

RESEARCH ARTICLE | *Control of Movement*

Both fast and slow learning processes contribute to savings following sensorimotor adaptation

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Coltman SK, Cashaback JGA, Gribble PL. Both fast and slow learning processes contribute to savings following sensorimotor adaptation. *J Neurophysiol* 121: 1575–1583, 2019. First published March 6, 2019; doi:10.1152/jn.00794.2018.—Recent work suggests that the rate of learning in sensorimotor adaptation is likely not fixed, but rather can change based on previous experience. One example is savings, a commonly observed phenomenon whereby the relearning of a motor skill is faster than the initial learning. Sensorimotor adaptation is thought to be driven by sensory prediction errors, which are the result of a mismatch between predicted and actual sensory consequences. It has been proposed that during motor adaptation the generation of sensory prediction errors engages two processes (fast and slow) that differ in learning and retention rates. We tested the idea that a history of errors would influence both the fast and slow processes during savings. Participants were asked to perform the same force field adaptation task twice in succession. We found that adaptation to the force field a second time led to increases in estimated learning rates for both fast and slow processes. While it has been proposed that savings is explained by an increase in learning rate for the fast process, here we observed that the slow process also contributes to savings. Our work suggests that fast and slow adaptation processes are both responsive to a history of error and both contribute to savings.

NEW & NOTEWORTHY We studied the underlying mechanisms of savings during motor adaptation. Using a two-state model to represent fast and slow processes that contribute to motor adaptation, we found that a history of error modulates performance in both processes. While previous research has attributed savings to only changes in the fast process, we demonstrated that an increase in both processes is needed to account for the measured behavioral data.

human; motor learning; prediction error; savings; two-state model

INTRODUCTION

A classic feature of human motor behavior, known as savings, occurs when the relearning of a motor skill is faster than the initial learning (Herzfeld et al. 2014; Huang et al. 2011; Kojima et al. 2004; Krakauer et al. 2005; Leow et al.

2016; Smith et al. 2006; Zarahn et al. 2008). It has been proposed that some component of memory from the initial training must contribute to the faster relearning (Herzfeld et al. 2014; Leow et al. 2016). However, currently, there are competing accounts of how this memory affects relearning (Herzfeld et al. 2014; Huang et al. 2011; Kojima et al. 2004; Krakauer et al. 2005; Leow et al. 2016; Smith et al. 2006; Zarahn et al. 2008). While some evidence suggests that savings can be accounted for by changes in the learning rate of a slow adaptation process, other studies suggest that changes in the learning rate of a fast process may also play a role. The goal of the present study was to characterize motor adaptation using a two-state model and test the idea that changes in both fast and slow processes underlie savings.

When participants learn to compensate for a systematic perturbation, such as an applied force during reaching, error reduction is thought to occur through a rapid initial improvement followed by slow incremental improvements, until a near-baseline level of performance is attained (Smith et al. 2006; Haith and Krakauer 2013). Adaptation is thought to occur through the updating of an internal model based on sensory prediction errors, characterized as the difference between predicted and measured sensory consequences (Scheidt et al. 2001; Shadmehr et al. 2010; Thoroughman and Shadmehr 2000; Tseng et al. 2007; Wolpert and Flanagan 2001; Wolpert and Kawato 1998). Researchers have modeled motor adaptation using “state-space” models of motor learning (Cheng and Sabes 2006; Donchin et al. 2003; Thoroughman and Shadmehr 2000), which have been shown to fit trial-to-trial adaptation to perturbations extremely well. These models incorporate a retention parameter and a learning rate parameter. The retention parameter characterizes how much learning is carried over from trial to trial, and the learning rate specifies what proportion of movement error is corrected for from trial to trial (Cheng and Sabes 2006; Donchin et al. 2003; Thoroughman and Shadmehr 2000). Variations of the state-space model suggest that adaptation is the result of multiple learning processes each with distinct timescales, resulting from the differences in their adaptation dynamics (Kording et al. 2007; Lee and Schweighofer 2009; Smith et al. 2006).

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A prominent account of adaptation is the two-state model proposed by Smith et al. (2006), in which a fast process learns quickly but has poor retention and a slow process has better retention but learns more slowly. The important assumptions in this model are that learning rate is higher for the fast process compared with the slow process and that retention is poorer for the fast process compared with the slow process. In this way, the distinguishing feature of the two-state model proposed by Smith et al. (2006) is the diversity in the characteristics of learning and retention of these two states.

To account for savings over short timescales (e.g., over a period of minutes), Smith et al. (2006) suggested that savings occurs due to a resistance of the slow process to change, which can be interpreted as meaning the learning rate and retention parameters are fixed. However, a number of recent studies suggest that learning rate can be modified depending on factors such as the uncertainty of movement error (Wei and Körding 2010), size of movement error (Marko et al. 2012), and a history of movement errors (Herzfeld et al. 2014). Of interest in the context of the current study is whether a history of movement error (Herzfeld et al. 2014) plays a role in modifying the learning rate parameters of both fast and slow components of a two-state model.

Some researchers have suggested that savings is due to an increase in the learning rate of the fast process with no changes in the learning rate for the slow process (Albert and Shadmehr 2018; McDougale et al. 2015; Trewartha et al. 2014), while other studies point to the possibility that the slow process contributes to savings (Joiner and Smith 2008). Some studies suggest that the implicit component of adaptation, which some have linked to a slow learning process (McDougale et al. 2015), does not exhibit savings (Haith et al. 2015; Morehead et al. 2015). Thus, it is inconclusive as to whether the slow process, in addition to the fast process, is influenced by previous errors and may therefore contribute to savings.

The goal of the present study was to test the hypothesis that both fast and slow learning processes contribute to savings. We asked participants to perform the same force field adaptation

task two times, separated by a 5-min break. We addressed the shortcomings of previous studies by using a large sample size and by using a resampling procedure to fit the two-state model to group data, rather than to individual data. We hypothesized that when a force field perturbation is reintroduced, savings would be associated with changes in both the fast and slow processes. We predicted that learning rates for both the fast and slow processes would increase when the force field is reintroduced and that changes in both fast and slow learning rates are required to account for the behavioral features associated with savings.

METHODS

Participants. Fifty-three healthy, young adults (36 female and 17 male, 21.3 ± 4.6 yr, age range 18–39 yr) participated in a force field adaptation experiment. Participants were recruited from the research participation pool maintained by the Department of Psychology at Western University and received either course credit or CAD\$12.00 for participation. All participants reported normal or corrected-to-normal vision and were right-handed. Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield 1971). Seven participants were excluded due to improper calibration of the testing apparatus during one of the two testing sessions. These seven participants were excluded from the analyses and results, reducing the reported sample size to 46. The protocol was approved by Western University's Research Ethics Board and all participants provided written, informed consent.

