Retention and interference of learned dexterous manipulation: interaction between multiple sensorimotor processes

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Fu Q, Santello M. Retention and interference of learned dexterous manipulation: interaction between multiple sensorimotor processes. J Neurophysiol 113: 144 –155, 2015. First published October 1, 2014; doi:10.1152/jn.00348.2014.—An object can be used in multiple contexts, each requiring different hand actions. How the central nervous system builds and maintains memory of such dexterous manipulations remains unclear. We conducted experiments in which human subjects had to learn and recall manipulations performed in two contexts, A and B. Both contexts involved lifting the same L-shaped object whose geometry cued its asymmetrical mass distribution. Correct performance required producing a torque on the vertical handle at object lift onset to prevent it from tilting. The torque direction depended on the context, i.e., object orientation, which was changed by 180° object rotation about a vertical axis. With an A1B1A2 context switching paradigm, subjects learned A1 in the first block of eight trials as indicated by a torque approaching the required one. However, subjects made large errors in anticipating the required torque when switching to B1 immediately after A1 (negative transfer), as well as when they had to recall A1 when switching to A2 after learning B through another block of eight lifts (retrieval interference). Classic sensorimotor learning theories attribute such interferences to multi-rate, multi-process mechanisms. However, our experiments indicated that the strength of this interference depends on the extent of the context switch (i.e., torque to be exerted in an opposite direction) and the effectiveness of context cues, we have shown that a learned manipulation has an inhibitory effect on the CNS’s ability to use visual cues for planning manipulation in an opposite context (i.e., torque to be exerted in an opposite direction) and that the strength of this interference depends on the extent of consecutive practice in the preceding context (Fu and Santello 2012). This interference shares common features with experimental evidence from reaching studies demonstrating an anterograde interference using similar A1B1A2 paradigms, where A and B denote opposite contexts. Specifically, we found interference occurring on the “transfer trial” when subjects switched to context B the first time after learning A, as well as on the “retrieval trials” when subjects switched back to A. We hypothesized that this interference is due to the extent of visual and disturbance transformations of manipulation might have been the net result of two different adaptation processes running in parallel: one features error-driven updates of internal models, whereas the other depends on the history of repeated actions. However, our previous study did not allow the quantification of the role of each of these processes in the interference on manipulation transfer and retrieval. To pursue this goal, in the present study we used a series of experimental variations of the A1B1A2 learning paradigm to thoroughly quantify the time course of the retention and interference phenomena. These new data allowed us to create a novel computational model that can account for the complex interaction between multiple sensorimotor processes.

MATERIALS AND METHODS

Subjects

Ninety-six healthy right-handed subjects (18–28 yr of age; 51 men) participated in this study. All participants were naive to the purpose of the study and gave their informed written consent according to the Declaration of Helsinki. The protocols were approved by the Office of Research Integrity and Assurance, Arizona State University. Subjects were randomly assigned to one of four experiments (see below).

DEXTEROUS MANIPULATION is thought to rely on building an internal representation of the task or object dynamics that can be updated through trial-by-trial learning to achieve a stable performance (Flanagan et al. 2001; Nowak et al. 2007; Salimi et al. 2000). However, the underlying sensorimotor mechanisms are not well understood. The properties of the learned representation of a motor task can be evaluated by generalization or retrieval protocols in which subjects are asked to generalize a previously learned task to a new context or recall the learned task in the same context. Until recently, such protocols have been mostly applied to reaching tasks (for review, see Wolpert et al. 2011), which has led to the establishment of several models of sensorimotor learning. For instance, error-based learning suggests that the central nervous system (CNS) updates the internal model of the task by using errors made in the previous trial(s) (Smith et al. 2006), whereas model-free learning is based on reinforcement and/or use-depended plasticity (Huang et al. 2011). Despite the insight provided by many studies of reaching movements, less is known about whether the proposed theoretical frameworks can account for sensorimotor learning underlying manipulation tasks.

A single object can be manipulated in different contexts, each requiring different forces and/or torques whose modulation, in turn, depends on object properties and hand-object spatial relations. A unique feature of manipulation task is the existence of rich visually based context cues that could result in fast adaptation (Ingram et al. 2011) and accurate initial estimation of task dynamics (Fu and Santello 2012). Despite the effectiveness of context cues, we have shown that a learned manipulation has an inhibitory effect on the CNS’s ability to use visual cues for planning manipulation in an opposite context (i.e., torque to be exerted in an opposite direction) and that the strength of this interference depends on the extent of consecutive practice in the preceding context (Fu and Santello 2012). This interference shares common features with experimental evidence from reaching studies demonstrating an anterograde interference using similar A1B1A2 paradigms, where A and B denote opposite contexts. Specifically, we found interference occurring on the “transfer trial” when subjects switched to context B the first time after learning A, as well as on the “retrieval trials” when subjects switched back to A. We hypothesized that this interference is due to the extent of visual transformation.
Apparatus

We asked subjects to grasp and lift a single L-shaped object. This object consisted of a handle and a rectangular base. The handle was equipped with two force/torque (F/T) sensors (Nano25, ATI Industrial Automation; Fig. 1A) that were used to measure digit forces and compute the center of pressure on each side of the handle (sampling rate: 1 kHz). Digit forces and center of pressure were used to calculate the compensatory torque subjects exerted on the object at lift onset (Fu et al. 2010). Note that in this study we do not attempt to analyze the change of digit level variables (e.g., digit force or center of pressure), but rather focus on the learning, interference, and retention at the task level (i.e., compensatory torque). We used the L-shaped object so as to have an asymmetrical mass distribution relative to the handle. The manipulation tasks required subjects to exert a torque to counter the external torque caused by the object’s mass distribution to prevent the object from tilting. Importantly, the L-shaped object geometry provided visual cues about its asymmetrical mass distribution, thus allowing subjects to anticipate the external torque direction (see below). We also measured peak object peak using an active marker-based motion tracking system (Impulse, Phasespace; sampling rate: 480 Hz) to obtain an additional motor performance index. The motion tracking system also provided measurement of object height with respect to the table surface, which was used to determine the instant at which object lift onset occurred (object height >0.5 mm for at least 400 ms). Recording of motion and force data was synchronized via TCP/IP protocols (delay <1 ms). Motion tracking data were linearly interpolated offline to 1 kHz to match the sampling rate of the F/T sensors.

