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Neural Averaging in Motor Learning

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Mattar AA, Ostry DJ. Neural averaging in motor learning. *J Neurophysiol* 97: 220–228, 2007. First published October 4, 2006; doi:10.1152/jn.00736.2006. The capacity for skill development over multiple training episodes is fundamental to human motor function. We have studied the process by which skills evolve with training by progressively modifying a series of motor learning tasks that subjects performed over a 1-mo period. In a series of empirical and modeling studies, we show that performance undergoes repeated modification with new learning. Each in a series of prior training episodes contributes such that present performance reflects a weighted average of previous learning. Moreover, we have observed that the relative weighting of skills learned wholly in the past changes with time. This suggests that the neural substrate of skill undergoes modification after consolidation.

INTRODUCTION

The ways in which skills depend on past learning have been examined in a number of recent studies (Brashers-Krug et al. 1996; Caithness et al. 2004; Shadmehr and Brashers-Krug 1997; Walker et al. 2003). These studies have used variants of a procedure known as an ABA design where A and B are often opposite patterns of force applied to the hand by a robotic device. In these experiments, subjects learn task A and then following a variable interval, they learn task B. Subjects are then re-tested on task A to assess retention of initial learning. The interval between A and B is manipulated to investigate the time course of consolidation of task A learning. Some studies suggest that once consolidated, skills are not affected by further learning. Evidence for this idea comes from studies in which the learning associated with task A was retained provided that the interval between A and B was sufficiently long [more than ~5 h (Brashers-Krug et al. 1996; Shadmehr and Brashers-Krug 1997)]. In contrast, other recent work suggests that new learning can displace original learning (Caithness et al. 2004; Walker et al. 2003). Evidence suggests that when A and B involve opposite patterns of force, learning B interferes with the retention of A regardless of whether the interval between A and B is 5 min, 1 day, or 1 wk. This suggests that consolidated skills, even those learned long ago, can be disrupted by new learning.

In the present study, we have tested the hypothesis that performance reflects a combination of past learning and that skills are neither fixed after consolidation nor displaced with new learning. Support for the idea that motor learning reflects a neural averaging of previous learning comes from studies that have explored generalization of learning across the workspace (Malfait et al. 2005). In these studies, subjects learned to make movements in each of two workspace locations. Different patterns of force were applied to the hand in each location. Performance at a location intermediate to the two training areas

could be predicted in modeling studies based on a spatial average of the commands learned at the flanking locations. It has also been shown that for movements to benefit from earlier training, they must be made in areas of the workspace intermediate to previously trained movement directions, where spatial averaging of prior learning is possible (Gandolfo et al. 1996). This generalization falls off sharply for movements outside of these boundaries. These studies and others (Gharamani and Wolpert 1997) suggest that motor skills learned separately in different spatial locations can be combined. Here we have tested whether a combinatorial process also applies to the development of skills over time.

We designed two experiments in which subjects were tested a number of times over an extended period. This allowed us to track performance as it evolved with repeated training. In *experiment 1,* we left delays of either 24 h or 1 mo between training sessions to allow for consolidation of learning. In *experiment 2,* subjects trained on two consecutive days followed by delays of 2 or 10 days prior to final testing. Results suggest that consolidated skills are modifiable, but they are not entirely replaced by new learning. Instead performance reflects a combination of prior learning that changes with time.

METHODS

Subjects

Eighty-nine young adults (48 females, overall mean age $\pm$ SE, 22.51 ± 0.38 yr) took part in the experiments described below. 48 and 41 subjects participated in *experiments 1* and *2,* respectively. The McGill University Ethics Review Board approved all procedures. Subjects were right-handed and neurologically healthy and had normal or corrected vision.

Apparatus

Subjects made movements while holding the handle of a two-joint robotic device (InMotion2, Interactive Motion Technologies, Cambridge, MA) that allows movements in the horizontal plane. An air sled supported the arm during movement and eliminated friction. Torque motors connected to the shoulder and elbow joints of the robot applied forces (see following text) to subjects' hands during movement. Sixteen-bit optical encoders (Gurley Precision Instruments, Troy, NY) sensed the robot's (and hence the subject's) joint angles. Data were sampled at 400 Hz and stored off-line for later analysis.

Experimental task

In each experimental session, subjects made movements to a set of five targets (Fig. 1*A*). The targets were 3 cm in diameter and were arranged around the upper arc of a circle with a radius of 15 cm. The starting position was defined by shoulder and elbow angles of 45° and 90° relative to the frontal plane and the upper arm, respectively.
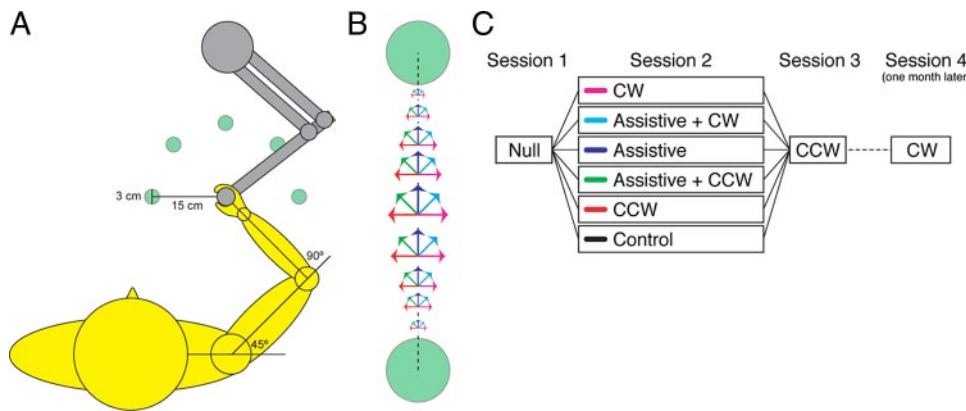

FIG. 1. Robotic device, force fields, and experimental protocol. *A*: subjects made movements to targets arranged in a semicircle about the hand. *B*: robotic device was programmed to apply velocity-dependent forces to the hand in 5 directions relative to the direction of movement (a straight out movement is shown as an example). The size of the arrows schematically represents the force magnitude as it scales with velocity. *C*: subjects in *experiment 1* were tested in 4 sessions over a 1-mo period. The colors shown identify each group in Figs. 1–4.