Apparatus. Participants were seated at a table with a working surface (53×65 cm) raised 90 cm from the floor (Fig. 1A). A chair was positioned relative to the table so that participants could comfortably see and reach within the working surface. Once the chair was adjusted it remained in the same position for both experimental sessions. A liquid crystal display (LCD) TV projected visual feedback onto a semisilvered mirror mounted horizontally above the robotic arm, such that the mirror blocked the participants' view of their arm and hand. Participants' right forearm was supported against gravity by a lightweight sled. Air jets in the sled reduced friction as participants moved their arm.

The display system was used to present the start and target locations to participants. In both experiments, participants held the

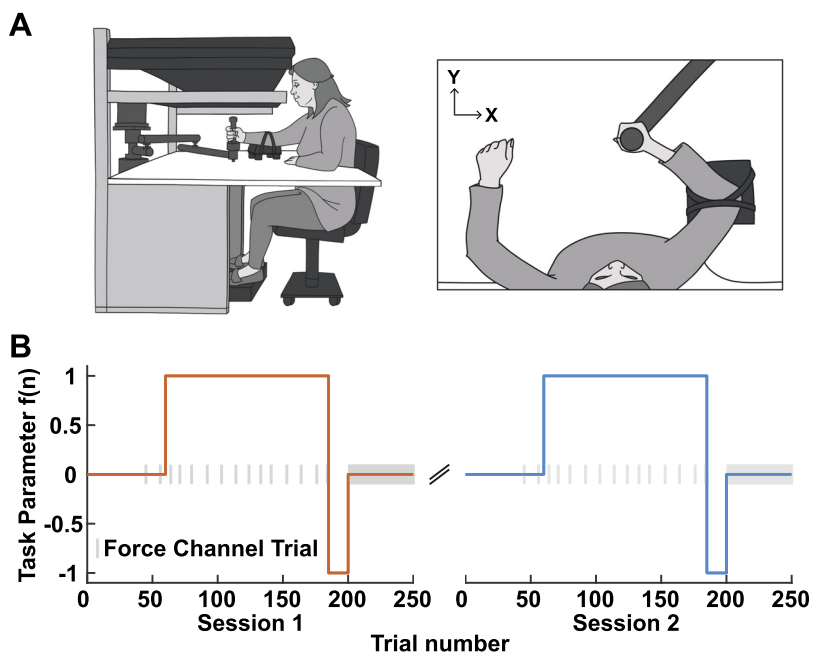


Fig. 1. Experimental apparatus and design. *A*: a seated participant grasped the robotic manipulandum, while visual feedback was presented veridically using a top-mounted TV viewed through a mirror. The participant's forearm was supported by an air-sled. *B*: the experiment was divided into two sessions, separated by a 5-min session break. Each session consisted of four blocks: 1) a baseline period of null field (no force) trials, 2) force field adaptation, 3) force field reversal, and 4) a series of channel trials. In the second session subjects reached in the same force field during adaptation. Randomly distributed during baseline and adaptation blocks and throughout the last block in each session, force channel trials (gray bars) were used to track the progression of learning.

handle of a planar robotic manipulandum (InMotion2, Interactive Motion Technologies, Cambridge, MA). A circular cursor (5-mm radius) was displayed on the semisilvered mirror and was used to represent the position of the center of the handle. Participants were presented with a circular start position target (10-mm diameter) and a circular movement target (10-mm diameter) located 15 cm forward of the start position.

On a given trial, the manipulandum applied either no force, a clockwise force field, a counterclockwise force field, or a force channel. During force field trials, the robotic manipulandum applied a force (F) to the hand. The strength of these forces was proportional to the velocity (v) of the hand, and force direction was perpendicular to hand movement as follows:

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = b \begin{bmatrix} 0 & 1 \\ -1 & 0 \end{bmatrix} \begin{bmatrix} v_x \\ v_y \end{bmatrix} \quad (1)$$

where x and y are the lateral and sagittal directions, F_x and F_y are the robot forces applied at the hand, v_x and v_y are hand velocities, and b is the field constant ($\pm 20 \text{ N}\cdot\text{s}\cdot\text{m}^{-1}$) whose sign determined the direction of the force field (positive = clockwise and negative = counterclockwise).

During the force channel trials, the robot motors were used to constrain movements to a straight line between the start position and target. This allowed for the removal of kinematic movement errors by effectively preventing any motion perpendicular to the target direction. This was implemented by applying a stiff virtual wall (spring constant 6,000 N/m and damping coefficient 1 N·s·m⁻¹) perpendicular to forward movement of the hand. An algorithm controlled the robot's torque motors and compensated for the dynamical properties of the robotic arm. The position of the robotic handle was recorded at 600 Hz and the data were stored for offline analysis.

Paradigm. Hadjiosif and Smith (2013) suggested that the duration of the intertrial interval modulates the amount of adaptation that can occur. To maintain a consistent intertrial interval throughout the experiment, we instructed participants to successfully reach the target within a narrow temporal window and used the manipulandum to guide the return of the participant's hand to the start position. At the beginning of each trial both the start position and target appeared in white. Participants were required to align the cursor within 5 mm of the center of the start position and hold this position for 200 ms, at which time the target changed color from white to green, representing a "go" signal for participants to initiate a movement to the target. Participants were instructed to reach for the target and bring the center of the handle to within 5 mm of the target within 350–500 ms. If a participant's movement time was less than 350 ms, the target turned red to indicate that the movement was "too fast." If the participant's movement time was within 350–500 ms, the target remained green to indicate that the movement was "good." And if the participant's movement was greater than 500 ms, the target would turn blue to indicate "too slow." Feedback related to movement time was displayed on the screen for 1,000 ms before the robotic arm returned the participant's hand to the starting position. Participants were instructed to try to obtain the "good" feedback as often as possible throughout the experiment.

