Lack of Adaptation to Random Conflicting Force Fields of Variable Magnitude

Rahul Gupta1,2 and James Ashe1,2,3

1Brain Sciences Center, Veterans Affairs Medical Center, Minneapolis; and 2Graduate Program in Biomedical Engineering and 3Departments of Neuroscience and Neurology, University of Minnesota, Minneapolis, Minnesota

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Gupta R, Ashe J. Lack of adaptation to random conflicting force fields of variable magnitude. J Neurophysiol 97: 738–745, 2007. First published November 8, 2006; doi:10.1152/jn.00773.2006. The concept of internal models has been used to explain how the brain learns and stores a variety of motor behaviors. A large body of work has shown that conflicting internal models could not be learned simultaneously; this suggests either a limited capacity or the unstable nature of short-term motor memories. However, it has been recently shown that multiple conflicting internal models of motor behavior could be acquired simultaneously if associated with appropriate contextual cues and random presentations. We re-examined this issue in a more complex environment in which the magnitude of the conflicting fields could vary randomly. Human subjects failed to show any evidence of learning the force fields themselves or the magnitude of the forces experienced, even with extended practice. Subjects did adapt to the applied perturbation when the field strength was kept constant but still did not form internal models. Our results show that neither random presentation nor specific contextual cues are sufficient for learning conflicting internal models when the magnitude of the forces is also unpredictable. The data suggest that multiple conflicting internal models cannot be learned in all environments, and provide support for the unstable nature or limited capacity of motor memories.

INTRODUCTION

Humans and other animals have the ability to learn a great variety of skilled movements and to perform them in many different environments. It is thought that the brain maintains a representation of each of these behaviors in the form of an internal model (Flanagan and Wing 1997; Jordan and Rumelhart 1992; Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi 1994; Wolpert et al. 1995), which is used to predict the effects of an object or a particular environment on the body and to calculate the motor output required to perform desired actions. The way in which internal models of different environments are acquired has been used to study the characteristics and capacities of motor memory.

Subjects readily learn to operate in new mechanical (Shadmehr and Mussa-Ivaldi 1994) or kinematic (Flanagan and Rao 1995; Krakauer et al. 1999) environments. However, simultaneous exposure to opposite or conflicting force fields (Brashears-Krug et al. 1996; Caithness et al. 2004; Kram et al. 1999; Krakauer et al. 2000, 2005; Tong et al. 2002; Wigmore et al. 2002; see Bock et al. 2003, for a different perspective) often interferes with the learning process. Interference has been observed both when the fields were alternated trial by trial or presented in alternating blocks. It is generally believed that the interference observed after exposure to opposite force fields in close temporal proximity is due to disruption in the consolidation of the short-term motor memory (but see Caithness et al. 2004).

This view has been recently challenged by demonstrating that simultaneous learning of conflicting viscous force fields is possible if these fields are presented randomly and appropriate contextual cues are provided (Osu et al. 2004; Wada et al. 2003). To explain this intriguing result, the authors of these studies proposed that the subjects formed two internal models simultaneously and were able to switch between them using the available contextual cues, in accordance with the MOSAIC model (Haruno et al. 2001; Wolpert and Kawato 1998). The MOSAIC model proposes that, during motor adaptation, many controllers (inverse models) can be simultaneously selected and learned. Before performing a task, the a priori information available from the extrinsic contextual cues guides the selection of the appropriate controller and thus facilitates rapid and effective switching.

This finding raised the question whether such simultaneous context-based learning of conflicting environments could be applied to other more general situations as well. One important generalization would be to uncertain environments in which the forces vary randomly in magnitude (Scheidt et al. 2001; Takahashi et al. 2001) as well as direction. Based on these earlier results, we reasoned that given sufficient practice and appropriate contextual cues, subjects should be able to adapt to a combined environment comprising two randomly switching identical distributions of field strengths, one generating clockwise (CW) and the other generating counter-clockwise (CCW) forces. Specifically, they would be expected to compensate for a perturbation close to the mean value of the applied environment (Scheidt et al. 2001; Takahashi et al. 2001). Our results, discussed in the following text, demonstrate that human subjects were not able to form internal models of such an unpredictable and conflicting environment.