Subjects were told to observe the workspace and wait for a target to be illuminated before moving. After waiting at the start position for 1,000 ms, subjects were required to move to a pseudorandomly selected target within 500 ± 50 ms and to stay within its boundaries for an additional 750 ms. Visual and auditory cues informed subjects about the duration of each movement, after which the robot brought the hand back to the start position.

Force fields

The robot was programmed to apply forces to the hand that were dependent on instantaneous movement velocity. Force, f_x and f_y, was applied according to the equation

$$\begin{bmatrix} f_x \\ f_y \end{bmatrix} = c \begin{bmatrix} \sin\theta & \cos\theta \\ -\cos\theta & \sin\theta \end{bmatrix} \begin{bmatrix} v_x \\ v_y \end{bmatrix}$$

where x and y are the lateral and sagittal directions, v_x and v_y are movement velocity, $c = 15 \text{ N} \cdot \text{s} \cdot \text{m}^{-1}$ and θ defined the direction of force relative to the direction of movement (see following text and Fig. 1*B*).

Procedure

We performed two experiments. In the first experiment, subjects were tested a number of times over a 1-mo period. This allowed us to track performance as it evolved with repeated training. On each of 4 sessions, subjects made movements to five targets while holding the handle of a robotic device that was programmed to apply forces to the hand that varied with movement velocity (see Fig. 1*A*). We left delays of either 24 h or 1 mo between training sessions to allow for consolidation of learning. During *session 1*, subjects familiarized themselves with the task and no forces were applied. One day later in *session 2*, subjects were divided into five groups ($n = 8$ for each group) and each made movements in one of the force-fields depicted in Fig. 1*B*. Two of these fields pushed the hand laterally ($\theta = 0°$ and $\theta = 180°$); an assistive field, acted in the direction of movement ($\theta = 90°$); two other fields had assistive and lateral components, resulting in forces that acted at 45° to the direction of movement ($\theta = 45°$, assistive + clockwise and $\theta = 135°$, assistive + counter-clockwise). A sixth group of control subjects ($n = 8$) did not make movements during *session 2*. One day later in *session 3*, all subjects made movements in a lateral field that pushed the hand in a counter-clockwise (CCW) direction relative to the direction of movement ($\theta = 180°$). This allowed us to determine the effect of *session 2* training on *session 3* performance. Approximately 1 mo later [*session 4*: mean delay 34.3 ± 7.2 (SD) days], to test the effect of the entire training history, subjects returned to make movements in a clockwise (CW) field that pushed the hand in a direction opposite to the *session 3* field ($\theta = 0°$). Figure 1*C* summarizes the experimental protocol. Four of the 48 subjects tested in *experiment 1* did not return for *session 4*

testing. Subjects made 100 movements each session. For each individual, testing sessions occurred at approximately the same time of day.

In the second experiment, we randomly selected the direction of load in each of two training sessions. By examining how performance on a final test session varied as a consequence of the wide variety of training histories, we could directly test the idea that performance reflects a combination of past learning. In this experiment, *session 1* (familiarization) was followed immediately by *session 2* training. For *session 2*, the field was chosen randomly from the five used in *experiment* 1. For *session 3* (24 h later), the training field was again chosen randomly. This resulted in 25 possible combinations of *session 2* and *3* training fields. During *session 4* (after a 2- or 10-day delay), subjects were tested in a clockwise lateral field ($\theta = 0°$ relative to the direction of movement). For the 2- and 10-day delay conditions, we ran 25 subjects (all combinations) and 16 subjects (a subset of the combinations), respectively.

Measures and statistics

Hand position data were numerically differentiated and then low-pass Butterworth filtered at 20 Hz to generate velocity profiles. Movement start and end were scored at 5% of peak tangential velocity. To assess movement curvature, we computed a measure of perpendicular error (PE), which is defined as the signed distance at maximum velocity from the vector linking movement start and end positions. We computed PE at the moment of peak velocity to assess movement curvature prior to any voluntary response to the load applied by the robot. We also computed initial angular deviation (the angle between the vectors linking start and end, and start with the point of maximum tangential velocity) and found results similar to those reported here. Throughout, we use the term performance to refer to movement path error in the lateral direction (PE).

Statistical tests were conducted using ANOVAs and were followed by post hoc Tukey comparisons where appropriate. In *experiment 1*, we divided subjects (48 in total) into groups of eight on the basis of the field in which they were trained during *session 2*. To compare *session 2* performance for the different directions of load application, we performed an ANOVA on movement curvature (PE). We compared PE for movements 6–25 (the 2nd-5th movement to each of 5 targets; the 1st movement to each target was excluded). We also compared the unsigned PE at the end of training (movements 91–100) to assess the extent to which the magnitude of final error differed between groups. Since the assistive loads did not curve movements laterally but instead applied force in the direction of movement, we also examined movement velocity profiles. We computed the difference between time-normalized velocity profiles for movements made in force fields and those made to the same target in the absence of load (Malfait et al. 2005). We used the sum of squared differences as a dependent measure of the force fields' effect on velocity, and per-

formed ANOVAs to determine whether velocity profiles changed over the course of training and whether final movements (91–100) were still affected by the force field.

To determine whether learning with assistive loads is retained over time in a fashion comparable to that observed with lateral loads, we examined the effects of training with assistive loads on movement duration. Our rationale for choosing this measure was that assistive loads affect timing along the intended trajectory, rather than error in the lateral direction. Since training with assistive loads was limited to *session 2*, our analysis focused on *session 3* performance with or without previous training with assistive loads. Specifically, we examined the duration of the initial movement segment (≤ 1.0 cm from movement start) to preclude possible voluntary correction for the load. We examined the first 5 movements and used an independent samples *t*-test to compare *session 3* movement durations for naïve subjects with those of subjects who trained in an assistive load in *session 2*.

For *session 3* and *session 4* we computed mean movement curvature (PE) for movements 6–25. We also computed PE for the final training movements in session 3 (91–100). Using ANOVA and *post hoc* comparisons, we assessed the dependence of movement curvature on the field in which subjects trained during *session 2*. For subjects that trained in the same lateral counter-clockwise field for both *session 2* and *session 3*, we tested whether initial *session 3* performance (movements 6–25) was facilitated relative to final *session 2* performance (movements 91–100) by performing a paired-samples *t*-test.