A typical method for the study of savings is a within-subject experiment in which the same group of participants adapt to a perturbation at one time point and readapt to the same perturbation at a later time point. Participants completed two sessions that were separated by a 5-min session break (Fig. 1B). Each session included a total of 250 forward reaching movements. The experimental sequence during a session was baseline (no force) trials, force field adaptation, brief force field reversal, and finally a series of force channel trials (Trewartha et al. 2014). The first 60 trials were baseline trials in which participants could reach freely to the target. On trials 61–185 (force field adaptation), a force field perturbation was applied by the manipulandum. On trials 186–200 (force field reversal), an opposite

force field perturbation was applied by the manipulandum. In trials 201–250 (force channel trials), a stiff virtual channel was introduced. In addition, the force channel was active for 15 of the trials during baseline and force field adaptation (trials 45, 56, 64, 71, 80, 92, 103, 114, 124, 133, 141, 153, 164, 176, and 184). The use of randomly interspersed force channel trials, in which the path of the robot handle was constrained to a straight line, allowed us to probe force field adaptation. In the first session participants adapted their reaches to a viscous (velocity-dependent) force field. In the second session participants reached in the same force field as in the first session. The experimental paradigm was designed to capture short-term adaptation that both occurs very quickly, and that decays with the passage of time. The experimental paradigm used in this study was based on a spontaneous recovery (also termed "rebound") paradigm used by Smith et al. (2006); this paradigm is useful for extracting the fast and slow processes of the two-state model. Spontaneous recovery is a signature of an adaptive system that is supported by multiple processes, each learning at different timescales. Smith et al. (2006) suggest that, at the end of the first force field adaptation, most of the motor output is dependent on the slow state. During the brief force field reversal, the motor output is dependent on the fast state. Because the fast state has poor retention, it decays fast, while the slow state has strong retention and decays much more slowly; the result is a spontaneous recovery of the previously learned adaptation behavior during the block of force channel trials. Rebound was characterized by the average adaptation index measured over the first five trials after participants reached asymptotic performance. Asymptote was determined using paired *t*-tests comparing consecutive trials in the force channel block (trials 201–250).

Data analysis. The position, velocity, and forces exerted by the manipulandum and the hand, in both x and y (Fig. 1A), were recorded at 600 Hz. The raw data were digitally smoothed using a fourth-order low-pass Butterworth filter with a cutoff frequency of 14 Hz. We performed data analysis using custom MATLAB R2017a (The MathWorks) scripts.

For each trial we computed the lateral deviation at peak velocity of the hand path relative to a straight line between the start position and target. We then computed the lateral force profiles that participants generated throughout movements in the force channel trials. To quantify the degree of adaptation in force channel trials, we computed an adaptation index defined by linear regression (without an intercept) of the measured lateral force profile produced by the hand (while velocity exceeded 2 cm/s) onto the ideal force profile that would have to be generated to fully compensate for the force field throughout the movement, had the force field been applied (see Smith et al. 2006 for more details). The adaptation index was zero if these force profiles were uncorrelated and one if these force profiles were identical to one another.

Model fitting. The response to a sensory prediction error can be mathematically described by a state-space model. The amount of trial to trial adaptation is based on two parameters that weigh the relative importance of recalling the previous motor commands, and of the sensory prediction error: a retention parameter, which is related to how much is remembered from trial to trial, and a learning rate parameter, which relates to the proportion of error that is corrected for trial to trial (Scheidt et al. 2001).

Smith et al. (2006) proposed that motor adaptation is supported by two separate processes, each with distinct timescales, one fast and one slow, that operate simultaneously. The fast process (f , Eq. 2) responds strongly to error, learns quickly (B_f), but has poor retention (A_f). The slow process (s , Eq. 3) has better retention (A_s) but is less sensitive to errors and thus learns more slowly (B_s). The two processes are combined to produce the net output $x_{net}(n)$ (Eq. 4). Error arises because there is a difference between the net output $x_{net}(n)$ and the task parameter $f(n)$ (Eq. 5). The model is as follows:

$$x_f(n+1) = A_f \cdot x(n) + B_f \cdot e(n) \quad (2)$$

$$x_s(n+1) = A_s \cdot x(n) + B_s \cdot e(n) \quad (3)$$

$$x_{net}(n) = x_f(n) + x_s(n) \quad (4)$$

$$e(n) = f(n) - x_{net}(n) \quad (5)$$

During the force channel trials, it was assumed $e(n)=0$ and thus there was no learning, and all updating resulted only from decay. By setting the perturbation magnitude $f(n)$ of the force field adaptation and brief force field reversal to ± 1 , the predicted motor output from the model (x_{net}) corresponds to the adaptation index (Smith et al. 2006; Trewartha et al. 2014). To estimate the model parameters, the model was fit (using the function *fmincon* in MATLAB R2017a) to minimize the squared difference between the model predicted motor output (x_{net}) and participant adaptation index, measured on force channel trials. It has been suggested that the inclusion of force channel trials and breaks between sessions improves the ability of a least-mean-squared-error optimization method to estimate model parameters (Albert and Shadmehr 2018). We used the 95% confidence interval for each parameter reported in Smith et al. (2006) to generate a uniform distribution of 100 different parameter values for each parameter in the model. The stability of the model fits and the sensitivity of the initial conditions were tested using a randomly selected value from each distribution as the starting parameter values. This was done to better ensure the identification of a global minimum within the constrained parameter space.

As in Albert and Shadmehr (2018), the constrained parameter space was defined by upper and lower bounds and by linear inequality constraints. Linear inequality constraints were specified to enforce traditional two-state model dynamics according to

$$A_s \geq A_f + 0.001 \quad (6)$$

$$B_f \geq B_s + 0.001 \quad (7)$$

To fit the model, we set the initial values of the fast and slow process to zero, on the first trial of the first session. At the end of the first session, our paradigm was designed to produce a rebound of the previously learned adaptation behavior during the block of force channel trials. The duration of the break between sessions was set to 5 min to allow for decay of the rebound from the first session. To account for the additional forgetting of the fast and slow processes across the 5-min break between sessions, the parameter d was used as a decay factor that parameterizes elapsed time between trials (Joiner and Smith 2008; Albert and Shadmehr 2018). The value of d was estimated by calculating the ratio of the duration of a session break to the average intertrial interval across the first session. As in Albert and Shadmehr (2018), we modeled the additional decay where the net output on *trial 250* of the first session was as follows:

$$x_f(250) = A_f^{d+1} \cdot x(249) + A_f^d \cdot B_f \cdot e(249) \quad (8)$$

$$x_s(250) = A_s^{d+1} \cdot x(249) + A_s^d \cdot B_s \cdot e(249) \quad (9)$$

The values for $x_f(250)$ (Eq. 8) and $x_s(250)$ (Eq. 9) from the first session were then used as the initial values for each process at the start of the second session.

The use of Eq. 8 and Eq. 9 allowed us to compare the estimate for the net output (as the sum of the two processes) to the measured behavior during the two force channel trials at the end of the block of baseline trials in *session 2*. This method acted as a control to ensure the state of the system had returned to baseline and therefore any measured changes in the model parameters could be attributed to the repetition of the environmental perturbation and history of the sensory prediction error.

