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RESEARCH NOTE

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# Does the motor control system use multiple models and context switching to cope with a variable environment?

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**Abstract** Studies of arm movements have shown that subjects learn to compensate predictable mechanical perturbations by developing a representation of the relation between the state of motion of the arm and the perturbing forces. Here, we tested the hypothesis that subjects construct internal representations of two different force fields and switch between them when presented with an alternating sequence of these fields. Our results do not support this hypothesis. Subjects performed reaching movements in four sessions over 4 days. On the 1st day the robotic manipulandum perturbed the movement by perpendicular force that alternated its direction after each movement. Subjects were unable to construct the two underlying models and switch between them. On the 2nd day only one field was applied and well learned. On the 3rd day only the other field was applied and well learned. Then the experiment of the 1st day was repeated on the 4th day. Even after this extensive training subjects showed no signs of improved performance with alternating fields. This result combined with previous studies suggests that the central nervous system has a strong tendency to employ a single internal model when dealing with a sequence of perturbations.

**Keywords** Multiple models · Reaching movement · Force fields · Adaptation · Memory consolidation · Human motor control

## Introduction

Reaching movements are typically performed in a straight line from the initial position of the hand to the target (Morasso 1981). When velocity-dependent perturbing forces are applied, subjects learn to generate compensatory forces and return to a rectilinear path. Moreover, when the perturbation is eliminated unexpectedly, subjects demonstrate erroneous movements, which are called aftereffects.

The concept of an internal model captures the ability of the brain to learn predictable perturbations and generate aftereffects. The notion of multiple models was suggested to describe the ability to adapt to diverse perturbations with different contexts (Wolpert and Kawato 1998; Flanagan et al. 1999; Vetter and Wolpert 2000) and to allow the exploitation of redundancy by performing the same task in different ways under different circumstances (Karniel et al. 2001). The goal of this study is to investigate the hypothesis that the central nervous system can adapt to a sequence of perturbations by developing multiple models and switching between them as required by the context of the sequence.

The movement of the limb can be described as a solution of the following system of ordinary differential equations:

$$D(q,\dot{q},\ddot{q}) = C(\circ) \tag{1}$$

where the operator $D$ represents the force generated by the limb dynamics, the vector $q$ may represent joint angles, and $C(\circ)$ represents the forces generated by the motor control system as it executes a desired movement. The circle in the parentheses indicates that we are uncertain about which variables the controller does actually depend upon.

If the dynamics of the limb are altered by an external force perturbation $E$, the control system has to develop an internal representation of the perturbation $\hat{E}$ in order to recover the planned motion:

$$D(q,\dot{q},\ddot{q}) + E(\dot{q},q,\ddot{q},t) = C(\circ) + \hat{E}(\circ) \tag{2}$$

In previous studies it was shown that the internal representation $\hat{E}$ can be a function of position velocity and acceleration (Shadmehr and Mussa-Ivaldi 1994; Flash and Gurevich 1997; Lackner and Dizio 1998; Sainburg et al. 1999), however it appears that it cannot be an explicit

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function of time (Conditt and Mussa-Ivaldi 1999; Karniel and Mussa-Ivaldi 2001). We expected that the brain would compensate for two alternating force fields by generating two separate models and then switching between them. This would be a particularly simple instance of control based on multiple models (for more general discussion of multiple internal models, see Wolpert and Kawato 1998; Vetter and Wolpert 2000). To test this hypothesis, we asked subjects to perform reaching movements while holding the handle of a robotic manipulandum that generated velocity-dependent forces. The direction of the forces alternated after each movement. Our null hypothesis asserts that the internal model is composed of two models that are alternated after each movement, i.e., that the internal model takes the form:

$$\hat{E}_{MM}(q,\sigma) = \begin{cases} E_1(\dot{q}) & \sigma = +1 \\ E_2(\dot{q}) & \sigma = -1 \end{cases} \tag{3}$$

where σ={+1,–1,+1,–1,...} is a "context variable", alternating after each movement.