We performed a further set of analyses to determine whether the rate of learning was affected by the direction of movement. For each of the five fields, we used repeated measures ANOVAs to examine whether adaptation rate varied across the 5 targets in the workspace. For these analyses we focused on movements 6–25.

In experiments 1 and 2, we used regression analyses to determine the relationship between performance on the test session and subjects' previous training histories. In *experiment* 1, we evaluated the dependence of initial *session 3* curvature (PE for movements 6–25) on the five fields learned during *session 2*. We decomposed the loads experienced in the five fields into their lateral and assistive components and used each to predict performance in the counter-clockwise lateral field that subjects learned during *session 3*. The analyses reported here focus on how *session 3* performance was affected by the lateral strength of the force fields. No relationship was found between performance with lateral loads in *session 3* and assistive loads in *session 2*.

We used regression again in *experiment* 2. We assessed the dependence of initial *session 4* curvature (after 2- or 10-days of rest) on the loads experienced during *session 2* and *session 3*. This allowed us to determine whether *session 4* performance could be accounted for by either *session 2* or *session 3* alone or both training sessions in combination. For these analyses, we decomposed both the *session 2* and *session 3* fields into lateral and assistive components. We carried out a regression in which *session 4* performance (PE) was assessed as a linear combination of *session 2* and *session 3* training. The coefficients of terms representing the lateral loads experienced during *session 2* and *session 3* were used to estimate the relative effects of *session 2* and *session 3* training on *session 4* performance. No relationship was found between *session 4* performance and the assistive loads experienced during *session 2* and *session 3*.

Statistical tests of differences in regression weights between the 2-day and the 10-day delay were conducted using the bootstrap function BOOTSTRP in Matlab (The Mathworks, Natick MA). We repeated each regression 100 times and performed an independent samples *t*-test on resulting weights.

Simulations

For simulations we used a model of planar two-joint arm movement (Gribble et al. 1998) based on the λ-version of the equilibrium point hypothesis (Feldman 1986). According to the model, movement and muscle co-contraction result from neural input that takes the form of time-varying shifts in the threshold muscle length for motor neuron recruitment (λ). Motor neuron activation depends on the difference between actual and threshold lengths as specified in the equation

$$A(t) = l(t - d) - \lambda(t) + \mu(t)\frac{dl}{dt}(t - d)$$

In this equation, A is positive or zero, l is the actual muscle length, λ is the centrally specified threshold length for motor neuron activation, μ is a constant specifying the dependence of threshold length on velocity, dl/dt is the rate of change of muscle length and d is a constant reflex delay. Muscle force, F, is generated in proportion to motor neuron activation according to the exponential function

$$F = \rho[\exp(A) - 1]$$

where each muscle's force generating ability varies with its cross sectional area, ρ. The model includes six muscles: biceps long head and triceps lateral head at the elbow, pectoralis and deltoid at the shoulder, and biceps short head and triceps long head spanning both joints. Passive muscle stiffness also contributes to total muscle force.

The coordinated control of muscle λs results in movement and muscle co-activation. We assume that movements are produced by time-varying shifts in the limb's equilibrium trajectory (and in the associated muscle λs), where each point on the trajectory is given by the set of λs that minimizes total muscle force. The co-contraction command is defined by a separate set of λ shifts that act to increase muscle force in the most equal proportions without changing net joint torque. As in Gribble et al. (1998), for purposes of these simulations the co-contraction command is defined initially in force space and hence its units are N and specify average muscle force. The vector in λ space associated with this muscle force in statics is used as the co-contraction command.

Force field adaptation was simulated using a learning algorithm in which the equilibrium trajectory and associated muscle λs are adjusted on a trial-by-trial basis in proportion to the difference between desired and actual trajectories (see Gribble and Ostry 2000 for details). In particular, we assumed that commands were updated on the basis of squared position error, such that large errors led to large adjustments in the modeled motor commands while small errors resulted in small adjustments. These adjustments were scaled by a constant such that differential rates of adaptation could be modeled. Control signals were thus updated according to the following equation

$$\Delta\lambda(t - d_{nm}) = r \cdot (l(t) - \lambda(t))^2$$

where $\Delta\lambda$ is a vector of changes to muscle threshold length which reflect position error. This vector is summed on a trial-by-trial basis with the vector of muscle threshold lengths, λ, that was used to produce movements on the preceding trial. The position error is calculated as the time-varying difference between centrally-specified and actual muscle lengths, λ and l. The parameter d_{nm} is a constant that time-advances the position error vector by an amount corresponding to the neuromuscular delay, and r is a gain parameter that scales the rate with which squared position error is minimized. In the modeling studies described below we varied rate and co-contraction parameters to best fit the empirical data (Table 1). We found similar results in a set of simulations in which these parameters were held constant.

TABLE 1. *Parameters used to fit simulations to empirical data*

	Session 1	Session 2	Session 3	Session 4
Rate, arbitrary units	10.5	10.5	10.5	6.0
Co-contraction, total force, N	45	47–80	42–70	73–95

The simulations replicated the experimental conditions in our month-long study. We began by simulating movements to 5 targets, arranged as they were for subjects (see Fig. 1*A*). Each movement direction was considered separately and then averaged for graphical presentation. Total movement duration (1200 ms) matched values observed empirically and for each session we simulated 100 movements.

We began with *session 1* by simulating movements in the absence of load. This generated five sets of modeled control signals (one for each movement direction) that compensated for the dynamics of the arm and produced straight-line movements. For *session 2* we used the five sets of final *session 1* control signals as initial commands for movements in each of the five force fields. For *session 3* and *session 4*, initial commands for each movement direction were based on a weighted average of the control signals for that direction from preceding sessions. For each movement direction, the modeled control signals were averaged according to the following equation

$$\lambda_{avg} = w_1\lambda_1 + w_2\lambda_2$$

where λ_1 and λ_2 are time-varying vectors of threshold muscle lengths associated (in this example) with *session 1* and *session 2* training, w_1 and w_2 are the relative weights for each session, and λ_{evg} is the vectorally averaged control signal. To obtain initial commands for *session 3*, *session 1* and *session 2* control signals were weighted 20%/80% (according to the 2-day delay group in Fig. 5*B*). The same weightings were used for all movement directions. To select weightings for *session 4*, we performed a number of simulations in which weights for *session 2* and *session 3* ranged from 0%/100% to 100%/ 0%. We then computed the sum of squared differences between actual and simulated *session 4* performance. Based on this analysis, *session 2* and *session 3* control signals were weighted 50%/50% to produce initial commands for *session 4*.