Statistical design. Pairwise comparisons were performed with non-parametric bootstrap hypothesis tests or paired *t*-tests. For statistical analyses that require multiple comparisons, we used the Holm-Bonferroni correction (Holm 1979). Statistical tests were considered significant at $P < 0.05$. For all reported and depicted values, we report the mean and SE.

RESULTS

In the first session participants adapted their reaches to a viscous (velocity-dependent) force field. In the second session participants reached in the same, previously experienced force field. We used both kinematic (Fig. 2A) and kinetic (Fig. 2B) behavioral measures to assess performance during the first and second sessions.

Figure 2A shows the lateral deviation for all trials in each session, averaged across participants. In both sessions participants exhibited learning during both the adaptation and reversal blocks. The mean \pm SD lateral deviation for all force channel trials was 0.51 ± 0.27 mm, indicating that the force channel trials were effective at minimizing kinematic errors. That is, the force channels effectively prevented the hand from deviating from the straight line connecting the start position and the target.

Figure 2B shows adaptation index for all force channel trials in each session, averaged over participants. We examined the adaptation index during four different epochs: early (first force channel trial during adaptation), late (last force channel trial during adaptation), reverse (first force channel trial postreversal), and rebound (average of the first five trials of the force channel trial block after performance reached asymptote). The

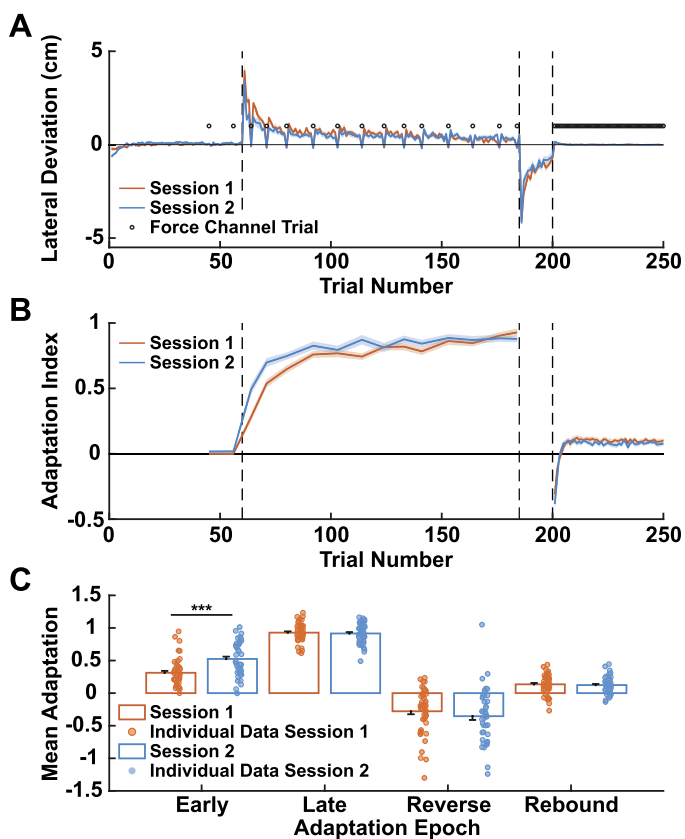


Fig. 2. *Experiment 1.* A: average, for *session 1* (orange) and *session 2* (blue), of the lateral deviation of the hand path at peak velocity throughout the experiment. The shaded region denotes \pm SE. Open circles represent channel trials. B: the average adaptation index for all channel trials in *session 1* (orange) and *session 2* (blue). The shaded region denotes \pm SE. C: comparisons between *session 1* (orange) and *session 2* (blue) for the mean adaptation index for (early) the first force channel trial of the adaptation block, (late) last force channel trial of the adaptation block, (reverse) the first force channel trial after the adaptation reversal, and (rebound) force channel trials 22–25. Circles represent individual data.

results of the analysis on the rebound epoch was consistent whether we considered 5 trials after asymptote or the entire block of 50 rebound trials. To provide a consistent basis for comparing across different epochs, in the analyses that follow to characterize rebound we used the first 5 trials after participants reach asymptote.

The adaptation index represents the proportion of compensation for the experienced force field. We compared the adaptation index estimated in the four epochs across sessions (Fig. 2C). The mean adaptation index in the early learning epoch of the second session was larger than that in the first session [paired *t*-test, $t(36) = 4.29$, $P < 0.001$]. This indicates the presence of savings. We did not detect a reliable difference between mean adaptation index in the late learning epoch in *session 1* versus *session 2* ($P = 0.165$), reverse ($P = 0.291$), or rebound epochs ($P = 0.145$). Thus, the influence of repeating the same force field in the second session was only statistically different during the early epoch.

We used a two-state model (Smith et al. 2006) to decompose the measured adaptation indices given in Fig. 2B in to a fast and slow learning process. Our aim was to test whether savings is associated with a change in learning rate for the fast process alone, as previously suggested (Trewartha et al. 2014; McDougle et al.

2015; Albert and Shadmehr 2016), or for both fast and slow processes.

As previously described in METHODS, we used a spontaneous recovery paradigm (Smith et al. 2006) to extract the fast and slow processes of the two-state model. The key components of this paradigm are the brief reversal of the force field adaptation used to return behavior to baseline and a block of force channel trials that reveal a spontaneous recovery of the previously learned force field adaptation. We observed that fitting the data with the two-state model appeared to be dependent on these two features. In addition to participants who were ideal representatives of the average data (Fig. 3, S7 and S32), we had participants who did not show a behavioral influence from the brief force field reversal and/or did not show spontaneous recovery, which resulted in estimates that appeared to be unrealistic after fitting the model to their individual data. For example, some individual fits suggest no retention (S17, *session 2*, $A_f = 0.000$; S14, *session 1*, $A_f = 0.000$), perfect retention (S17, *sessions 1 and 2*, $A_s = 1.000$; S14, *session 1*, $A_s = 1.000$), virtually no learning (S37, *session 1*, $B_f = 0.043$, $B_s = 0.009$), or perfect learning (S26, *session 2*, $B_f = 1.000$).

