaiming and implicit motor adaptation. *J Neurophysiol* 120: 2640–2648, 2018. doi:10.1152/jn.00283.2018.
- Imamizu H, Miyauchi S, Tamada T, Sasaki Y, Takino R, Pütz B, Yoshioka T, Kawato M.** Human cerebellar activity reflecting an acquired internal model of a new tool. *Nature* 403: 192–195, 2000. doi:10.1038/35003194.
- Johnson H, Van Beers RJ, Haggard P.** Action and awareness in pointing tasks. *Exp Brain Res* 146: 451–459, 2002. doi:10.1007/s00221-002-1200-z.
- Kagerer FA, Contreras-Vidal JL, Stelmach GE.** Adaptation to gradual as compared with sudden visuo-motor distortions. *Exp Brain Res* 115: 557–561, 1997. doi:10.1007/PL00005727.
- Kim HE, Morehead JR, Parvin DE, Moazzezi R, Ivry RB.** Invariant errors reveal limitations in motor correction rather than constraints on error sensitivity. *Commun Biol* 1: 19, 2018. doi:10.1038/s42003-018-0021-y.
- Kim HE, Parvin DE, Ivry RB.** The influence of task outcome on implicit motor learning. *eLife* 8: e39882, 2019. doi:10.7554/eLife.39882.
- Kim S, Ogawa K, Lv J, Schweighofer N, Imamizu H.** Neural substrates related to motor memory with multiple timescales in sensorimotor adaptation. *PLoS Biol* 13: e1002312, 2015. doi:10.1371/journal.pbio.1002312.
- Kitazawa S, Kohno T, Uka T.** Effects of delayed visual information on the rate and amount of prism adaptation in the human. *J Neurosci* 15: 7644–7652, 1995. doi:10.1523/JNEUROSCI.15-11-07644.1995.
- Klassen J, Tong C, Flanagan JR.** Learning and recall of incremental kinematic and dynamic sensorimotor transformations. *Exp Brain Res* 164: 250–259, 2005. doi:10.1007/s00221-005-2247-4.
- Krakauer JW, Mazzoni P, Ghazizadeh A, Ravindran R, Shadmehr R.** Generalization of motor learning depends on the history of prior action. *PLoS Biol* 4: e316, 2006. doi:10.1371/journal.pbio.0040316.
- Landi SM, Baguear F, Della-Maggiore V.** One week of motor adaptation induces structural changes in primary motor cortex that predict long-term memory one year later. *J Neurosci* 31: 11808–11813, 2011. doi:10.1523/JNEUROSCI.2253-11.2011.
- Leow LA, de Rugy A, Marinovic W, Riek S, Carroll TJ.** Savings for visuomotor adaptation require prior history of error, not prior repetition of successful actions. *J Neurophysiol* 116: 1603–1614, 2016. doi:10.1152/jn.01055.2015.
- Leow LA, Loftus AM, Hammond GR.** Impaired savings despite intact initial learning of motor adaptation in Parkinson's disease. *Exp Brain Res* 218: 295–304, 2012. doi:10.1007/s00221-012-3060-5.
- Leow LA, Marinovic W, de Rugy A, Carroll TJ.** Task errors contribute to implicit aftereffects in sensorimotor adaptation. *Eur J Neurosci* 48: 3397–3409, 2018. doi:10.1111/ejn.14213.
- Li CS, Padoa-Schioppa C, Bizzi E.** Neuronal correlates of motor performance and motor learning in the primary motor cortex of monkeys adapting to an external force field. *Neuron* 30: 593–607, 2001. doi:10.1016/S0896-6273(01)00301-4.
- Leow L-A, Marinovic W, de Rugy A, Carroll TJ.** Task errors drive memories that improve sensorimotor adaptation (Preprint). *bioRxiv* 538348, 2019. doi:10.1101/538348.
- Lilliefors HW.** On the Kolmogorov-Smirnov test for normality with mean and variance unknown. *J Am Stat Assoc* 62: 399–402, 1967. doi:10.1080/01621459.1967.10482916.
- Marko MK, Haith AM, Harran MD, Shadmehr R.** Sensitivity to prediction error in reach adaptation. *J Neurophysiol* 108: 1752–1763, 2012. doi:10.1152/jn.00177.2012.
- Mawase F, Lopez D, Celnik PA, Haith AM.** Movement repetition facilitates response preparation. *Cell Rep* 24: 801–808, 2018. doi:10.1016/j.celrep.2018.06.097.
- Mazzoni P, Krakauer JW.** An implicit plan overrides an explicit strategy during visuomotor adaptation. *J Neurosci* 26: 3642–3645, 2006. doi:10.1523/JNEUROSCI.5317-05.2006.
- McDougle SD, Bond KM, Taylor JA.** Explicit and implicit processes constitute the fast and slow processes of sensorimotor learning. *J Neurosci* 35: 9568–9579, 2015. doi:10.1523/JNEUROSCI.5061-14.2015.
- McDougle SD, Ivry RB, Taylor JA.** Taking aim at the cognitive side of learning in sensorimotor adaptation tasks. *Trends Cogn Sci* 20: 535–544, 2016. doi:10.1016/j.tics.2016.05.002.
- McDougle SD, Taylor JA.** Dissociable cognitive strategies for sensorimotor learning. *Nat Commun* 10: 40, 2019. doi:10.1038/s41467-018-07941-0.