RESULTS

The data support the idea that skills reflect a neural averaging of past learning. The evidence is as follows: during *session 2* (the first training session) subjects learned to move in one of the five force fields. Initial movements (Fig. 2*A*) were deflected consistent with the direction of the loads but straightened over the course of *session 2* training (Fig. 2*B*) such that final movements did not differ in terms of the magnitude of movement curvature ($P > 0.05$). Fields that had assistive components resulted in velocity profiles that were initially different from those of reference movements (Fig. 2*C*). However, with training these differences decreased ($P < 0.05$) such that by the end of training, with one exception, velocity profiles were no different from those of reference movements ($P > 0.05$). These findings suggest that neural control was modified to normalize movements in the presence of load (Fig. 2*C*).

Subjects returned 24 h later for *session 3* to make movements in a lateral field that displaced the hand in a counterclockwise direction. Movements during *session 3* were initially curved consistent with the lateral load (Fig. 3*A*) and straightened over time (Fig. 3*B*). *Session 3* performance was affected by what subjects learned during *session 2*. This effect could be quantified in terms of the angle between the loads experienced during *session 2* and *session 3*. As the difference increased from 0° to 180° we observed effects that ranged from facilitation to interference (Fig. 3*C*). When the directions of load were the same for both *session 2* and *session 3*, facilitation was observed. Initial *session 3* movements were straighter than those of naïve controls ($P < 0.001$). For these subjects, movements at the start of *session 3* were also straighter than those made at the end of *session 2* ($P < 0.05$) indicating that *session 2* learning facilitated *session 3* performance. When the directions of load were opposite for *session 2* and *session 3*, we observed interference. Initial *session 3* movements were worse than naïve controls' ($P < 0.01$). Subjects who trained in an assistive field during *session 2* performed no different from naïve controls in terms of movement curvature during *session*
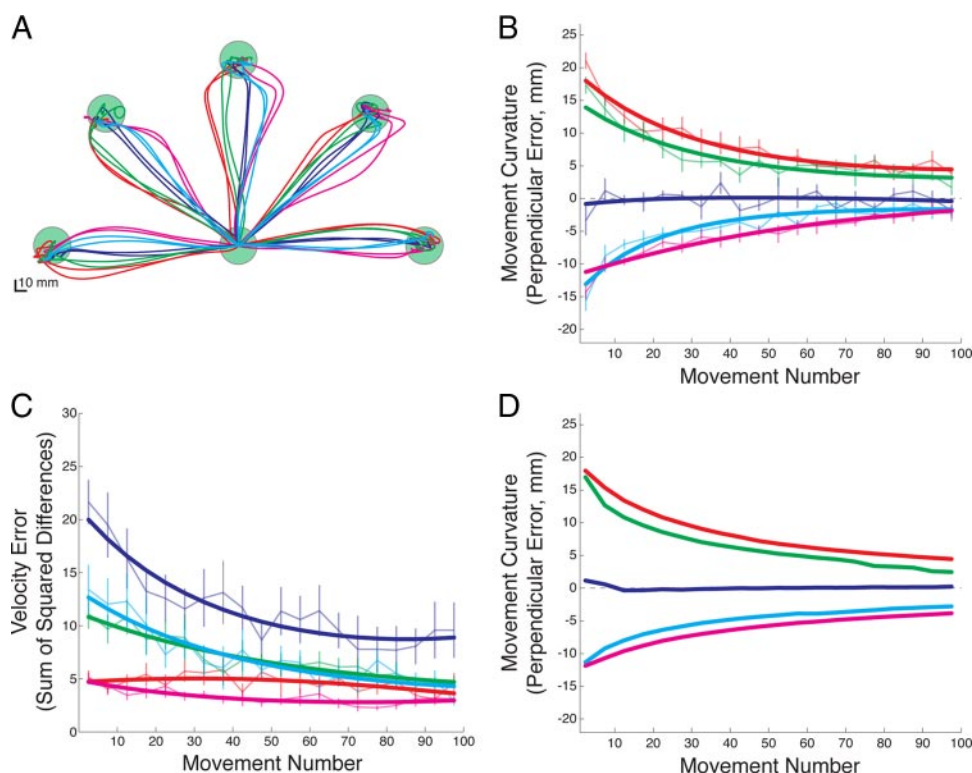