Subjects were unable to construct the two underlying models and switch between them. However, one may suggest that if the two fields were learned separately, at an earlier stage, and if consolidation were allowed to take place (Brashers-Krug et al. 1996; Shadmehr and Brashers-Krug 1997), then their internal models could be switched when, in a following session, the fields will be presented in sequence. To test this hypothesis, we developed an extended experiment where each field was applied and well learned separately. Even after this training subjects were not able to counteract the sequence of perturbing fields. This result casts some doubt on the ability of subjects to employ multiple models and/or to switch them according to the context of a sequence.

## Materials and methods

Five subjects, four male and one female ranging in age from 30 to 47 years, participated in this study after giving their written informed consent as stipulated by the University's Institutional Review Board. Each subject performed reaching movements in four sessions of about 50 min on 4 consecutive days according to the detailed description provided below.

### Experimental setup

Seated subjects held the handle of a two-degrees of freedom robotic manipulandum, and looked at a screen that displayed the location of the hand and the location of the target. The movements were performed in the horizontal plane. The robotic manipulandum exerted forces on the subject's hand and measured its trajectory. For further details about the robotic manipulandum, see Shadmehr and Mussa-Ivaldi (1994), Conditt and Mussa-Ivaldi (1999), and Scheidt et al. (2000).

### Experimental protocols

Subjects were asked to execute fast reaching movements to a target displayed on the screen. A small round cursor represented the position of the hand and a rectangular one represented the target. As soon as the cursor reached the target, the target changed color according to the following rules. If the target was reached after 633 ms from its presentation, the rectangle became blue to inform the subject that the movement was too slow, if the target was reached within 533–633 ms, the rectangle exploded (i.e., become gradually bigger over a period of 200 ms), and if the target was reached before 533 ms, the target become red, to inform the subject that the movement was too fast. The subject was instructed to start moving as soon as the target appears and to try to "explode" the targets. The sequence of target locations was randomized. The movement time implicitly instructed by the target display was designed to induce movement durations similar to other related experimental studies (Conditt and Mussa-Ivaldi 1999).

A viscous curl force field was applied as follows:

$$F = \begin{bmatrix} 0 & -15\sigma \\ 15\sigma & 0 \end{bmatrix} V \tag{4}$$

where **F** is the force, **V** is the velocity, and σ⊂{+1,–1}. On the 1st and 4th days the force reversed its direction after each movement. Both fields acted perpendicular to the direction of motion and the magnitude of the forces were proportional to the velocity. The direction (right and left relative to the direction of movement) alternated after each movement. On the 2nd day only one field was applied (σ=–1) and on the 3rd day only the other field was applied (σ=+1).

The experiments included three possible targets, which allowed six possible movements of 10 cm (Fig. 1 *first row*). The set