The direction of the torque depended on the manipulation context. Specifically, depending on the object presentation, the object could appear to have a left (L) or right (R) center of mass relative to the subject, therefore requiring a clockwise (CW) or a counterclockwise (CCW) torque (“task torque”), respectively, of 320 N·mm (Fig. 1B). The two contexts were switched by instructing the subjects to rotate (CCW) torque (“task torque”), respectively, of 320 N·mm (Fig. 1C) was defined as $T_{\text{comp}}$, which is an indicator of the anticipatory control, because the feedback-driven torque correction could only occur after the object starts to move. We also found in our previous work that the behavioral error subjects made (peak object roll) was linearly dependent on the torque error they made at lift onset. This correlation was found in the present work, too ($r = 0.77, P < 0.001$, for all trials combined). Therefore, in all experiments, we measured $T_{\text{comp}}$ at object lift onset to quantify subjects’ ability to predict the required compensatory torque.

Experimental Procedures

In all conditions, subjects sat comfortably and the object was presented 30 cm in front of them. The handle of the object was aligned with the subjects’ right shoulder to ensure a comfortable grasp with the right hand. On hearing a “go” signal, subjects reached to grasp and lifted the object ~10 cm above the table, held it in a stationary position for ~2 s, and replaced it on the table. Subjects were required to grasp the handle with the tip of the thumb on the left graspable surface of the handle and the tip of the index and middle fingers on the right graspable surface of the handle (Fig. 1B) and to prevent the object from tilting, as if they were lifting a cup of water. All tasks required subjects to plan and generate torques in an anticipatory fashion to compensate the torque caused by asymmetric mass distribution with respect to the hand. Subjects were also instructed to rotate the object 180°, as described above, following the experimenter’s command.

Fig. 1. Experimental apparatus and protocol. A: design of the handle with embedded force/torque sensors and graspable surface. B: 2 alternative presentations [context right (R) and left (L)] of the L-shaped object and their corresponding compensatory torque directions (clockwise and counterclockwise arrows). C: time course of compensatory torque ($T_{\text{comp}}$, solid line) and object roll (dotted line) on trials 1 and 8 of the first block of trials (left center of mass) performed by a representative subject (S35). The horizontal dashed line denotes the task torque, whereas the 2 vertical solid lines denote object lift onset and peak object roll, respectively. D: sequence of manipulation contexts, transfer and retrieval trials, and breaks for each experimental condition.
Before the experiments started, the object was visually presented to the subjects and they were allowed to briefly touch the graspable surfaces to familiarize themselves with the frictional properties of the handle. All experimental conditions consisted of four blocks of eight consecutive trials with the exception of the random condition (see below), and each block was performed in the same context. Because there were two manipulation contexts (i.e., left or right center of mass), the order of presentation of R and L contexts was counterbalanced across subjects for each experimental condition. We also define the first context experienced by the subjects as context A and the following one as context B. The intertrial and interblock duration lasted less than 10 s, unless otherwise stated for specific experimental conditions.

Experiment 1: control group. To establish a baseline of manipulation performance, the first experiment consisted of the block sequence A1B1A2B2, and no break was given between blocks. In addition, subjects in the control group (Ctrl; n = 16) were recalled after 2 wk to perform another four blocks following the same block sequence (Fig. 1D).

Experiment 2: retention and interference groups. The second experiment was designed to assess the effect of time on the retention and interference of learned manipulation (Fig. 1D). Subjects were divided into six groups that differed in terms of when the break occurred between blocks as well as its duration. Specifically, subjects in the retention groups (RT10, RT20, and RT60; n = 12, 8, and 8, respectively) were given a 10-, 20-, or 60-min break after learning the first context, A1, followed by another three blocks in the sequence of A2B1A2. In contrast, subjects in the interference groups (IF10, IF20, and IF60; n = 12, 8, and 8, respectively) were given a 10-, 20-, or 60-min break after learning both contexts A1B1, followed by another two blocks (A2B2). Note that for the IF groups, all breaks were given after the object rotation.

Experiment 3: transfer group. The third experiment was designed to quantify subjects’ ability to generalize a learned manipulation from block 1 to the new context in block 2 after the effect of interference had decayed. A 1-h break was inserted after subjects in the transfer group (TF60; n = 12) performed manipulation in context A1 and rotated the object (Fig. 1D). Subjects then performed another three blocks (B1A2B2) after the break.

These instructions for the activities allowed during breaks were the same as those used by previous retention studies using force-field reaching tasks (Cris CIMagna-Hemminger and Shadmehr 2008; Shadmehr and Brashears-Krug 1997). For experiments 2 and 3, subjects were asked to remain seated in the chair if the break time was 10 min. For longer breaks, subjects could leave the room during the break to resume normal activity. All subjects were also asked to avoid activities that involved large forces (e.g., heavy lifting) during the breaks.

Experiment 4: random group. We also tested a group of subjects (Rand; n = 12) who performed the first 16 trials with a pseudorandom presentation of the 2 contexts (trial sequence: ABABABABABBAA), followed by 2 blocks of 8 consecutive trials in each context (Fig. 1D). Similarly to the Ctrl group, breaks between trials lasted less than 10 s.

Data Analysis

As mentioned above, we use T\textsubscript{com} to quantify the anticipatory control of manipulation. In addition, we do not distinguish between L and R contexts, because we have already shown that there was no difference between the two contexts from the perspective of torque production (Fu and Santello 2012). Therefore, we define the sign of the ideal T\textsubscript{com} (T\textsubscript{target}, i.e., the torque that can perfectly counterbalance the external torque caused by the object asymmetric mass distribution) based on the order of the contexts (A or B), rather than the actual torque direction (CW or CCW). Thus contexts A and B were defined as being characterized by a positive and negative T\textsubscript{target}, respectively. Moreover, the T\textsubscript{com} exerted by the subjects would have the same sign as the T\textsubscript{target} if the direction of the exerted torque was the same as that of the T\textsubscript{target}. For instance, if the T\textsubscript{target} in context B was in CW direction, T\textsubscript{com} would be positive and negative if subjects exerted a torque in CCW and CW direction, respectively.

We were interested in quantifying subjects’ ability to recall a learned context or transfer to a new context (i.e., from context A to B; Fig. 1D). To evaluate retrieval of previously learned manipulation context, we calculated the retrieval index (RI) as the difference between the T\textsubscript{com} exerted on the retrieval trial and the averaged T\textsubscript{com} exerted across the last five trials performed in the same context, normalized by the sign of T\textsubscript{target}. For instance, for the Ctrl group, the RI of context A was calculated as the difference between T\textsubscript{com} exerted on trial 1 of block 3 and T\textsubscript{com} averaged across trials 4–8 of block 1. Therefore, a negative or positive RI would indicate imperfect recall of a learned manipulation context, and the magnitude of RI would correlate with subjects’ inability to retrieve learned manipulation.