Previous studies that have suggested savings is due to an increase in the learning rate of the fast process with no changes

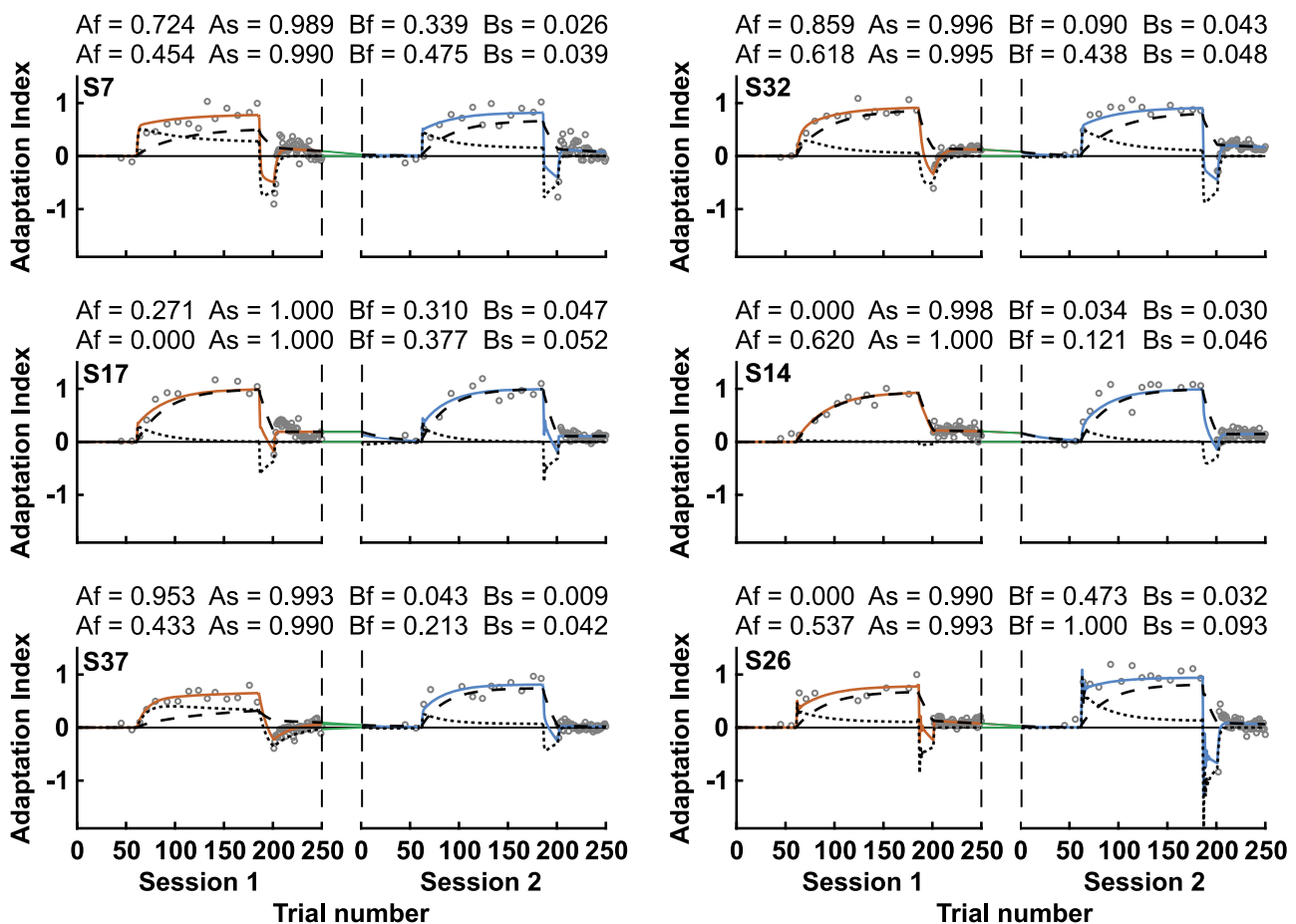


Fig. 3. Model fitting representative individual data. The data and two-state model fit for six individual participants (S7, *top left*, S32, *top right*, S17, *middle left*, S14, *middle right*, S37, *bottom left*, S26, *bottom right*). *Top row*, two ideal participants; *middle row*, two participants with a two-state model fit that included zero or perfect retention; *bottom row*, two participants with a two-state model fit that included zero or perfect learning. Circles represent the adaptation index values plotted for each force channel trial. The overall output predicted by the model for *session 1* (orange traces), *session 2* (blue traces), the fast process (dotted lines) and the slow process (dashed lines) are shown as a function of trial. The estimated decay during the session break is shown in green. The four parameters of the model are fast retention (A_f), fast learning rate (B_f), slow retention (A_s), and slow learning rate (B_s).

in the learning rate for the slow process relied on using individual data to estimate model parameters characterizing fast and slow learning processes (Albert and Shadmehr 2018; Trewartha et al. 2014). When we estimated the slow and fast learning processes by fitting the two-state model to the time course of adaptation index of each participant individually, we found a similar result. Using the estimates from the individual data, we compared the average within-subject differences between *session 1* and *session 2* for each of the four parameters of the model (i.e., A_f , A_s , B_f , B_s). We found that the fast process learning rate (B_f) changed from *session 1* to *session 2* [paired t -test, $t(45) = -4.19$, $P < 0.001$, Fig. 4]. No other parameters showed statistically reliable changes from *session 1* to *session 2*. The nature of the unreasonable fits for some participants (Fig. 3) raises concerns about the ability to use individual data to estimate model parameters characterizing fast and slow learning processes, without also considering how the model fits data averaged across participants.

Here we describe a procedure based on fitting data averaged across participants. For each session we fit the model to data averaged across participants, and we used a bootstrapping procedure to estimate distributions of parameter values. We generated resampled populations of subjects by selecting, with replacement, the entire time course of adaptation index values for *session 1* and *session 2*, for each selected subject. We fit the two-state model to the time course of the adaptation index, averaged across the resampled population. We did this 10,000 times to generate a distribution of estimated parameter values. To perform within-subject comparisons across session, in each of the 10,000 model fits we used the same set of resampled subjects for *session 1* and *session 2*. Model fits were performed using the *fmincon* function in MATLAB. After obtaining the 10,000 parameter sets, we tested whether parameter estimates changed from *session 1* to *session 2*.