FIG. 2. Empirical and modeled performance for *session 2*. *A*: initial movements made in the 5 fields during *session 2*. For each group, 2 movements representative of the mean curvature for movements 6–25 are shown. Curvature was consistent with the direction of loads applied by the robot. *B*: change in movement curvature over the course of *session 2* training. Movements straightened with training during *session 2*. *C*: change in velocity profiles over the course of *session 2* training. With training, differences between velocity profiles for movements made in force fields and those of movements made in the absence of load decreased. *D*: simulated movements in the 5 force fields were initially curved but straightened as modeled control signals were updated to account for position error (compare with *B*).
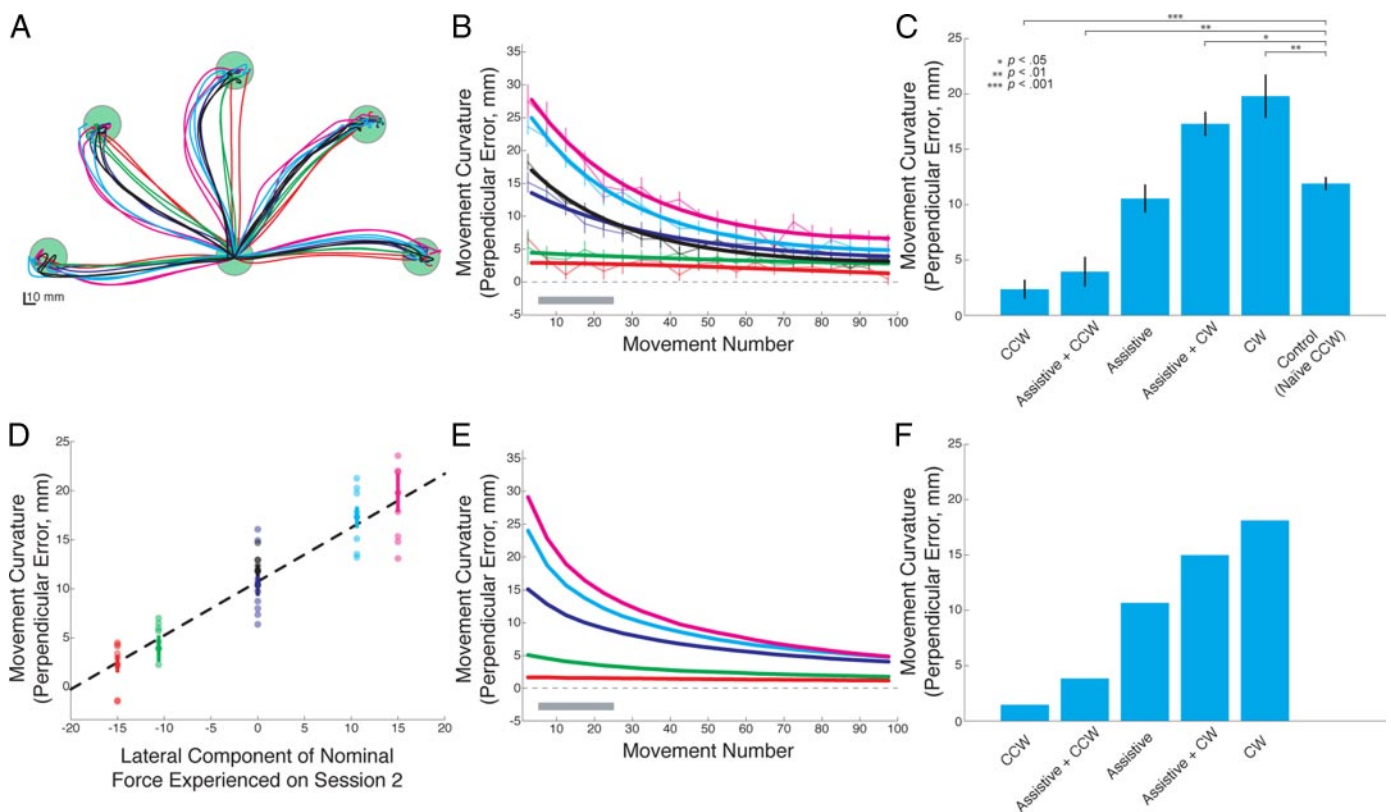
FIG. 3. Performance during *session 3*: effects of *session 2* training ranged from facilitation to interference. *A*: initial movements in a counter-clockwise (CCW) lateral field: Movement curvature depended on the field in which subjects were trained during *session 2*. For each group, 2 movements representative of the mean curvature depicted in *C* are shown. *B*: change in movement curvature over the course of *session 3* training. *C*: initial curvature (average PE for movements 6–25, highlighted by the horizontal gray bar in *B*) differed depending on the field in which subjects trained during *session 2*. Facilitation, interference and effects in between were observed. *D*: regression revealed that *session 3* performance could be predicted on the basis of the lateral loads learned during *session 2*. *E*: simulated movements show a pattern similar to that observed empirically (compare with *B*). The simulations used a weighted average of final *sessions 1* and *2* control signals (20%/80%) as initial movement commands for *session 3*. *F*: initial curvature (PE) for simulated movements 6–25 (highlighted by the horizontal gray bar in *D,* compare with *C*).

3 ($P > 0.05$). This indicates that when learned forces were orthogonal (90°), performance in the lateral direction in *session 3* was unaffected. When the angle between loads for *session 2* and *session 3* was 45° or 135° we saw movement curvature consistent with partial facilitation ($P < 0.01$) and partial interference ($P < 0.05$), respectively (Fig. 3*C*). By the end of *session 3*, all subjects learned the counter-clockwise field such that performance for all groups was no different from that of controls ($P > 0.05$). A regression analysis showed that initial *session 3* performance could be predicted on the basis of the magnitude of lateral load experienced during *session 2* (Fig. 3*D*, $P < 0.001$, 82.5% of variance accounted for).

In a separate analysis, we examined the effects of having previously learned assistive loads on the temporal characteristics of movements one day later. We focused on the duration of the initial segment of *session 3* movements. We found that subjects who trained in an assistive field during *session 2* moved slower than naïve controls over the first 5 movements of *session 3* ($P < 0.05$). This indicates that modifications in the timing of movements that compensate for assistive loads are retained even when the original learning did not alter the spatial profile of the movement.

Subjects returned one month later (*session 4*) to be tested in a clockwise field that pushed the hand laterally in a direction opposite to that in *session 3* (mean 34.3 ± SD 7.2 days). Movements during *session 4* were initially curved in a direc-

tion that was consistent with the clockwise load (Fig. 4*A*) and straightened over the course of training (Fig. 4*B*). The initial movement curvature differed depending on subjects' training history ($P < 0.001$, Fig. 4*C*).

The performance we observed during *session 4* is not consistent with the idea that after consolidation, skills are resistant to modification by new learning (Brashers-Krug et al. 1996; Shadmehr and Brashers-Krug 1997). It is similarly inconsistent with the idea that new learning eliminates earlier learning (Caithness et al. 2004). The evidence that consolidated skills can be modified is that subjects who experienced the same field in both *session 2* and *session 4* showed no benefit from their *session 2* learning (and performed no differently than naïve subjects ($P > 0.05$) when tested in *session 4* in a clockwise field). The evidence that new learning does not simply displace earlier learning is that even though all subjects adapted to the same field during *session 3*, they performed differently when tested in *session 4*. The differences observed during *session 4* reflect subjects' original *session 2* training (*posthoc* comparisons are summarized in Fig. 4*C*). Taken together, our results suggest that neither of the individual previous training sessions could account for the performance we observed, but instead that both prior training sessions were important one month later.