The assessment of transfer performance was based on the within-subject comparison between the T\textsubscript{com} exerted on the transfer trial and the T\textsubscript{com} exerted on first trial, in which subjects had no prior manipulation experience with the object. For this comparison, we normalized the T\textsubscript{com} from the transfer trial (context B) by the negative sign of its T\textsubscript{target}, therefore avoiding the statistical complication caused by the different signs of the two contexts.

Statistical Analysis

Statistical analyses were designed to assess within-block learning, interblock interactions, and the effect of break duration by using T\textsubscript{com} and RI for different experimental conditions (Matlab and SPSS). All tests were performed at the \( P < 0.05 \) significance level. Comparisons of interest exhibiting statistically significant differences were further analyzed using post hoc tests with Bonferroni corrections.

Model and Simulation

To facilitate the interpretation of our experimental findings, we first tested a modified version of a dual rate multiple context model (DRMC; Lee and Schweighofer 2009), which supports the protection of a learned context by assuming a context-independent fast process and a context-dependent slow process. This model can successfully explain anterograde interference as inability of the fast process to be switched to the opposite direction on the first trial following a context switch, therefore competing with the slow process, which is sensitive to contextual cues. Specifically, the model can be described with the following equations. On trial \( n \), the motor error \( \epsilon \) is determined by the difference between the motor output \( y \) and the ideal compensatory torque to be generated at lift onset (i.e., \( T\text{\textsubscript{target}} \)):

\[
\epsilon(n) = T\text{\textsubscript{target}}(n) - y(n).
\]  (1)

This torque error has been shown to be strongly correlated with the behavioral error (i.e., peak object roll). Therefore, the state update process follows:

\[
x_i(n + 1) = A_i \cdot x_i(n) + B_i \cdot \epsilon(n)
\]  (2)

\[
x_f(n + 1) = A_f \cdot x_f(n) + B_f \cdot \epsilon(n) \cdot e(n),
\]  (3)

where \( x_i \) is a two-dimensional vector that represents the internal states of the two contexts in a slow-learn-slow-forget process, \( x_f \) is a single state of a fast-learn-fast-forget process, and \( e \) is the context-selection vector. \( A_i \) and \( B_i \) are the learning and forgetting rates of the fast process, whereas \( A_f \) and \( B_f \) are the learning and forgetting rates of the slow process, respectively. Finally, the motor output is determined by the sum of two states:

\[
y(n) = x_i(n) + x_f(n) \epsilon(n)
\]  (4)

However, this model did not account for the decay of internal representations during break time. Here we assume that subjects can retain well the context-dependent representation. In contrast, we
assume that context-independent and use-dependent memory decays exponentially:

\[ x_i(n + 1) = x_i(n) \cdot e^{-RT} \]  

(5)

such that half-life of the decay is \( V \cdot \ln(2) \). Note that the additional parameter \( V \) is necessary because decay rates during active learning and break would likely be different (Criscimagna-Hemminger and Shadmehr 2008). Furthermore, note that our object manipulation task has salient visual geometric cues about the object mechanical properties and, therefore, the dynamics of the task, i.e., direction of the compensatory torque. Therefore, we set the initial value of \( x_i(1) \) to \((180, -180)^T\) instead of zero initialization, which was usually assumed in motor learning models. We also set \( x_i(1) \) to 0 because it is context independent.

However, we found it challenging to fit the DRMC model to our data (see RESULTS). Therefore, we propose a novel computational model based on the nonlinear interactions between two sensorimotor processes (dual processes nonlinear interaction model, DPNI). Similar to the DRMC model, the DPNI model also consists of two sensorimotor adaptation processes. However, to account for our data, we model the context-independent process differently and propose a nonlinear interaction between the two processes instead of linear summation. Specifically, this model combines an error-based learning process and a use-dependent memory (i.e., sensorimotor memory; see DISCUSSION). The error-based update equation follows:

\[ x(n + 1) = A(n) \cdot x(n) + B(n) \cdot e(n), \]  

(6)

where \( x \) is a two-dimensional vector that represents the internal estimate of the task dynamics of the two contexts. \( A \) and \( B \) denote the retention and learning rates, respectively, that can vary trial by trial for context \( B \). In fact, \( A \) usually was assumed in motor learning models. We also set \( x_i(1) \) to 0 because it is context independent.

Most importantly, we think that the bias caused by use-dependent memory is also a function of the internal state \( x \) that is actively engaged for the context in the current trial. Specifically, this bias is small when the direction of the use-dependent memory of the torque is the same as that of the engaged internal state, whereas the bias is large when they have opposite directions. To generate motor output on trial \( n \), the sensorimotor system has to first generate a plan based on visual context cues:

\[ x_i(n) = x_i(n)^T \cdot e(n). \]  

(8)

where \( e(n) \) is a selection vector that takes the value of \([1, 0]^T\) or \([0, 1]^T\) for context \( A \) and \( B \). The final motor output, however, is biased due to nonlinear interaction between two internal states \( x_i \) and \( n \):

\[ y(n) = x_i(n) + bias(n) \]  

(9)

bias(n) = D \cdot u(n)/(1 + \exp(sign[u(n)] \cdot E \cdot x_i(n))), \]  

(10)

where sign(u) is 1 and -1 if \( u \) is positive and negative, respectively. Although Eq. 10 seems to be arbitrary, it smoothly describes the nonlinear combination of two sensorimotor processes with only two parameters (\( D \) and \( E \)). Note that two parameters are necessary to account for such a context-dependent combination of two processes. In fact, Eq. 10 is essentially a sigmoid function whose shape (both magnitude and direction) is modulated by \( u \). A positive \( u \) generates small and large positive bias to positive and negative \( x_i \), respectively, whereas a negative \( u \) generates small and large negative bias to negative and positive \( x_i \), respectively.

Last, to model the effect of break duration, we again assume that subjects can retain well the context-dependent memory component, and that context-independent and use-dependent memory decays exponentially:

\[ u(n + t) = u(n) \cdot e^{-RT} \]  

(11)

such that half-life of the decay is \( F \cdot \ln(2) \).