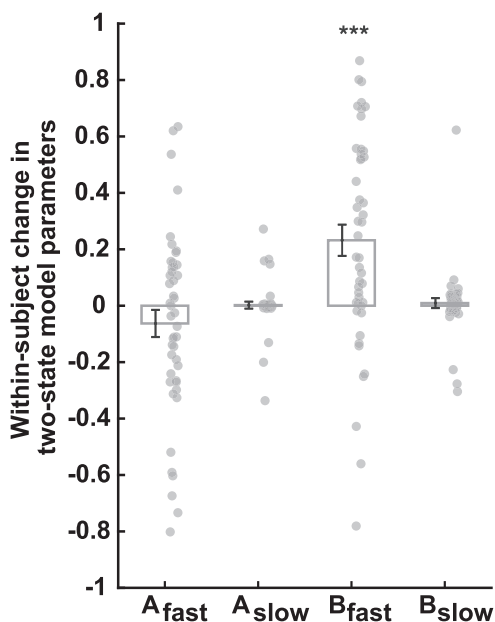


Fig. 4. Estimated model parameters based on fitting individual data. Bars indicate the mean change in model parameters between sessions. Error bars indicate \pm SE. Circles represent individual subject differences between sessions. The four parameters of the model are fast retention (A_{fast}), fast learning rate (B_{fast}), slow retention (A_{slow}), and slow learning rate (B_{slow}).

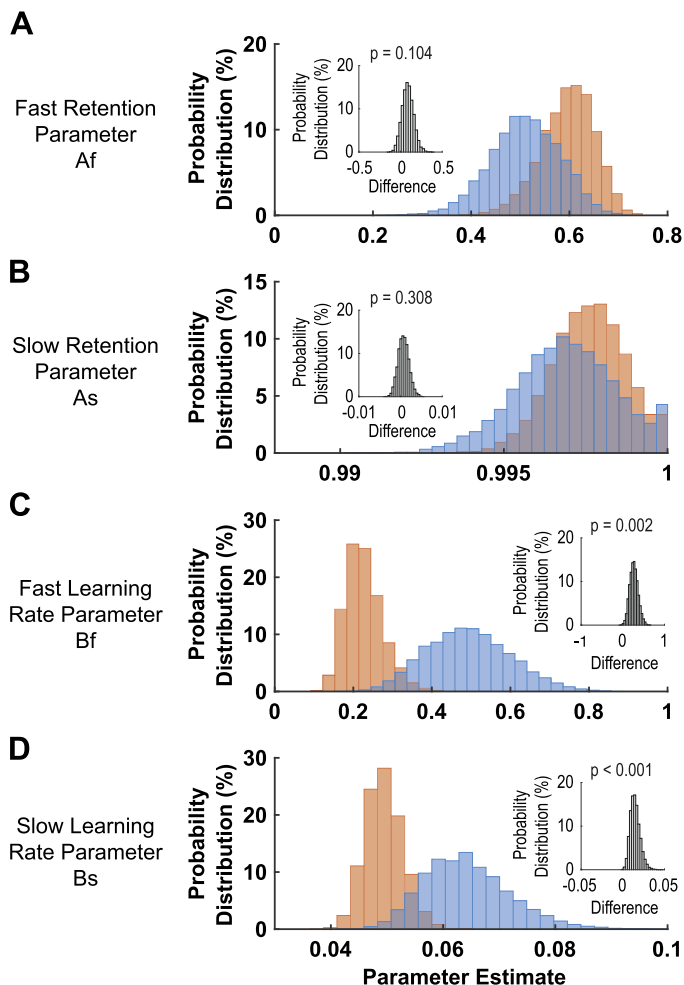


Fig. 5. Probability distribution of the model parameters given the data. Orange and blue represent *session 1* and *session 2*, respectively. *Inset* represents the difference between sessions. The four parameters of the model are fast retention (A_f), fast learning rate (B_f), slow retention (A_s), and slow learning rate (B_s).

Figure 5 shows the distribution of each of the four parameter values. To determine whether the difference between the mean of each distribution was statistically reliable, we calculated the value of the difference between the two sessions. The *insets* in Fig. 5 show the distribution of differences found. To consistently analyze the proportion of values that fell below zero, we subtracted the session distribution with smaller values from the distribution with larger values. When participants experienced repetition of the same perturbation, we found an increase in learning rate both in the fast (B_f , $P = 0.002$) and slow (B_s , $P < 0.001$) processes. This suggests that the observed increase in level of adaptation during the early learning epoch, representing savings, results from an increased learning rate in both the fast and slow process.

From the bootstrap distributions we then calculated the mean value for each parameter, for *session 1* and *session 2* separately. Using these estimates we simulated our experimental design using the two-state model, to produce simulated learning curves. As seen in Fig. 6, the simulated learning curves match well with the measured behavioral data. Additionally, the model successfully captures both the initial improvement in the adaptation index seen over the course of adaptation, as well

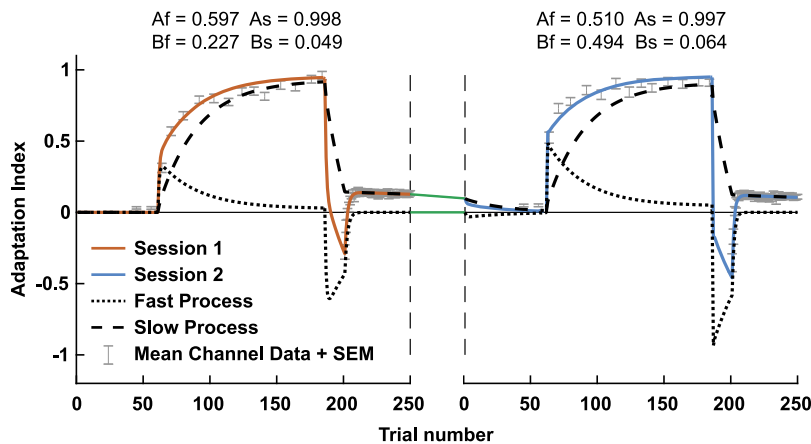


Fig. 6. Model simulations. Parameter estimates for each session were based on the mean values from the bootstrap distributions shown in Fig. 5. Gray bars represent average behavioral data. The overall output predicted by the model for *session 1* (orange traces), *session 2* (blue traces), the fast process (dotted lines), and the slow process (dashed lines) are shown as a function of trial. The estimated decay during the session break is shown in green. The four parameters of the model are fast retention (A_f), fast learning rate (B_f), slow retention (A_s), and slow learning rate (B_s).

as the rebound of the adaptation index seen in the final block of force channel trials.

DISCUSSION

Using a rebound paradigm, we found that both fast and slow processes contribute to savings. When the motor system was exposed to a force field during the second session that was the same as the one from the previous session, we found increased learning rates of both fast and slow processes. This suggests that a history of errors modulates both fast and slow processes, and more importantly, that both fast and slow processes have access to this history of errors.