METHODS

Twenty-two right-handed human subjects (20–36 yr) participated in one of three experiments after providing informed consent. The study protocol was approved by the local Institutional Review Board.

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Overview of experiments

The experiments involved subjects performing reaching movements in a single direction against perpendicular velocity-dependent forces that pushed either to the right or to the left, were randomly switched and were cued by two different colors. For the first two experiments, the magnitude of the field strength was stochastic from trial to trial. Experiment 1 was performed over 1 day, whereas subjects in experiment 2 performed the task over two consecutive days to allow them more practice with the fields. Experiment 3 was also performed over 2 days, but in this case, the magnitude of the field strength was fixed to control for the trial-to-trial stochastic variation in the force magnitude.

Experimental setup

For all experiments, subjects sat in a chair holding the handle of a two-joint, planar robotic manipulandum (Interactive Motion Technologies, Cambridge, MA) and executed timed reaching movements in the horizontal plane. A vertical LCD monitor in front of the subjects displayed “start” and “end” target circles, both of 3 cm diameter, and a 1.5 cm-diameter cursor representing the hand (equivalent to the robot endpoint) position; the hand and the arm were visible throughout the experiment. The reach was a 15 cm movement and corresponded to an upward motion of the cursor on the screen and a movement of the subjects’ hand away from the body in a para-sagittal plane. Subjects were asked to position themselves so as to approximately align the forward movement with the axis of the shoulder joint. However, their posture and position were not constrained in any way.

On most trials, the robotic device produced forces on the subjects’ hand (see following text for details). The forces were applied only during the outward movement from the start to the end target, and subjects were allowed to return to the start circle whenever they chose (the start circle was visible at all times). A trial began when the subject positioned the cursor completely within the start circle. On force trials in all three experiments, a colored rectangular frame was displayed around the workspace on the monitor at the beginning of the trial, as a contextual cue. For experiment 1, the frame was blue for rightward forces and red for leftward forces (vice versa for the other 2 experiments). For the initial “null trials” in the absence of forces, a cue was irrelevant and was therefore not provided. After the cue was displayed for 300 ms, the end target came on following a random delay of 200–500 ms. Subjects were instructed to wait for the target to come on and then make point-to-point reaching movements that were “as straight and smooth as possible” and to “stop and hold at the target.” During force trials, the forces were applied once the subject crossed a circular window that was 1.5 times the radius of the start circle and concentric with it (except in experiment 3; see following text). The movement was required to be completed within 400–700 ms; this relatively large time window was used because of the wide variation in the magnitudes of the field strengths that were used. A trial was complete after a target hold time (700 ms). At the end of each trial, feedback was provided regarding the movement timing: the target turned red if the movement was too slow, turned green if it was too fast, and turned black if subjects did not stop and hold at the target for the required time. After that, the trajectory of the movement was shown as feedback to the subjects for 300 ms.

Incorrect movements were classified into four types: limit errors, when the subjects’ hand strayed outside a virtual boundary in the workspace (the extent of the virtual boundary was the same as the movement amplitude in the direction of the movement and 1.5 times the movement amplitude in the direction perpendicular to the movement); fast and slow errors, when the movement was <400 ms and >700 ms respectively; and target hold errors, when the subject did not stop and hold at the target for the required time.

Experiment 1

Six subjects (1 male, 5 females) participated in experiment 1. The experiment consisted of 27 blocks of 20 trials each performed in a single session. A break of 12 s was provided after each block.