We used a nonlinear optimization procedure in Matlab ("fmincon") to estimate the five parameters (\( A, B, A, B, V \)) of the DRMC model and the six parameters (\( A, B, C, D, E, F \)) of our DPNI model. This procedure minimizes mean squared error between the output of the model and experimental data (\( T_{\text{com}} \)) from selected trials in multiple groups. Specifically, we used \( T_{\text{com}} \) from selected trials of the Rndm group, Ctrl group, and IF groups. The mean \( T_{\text{com}} \) averaged within each of these trials was used because the data from individual subjects were too noisy for us to obtain reliable fits. Confidence intervals for parameter estimates were calculated using a bootstrap procedure (Ingram et al. 2011; Smith et al. 2006) that resamples the experimental data with replacement to obtain 1,000 bootstrap data sets. The model was fitted separately to the mean \( T_{\text{com}} \) of each of these data sets. The 95% confidence intervals were calculated as the 2.5 and 97.5 percentile values from the distribution for each parameter obtained across the 1,000 individual fits. Finally, we used the Bayesian information criterion (BIC) to compare the DRMC model and our DPNI model. Specifically, BIC evaluates goodness of fit and penalizes larger number of parameters:

\[ \text{BIC} = N \cdot \ln(\sigma^2_k) + k \cdot \ln(N), \]  

(12)

where \( \sigma^2_k \) is the summed square error of the fit, \( k \) is the number of parameters, and \( N \) is the number of data points (i.e., trials). A BIC difference of 4.6 is considered to provide strong evidence that the model with lower BIC is better (Burnham and Anderson 2002).

RESULTS

Learning Manipulation in Context A: First Block of Trials

All experimental groups except the Rndm group started with learning context A through a block of eight consecutive trials. Based on our prior work (Fu and Santello 2012), we expected
subjects to start with an estimation of the object weight distribution based on visual geometric cues. Therefore, we expected subjects to generate the compensatory torque ($T_{\text{com}}$) in the correct direction on the first trial of block 1. Through subsequent trial-by-trial learning, subjects would then be able to quickly improve the estimation of the torque magnitude and its timing within the first three trials. Our results are consistent with these predictions and our previous study using the same L-shaped object (Fu and Santello 2012). Specifically, subjects started by underestimating the task torque ($T_{\text{com}} = 182.25 \pm 9.41$ N-mm, mean ± SE; $n = 84$) but quickly approached the target torque within the first three trials. Repeated-measures ANOVA across the first three trials revealed a significant main effect of trial [$F_{(2,152)} = 50.40$, $P < 0.001$] and no effect of group [$F_{(7,76)} = 0.627$, $P = 0.732$]. Furthermore, repeated-measures ANOVA across the last five trials showed no effect of trial [$F_{(4,304)} = 1.308$, $P = 0.256$] or group [$F_{(3,76)} = 1.76$, $P = 0.108$].

After subjects learned context A in the first block, we examined how the preceding manipulation context could affect the retrieval of a learned context or the transfer to a new context by systematically varying the block sequence and break time between certain blocks (Fig. 1D).

### Experiment 1: Interference Occurs at Both Transfer Trial and Retrieval Trial

Subjects in the Ctrl group rotated the object $180^\circ$ after every block of eight trials, thus switching the manipulation context three times on the first day (Fig. 1, B and D). It has been demonstrated that when the manipulation context (i.e., the direction of compensatory torque) was reversed after a block of consecutive trials in context A, subjects made a significantly large error on the first trial following the change to context B (Fu and Santello 2012). In the present study, we found a similar result in the Ctrl group despite the fact that the change of contexts was induced by object rotation instead of changing where the object had to be grasped. Specifically, on the transfer trial, subjects generated a $T_{\text{com}}$ of $-75.05 \pm 11.01$ N-mm, which had a correct direction but significantly smaller magnitude than the $T_{\text{com}}$ generated on trial 1 of block 1 [Fig. 2, A and C; repeated-measures ANOVA, $F_{(1,15)} = 10.74$, $P = 0.005$]. This suggests that subjects not only failed to generalize what they had learned in context A to context B but also performed worse than when starting without prior manipulation experience, thus indicating negative learning transfer.

When switching back to context A on trial 1 of block 3 after eight trials in context B, subjects were not able to perfectly recall the manipulation previously learned in context A, as indicated by the underestimation of $T_{\text{com}}$ (113.91 ± 15.76 N-mm; Fig. 2A). Therefore, the retrieval index quantifying the extent of performance degradation was significantly negative (Fig. 2B; RI = $-174.60 \pm 15.76$ N-mm; 1-sample t-test, $P < 0.001$). Furthermore, we found that subjects also failed to perfectly recall context B on the first trial of block 4 (RI = $-106.86 \pm 12.96$ N-mm; 1-sample t-test, $P < 0.001$). The retrieval of context B, however, was better than the retrieval of context A in block 3, as indicated by a less negative RI [repeated-measures ANOVA, significant main effect of context, $F_{(1,15)} = 12.13$, $P = 0.003$].

We hypothesized that both the negative transfer and the retrieval failure were caused by an interference effect generated by the preceding trial blocks. The following two experiments were designed to examine the extent to which break duration could affect the magnitude of the interference and retention.

### Experiment 2: Effect of Time on the Magnitude of Interference on Retrieval Trials

There are two possible explanations for the interference on the retrieval trials: 1) learning of context B caused context A to be unlearned, or 2) performing context B temporarily contaminated the retrieval of A through a secondary process without erasing learned context A. The latter scenario would indicate that subjects could be able to recall context A if the “contamination” could be washed out by giving subjects a break, whereas the former scenario would indicate that context A has to be relearned regardless of the break duration before the retrieval. Therefore, we asked subjects in the IF10, IF20, and IF60 groups to take breaks of different durations after rotating the object at the end of block 2. Moreover, we asked subjects in the RT10, RT20, and RT60 groups to take breaks after block 1 (Fig. 1D). The protocols used in the IF groups were designed to test the decay of interference from context B, whereas the protocols used in the RT groups were designed to provide a baseline for the ability to retain context A over time without performing the second context.

For the RT groups, we found that the duration of the break did not significantly affect subjects’ ability to recall the manipulation context learned before the break (Fig. 2B). Subjects could recall context A almost perfectly (RI = $-27.59 \pm 14.64$, $-12.64 \pm 20.64$, and $-18.98 \pm 23.99$ N-mm for the RT10, RT20, and RT60 groups, respectively) with no significant differences in RI across the three groups (one-way ANOVA, $P = 0.839$). In contrast, we observed a significant negative linear effect of break duration on the interference index for the IF groups [1-sample t-test, $t = -2.060$, $P = 0.049$]. Moreover, the interference index was significantly lower in the RT groups than in the IF groups (Tukey’s HSD post-hoc test, $P = 0.028$).