It is well established that when participants are reexposed to the same perturbation, adaptation occurs more rapidly (Herzfeld et al. 2014; Huang et al. 2011; Kojima et al. 2004; Leow et al. 2016; Smith et al. 2006). The presence of savings in the current study was confirmed by comparing the estimated learning rate parameters from initial adaptation and readaptation to the same perturbation. In line with the findings of Herzfeld et al. (2014), participants adapted more quickly during the second session compared with the first, not because the motor system recalled the motor commands to counter the repeated perturbation, which would have resulted in better retention, but rather because it recognized the errors and adapted its overall rate of learning.

During adaptation to a novel task the learning curve exhibits two stereotypical phases: an early rapid phase that accounts for the majority of performance gains, and a second slower phase that provides only modest and gradual improvements (Smith et al. 2006; Haith and Krakauer 2013). During the early rapid phase of learning, the fast process dominates, leading researchers to suggest that savings is due to an increase in the learning rate of the fast process with no change in the learning rate for the slow process (Albert and Shadmehr 2018; McDougale et al. 2015; Trewartha et al. 2014). This finding is often expected as the qualitative difference in early learning between initial learning and relearning is better explained by the learning rate of the fast process, not the slow process. Additionally, some have proposed that the fast process is influenced by explicit learning strategies, whereas the gradual improvements in performance that follow are thought to be due to a slow process that has been linked to implicit learning (Bond and Taylor 2017; McDougale et al. 2015; Taylor et al. 2014). Note, however, that in the context of visuomotor rotation experiments it

has been proposed that explicit and implicit systems can be mapped onto fast and slow processes and can be behaviorally separated (McDougale et al. 2015; Morehead et al. 2015; Taylor et al. 2014). In the present study we use force field adaptation

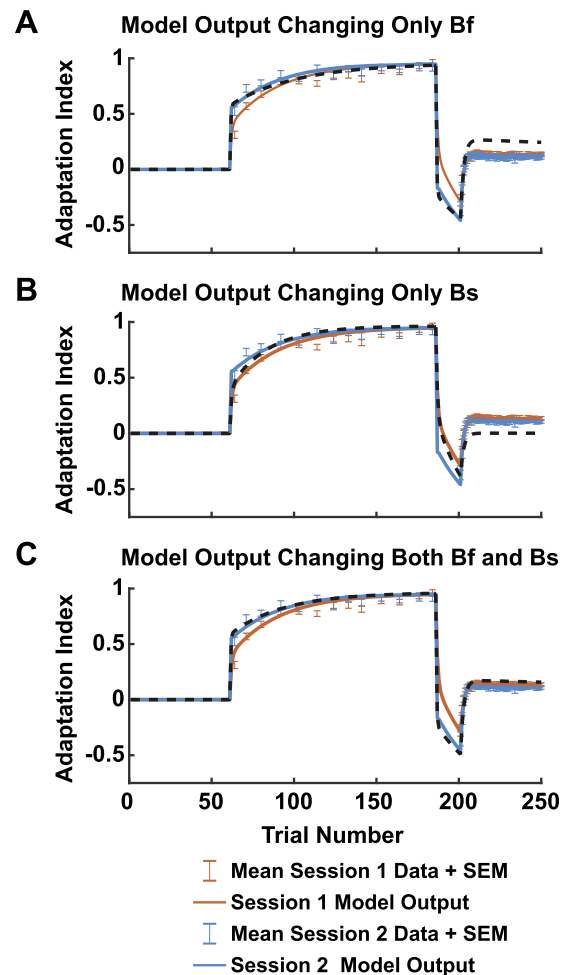


Fig. 7. Sensitivity analysis. We simulated net motor output using the mean values from the bootstrap analysis as the parameter estimates for the fast and slow processes from *session 1* (orange) and *session 2* (blue). Orange and blue bars represent average behavioral data from *sessions 1* and *2*, respectively. *A*: *session 1* parameters were held constant with only a change in the fast learning rate parameter. *B*: *session 1* parameters were held constant with only a change in the slow learning rate parameter. *C*: *session 1* retention parameters were held constant with a change in both fast and slow learning rate parameters.

and to our knowledge no such direct measures exist to assess the fast and slow processes.

Recently, however, Albert and Shadmehr (2018) highlighted that estimates using least-mean-squared-error to fit individual data can lead to overfitting the noise in the data and can produce errant fits. In the present study, when we fit the two-state model to data from each participant individually and we estimated the model parameters in each session separately, we found that only the change in the fast process learning rate was statistically reliable. That is, we found no reliable changes in the retention parameters or the slow process learning rate. However, using a bootstrap method to fit the model to group data, we observed an increase in learning rate for both the fast and slow processes. This suggests that the increased learning rate of the slow process seen at the group level may not occur for all individual participants or that the method of fitting individual data fails to uncover this increase.

To assess the importance of an increased learning rate of the slow process, we simulated the net motor output during our experimental paradigm using the mean value for each parameter estimate from the bootstrap analysis for *session 1* and *session 2* (Fig. 7). Next we simulated the net output of three separate conditions to assess whether the change in behavior observed in *session 2* could be accounted for by a change in the fast learning rate (B_f) alone (Fig. 7A) or a change in the slow learning rate (B_s) alone (Fig. 7B) or whether it required a change in both the fast and slow learning rates (B_f and B_s) (Fig. 7C).

In Fig. 7A we took the average parameter values for A_f , A_s , and B_s from *session 1* and the average parameter value for B_f from *session 2* and simulated the motor output that would result from a change in only the fast learning rate in *session 2*. While the increase in the learning rate for the fast process can account for the initial increase in rate of adaptation, it cannot account for the same level of rebound observed in the block of force channel trials at the end of each session. As previously noted in RESULTS, we found no reliable difference between the level of rebound in each session. Next we took the average parameter values from the bootstrap analysis for A_f , A_s , and B_s from *session 1* and the average parameter value for B_s from *session 2* and simulated the motor output that would result from a change in only the slow learning rate in *session 2*. In this condition, we observed that the simulated output failed to account for savings and, in addition, predicted a decrease in rebound that was not observed in the behavioral data (Fig. 7B). Qualitatively we observed that the simulated output fails to account for the observed behavioral data with a change to the fast or slow learning rate alone. Only when we changed the learning rate for both the fast and slow processes together could we account for both the savings and rebound measured in the behavioral data (Fig. 7C). Therefore, the inclusion of the increase in learning rate for the slow process is needed to fully account for the pattern of results seen in the behavioral data.