We tested whether the adaptation rate was affected by the direction of movement. We found no systematic effects of
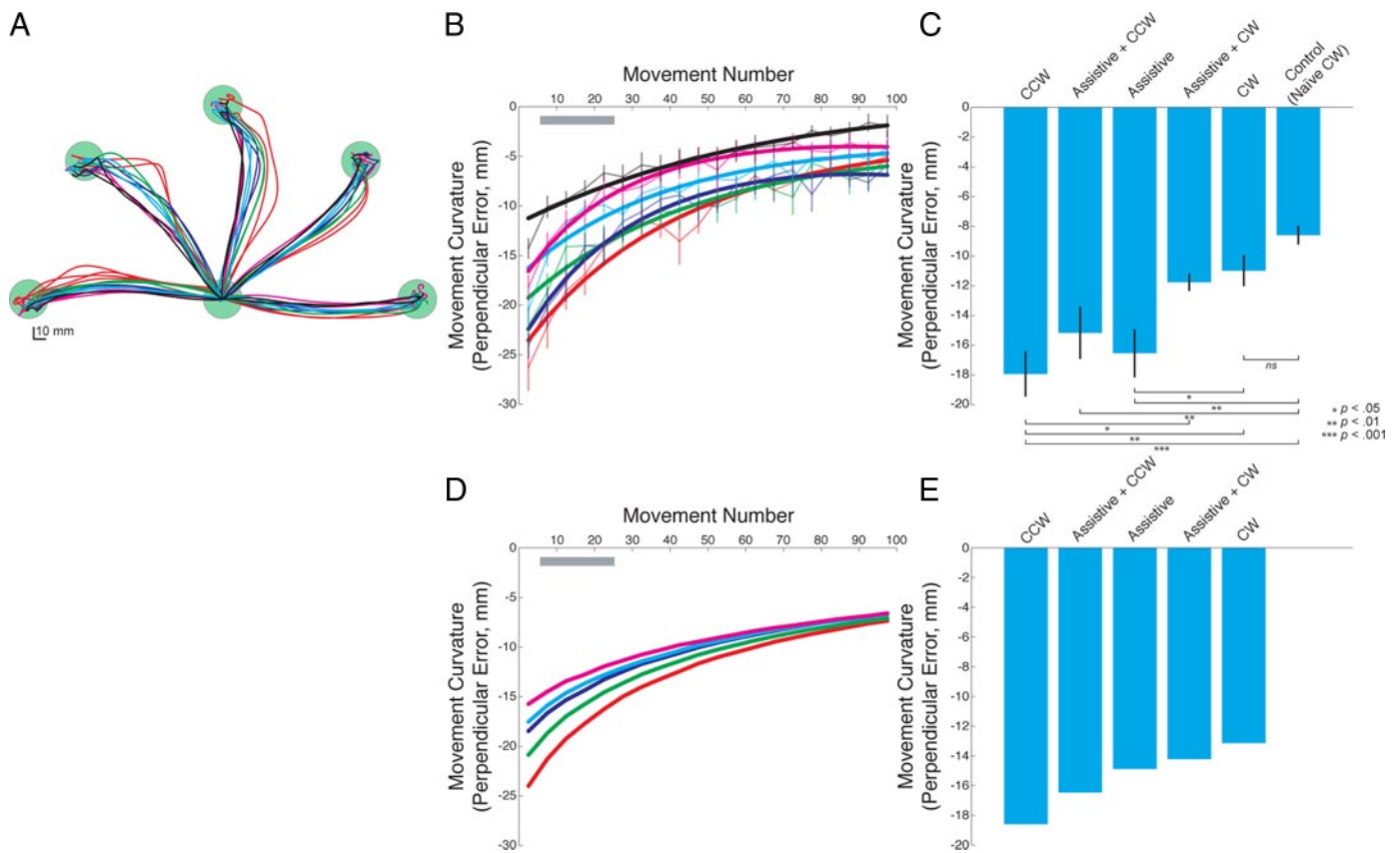
FIG. 4. *Session 4* performance reflects both *sessions 2* and *3* learning. *A*: initial movements in a clockwise (CW) lateral field. For each group, 2 movements representative of the mean curvature depicted in *C* are shown. *B*: change in movement curvature over the course of *session 4* training. *C*: initial curvature (average PE for movements 6–25, highlighted by the horizontal gray bar in *B*) differed depending on training history. *D*: simulations in which initial *session 4* commands were an equally weighted average (50%/50%) of the final *sessions 2* and *3* control signals (compare with B). *E*: initial curvature (PE) for simulated movements 6–25 (highlighted by the horizontal gray bar in *D,* compare with *C*).

movement direction on rate of learning. Out of 20 possible combinations (5 force field directions X 4 sessions), only 3 showed a dependence of adaptation rate on movement direction ($P < 0.05$).

We designed a second experiment that directly tested the idea that performance reflects a combination of prior skill learning. In this experiment we randomly varied each subject's training history and assessed the effects on later performance. The study involved an initial familiarization session, two subsequent training sessions separated by 24-hours and a final test session. For each of the two training sessions (*session 2* and *session 3*) the training field was selected randomly from the five shown in Fig. 1*B*, resulting in 25 possible training sequences. During *session 4*, subjects were tested in a field that perturbed the hand laterally in the clockwise direction. Two separate experiments followed this basic procedure, with either a 2-day or 10-day delay between the training sessions and final *session 4* testing.

Subjects' training histories (*session 2* and *session 3* learning) strongly influenced initial performance in the final test session (Fig. 5*A*, $P < 0.001$ for both the 2-day and 10-day delays, 91.1% and 80.4% of variance accounted for, respectively). *Session 4* performance could be predicted on the basis of both *session 2* ($P < 0.001$, $P < 0.05$ for the 2-day and 10-day delays) and *session 3* ($P < 0.001$ for both delays) training. *Session 3* training had a stronger influence on *session 4* performance, but its relative effect decreased ($P < 0.01$ using

bootstrap tests) as the interval between the training and testing sessions grew from 2 days to 10 days (Fig. 5*B*). Representations of skill thus involve a weighted average of past training that changes over time.