![Fig. 2. Experimental results from experiments 1–3. A: trial-to-trial compensatory torque ($T_{\text{com}}$) from blocks 1–4 for the control (Ctrl) group. The task torque ($T_{\text{com}}$; thin black dashed line) is defined as positive for the first context (A) and negative for the second context (B). B: Retrieval index (RI) plotted against the duration of the break between blocks. C: comparisons of first trials and transfer trials from the Ctrl vs. transfer (TF60) groups. Data are averages of all subjects (±SE). *$P < 0.05$.](http://jn.physiology.org/content/early/2017/06/10/jn.00348.2014/Fig2)

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RT20, and RT60 groups, respectively). One-way ANOVA revealed no main effect of group ($F_{(2,25)} = 0.10, P = 0.904$). Furthermore, one-sample $t$-test using RI from each group confirmed that these RI values were not statistically different from zero ($P = 0.10, 0.56,$ and $0.45$ for RT10, RT20, and RT60 groups, respectively). In contrast, we found that the retrieval of context A improved with longer break durations for the IF groups, suggesting a weaker interference as a function of break duration ($RI = -102.14 \pm 23.36, -57.76 \pm 21.82,$ and $-27.83 \pm 16.43$ N-mm for the IF10, IF20, and IF60 groups, respectively; Fig. 2B). Together with the RI computed from Ctrl group performing context A, one-way ANOVA confirmed a significant main effect of group ($F_{(3,40)} = 14.50, P < 0.001$). Moreover, one-sample $t$-test revealed that only the IF10 and IF20 groups had significantly negative RI ($P = 0.003$ and $0.033$ for IF10 and IF20 groups, respectively), but not the IF60 group ($P = 0.118$). This result suggests that the learning of manipulation in the second context B did not erase learning of context A. Instead, learning in context B temporarily impaired subjects’ ability to retrieve learned context A, which could be washed out by a 60-min break. One-way ANOVA confirmed that the RIs of context A from IF60 and RT60 groups were not significantly different from each other [no main effect of group, $F_{(1,22)} = 0.09, P = 0.764$]. Additionally, we found that the blocking effect on context retrieval was likely induced by the most recently performed trials. Specifically, for the IF groups who were asked to retrieve context B in block 4, they all exhibited imperfect retrieval again to a similar extent [1-way ANOVA, $F_{(2,25)} = 0.384, P = 0.685$; RI = $-139.42 \pm 14.7143$ N-mm, averaged across the 3 groups] despite the different break durations before block 3.

Importantly, our data also suggest that subjects were able to retain well the learned context regardless of the decay of the temporary interference. To further verify subjects’ ability to retain learned manipulation, we asked the Ctrl group to come back after 2 wk (IF2W) and recall the manipulation tasks with the same block sequence (Fig. 1D). We found that subjects were able to retrieve context A to a similar extent as the IF60 group [RI = $-23.14 \pm 22.12$ N-mm; 1-way ANOVA, $F_{(1,26)} = 0.03, P = 0.874$; Fig. 2B]. This result extends previous observations of 24-h retention of learned manipulation, i.e., retention of anticipatory control of fingertip forces to object mass learned through object lifting (Gordon et al. 1993; Nowak et al. 2007). Additionally, we found interference again when subjects had to recall context B in the second session after 2 wk (RI = $-181.46 \pm 21.67$ N-mm) due to the most recent performance in the preceding context A (Fig. 1D).

**Experiment 3: Time-Dependent Interference on the Transfer Trial**

We have demonstrated that learning manipulation in context B temporarily interferes with the retrieval of previously learned manipulation in context A. This raises the question of whether learning context A in the first block would exert a similar anterograde interference on the subsequent manipulation in context B. We hypothesized that if a long enough break was given after block 1, subjects could have started learning context B with a smaller initial error. In the third experiment, subjects performed one block of eight trials and rotated the object at the end of the block (Fig. 1D). After a 1-h break, subjects came back and started to learn the manipulation in context B. As expected, $T_{com}$ on trial 1 of block 2 for the TF60 group ($-159.35 \pm 16.17$ N-mm) was significantly closer to the $T_{target}$ than $T_{com}$ on the transfer trial of the Ctrl condition [1-way ANOVA, $F_{(1,26)} = 14.75, P = 0.001$; Fig. 2C]. Additionally, paired-sample $t$-test revealed that, for the TF60 group, the magnitude of $T_{com}$ on the transfer trial was not significantly different from $T_{com}$ on the first trial of block 1 [$F_{(1,11)} = 0.60, P = 0.455$]. These findings suggest that subjects started learning context B without any transfer from the previously learned context A, even when the 1-h break was long enough for the interference effect to decay to a minimum level. This phenomenon is consistent with those reported by previous studies (Bursztyn and Flanagan 2008; Fu and Santello 2012; Zhang et al. 2010), which showed no task-level learning transfer from context A to B. Furthermore, here we demonstrate that lack of learning generalization in manipulation tasks was not due to lack of context cues or anterograde interference caused by learning a context immediately preceding the new context.

**Experiment 4: One Trial is Sufficient to Induce Interference on Manipulation in the Following Context**

The last experimental condition, Rndm, consisted of pseudorandom presentation of the two manipulation contexts. This design prevented subjects from being exposed to the same context for more than three consecutive trials during the first half of the experiment (Fig. 3A). The first feature of the context presentation was that the first context switch occurred after the first trial, instead of after eight trials as in all other groups (Fig. 1D). We found that subjects in the Rndm group exerted a torque ($T_{com} = -138.33 \pm 22.52$ N-mm) closer to the $T_{target}$ than the torque exerted by the Ctrl group on the first trial of context B (Fig. 3B). One-way ANOVA confirmed a significant main effect of group [$F_{(1,26)} = 7.44, P = 0.011$]. Additionally,
the magnitude of the $T_{\text{com}}$ subjects exerted for the first trial of context B was significantly smaller than the $T_{\text{com}}$ exerted for trial 1 of context A [repeated-measures ANOVA, $F_{(1,11)} = 6.38, P = 0.028$. These two findings are consistent with our previous work using a U-shaped object (Fu and Santello 2012) with the same context switch sequence, suggesting that one trial was sufficient to induce interference on the next context, whereas further practice in the same context would have increased the strength of the interference.