One criticism of the two-state model is that while it is able to explain savings over short timescales, it fails to account for savings observed after a prolonged period of washout following the initial learning of a perturbation (Krakauer et al. 2005; Zarahn et al. 2008). While savings is traditionally explained by an increase in the rate of learning for the fast process, the observed increase in the slow process learning rate in the present study may reflect that the history of error influences

both processes. Joiner and Smith (2008) observed that maximizing the long-term benefit of initial training in a force field perturbation task related to the amount of learning achieved by the slow process, providing a possible role for the slow process in savings. Therefore, the increase in the rate of adaptation in early learning maybe be represented by the increase in the fast process learning rate, while the increase in the slow process learning rate may represent savings over longer timescales.

The increase in learning rate for both the fast and slow process is believed to rely on the stored history (i.e., memory) of error (Herzfeld et al. 2014; Leow et al. 2016). One possible theory of the mechanism behind storing a history of error is structural learning. Structural learning is thought to be essential to capturing the initial rapid phase of learning that leads to structure-specific learning-to-learn effects (Braun et al. 2009), often interpreted as an explicit strategy used in the visuomotor rotation literature (Bond and Taylor 2017). Structural learning is essentially about reducing the dimensionality of the space to be searched to adapt and speed learning. This becomes increasingly important for skilled performance that requires the effective and efficient gathering and processing of sensory information relevant to an action.

Our findings show that both fast and slow processes contribute to savings. In particular, the theory of storing a history of errors (Herzfeld et al. 2014) has been shown to allow both hidden processes to modulate their output, as measured via the rate of learning. Critically, the significant change in adaptation in the present study seen during the early learning of the second perturbation was clearly attributed to the fast process, while the rebound seen in the force channel trials at the end of the second session was clearly attributed to the slow process.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

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

REFERENCES

- Albert ST, Shadmehr R. The neural feedback response to error as a teaching signal for the motor learning system. *J Neurosci* 36: 4832–4845, 2016. doi:10.1523/JNEUROSCI.0159-16.2016.
- Albert ST, Shadmehr R. Estimating properties of the fast and slow adaptive processes during sensorimotor adaptation. *J Neurophysiol* 119: 1367–1393, 2018. doi:10.1152/jn.00197.2017.
- Bond KM, Taylor JA. Structural learning in a visuomotor adaptation task is explicitly accessible. *eNeuro* 4: ENEURO.0122-17.2017, 2017. doi:10.1523/ENEURO.0122-17.2017.
- Braun DA, Aertsen A, Wolpert DM, Mehring C. Motor task variation induces structural learning. *Curr Biol* 19: 352–357, 2009. doi:10.1016/j.cub.2009.01.036.
- Cheng S, Sabes PN. Modeling sensorimotor learning with linear dynamical systems. *Neural Comput* 18: 760–793, 2006. doi:10.1162/neco.2006.18.4.760.

- Donchin O, Francis JT, Shadmehr R.** Quantifying generalization from trial-by-trial behavior of adaptive systems that learn with basis functions: theory and experiments in human motor control. *J Neurosci* 23: 9032–9045, 2003. doi:10.1523/JNEUROSCI.23-27-09032.2003.
- Hadjiosif A, Smith MA.** Savings is restricted to the temporally labile component of motor adaptation. *Translational and Computational Motor Control*. San Diego, CA, November 8, 2013.
- 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.** Theoretical models of motor control and motor learning. In: *Routledge Handbook of Motor Control and Motor Learning*, edited by Gollhofer A, Taube W, Nielsen JB. Milton Park, UK: Routledge, 2013, p. 7–28.
- 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.
- Holm S.** A simple sequentially rejective multiple test procedure. *Scand Stat Theory Appl* 6: 65–70, 1979.
- 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.
- Joiner WM, Smith MA.** Long-term retention explained by a model of short-term learning in the adaptive control of reaching. *J Neurophysiol* 100: 2948–2955, 2008. doi:10.1152/jn.90706.2008.
- Kojima Y, Iwamoto Y, Yoshida K.** Memory of learning facilitates saccadic adaptation in the monkey. *J Neurosci* 24: 7531–7539, 2004. doi:10.1523/JNEUROSCI.1741-04.2004.
- Kording KP, Tenenbaum JB, Shadmehr R.** The dynamics of memory as a consequence of optimal adaptation to a changing body. *Nat Neurosci* 10: 779–786, 2007. doi:10.1038/nn1901.
- Krakauer JW, Ghez C, Ghilardi MF.** Adaptation to visuomotor transformations: consolidation, interference, and forgetting. *J Neurosci* 25: 473–478, 2005. doi:10.1523/JNEUROSCI.4218-04.2005.
- Lee J-Y, Schweighofer N.** Dual adaptation supports a parallel architecture of motor memory. *J Neurosci* 29: 10396–10404, 2009. doi:10.1523/JNEUROSCI.1294-09.2009.
- Leow L-A, 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.
- 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.
- 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.
- 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.
- Oldfield RC.** The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9: 97–113, 1971. doi:10.1016/0028-3932(71)90067-4.
- Scheidt RA, Dingwell JB, Mussa-Ivaldi FA.** Learning to move amid uncertainty. *J Neurophysiol* 86: 971–985, 2001. doi:10.1152/jn.2001.86.2.971.
- Shadmehr R, Smith MA, Krakauer JW.** Error correction, sensory prediction, and adaptation in motor control. *Annu Rev Neurosci* 33: 89–108, 2010. doi:10.1146/annurev-neuro-060909-153135.
- 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.
- 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.
- Thoroughman KA, Shadmehr R.** Learning of action through adaptive combination of motor primitives. *Nature* 407: 742–747, 2000. doi:10.1038/35037588.
- Trevartha KM, Garcia A, Wolpert DM, Flanagan JR.** Fast but fleeting: adaptive motor learning processes associated with aging and cognitive decline. *J Neurosci* 34: 13411–13421, 2014. doi:10.1523/JNEUROSCI.1489-14.2014.
- Tseng Y-W, Diedrichsen J, Krakauer JW, Shadmehr R, Bastian AJ.** Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *J Neurophysiol* 98: 54–62, 2007. doi:10.1152/jn.00266.2007.
- Wei K, Körding K.** Uncertainty of feedback and state estimation determines the speed of motor adaptation. *Front Comput Neurosci* 4: 11, 2010. doi:10.3389/fncom.2010.00011.
- Wolpert DM, Flanagan JR.** Motor prediction. *Curr Biol* 11: R729–R732, 2001. doi:10.1016/S0960-9822(01)00432-8.
- Wolpert DM, Kawato M.** Multiple paired forward and inverse models for motor control. *Neural Netw* 11: 1317–1329, 1998. doi:10.1016/S0893-6080(98)00066-5.
- 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.