Computational modeling of neural averaging in motor learning

We carried out simulation studies using a computer model of two-joint arm movement and our results were consistent with the idea that performance reflects a weighted combination of past training. Control signals in the model were updated on a trial-by-trial basis based on the difference between the desired and actual trajectory on the most recent movement trial (Gribble and Ostry 2000). This iterative adjustment of modeled neural commands permits compensation for externally applied loads.

In the simulation studies the model was trained over four successive "sessions" to mirror the experimental manipulation. For the initial training session (simulated *session 1*), we modeled movements in the absence of external load. This resulted in modeled control signals that produced straight movements to each of the five targets and effectively compensated for the mechanical behavior of the two-joint arm.

To simulate *session 2*, we modeled movements in the presence of each of the five fields depicted in Fig. 1*B*, using the final *session 1* control signals as initial commands for *session 2*. Like in *session 2* of our experiment, the five fields resulted
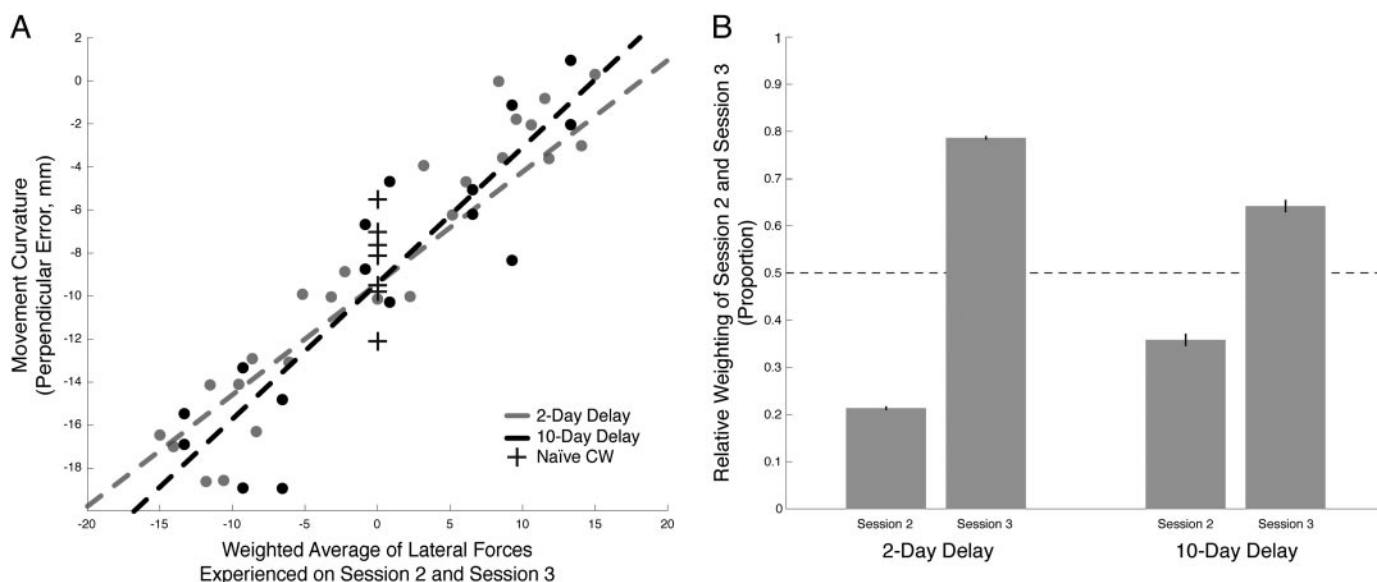
FIG. 5. Motor learning reflects a weighted combination of previous training. *A*: for both 2- and 10-day delays, regression showed that *session 4* performance depended on a weighted average of the lateral loads learned during *session 2* and *session 3*. *B*: as the delay between training and testing increased from 2- to 10-days, the relative influence that *session 2* and *session 3* training had on *session 4* performance shifted toward equivalence. Bars depict the relative influence of each session (mean ± SE, derived from bootstrap tests).

in movements whose curvature was consistent with the externally applied load. As control signals were updated on the basis of position error this curvature was eliminated as it was in our experimental subjects (compare Figs. 2*B* and 2*D*). Velocity profiles were also altered by the presence of load but returned to normal with training. The iterative procedure resulted in five different sets of modeled control signals (one for each movement direction in each field) that reflected learning at the end of simulated *session 2*.

For *session 3*, we modeled movements in a lateral field that pushed the hand in a counter-clockwise direction. Initial performance during *session 3* depended on what the model learned previously. By using a weighted vector average of the final *session 1* and *session 2* control signals (20% *session 1* and 80% *session 2*) as initial *session 3* commands we observed effects that were similar to those obtained empirically during *session 3* of the experiment (compare Figs. 3*B* and 3*E*, 3*C* and 3*F*).

Session 4 simulations involved movements in a field that pushed the hand laterally in a clockwise direction. We used a weighted vector average of the control signals generated during *session 2* and *session 3* (50% *session 2*, 50% *session 3*) as initial commands for *session 4* (see following text). We found that the model produced a pattern of performance similar to that observed empirically during *session 4* (compare Fig. 4*B* and 4*D*, 4*C* and 4*E*). This suggests that the training history affected *session 4* performance and skills reflect weighted combinations of the control signals learned on previous training episodes.

Figure 6 shows that a weighted average of *session 2* and *session 3* control signals best accounts for the pattern of performance observed empirically. When the final control signals from *session 2* alone (Fig. 6*A*) or *session 3* alone (Fig. 6*C*) were used as initial commands for *session 4*, performance was not well simulated. Instead, error between actual and simulated *session 4* performance was minimized (Fig. 6*D*) when initial control signals comprised an equally weighted

combination of final *session 2* and *session 3* commands (Fig. 6*B*).

DISCUSSION

Here we have shown that motor performance is affected by previous learning, which can produce effects that range from facilitation to interference. Consolidated skills do not appear to be resistant to change nor are they entirely replaced by new learning. Instead performance reflects a combination of prior learning. These combinations are not fixed but rather change over time in a fashion consistent with the idea that relative recency weights the influence of prior training sessions. Modeling studies suggest that the neural basis for performance is a weighted combination of the control signals learned during prior training episodes.