The Rndm condition also required subjects to frequently switch manipulation context multiple times during the first half of the experiment. We found that the performance on the context switch trials was generally worse than on preswitch trials, despite the fact that manipulation on the preswitch context was performed no more than three consecutive times. To illustrate this, for each context, we compared the average of the least three preswitch trials (trials 5, 12, and 16 for context A; trials 9, 10, and 14 for context B), the average of the last three context switch trials (trials 7, 11, and 15 for context A; trials 8, 13, and 17 for context B), and the average of the last three blocked trials (trials 30–32 for context A; trials 22–24 for context B; open, shaded, and filled circles in Fig. 3A). For context A, repeated-measures ANOVA revealed a significant main effect of trial [$F_{(2,22)} = 19.91, P < 0.001$; Fig. 3D]. Post hoc $t$-test confirmed that $T_{\text{com}}$ exerted on preswitch trials was significantly different from $T_{\text{com}}$ exerted on context switch trials ($P = 0.001$), but not from blocked trials ($P = 0.26$). Similarly, for context B, repeated-measures ANOVA revealed a significant main effect of trial [$F_{(2,22)} = 7.88, P = 0.005$; Fig. 3C]. Post hoc $t$-test confirmed that $T_{\text{com}}$ from preswitch trials was significantly different from $T_{\text{com}}$ exerted on context switch trials ($P = 0.01$), but not from blocked trials ($P = 0.73$). This result suggests that the interference from preceding contexts can be established within a few trials.

Interpretation of Experimental Data Using Model Simulation

Our data clearly revealed several important features of retention and interference in learning of dexterous manipulation tasks. Specifically, if manipulation A is learned, learning of the second manipulation B does not erase the learned manipulation A, but rather generates temporary interference when retrieval of A is required. Furthermore, the first block of context A also generates a temporary interference on the initial performance of context B. Despite these interferences, the learned manipulation was shown to be quite robust with respect to time and retrievable after the interference was washed out. These findings suggest that there are at least two processes underlying learning of dexterous manipulation. The first process updates the context-dependent internal representation of the manipulation leading to trial-to-trial error reduction as well as long-term retention. The second process quickly generates a short-term “bias” through the performance of manipulation within only a few trials (1 to 3) that competes with the internal representation. The question arises whether existing computational models of motor learning could capture these features.

We first rule out models that suggest that memory of manipulation in the first context is fragile and that learning of the second context would overwrite the previously learned manipulation in the first context (i.e., unlearned). Such unlearning of the first context during learning of the second context has been proposed to be due to either a single learning process (Ingram et al. 2011) or to be insensitive to contextual cues (Criscimagna-Hemminger and Shadmehr 2008; Smith et al. 2006). Specifically, these models predict that a break given after the AB paradigm would not reduce the interference on the recall of context A. We then considered the DRMC model (Lee and Schweighofer 2009), which supports the protection of a learned context by assuming a context-independent fast process and a context-dependent slow process. This model can successfully explain anterograde interference as inability of the fast process to be switched to the opposite direction on the first trial following a context switch, therefore competing with the slow process, which is sensitive to contextual cues. However, the original DRMC model did not include the decay of memory during inactive period, i.e., break. Therefore, we added the decay to the DRMC model, which had five free parameters (Eqs. 1–5). These parameters were determined using nonlinear optimization with data from the Rndm group and Ctrl group, as well as the IF groups. These trials were selected because they best cover the behavioral findings across all experiments. Specifically, we used $T_{\text{com}}$ from the first 16 trials from the Rndm group and first 16 trials from the Ctrl group, which were important to determine the parameters of the adaptation processes. We also used the first retrieval trials (trial 17) from three IF groups and the Ctrl group, which were important to determine the parameters of the retention. The rest of the trials could be used to test how well the model could perform in different interference (i.e., TF group) and retention scenarios (i.e., RT groups).

We found that it is challenging for the DRMC model to account for our data from both the IF and RT groups, although the DRMC model could reasonably predict the behavior of the Ctrl and Rndm groups. Specifically, the output of the DRMC model results from the linear summation of the slow and fast processes; therefore, the decay of the fast component would cause a decrease of the interference for the IF group, as well as a decrease of retention for the RT groups in a similar fashion (Fig. 4). This contradicts our data showing that the longer break duration only significantly reduced the interference, not the retention (Fig. 2B). In fact, other models, such as use-
dependent learning model from Diedrichsen et al. (2010), that use linear combination of multiple sensorimotor processes when generating total motor output would have come to the same conclusion.

To better account for our data, here we propose a new model that combines an error-based learning process and a use-dependent memory (Eqs. 1, 6–11) with six free parameters (A, B, C, D, E, F), which were determined using nonlinear optimization with data from the Rndm group and the Ctrl group, as well as the IF groups (same as the data used to fit the DRMC model). By implementing the boot-strap technique, we estimated parameters with 95% confidence intervals as follows: $A = 0.9771 (0.9321, 0.9891)$, $B = 0.2613 (0.1848, 0.4435)$, $C = 0.4865 (0.2746, 0.7212)$, $D = 0.5513 (0.4619, 0.6410)$, $E = 0.0057 (0.0031, 0.0097)$, and $F = 13.37 (7.21, 28.19)$.

Overall, the BCI of the DPNI model was much smaller than the BCI of the DRMC model (BCI difference = 33.28), suggesting the DPNI model better fits the training data. Additionally, the new model also correctly predicted the data from RT and TF groups, which were not used in the parameter search. Specifically, the new model predicts the 32-trial data averaged across subjects from the Ctrl and Rndm groups well (for Ctrl group, compare Fig. 5A with Fig. 3A, $r = 0.95$; for Rndm group, compare Fig. 5B with Fig. 3A, $r = 0.93$). Most importantly, the DPNI model predicts the differential effect of break duration on the phenomena of interference and retention of learned manipulation reported here (Fig. 5E vs. Fig. 2B), as well as the time-dependent interference on the transfer trial (Fig. 5D vs. Fig. 2C).

We found that subjects could update the internal representation of the manipulation rapidly as indicated by the relatively large value of learning rate $B$ compared with those found in reaching studies. This is consistent with previous findings that demonstrated fast adaptation rates for learning object manipulation when contextual cues are available (Ingram et al. 2011). The parameter $C$ suggests that the use-dependent memory $u$ is heavily dependent on manipulations performed on the most recent trials (Fig. 5, A and B). This result is consistent with the fast establishment of use-dependent memory observed in different manipulation tasks (Jenmalm et al. 2006; Lukos et al. 2013; Witney et al. 2001) but differs from the finding that use-dependent bias was built through repeated reaching tasks with a much slower timescale (Diedrichsen et al. 2010). The parameter $F$ suggests that when not actively involved in the task (i.e., during break), the use-dependent memory $u$ decays with a half-life of 9.27 min with 95% confidence interval (4.99, 19.54). Last, parameters $D$ and $E$ shape the nonlinear bias function (Eq. 6; Fig. 5C). Specifically, the use-dependent memory $u$ would induce bias to the visually engaged motor plan $x(n)\dot{c}$ to a greater extent when $x(n)c$ is in the direction opposite to $u$.