- Morehead JR, Qasim SE, Crossley MJ, Ivry R.** Savings upon re-aiming in visuomotor adaptation. *J Neurosci* 35: 14386–14396, 2015. doi:10.1523/JNEUROSCI.1046-15.2015.
- Morehead JR, Taylor JA, Parvin DE, Ivry RB.** Characteristics of implicit sensorimotor adaptation revealed by task-irrelevant clamped feedback. *J Cogn Neurosci* 29: 1061–1074, 2017. doi:10.1162/jocn_a_01108.
- Parvin DE, McDougle SD, Taylor JA, Ivry RB.** Credit assignment in a motor decision making task is influenced by agency and not sensory prediction errors. *J Neurosci* 38: 4521–4530, 2018. doi:10.1523/JNEUROSCI.3601-17.2018.
- Reichenthal M, Avraham G, Karniel A, Shmuelof L.** Target size matters: target errors contribute to the generalization of implicit visuomotor learning. *J Neurophysiol* 116: 411–424, 2016. doi:10.1152/jn.00830.2015.
- Ruitenberg MF, Koppelmans V, De Dios YE, Gadd NE, Wood SJ, Reuter-Lorenz PA, Kofman I, Bloomberg JJ, Mulavara AP, Seidler RD.** Neural correlates of multi-day learning and savings in sensorimotor adaptation. *Sci Rep* 8: 14286, 2018. doi:10.1038/s41598-018-32689-4.
- Scheidt RA, Reinkensmeyer DJ, Conditt MA, Rymer WZ, Mussa-Ivaldi FA.** Persistence of motor adaptation during constrained, multi-joint, arm movements. *J Neurophysiol* 84: 853–862, 2000. doi:10.1152/jn.2000.84.2.853.
- Schlert J, Ivry RB, Diedrichsen J.** Encoding of sensory prediction errors in the human cerebellum. *J Neurosci* 32: 4913–4922, 2012. doi:10.1523/JNEUROSCI.4504-11.2012.
- Schween R, Hegele M.** Feedback delay attenuates implicit but facilitates explicit adjustments to a visuomotor rotation. *Neurobiol Learn Mem* 140: 124–133, 2017. doi:10.1016/j.nlm.2017.02.015.
- Shmuelof L, Huang VS, Haith AM, Delnicki RJ, Mazzoni P, Krakauer JW.** Overcoming motor “forgetting” through reinforcement of learned actions. *J Neurosci* 32: 14617–14621a, 2012a. doi:10.1523/JNEUROSCI.2184-12.2012.
- Shmuelof L, Krakauer JW, Mazzoni P.** How is a motor skill learned? Change and invariance at the levels of task success and trajectory control. *J Neurophysiol* 108: 578–594, 2012b. doi:10.1152/jn.00856.2011.

- Smith MA, Ghazizadeh A, Shadmehr R.** Interacting adaptive processes with different timescales underlie short-term motor learning. *PLoS Biol* 4: e179, 2006. doi:[10.1371/journal.pbio.0040179](https://doi.org/10.1371/journal.pbio.0040179).
- Taylor JA, Ivry RB.** Flexible cognitive strategies during motor learning. *PLOS Comput Biol* 7: e1001096, 2011. doi:[10.1371/journal.pcbi.1001096](https://doi.org/10.1371/journal.pcbi.1001096).
- Taylor JA, Ivry RB.** Cerebellar and prefrontal cortex contributions to adaptation, strategies, and reinforcement learning. *Prog Brain Res* 210: 217–253, 2014. doi:[10.1016/B978-0-444-63356-9.00009-1](https://doi.org/10.1016/B978-0-444-63356-9.00009-1).
- Taylor JA, Klemfuss NM, Ivry RB.** An explicit strategy prevails when the cerebellum fails to compute movement errors. *Cerebellum* 9: 580–586, 2010. doi:[10.1007/s12311-010-0201-x](https://doi.org/10.1007/s12311-010-0201-x).
- Taylor JA, Krakauer JW, Ivry RB.** Explicit and implicit contributions to learning in a sensorimotor adaptation task. *J Neurosci* 34: 3023–3032, 2014. doi:[10.1523/JNEUROSCI.3619-13.2014](https://doi.org/10.1523/JNEUROSCI.3619-13.2014).
- Vandevorde K, Orban de Xivry J-J.** Internal model recalibration does not deteriorate with age while motor adaptation does (Preprint). *bioRxiv*, 2018. doi:[10.1101/292250](https://doi.org/10.1101/292250).
- Welch RB.** Adaptation to prism-displaced vision: the importance of target-pointing. *Percept Psychophys* 5: 305–309, 1969. doi:[10.3758/BF03209569](https://doi.org/10.3758/BF03209569).
- Wolpe N, Ingram JN, Tsvetanov KA, Henson RN, Kievit RA, Wolpert DM, Rowe JB; Cambridge Centre for Ageing and Neuroscience.** Motor learning decline with age is related to differences in the explicit memory system (Preprint). *bioRxiv*, 2018. doi:[10.1101/353870](https://doi.org/10.1101/353870).
- Zarahn E, Weston GD, Liang J, Mazzoni P, Krakauer JW.** Explaining savings for visuomotor adaptation: linear time-invariant state-space models are not sufficient. *J Neurophysiol* 100: 2537–2548, 2008. doi:[10.1152/jn.90529.2008](https://doi.org/10.1152/jn.90529.2008).

