Sequence, time, or state representation: how does the motor control system adapt to variable environments?

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Abstract. Does the observation of well-timed movements imply the existence of some internal representation of time, such as a hypothetical neural clock? Here we report the results of experiments designed to investigate whether subjects form a correct adaptive representation of mechanical environments that change in a very predictable manner. In these experiments, subjects were asked to execute arm movements over a two-dimensional workspace while experiencing time-dependent disturbing forces. We provide a formal definition for time representation and conclude that our subjects didn't use time representation for motor adaptation under the tested conditions.

Subjects performed arm-reaching movements in the following experiments: (1) six experiments in a sinusoidal time-varying force field; (2) six experiments in a simple sequence of alternating viscous force fields, in which the number of targets allowed for the approximation of the force by a complex state-dependent force field; and (3) six experiments in the same simple sequence of alternating viscous force fields, in which no state-dependent force field approximation was possible. We found that the subjects did not adapt to the time-varying force field and were unable to form an adequate representation of the simple sequence of force fields. In the latter case, whenever possible, they adapted to a single state-dependent field that produced forces similar to the two alternating fields. This state-dependent field produced the same forces as the applied sequence of fields *only over the trajectories that subjects executed during the training phase*. However, the state-dependent field was inadequate to produce the correct forces generated by the field sequence over a new set of trajectories.

These results are not consistent with the hypothesis that subjects would develop a correct representation of time-dependent forces, at least under the tested

circumstances. We speculate that the system responsible for adaptation of movements to external forces may be unable to employ temporal representation. While it is possible that such a representation may emerge in a more prolonged and/or intense training, our findings indicate a preference by the adaptive system to generalize based on representing dependence of external forces upon state rather than upon time.

1 Introduction

When moving their arms, people learn to adjust motor commands to compensate for disturbing forces depending consistently on the state of motion of the limb (Shadmehr and Mussa-Ivaldi 1994; Flash and Gurevich 1997; Flanagan and Wing 1997; Lackner and Dizio 1998; Wolpert and Ghahramani 2000). This compensatory mechanism is a form of adaptation critical to our ability to cope with changes in body dynamics due to natural development, aging, and traumatic events.

Many tasks involve manipulating objects that generate time-varying forces. For example, when we carry a container full of liquid, the reaction forces generated by the container depend on state variables, such as the configuration of the liquid, that are not observed. Consequently, these forces vary with time but do not appear to vary consistently with the state of motion of the arm. Some tasks are performed in a time-varying environment. This may be due to a pathological state, such as tremor, that can be regarded as a quasiperiodic perturbation arising from noncontrolled internal processes. In the case of intentional tremor, these processes are associated with the execution of a motor command. We examined the ability of the adaptive system to cope with time-varying perturbations by correctly representing forces as functions of time instead of as functions of the state of motion of the arm. This ability would require access to some neural structure representing time.

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Numerous studies suggest the existence of explicit timing structures in the central nervous system. Accurate music performance is frequently explained based on biological clocks or internal timekeepers (see, e.g., Palmer 1997). Ivry (1996) describes two computational options for time representation in the brain. One option is a clock-counter model involving a single pacemaker and multiple counters to construct time intervals. The second option is a combination of multiple internal mechanisms, each representing a specific time interval. According to Ivry, there is evidence for the involvement of many neural structures in the task of time representation including the cerebellum, basal ganglia, and even some cortical structures. Buonomano and Merzenich (1995) suggested a physiologically plausible artificial neural network model for time representation, and Meck (1996) provided a review of internal clocks and memory of time. Llinas suggested the olivocerebellar system as a possible location for an internal representation of time (Welsh et al. 1995). However, Keating and Thach (1997) found no evidence for clock signals in this system. This is not an exhaustive review of the many studies that have addressed the issue of time representations in the central nervous system (see also the numerous references about biological clocks mentioned in the papers above; Block 1990; Winfree 2000). Yet it appears that the words of Block in the introduction to his book are still valid today: "no simple model can purport to explain the variety of temporal behaviors and phenomena that are experienced by individuals" (Block 1990). Regarding discrete temporal representation, many studies have addressed the ability of subjects to implicitly learn sequences of events (Reber 1989; Cohen et al. 1990; Berns et al. 1997; Dominey et al. 1998; Beiser and Houk 1998; Seidler et al. 2002). How the brain generates temporal behaviors and whether it uses structures such as clocks and counters are still open questions.

Following the vast apparent evidence for time and sequence representation in the central nervous system, our null hypothesis is that sequence, time, and state representation are all equally available for adaptation by the motor control system. The critical implication of this hypothesis is that subjects should be able to adapt to perturbations that depend on time as rapidly and efficiently as to perturbations depending on the position and/or velocity of the hand. Our results reject this hypothesis and suggest that the ability of the motor control system to employ representation of time is limited. In Sect. 2, we present a formal definition of time representation and speculate on its relevance to motor adaptation.