Subjects started with a block of reaching movements under full on-line visual feedback, in the absence of forces (the null field), to get them acquainted with the apparatus. This was followed by another block without the forces but now without on-line visual feedback of the cursor on the display monitor. This was accomplished by blanking out the cursor when a window, of radius 1.5 times the radius of the start circle, was crossed. After these two blocks in the null field, subjects were asked to perform 25 blocks in the presence of forces without real-time visual feedback of the cursor (similar to the 2nd block). The real-time feedback of the cursor was suppressed to avoid on-line error corrections during the movement.

The forces were generated by two torques motors acting on the handle of the robotic arm, which the subjects held with their right hand. The forces were proportional to the hand velocity and directed perpendicular to the desired direction of motion; i.e., the forces tended to perturb the subject’s hand either to the left (left-directed force field, LF) or to the right (right-directed force field, RF). The force fields can be expressed as

\[ F_x = b \times y; \quad F_y = 0 \]  

where \( y \) represents the \( y \) component of the hand velocity, \( F_x \) and \( F_y \) are the \( x \) and \( y \) components of the force, and \( b \) is the gain coefficient. This gain coefficient was picked at the beginning of each trial, randomly (i.e., with a probability of 0.5) from either of two Gaussian distributions of identical variance (22 N²/m²/s²) and respective means +15 and −15 N/m/s. The gain coefficients were selected before each trial without any sort of constraint (on number or order). As a consequence, the sequence of coefficients was different for individual subjects (in contrast, for example, with Scheidt et al. 2001).

Experiment 2

In experiment 2, six subjects (5 males, 1 female) performed exactly the same task as in experiment 1 with the addition of a second session of 25 force blocks on the following day (a separation of ~24 h). This was followed by two more blocks in which the forces were not applied on certain trials (catch trials), randomly chosen with a probability of 0.25. The catch trials were never allowed to occur consecutively, irrespective of whether a trial was completed correctly or not, to ensure that they maintained the quality of surprise. Furthermore, for the catch trials, the cues were presented as for the force trials so that the subjects could not predict their occurrence. One subject (male) showed hand-path deviations in only one direction (for both the left- and right-directed forces) and was excluded from further analyses.

Experiment 3

Ten subjects (7 females, 3 males) participated in a third experiment, which had the same structure as the second one with two main differences. First, the magnitudes of the gain coefficients were kept fixed at one of three different levels (16, 20 and 23 N/m/s) for individual subjects instead of selecting from Gaussian distributions (the direction of the force was still random), and second, the forces were turned on when the subject entered the center circle, instead of waiting till the subject exited the center as in the previous experiments. Because the forces are proportional to the velocity, subjects would not have felt much force until they started their movement. This is in accordance with the usual paradigm to study movements in viscous force fields. Three subjects (2 females, 1 male) were excluded from further analyses: one was not perturbed, one was perturbed in only one direction and the third showed inconsistent behavior.
Data analysis

To assess the performance of the subjects, we calculated an average signed hand-path deviation for each trial by first computing a sample-by-sample difference between the hand trajectory of the subject and the straight line connecting the start to the end target and then averaging it over the movement (Eq. 2). This approach was motivated by several studies that have shown the straight-line path to be the “desired” trajectory of such reaching movements and that the hand-paths of subjects deviate in the direction of the force (Gandolfo et al. 1996; Morasso 1981; Shadmehr and Mussa-Ivaldi 1994).

\[
\text{Signed deviation} = \frac{1}{N_{\text{samples}}} \sum (v_{\text{actual}} - v_{\text{straightline}}) \tag{2}
\]

The coordinate system was such that “up” on the screen and “forward” in the movement plane corresponded to the positive-y axis, whereas “right” on the screen, as well as in the movement plane, was the positive-x axis. For the first two experiments, the start of the movement was taken as the moment the subject exited the window around the center (also when the force turned on), whereas the end of the movement was when the subject touched the end target circle. For experiment 3, the start and end of the movement were determined using a velocity threshold of 4 cm/s (the force was already on then).