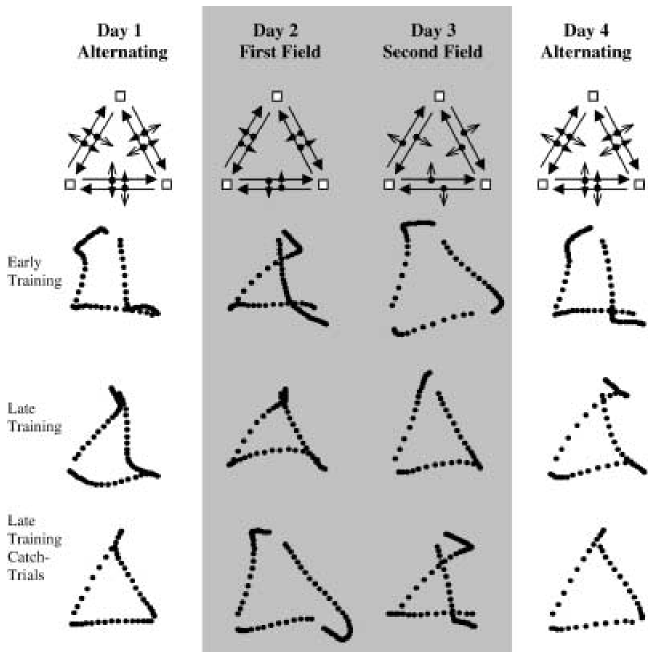


**Fig. 1** The *first row* is a sketch of the three targets, six movements, and forces directions (*small arrows*). Each *column* describes 1 day of the experiment. For each day (*column*) and for three experimental conditions (*row*) the clockwise hand trajectories of one subject are plotted. The *second row* shows the first movement in the early learning part, the *third row* shows the last movements in the late learning part, and the *last row* describes catch trials, i.e., trials where the force was eliminated unexpectedly (last catch trials in the late learning part). The distance between each two targets is 10 cm and the temporal distance between two points is 20 ms. The return to a straight line and the aftereffects at catch trials on the 2nd and 3rd days demonstrates that each perturbation was well learned separately. Still, the combination of the perturbations in a simple predictable sequence was not compensated as predicted by our null multiple model hypothesis, neither on the 1st day nor on the 4th day

**Table 1** The experiment protocol. Each entry in the table describes part of the experiment that was performed continuously; a few minutes rest was allowed between each part. The *number* in each entry is the number of trials and the *letter* represents the type of force: *N* null field, i.e., no force; *R* force to the right, σ=–1; *L* force to the left, σ=+1; *A* left and right alternating after each movement σ={+1,–1,+1,–1,...}. When a force field was applied it was always in the form of Eq. (4)

| | Day 1 | Day 2 | Day 3 | Day 4 |
|---|---|---|---|---|
| Baseline | 118 N, 12A | 118 N, 12R | 118 N, 12L | 118 N, 12A |
| Early training | 156A, 12 N | 156R, 12 N | 156L, 12 N | 156A, 12 N |
| Midtraining | 168A<br>168A | 168R | 168L | 168A<br>168A |
| Late training | 156A, 12 N | 156R, 12 N | 156L, 12 N | 156A, 12 N |

of targets were randomly generated, one set was generated for day 1 and 4, and another for day 2 and 3. The same targets set was presented to all the subjects. The first part of each day was a baseline, where no forces were applied. This part was introduced in the 1st day in order to get the subject acquainted with the manipulandum and the display, and in the rest of the days in order to washout any expectation from the previous day. The subsequent parts were carried out in the presence of a force field. Catch trials (i.e., force field in the first part and null field in the other parts) were introduced in the first two parts and in the last part of each day. It has been demonstrated that catch trials interfere with learning (Thoroughman and Shadmehr 2000). Therefore we excluded each movement that immediately followed a catch trial from the data analysis. Table 1 summarizes the number of movements and the types of force fields that were presented in each day.

## Data analysis

To quantify learning and aftereffects we measured the deviation from a straight-line movement from the initial position to the target position. The direction error (DE) was developed to account for the alternating force direction. The DE was calculated as follows: at the point of maximum velocity, which is well before the influence of corrective movement, the Euclidian distance from the actual position to its projection onto a straight line trajectory was measured. Distance to the left (with respect to the direction of movement) was assigned a positive value and distance to the right was assigned a negative value. This error was multiplied by σ, both for regular trials where σ represents the direction of the applied field (Eq. 4), and for catch trials where it represents the direction of the expected field. Positive DE thus means yielding to the force field (for example, because of under estimation of the force amplitude). Negative DE means over estimation of the force field (in catch trials it indicates an aftereffect).

## Internal models

In the Results section we demonstrate that subjects remember implicitly the error experienced in the previous time that the same movement was performed. In order to account for this “learning attempt”, we fitted the sequence of errors produced by each subject for each of the six types of movements with the following error model (Thoroughman and Shadmehr 2000):

$$\begin{aligned} z_{n+1} &= a \cdot z_n + b \cdot \sigma_n \\ y_n &= z_n + d \cdot \sigma_n \end{aligned} \tag{5}$$

where $y_n$ is the directional error at the *n*th trial, $z_n$ represents the influence of the internal model, and $\sigma_n$ is plus or minus one according to the direction of the applied perturbation (Eq. 4) at the *n*th trial. Due to the non-linear mechanics of the arm, it is not expected that a perturbation to the right would generate an equal deviation with opposite sign to that caused by a similar left perturbation. Therefore we also considered a non-linear output function, i.e., two different values of *d*, one for each force perturbation. Note that the internal model is represented here by the parameter *z*, and therefore this non-linear model is still a single model. According to the multiple models hypothesis, if one assumes that the context is easily recognizable (in this case the simplest possible sequence of two alternating perturbations), one expects the system to generate two internal models. Therefore we also considered the following multiple model:

$$\begin{aligned} &\begin{cases} z1_{n+1} = a1 \cdot z1_n + b1; \quad z2_{n+1} = z2_n \quad if \quad \sigma_n = +1 \\ z2_{n+1} = a2 \cdot z2_n + b2; \quad z1_{n+1} = z1_n \quad if \quad \sigma_n = -1 \end{cases} \\ &y_n = \begin{cases} z1_n + d \quad if \quad \sigma_n = +1 \\ z2_n - d \quad if \quad \sigma_n = -1 \end{cases} \end{aligned} \tag{6}$$

Altogether we report here the fitting of four models: (1) the linear single model (Eq. 5), (2) the non-linear single model, (3) the multiple-model (Eq. 6), and (4) the multiple models with non-linear output function. Since each of the six movements directions were modeled separately, the number of parameters used for the fitting were 18, 24, 30, and 36, respectively. For each subject, for day 1 and 4, the model was fitted to the data of the first part of the midtraining and tested on the data of the second part (and vice versa).

# Results

## No evidence for context switching between multiple models

The main results could be appreciated from Fig. 1, which describes a sample of movements from a single subject. One can see that the subject was unable to compensate for the alternated force fields even after extensive practice and learning of each force field separately. In particular, by comparing movements on day 4 with movements on day 1 one can see that the exposure to the two fields, separately, on days 2 and 3, did not lead to a change in performance with the alternating fields. Figure 2 demonstrates the same results over all the movements and for the five subjects. All subjects showed significant learning and significant aftereffects on days 2 and 3. In contrast, on days 1 and 4, either minor or not significant changes were observed without any consistent pattern of aftereffects. These results clearly contradict our expectation, based on the multiple models hypothesis, that subjects would switch two internal representations according to the sequence context so as to improve performance with alternating fields. In the rest of the Results section we describe an analysis of the time series of the errors, and present evidence for a learning attempt by the subjects. Since our results (Figs. 1, 2) in-

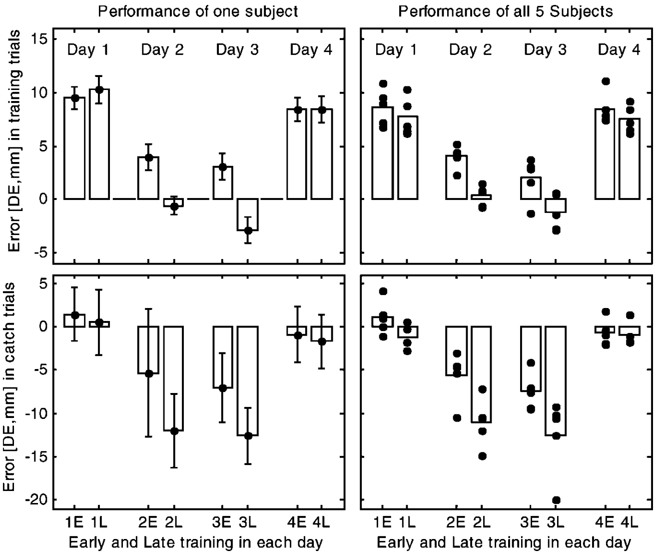


**Fig. 2** The directional error at the early and late learning of each day in training trials (*upper figures*) and in catch trials (*bottom*). The mean directional errors and 95% confidence interval of one subject appear on the *left side*. On the *right side*, each *bar* is the mean error of all subjects and each *dot* is the mean error of one subject. The directional error is a measure of distance from a straight line. A negative value of the directional error in the catch trials indicates an internal representation of the force perturbation. Such representation is evidence for each perturbation separately on the 2nd and 3rd day but is not apparent on the 1st and the 4th days where a multiple model is required in order to represent the external perturbation

dicate lack of successful implementation of multiple models, we suspect that a single model underlies this learning attempt.