**DISCUSSION**

Through four experiments and a theoretical model, we have demonstrated that a complex interaction between two sensorimotor mechanisms underlies learning, retention, and interference of dexterous manipulation. One mechanism is an error-based update of context-dependent internal estimates of the task dynamics, whereas the other is a use-dependent memory that is not selectively associated with a specific context. We discuss our results with respect to other motor adaptation studies of hand and arm movements, as well as their underlying neural mechanisms.

**Effect of Previous Motor Experience on Current Manipulation**

There has been extensive evidence that the current manipulation could be influenced by previous manipulations. Specifically, it has been shown that the CNS is capable of fast trial-by-trial adaptation to changes in manipulation context, e.g., object weight (Johansson and Cole 1992), surface friction (Westling and Johansson 1984), and weight distribution (Fu et al. 2010). Such adaptations are thought to rely on a “sensori-motor memory,” which was initially defined as the memory of an object’s physical properties (Johansson and Westling 1988). However, more recent data suggest that the CNS may maintain multiple internal representations of manipulatory skills. Quaney et al. (2003) demonstrated that squeezing an object generates a bias to grip force for object lifting in the following

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**Fig. 5.** Simulation results with the dual processes nonlinear interaction (DPNI) model. A: model output (circles) for the Ctrl group with block ABAB paradigm. B: model output for the Rndm group with pseudorandom context sequence. C: nonlinear bias as a function of visually engaged internal estimate of task dynamics $x\dot{c}$ and use-dependent memory $u$. D: output of model simulation for transfer after a 1-h break (TF60 group). E: output of model simulation for temporal characteristics of retention and interference (with 95% confidence intervals).
trial, and that the grip force bias induced by strong pinch disappeared for object lifting after 24 h (Quaney et al. 2005). These results suggested that there might be an object-based memory for object weight and an action-based memory for pinch force. Our findings provide direct evidence that support the concept that multiple sensorimotor mechanisms underlie the fast trial-to-trial adaptation (i.e., establishment of the sensorimotor memory) of object manipulation. Most importantly, we revealed that one component of these adaptation processes lasts a relatively short time, whereas the other could be correctly recalled after a long period of time. Furthermore, these two mechanisms with different timescales interact during the generation of motor commands for subsequent manipulation, thus inducing interference when they were incongruent with each other (Fig. 5, A and B).

Our experimental design used an object that provides strong visual geometric cues about the properties of the object (Fu and Santello 2012), which promotes context-dependent learning (Eq. 2) as well as visually based motor planning (Eq. 4). Interestingly, we also found that our theoretical framework can be used to explain unpredictable trial conditions when context cues are absent. In simple object lifting tasks, digit forces are scaled to the object weight experienced in the previous trial if information about object weight is unavailable on the current trial (Jenmalm et al. 2006). In bimanual manipulation tasks where subjects cannot reliably predict whether the object is mechanically linked between two hands, the scaling of the finger forces depends on the presence of the linkage experienced in the previous trials, with three consecutive presentations of the linkage causing greater force scaling bias than one presentation (Witney et al. 2000). It should be emphasized that lack of context cues and randomization of object properties with same visual appearance in these studies prevent context-dependent error-based learning from occurring, therefore making the use-dependent adaptation the dominant process influencing motor output on the subsequent trials. For instance, it was recently demonstrated that the compensatory torque exerted by the subjects during trial sequences with randomized target torque directions was biased toward the torque direction experienced on the previous trial and with magnitude of about 60 N-mm (Lukos et al. 2013). By using the parameter obtained for our DPNI model, we can simulate this process by setting the error-driven process to zero for all trials, therefore obtaining a compensatory torque of \( \sim 50 \text{ N-mm} \), which is in qualitative agreement with the experimental results of Lukos et al. (2013).

Use-Dependent Adaptation in Manipulation Tasks

Our framework assumes the secondary sensorimotor process to be use-dependent (Diedrichsen et al. 2010), rather than an error-based one with different timescales (Lee and Schweighofer 2009). This is because previous studies suggested that sensorimotor memory could be established in the absence of behavioral error (Quaney et al. 2003). Additionally, such use-dependent adaptation of manipulation may be interpreted as a process that encodes the likelihood of the occurrence of a context (Witney et al. 2001), similar to the establishment of a fast-adaptive prior of the statistical properties of reaching movement independent of movement errors (Verstynen and Sabes 2011). Use-dependent plasticity was recently proposed to be involved in motor learning of reaching movements (Diedrichsen et al. 2010; Huang et al. 2011). Such use-dependent learning in movement tasks is usually manifested as a bias in the movement direction. The encoding of bias direction could be modeled as a set of Gaussian-like tuning functions whose weightings are modulated by recent actions. Moreover, it has been demonstrated that the directional bias had a larger influence on movements made to angular targets further away from the repeated movement direction (Verstynen and Sabes 2011). This is consistent with our model, in which a greater bias was generated when the subsequent target torque was in the opposite direction to that which had been previously experienced. However, use-dependent learning of movement direction is often considered as a slow process that requires many repetitions of the same action (Classen et al. 1998; Diedrichsen et al. 2010). In contrast, our model seems to suggest a rather fast process that requires only a few trials. We suspect that this was due to fundamental differences between movement tasks and grasping tasks such as the one studied here. Specifically, movement tasks are usually dynamic and require changes in muscle activation in a short time to accelerate and decelerate the hand/fingers. In contrast, object lifting tasks usually feature a holding phase that requires subjects to produce a significantly large constant torque/force in addition to a short object lifting movement (Fig. 1C). This isometric force production may play an important role for building up the motor bias. Furthermore, reaching could be potentially executed toward an infinite number of continuously distributed directions, whereas object balancing tasks are bidirectional tasks (CW and CCW) whose performance relies on the distribution of force magnitude across agonist and antagonist muscle groups. The binary choices of torque direction might make our task more deterministic, therefore leading to faster adaptation.