To analyze the trend of the deviations over the course of the experiment, we divided the trials in the force blocks into bins of 50. In each such bin, trials performed in RF were separated from those in LF and then pooled over all the subjects in a particular experiment. These were then averaged to calculate the average signed hand-path deviation for the group. For the null trials, one average was calculated for each of the two blocks (of 20 trials each). To analyze the catch trials, we first assigned them to LF or RF according to the color of the cue that was displayed before the trial and then averaged the deviations on these trials over the subjects. We also calculated the average by pooling all the catch trials together, ignoring the color of the cue.

To study the relationship between the hand-path deviation and the applied field strength for the first two experiments, we binned the gain coefficient values in 2 N/m/s bins and calculated the mean deviation in each bin. These were then plotted against the gain coefficients at the bin centers (Fig. 3).

RESULTS

Time course of adaptation

We initially asked a group of six subjects to perform a single session of reaching movements during which their arm was perturbed by two randomly presented conflicting viscous force fields (experiment 1). The gain coefficient was selected randomly at the beginning of each trial from either of two Gaussian distributions (Fig. 1A; see Methods for details). Figure 1B depicts the hand paths of a typical subject from the group during an early (left) and a late force block (right). As expected, the initial trajectories of the subjects deviated in the direction of the forces in both fields. However, the pattern of deviation persisted throughout the experiment so that the hand paths were still curved at the end of the experiment; in fact, for some subjects, the curvature of the trajectory appeared to increase over time. This indicates that the subjects were unable to adapt to the applied forces.

The time course of the average performance across the subjects is plotted in Fig. 2A separately for the left-directed (LF; blue) and the right-directed (RF; red) force fields. It can be seen that, on average, the hand-path deviations did not decrease with practice, confirming that the subjects were not able to adapt to the force fields. The deviations at the end of the experiment (in the last bin of 50 trials, see Methods) were significantly different from zero (P < 0.01; 2-tailed t-test) for all six subjects in RF and four subjects in LF (P > 0.2 for the other 2 subjects, S3 and S5). Further, they were not significantly smaller in magnitude (P > 0.2; 1-tailed t-test) than the deviations at the start (in the first bin of 50 trials) for all subjects in RF and three subjects in LF (P < 0.01 for the other 3 subjects, S3–S5). Subjects seem to have performed, both quantitatively and qualitatively (Fig. 2A), slightly better in LF than RF; this may have been due to possibly greater stability in the posture when the forces pushed their arms inward in LF as against outward in RF (all subjects were right-handed and the desired movement was approximately aligned with the right-shoulder joint).

To test for the possibility that the subjects may not have received sufficient practice on the task, we repeated the experiment with a second group of six subjects who performed two sessions over consecutive days (experiment 2; 1 subject was excluded from further analyses, see Methods). Figure 1C shows the trajectories from a representative subject early on (left) and toward the end (right) of the experiment. Trajectories remained curved even after extended practice, as was the case for experiment 1. The average performance of the subjects is plotted in Fig. 2B for both days. Again, there is no evidence of adaptation; in fact the deviations seem to have increased in magnitude over the course of the experiment, indicating that the extra day of practice did not help. The deviation at the end of the experiment (in the last bin of 50 trials) was again significantly different from zero (P < 0.001) for all five subjects in RF and three subjects in LF (P < 0.001 for 2, P = 0.01 for the third; for the other 2 subjects, S3 and S5, P > 0.1) and not significantly smaller in magnitude than the deviation at the start (P > 0.5) for all subjects in RF and two subjects in LF (for the other 3, P < 0.005 for S3–S5). Subjects in this experiment also fared better in LF than in RF. A comparison of the deviations at the start of day 1 with those at the start of day 2 showed that the average deviation at the start of day 2 was not significantly smaller (P > 0.4; t-test) for all subjects in RF and three subjects in LF (P > 0.9 for 2, P = 0.044 for the third; P < 0.01 for the rest).