### A single model can explain the "learning attempt" in the data

The influence of the previous movement was observed by Thoroughman and Shadmehr (2000) and by Scheidt et al. (2001). In the sequence of alternating force fields, the previous movement was always performed with the opposite force perturbation, however the previous performance of a movement from the same initial and target positions could occur with the same force perturbation (if the number of movements between the last similar movement was odd). We compared the directional error of trials where the previous perturbation was equal to the current, to the error of trials where the previous perturbation was different from the current trial. All the subjects demonstrated smaller mean error for the trials that were performed under the same force field as the previous movement between the same targets (see Table 2). This result indicates the existence of "learning attempt" of some internal model, for example in the form of Eq. (5).

A comparison of the four different models (see Materials and methods) indicates that a parsimonious single model can explain the data. The root mean square (RMS) errors over the fitting data set for the four models were 6.6, 4.9, 5.5, and 5.3 mm, respectively. The generalization RMS errors for the four models were 6.9, 5.7, 6.1, and 6.0 mm, respectively. There was large variance in the fitting (95% confidence intervals were in the order of 1 mm), which suggests that further experiments and analysis are required to establish the detailed structure of the internal representation [for example, one could also consider interference between movement directions as in Thoroughman and Shadmehr (2000)]. Nevertheless, even in this simple analysis we observed that for each subject and for both days (1 and 4) the smallest RMS error was *always* obtained with the single non-linear model. This analysis is consistent with the lack of evidence for context switching between multiple models that is apparent in Figs. 1 and 2.

## Discussion

We tried to demonstrate utilization of context switching between multiple models by the motor control system during adaptation to alternating force-field perturbations. Even after extensive and effective exposure to each force field separately, subjects showed no evidence for improved performance in the alternating field. This finding contradicts our hypothesis that subjects would employ two separate models and learn to switch between them

**Table 2** The mean absolute value of the directional error in parts three and four (when no catch trials were introduced) of days 1 and 4, measured in millimeters. *EQ* Trials where the perturbation in the previous time that the same movement was performed was equal to the current perturbation ($n$=201, for each subject at each day). *DF* Trials where the previous perturbation of the same movement was different from the current ($n$=123, for each subject on each day). Note that the same movement refers to the same initial and target positions (see the six possible movements in Fig. 1). A $t$-test showed statistically significant difference between these sets of trials for all subjects

| | First day | | | | | Fourth day | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Subject | A *** | B *** | C ** | D ** | E *** | A *** | B * | C ** | D *** | E *** |
| EQ | 5.8 | 10.0 | 8.0 | 6.8 | 7.9 | 5.5 | 10.6 | 7.3 | 6.5 | 8.2 |
| DF | 8.8 | 13.5 | 9.7 | 8.6 | 11.0 | 8.6 | 12.6 | 9.3 | 11.0 | 11.6 |

*$P$<0.05; **$P$<0.01; ***$P$<0.001

according to the sequence context. In contrast, the subject's behavior could be accounted for by a parsimonious model in which subjects try to represent the alternating perturbations with a single internal model.

We wish to stress that our results do not reject the explanatory power of multiple models for many other motor behaviors; our conclusions may not be applicable beyond the tested conditions. Indeed a recent study by Rao and Shadmehr (2001) demonstrated context switching between perturbations after long training of one movement with spatial cues. The reason for that apparent conflict might be the different cues or the different training regime. If one movement required 4 days of practice, our protocol that includes six movements may require an extremely long training with proper cues in order to employ multiple models. One may further speculate that adaptation mechanisms are limited, and complex tasks require higher motor mechanisms, such as those subserving skill-learning. Further research is required to determine the exact conditions that may facilitate the employment of multiple models and context switching.

One unique feature of this study is the attempt to learn the two fields separately in order to facilitate the employment of context switching. Shadmehr and Brashers-Krug (1997) demonstrated that two conflicting fields can be learned and retained if the training sessions are separated by an interval of about 5 h. It is striking that the subjects in our study did not employ the sequence cue even after learning the two fields in 2 separate days.

Combined with other recent data that demonstrate lack of time and sequence representation and difficulties to acquire multiple models simultaneously (Conditt and Mussa-Ivaldi 1999; Karniel and Mussa-Ivaldi 2001; Korenberg and Ghahramani 2001), our results suggest that the brain tends to employ one state-based mapping and may not easily employ structures such as clocks, counter, or switches for the purpose of motor adaptation to force perturbations.

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