Learning Retention and Interference in Sensorimotor Learning Tasks

Our study examined retention and interference of manipulation using tasks that require torque production and suggest that interference occurring at context switch was due to conflict between two sensorimotor processes. However, because the use-dependent component decays fast, retrieval of learned manipulation was successful even after 2 wk. Interestingly, the interference found when switching context did not completely disappear after multiple switches (Fig. 3A). This indicates that even strong visual geometric cues could not completely override the effect of preceding manipulations. However, visual cues about object weight have been shown to completely override the effects of previous lifts on grip force scaling (Ameli et al. 2008; Loh et al. 2010). This can be explained by the subtle difference between grip force scaling and torque production. Specifically, whereas torque generation in object balancing is bidirectional, the grip force scaling in object lifting is essentially unidirectional. Our nonlinear bias framework indicates that the bias from the previous motor action could be quite small if the subsequent action is performed in the same direction (Fig. 5C). Therefore, bias from previous object lifting may not be strong enough to cause measurable difference when visual cue about object weight is provided. Despite this difference, our result is consistent with early grasping studies showing that memory of object weight distri-
bution with context cues could last more than 24 h (Gordon et al. 1993; Nowak et al. 2007).

Studies of other sensorimotor tasks have provided a large body of experimental evidence of interference and retention, such as reaching in force fields, visuomotor rotations (Bock et al. 2001; Caithness et al. 2004; Flanagan et al. 1999; Tong et al. 2002), interlimb coordination (Swinnen 2002), and verbal learning (Atkins 2001). Here we only compare our results with the data from force field studies due to the fact that reaching in force field could be seen as manipulation of an object (i.e., a robotic handle). It should be emphasized that the interference and retention reported in these studies have often been described as change in learning rate, whereas in our task they are manifested as an error on the first trial following the context switch and/or break. Although it is difficult to determine how much first-trial recall/transfer effects can be related to learning rate effects, in the present study we compare these effects because both means of quantification denote an influence from the action learned before switching context.

We found common features that are shared across learning of hand and arm movements using A1B1A2 paradigms. For reaching in force field tasks, the strength of anterograde interference on context B1 increased with the number of trials in context A1 (Sing and Smith 2010). Furthermore, the anterograde interference gradually decreased with time such that subjects learn B2 as if starting from scratch if the break duration between A1 and B1 is longer than 5.5 h (Shadmehr and Brasbers-Krug 1997). Initially, it was thought that the learned task was fragile and that without sufficient time to consolidate it, the second task in the opposite direction could erase the previously learned one. However, recent studies have attributed interference to competing sensorimotor processes (Caithness et al. 2004; Flanagan et al. 1999; Tong et al. 2002). Our current results also consistently support multiple sensorimotor processes underlying interference.

However, we also found significant differences in the temporal characteristics of the retention and interference between our task and reaching tasks. Specifically, several studies have found that if B1 is learned immediately after learning A1, the context retrieval in A2 would be always interfered by having learned B1 regardless of the break duration between B1 and A2 (Brasbers-Krug et al. 1996; Caithness et al. 2004; Krakauer et al. 2005). In contrast, we have shown that a short break between B1 and A2 could greatly decrease the strength of the interference (Fig. 2B). We also showed that context A could be retained well after 2 wk even if the last context performed by the subjects was B (Fig. 2B). This difference may be explained by the existence of contextual cues, which have been shown to be crucial to promote formation of distinct representations for different contexts (Cothros et al. 2009; Hirashima and Nozaki 2012; Howard et al. 2012; Osu et al. 2004), although the effectiveness of context cues relies on the type of cues (Howard et al. 2013; Salimi et al. 2003). Since most of the studies on temporal characteristics of retention and interference used few or weak context cues, it is possible that learning an opposite motor task immediately after the first one would result in, at least partially, erasing the memory of the first task. Therefore, context-independent learning models may be sufficient to explain interference under these circumstances (Smith et al. 2006). In contrast, our task affords learning across multiple unambiguously cueable contexts that all use the same effector.

Furthermore, the visual geometric cues about object dynamics are very strong, as shown by the non-zero initial estimation of \( T_{com} \) and correct estimation of \( T_{com} \) direction (Fig. 2A). Therefore, in our proposed model we implement a context-selection vector that works similarly to those used in the model proposed by Lee and Schweighofer (2009). Such context-dependent learning supports protection of learned motor tasks even in the presence of competing motor memory (Ingram et al. 2013; Pekny et al. 2011).

Possible Neural Substrates of Multiple Sensorimotor Processes

An important finding of the present study is the larger effect of break duration on interference than on retention. We interpreted this result as being due to a nonlinear interaction between two sensorimotor processes. There has been growing evidence for multiple different mechanisms in motor learning, such as error-based internal models (Smith et al. 2006), use-dependent plasticity (Diedrichsen et al. 2010), and reinforcement learning (Izawa and Shadmehr 2011). These mechanisms have been shown to have different timescales, to rely on different sensorimotor states and signals (Wolpert et al. 2011), and to be governed by different brain areas. Although the neural correlates of internal models remain unclear (Franklin and Wolpert 2011), the cerebellum (Nowak et al. 2004, 2009) is thought to maintain and update internal models for manipulation due to its role in comparing motor and sensory signals, hence in supporting error-driven learning. Furthermore, premotor and parietal cortices are thought to recall stored internal representations with contextual cues (Davare et al. 2011; Grafton 2010). With regard to use-dependent sensorimotor memory, evidence suggests that it could be stored in the primary motor cortex (M1), since repetitive movement could alter the kinematics elicited by transcranial magnetic stimulation targeting the same cortical network in M1 (Classen et al. 1998). It is also worth pointing out that arm isometric force production is coupled with more consistent M1 activities than reaching movement in nonhuman primates neuron recordings (Sergio and Kalaska 1998; Sergio et al. 2005), which could potentially explain the fast establishment of use-dependent sensorimotor memory in tasks like ours (i.e., with a hold phase).

It remains unclear how different sensorimotor processes interact to generate final motor output. Many existing theoretical models assume linear combinations, whereas our findings favor nonlinear summations. Such interactions could have occurred in M1, since a recent study found that motor evoked potentials (MEP) in M1 were scaled on the basis of lifting forces experienced in the previous trial, but such MEP modulation could be overwritten 150 ms after visual information about the object weight was available (Loh et al. 2010). However, further work is needed to identify the neural correlates of the parallel or serial neural processing that may underlie the integration of multiple sensorimotor processes.

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Author contributions

Q.F. and M.S. conception and design of research; Q.F. performed experiments; Q.F. analyzed data; Q.F. and M.S. interpreted results of experiments; Q.F. prepared figures; Q.F. drafted manuscript; Q.F. and M.S. edited and revised manuscript; Q.F. and M.S. approved final version of manuscript.

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