The points on the far right in Fig. 2B show the average deviation on the catch trials. The points shown in red and blue were calculated by separating trials on the basis of the color of the cue provided (which would indicate the expected direction of the force) and then taking averages. The point in black was calculated by pooling all the catch trials together irrespective of the cue. There is clearly no aftereffect for RF (red), and the one for LF (blue) is not significantly different from zero (P = 0.1142, 2-tailed t-test).

We found similar results using as error measure the deviation at peak y-velocity, normalized by the velocity. Further, to consider only the feed forward component of the movement, we calculated the signed hand-path deviation using only the first 250 ms of the movement and found similar results.

Variation of hand-path deviations with the applied forces

Having not found any signs of adaptation to the force fields, we wondered if there was any pattern in the variation of the deviations with force magnitude, which was proportional to the gain coefficient. As expected, the hand-path deviation varied...
almost linearly with the gain, both in LF and RF, with higher forces producing proportionally higher deviations (Fig. 3). A simple linear regression of the deviations on the gain coefficients (LF and RF combined) yielded a $R^2$ between 0.65 and 0.83 for experiment 2 (mean $/H11006 SD$: 0.75 $/H11006 0.07$, $n=5$). For experiment 1, the corresponding range was $[0.38, 0.87]$ ($0.65$ $/H11006 0.19$, $n=6$). To estimate the value of the field strength that was “best compensated for,” we calculated the gain coefficient at which the deviation was equal to the baseline control (calculated from the 2 null blocks at the start of the experiment). This was found to be inconsistent among the subjects and, in particular, was not always close to the mean. Specifically, we first compared the baseline-crossing gain coefficient of each individual subject with the mean value of the gain x−position ($m$) x−position ($m$) −0.1 −0.05 0 0.05 0.1 −0.1 −0.05 0 0.05 0.1 y−position ($m$) Block 4 y−position ($m$) Block 27 y−position ($m$) Block 4 y−position ($m$) Block 52 B and C: plots of hand trajectories of a typical subject in experiments 1 (B, top) and 2 (C, bottom) for the 2nd block (20 trials) in the force-field (left) and the last block in the force field (right). Trials in left-directed force fields (LF) are shown in blue, whereas those in right-directed force fields (RF) are in red. It can be seen that, for both subjects, the hand paths deviate in the direction of the forces when the fields are introduced and remain perturbed even after extensive practice.

FIG. 1. Gain coefficients and hand-paths. A: histogram plot of the gain coefficients used in experiments 1 (left) and 2 (right). There was no overlap between the right- and left-centered distributions. The range of gain coefficients for experiment 1 was: $+ve: [1.4177, 28.7084]$; $−ve: [−28.9020, −1.2372]$. For experiment 2, the range was: $+ve: [1.0764, 28.7678]$; $−ve: [−28.7091, −1.2534]$. B and C: plots of hand trajectories of a typical subject in experiments 1 (B, top) and 2 (C, bottom) for the 2nd block (20 trials) in the force-field (left) and the last block in the force field (right). Trials in left-directed force fields (LF) are shown in blue, whereas those in right-directed force fields (RF) are in red. It can be seen that, for both subjects, the hand paths deviate in the direction of the forces when the fields are introduced and remain perturbed even after extensive practice.

FIG. 2. Average performance of the subjects. The time course of the average signed hand-path deviations ($m$) $±$ SE is plotted against trial bins for subjects in experiments 1 (A) and 2 (B); null trials (green), rightward deflecting force field (RF; red) and leftward deflecting force field (LF; blue). See METHODS on details of how the averages were calculated. For experiment 2, the left curves represent the performance on day 1, while the right curves are for day 2. Regular trials in the last 2 blocks that contained random catch trials (“catch blocks”) have been omitted in these calculations. It can be seen that the deviation does not decrease with time and, in fact, increases for experiment 2. The points on the far right of the plot for experiment 2 show the average $±$ SE deviation ($m$) of the catch trials (see METHODS); the ones in red and blue are for the trials on which the cue indicated a RF and a LF, respectively, whereas the black point is the average over all the catch trials, irrespective of the cue.
over the subjects were 3.64.