Much recent research on learning and memory has focused on the idea that after recall, memories are labile and subject to displacement. Reactivated memories can be displaced by interfering events such as disruption of cellular protein synthesis (Kleim et al. 2003; Nader et al. 2000) and also appear to be displaced by new learning (Caithness et al. 2004; Walker et al. 2003). The present studies point to a further possibility, that original learning is not replaced by new learning but rather that old and new learning are combined at a neural level and that subsequent performance is mediated by this neural average. Consistent with this idea, when subjects complete multiple training episodes, one can observe a continuum of effects that range from facilitation to interference. When training episodes repeat the same sensorimotor mapping, the two training sessions facilitate each other. When training episodes involve opposite sensorimotor mappings, interference results and on later testing performance is no different from naïve. In between these extremes, training sessions produce a range of effects on one another from partially facilitating to partially interfering. Thus when a range of sensorimotor mappings is examined, a gradation of effects results that is not consistent with the idea
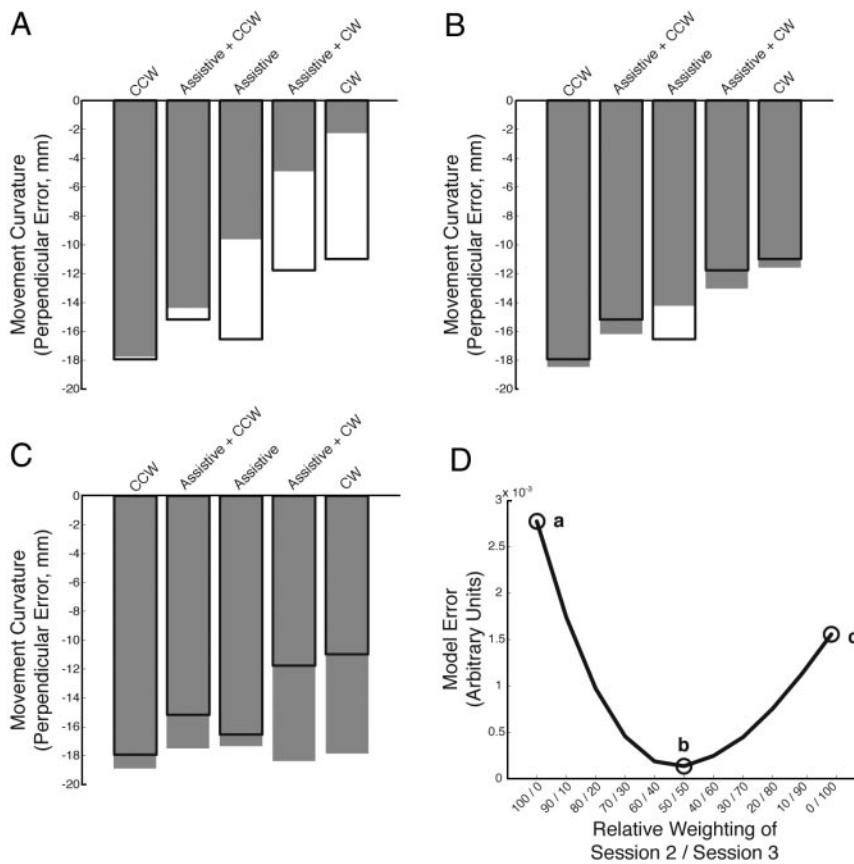
FIG. 6. A combination of *session 2* and *session 3* control signals provide the best simulation of *session 4* performance. *A*: predicted *session 4* movement curvature when initial commands comprised final *session 2* control signals. Black outlines show empirical *session 4* performance (as in panels *B* and *C*). *B*: predicted movement curvature when initial commands were an equal combination of final *session 2* and *session 3* control signals. *C*: predicted curvature when initial commands comprised final *session 3* control signals. *D*: error between empirical and simulated *session 4* performance was minimized by using an equal weighting of *session 2* and *session 3* control signals as initial values on *session 4*. *Session 4* performance associated with small letters a–c is shown in panels *A–C*.

that new learning simply displaces old. Rather it suggests that the neural substrate of skill is a combination of previous training.

Recent studies have also shown that consolidation does not permanently fix learning within the brain. Studies have shown that during periods of sleep after training, skills improve (Walker et al. 2002) and neural activation patterns shift location (Walker et al. 2005). These studies highlight that there is substantial "off-line" processing of learning after consolidation. Here we report a complementary result. As the delay between the end of training and final performance increases, the relative influence of each training session on final performance shifts toward equivalence. These changes in relative weighting suggest that the neural substrate of skill can change after consolidation of learning.

A number of studies have reported that subjects can learn two different fields simultaneously and independently access both encodings. This has been observed after extensive training (Krouchev and Kalaska 2003) or when each field is tied to a particular posture (Gandolfo et al. 1996) or other contextual cues (Osu et al. 2004) [note, however, that in some cases these arbitrary cues are insufficient (Gandolfo et al. 1996)]. Other cues, such as temporal separation, are not useful (Karniel and Mussa-Ivaldi 2002). Here we have shown that subjects do not have separate access to the learning associated with individual training sessions even when the fields involved orthogonal mappings between state of the limb and perturbing force. Instead, later performance was affected by a weighted combination of past learning. The situations in which the nervous system can separately access prior learning seem to involve

information beyond the different forces each field involves. Perhaps, by engaging processing elements related to more cognitive or conceptual abilities, these cues allow the nervous system to categorize new learning as a component of one skill without affecting others.

Our modeling studies produced results that closely matched the performance of experimental subjects. For *session 4,* the best match was produced when the rate of adaptation was slower and muscle co-contraction was elevated relative to the previous three sessions. Although the source of this effect is unclear, previous research has shown that when subjects encounter environments the mechanical properties of which vary, they respond by elevating limb impedance (Takahashi et al. 2001). In the present study, it is possible that having learned different force fields on *sessions 2* and *3* may have resulted in increased limb stiffness on *session 4*. At the same time, it should be emphasized that the overall pattern of results in our modeling studies is not dependent on the particular values for co-contraction and learning rate. As noted in the preceding text, we found similar results in a set of simulations in which these parameters were held constant.

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