Experiment 2 and one in experiment 1 came close to the means. The averages over the subjects were $3.64 \pm 4.08 \text{ N/m/s (n} = 5\text{) for experiment 2 and } -10.7 \pm 8.84 \text{ N/m/s (n} = 6\text{) for experiment 1.}

Finally, we repeated the preceding analyses using the gain coefficient values at which the deviation was equal to zero, rather than the baseline for each subject, and found similar results.

Another independent measure of performance

One might argue that the force distribution may have been a little too complex, making the task too difficult for the subjects. This may, then, explain the lack of improvement we noted in the performance of the subjects. To test this, for the second experiment we used an additional independent measure of performance—the number of incorrect movements that a subject makes during the course of the task. Figure 4 plots the number of four different types of incorrect movements (see METHODS) averaged over the six subjects. It can be seen that the numbers progressively decline during the course of a single day as well as for the overall experiment. A peak is observed at the start of the second day, but the magnitude of this peak is substantially lower than that at the start of day 1. Indeed, for all the subjects pooled together, the proportion of incorrect movements in the first two blocks of day 1 was significantly greater than that in the first two blocks on day 2 (difference of proportion test, $z = 7.0824, P < 0.0001$), indicating that there was a consolidation of whatever the subjects learned on day 1.

This figure thus indicates that although the hand-path deviation of the subjects did not decrease with time, the number of incorrect movements certainly did. Therefore we can safely conclude that the subjects could perform the task satisfactorily under the conditions and in fact improved in some aspects of their performance. Thus we have shown that the subjects were unable to form internal models of either the individual force distributions or of the combined distribution over a learning
period in which internal model acquisition has typically been observed. However, they did learn some aspects of the task in that they demonstrated a reduction in the number of incorrect movements as the task progressed.

Role of variation in force magnitude

Even though we have shown that subjects were unable to adapt to the conflicting force fields that had both unpredictable direction and magnitude, it was not completely clear what may have been the factor that prevented learning. Because an important novel aspect of our task was the random variation in force magnitude, to isolate its effect, we repeated experiment 2 with the modification that the gain coefficients were of fixed magnitude instead of being selected from a Gaussian distribution. Figure 5 shows the time course of the signed hand-path deviations averaged over seven subjects. Modest “adaptation” seems to have occurred in that the hand-path deviation decreased with time. However, in general, aftereffects were found to be absent. This suggests that instead of acquiring internal models of the conflicting fields, the subjects may have adopted some other strategy (e.g., stiffening the arm) that enabled them to effectively compensate for the applied perturbation. This appears plausible because adaptation with only one movement direction need not require global adaptation and therefore can be accomplished without learning the force field in its generality.

Discussion

In this experiment, we investigated the role of random presentation and context-based switching in the learning of conflicting dynamic force fields. Our results show that subjects were not able to adapt to force fields of stochastically varying strength via the formation of internal models of the fields themselves or of the overall distribution of force magnitudes. However, they did exhibit an improvement in performance in terms of a reduction in the number of incorrect movements, showing that they did learn some of the task properties. Furthermore, signs of modest adaptation, but not internal model formation, were seen when the strength of the field was kept fixed but allowed to switch randomly in direction.

It has been shown repeatedly in previous studies that exposure to conflicting dynamic force fields in close proximity results in interference, such that no net performance improvement is observed (Brashers-Krug et al. 1996; Caithness et al. 2004; Karniel and Mussa-Ivaldi 2002; Shadmehr and Brashers-Krug 1997). However, subjects do appear to simultaneously learn multiple dynamic fields of similar construction within different state spaces (Fukushi and Ashe 2003). The exact mechanism of the interference seen with conflicting dynamic fields is not clear, but it is generally believed that exposure to a second conflicting field results in retrograde interference leading to disruption of the short-term motor memory associated with the first (Brashers-Krug et al. 1996; Shadmehr and Brashers-Krug 1997) unless sufficient time has elapsed for consolidation of the first field to occur (for another view, see Caithness et al. 2004). Recent work (Osu et al. 2004; Wada et al. 2003), however, has challenged the belief that simultaneous learning of internal models of conflicting force fields is not possible by showing that if the force fields are presented in a random order (vs. a predictable sequence) using appropriate contextual cues in each trial, then learning does appear to occur. The authors explained this as a context-based switching of multiple internal models, although it was not clear what exactly the role of random presentation was and why such context-based switching was not possible under predictable exposure conditions (in alternating trials, for example). Our experiment was designed to test whether their observation could be generalized to more complex dynamic environments in which the conflicting fields could have a variety of different magnitudes, as one might experience in everyday life. Our experimental set-up was, in principle, very similar to that of Osu and colleagues (2004) except for the important difference that we sampled from a distribution of gain coefficients for each field (for the first two experiments), whereas in the task of Osu and colleagues, two fixed coefficients were used to generate the CW and CCW force fields. It has been shown (Scheidt et al. 2001; Takahashi et al. 2001) that subjects tend to learn approximately the mean value of force distributions, if applied only in one direction, both for uni- and bimodal distributions. We wondered if such learning would be observed even when the force distributions are presented simultaneously, randomly in opposite directions, as would be expected if the results of Osu and colleagues were generalizable.

The subjects in our first two experiments failed to show any learning of the conflicting force fields. We also investigated whether the subjects learned the distribution of forces even though they did not acquire an internal model of the fields themselves. Learning of the magnitude could be accomplished in one of two different ways. Subjects might learn the approximate mean of both the “left-centered” and the “right-centered” distribution of gain coefficients. However, if subjects were not able to separate the conflicting force fields, they might treat the distribution of magnitudes to the right and the left as being part of one field in which case they would tend to learn the approximate mean of the combined (bimodal) distribution (theoretically zero). In any case, the hand-path deviation of the subjects in trials in which the learned force strength was applied would be expected to be close to the baseline (control).
deviation (or zero). The baseline-deviation gain values (as well
the zero-deviation values) that we calculated were in general
not found to be close to the appropriate means and thus provide
evidence against either form of magnitude learning on the part
of the subjects.

The efficacy of contextual cues in enabling subjects to
simultaneously adapt to, and predictively switch between,
multiple conflicting environments is a matter of debate. Some
studies have shown that the simultaneous learning of opposite
environments, with appropriate switching (presumably of the
two internal models), is possible if appropriate postural (Gan-
dolfo et al. 1996) or spatial (Rao and Shadmehr 2001) cues are
provided, but not with arbitrary color cues (Gandolfo et al.
1996), even after extensive training (Shadmehr et al. 2005).
Krouchev and Kalaska (2003), however, demonstrated that
switching between opposite viscous fields based only on color
cues is possible if monkeys are recalling a previously learned
task (after extensive practice). One common aspect of the
training schedule in these studies is that they used predictable
sequences of fields, either trial-by-trial switching or alternating
blocked presentation (except Shadmehr et al. 2005, where the
authors presented the cue-field associations in a random order).
In contrast, other studies (Osu et al. 2004; Wada et al. 2003)
demonstrated that switching based entirely on color cues is
possible only if the fields are presented randomly. Our results
show that, for two opposite distributions of field strengths,
switching based only on color cues is not possible, even with
random presentation.

To isolate the significance of the unpredictable variation in
the field strength, we repeated our experiment using fixed gain
coefficients. With only this modification, subjects showed a
decrease in the hand-path deviation over time (Fig. 5), sug-
uggesting that the primary feature that prevented the subjects
from adapting to the forces and improving their performance in
the first two experiments was the randomly varying field
strength. However, the aftereffects in this experiment were not
significant, indicating that, even under the condition of fixed
field strength, subjects were unable to form internal models of
the conflicting dynamic environments. It is possible that the
subjects used impedance control (Franklin et al. 2003; Taka-
hashi et al. 2001) as a strategy for behavioral improvement in
experiment 3, given the fixed field strengths, as opposed to the
other two experiments in which the magnitude of the fields
varied.

Some potential reasons for the discrepancy between our
results and those of Osu et al. (2004) and Wada et al. (2003)
could be the differences in the saliency of the cues and the
number of training days. The color cues we used were dis-
played only for a short time (300 ms) as opposed to 1.5-3.5 s
in Wada et al. (2003) and 2 s in Osu et al. (2004). We chose a
short interval to decrease the total amount of experimental time
for the subjects and thus avoid boredom. However, we believe
that the short cue interval cannot account for our findings. This
is supported by the results of experiment 3 in which subjects
did show adaptation with exactly the same cue structure. As
regards the period of training, although we had more than
1,000 trials in one direction, the training was done over only 2
days, and it might be argued that subjects may be unable to
consolidate complex fields within that time frame. However,
Scheidt et al. (2001), using a very similar experimental setup
to ours except that the perturbation was applied only in one
direction (no conflict), demonstrated the formation of internal
tions despite the fact that they used a lot fewer trials (400
trials for the bimodal distribution, 200 for the unimodal dis-
tribution). Furthermore, subjects in experiment 2, who had an
overnight break that might have been expected to consolidate
their learning, did not fare better than subjects who practiced
for only 1 day (see Fig. 2). Therefore, although we cannot
know for certain whether subjects would develop internal
models of the fields we used if they practiced for several hours
daily over a period of months, we feel confident in claiming
that subjects do not learn the fields using training criteria that
have been used in many other experiments. Perhaps the most
plausible explanation for the discrepancy between our findings
and those of Osu et al. (2004) is that the development of
internal models in their experiment may have been direction
dependent. If one inspects the single-subject data (Fig. 2) in
their experiment, no aftereffects are evident in the single
direction we used in the current experiment. It is possible that
the development of internal models of conflicting fields using
random presentations and contextual cues may be influenced
by limb biomechanics.

Although subjects did not develop internal models, the
amount of exposure they received to the task did enable them
to learn some aspects of the behavior. This is seen in the plots
in Fig. 4, which clearly show an improvement in performance
in terms of a reduction in the number of incorrect movements
as the task progressed. This was observed on both experimental
days. We also observed an increase in the number of errors at
the beginning of the second day, and, interestingly, this number
was significantly smaller than that at the start of the first day.
We interpret the reduction in the number of incorrect move-
ments as indicating that subjects really did learn some aspects
of the behavior although in a different “dimension” from the
one of interest. The formation of an internal model likely
involves a number of interacting processes working simulta-
neously, and it is possible that these different processes follow
different learning dynamics.

In conclusion, human subjects were unable to form internal
models of conflicting dynamic environments that were pre-
sented randomly in the presence of contextual cues, even after
practice on more than a thousand trials. In a generalized
setting, where both the force magnitude and the direction were
unpredictable, subjects showed no signs of being able to adapt
their hand paths, whereas limited adaptation was seen in
exactly the same setup when the field strengths were kept fixed.
However, our data show no evidence supporting the formation
of internal models of the conflicting fields in either condition.
Although it is possible that the amount of practice may not be
sufficient to allow learning, this by itself is not sufficient to
to account for the discrepancies between our findings and those
of Osu et al. (2004) and Wada et al. (2003). Rather, our results
indicate that the effects of random presentation and context-
based switching documented in these latter studies may not
apply to more general settings.

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