Our findings relate to the role of internal models in the control of movements. Several studies suggest that the central nervous system constructs internal models of arm dynamics to generate the motor commands needed to drive the hand along a planned trajectory (see, e.g., Inbar and Yafe 1976; Gottlieb 1994; Bhushan and Shadmehr 1999; Kawato 1999; Karniel and Inbar 2000; Mussa-Ivaldi and Bizzi 2000; Wolpert and Ghahramani 2000). The normal unperturbed trajectory of the hand

reaching for a target is typically a straight line from the initial position of the hand to the target (Morasso 1981; Flash and Hogan 1985). When perturbing forces are applied, the trajectory of the hand initially deviates from this straight line. After prolonged exposure to forces that depend on the state of motion of the hand – i.e., on its position and velocity – subjects learn to generate compensatory forces that cancel the force perturbation (Shadmehr and Mussa-Ivaldi 1994). At this point, an unexpected removal of the perturbation (called a catch-trial) results in an erroneous movement approximately the mirror image of the initial deviation caused by the perturbing force. This is called an after-effect of adaptation. After-effects reveal the existence of a predictive mechanism and support the hypothesis that the central nervous system has indeed formed an internal model of the external perturbation. It is important to note that this type of motor adaptation is not a transitory change and that it gives rise to long-term retention and interference effects that have been found to last across different days (see Brashers-Krug et al. 1996).

Here we examine the problem of adapting movements to disturbing forces that depend periodically on time rather than on the state of motion of the arm. Subjects were required to reach with the hand toward several target locations while holding the handle of a robotic manipulandum (Fig. 1a). In one experiment (Experiment 1), the manipulandum exerted a perturbing force with constant direction and with amplitude that varied periodically with time (Fig. 1). The amplitude and frequency of the force were not particularly challenging. Indeed subjects in these and other experiments were able to compensate for forces of similar amplitude and frequency if these forces were correlated with the velocity of the hand (Conditt and Mussa-Ivaldi 1999). However, in the first experiment reported here, the force was uncorrelated with the arm movement (see Fig. 1). The lack of correlation between the force perturbation and the state of the arm is essential to insure that adaptation may only result from the explicit representation of the dependence of force upon time.

A dynamic environment may also depend on time in a discrete sequential manner. For example, in some industrial tasks, one must move around items of different size and weight. How do we adapt to a sequence of loads? To address this question, we carried out a second set of experiments (Experiments 2 and 3) in which subjects were exposed to a very simple sequence of disturbances. As in the first experiment, subjects were required to reach targets with their hand. However, in these experiments the manipulandum applied force disturbances with alternating directions in subsequent movements. This allowed us to explore the subjects' ability to counteract the disturbances by forming an internal representation of their sequential order.

When a perturbation is applied to reaching movements of the hand, two signs are generally considered to be evidence for the development of an internal model of the perturbation. The first sign is a progressive recovery of a rectilinear motion. The second sign is the appearance of after-effects in catch-trials, when the force is
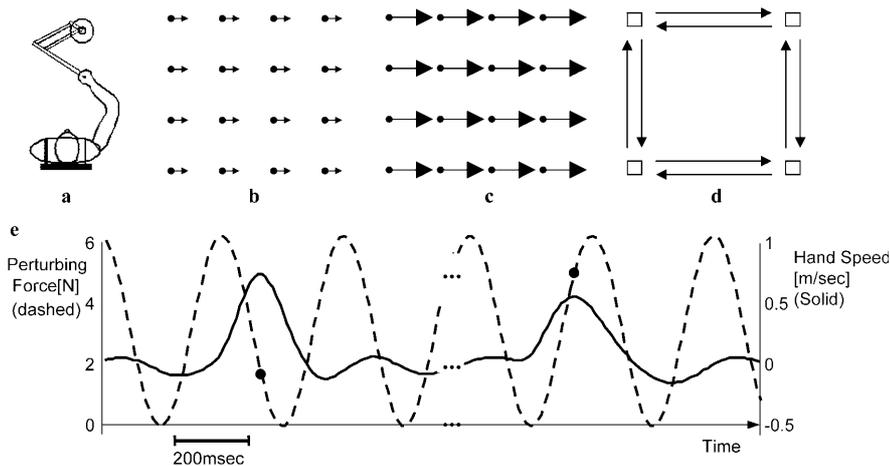
Fig. 1. The manipulandum and the time-dependent force perturbation. **a** Plan view of a subject holding the manipulandum. **b, c** Two examples of force fields in the first experiment. **d** The four targets and eight movements that were performed. **e** The amplitude of the applied force field (*dashed line*) over the velocity profiles of two movements. The applied force perturbation at the peak velocity of the first movement is illustrated in **b** and of the second movement in **c**

unexpectedly removed. In the experiments reported here, we observed both signs if the perturbation could be unambiguously associated with the position and velocity of the hand (in a control experiment and in Experiment 2) but not when the perturbation could only be predicted on the basis of its dependence on time (sinusoidal dependent in Experiment 1 and simple sequence of alternating forces in Experiment 3). Taken together, these results contradict the hypothesis that sequence, time, and state representation are equally available for adaptation by the motor control system.

2 Internal model and time representation. Formal definitions

In this section, we provide a rigorous description of our underlying assumptions in constructing the null hypothesis.

Under rather broad assumptions, the nonlinear dynamics of the limb are described by a system of ordinary differential equations, which collectively may be written as:

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

Here the vector q represents the spatial configuration of the limb as a collection, for example of joint angles. The dot represents time derivative. The term on the right, $C(\circ)$, represents the forces generated by the motor control system as it executes a desired movement $q_d(t)$. The circle in the parentheses indicates that we are uncertain about which variables the controller does actually depend on. It may or may not include a representation of time. Regardless of the explicit dependency of $C(\circ)$ on time, the solution of the dynamics (Eq. 1) is a trajectory of the arm, $q(t) = q_d(t)$, which consists of a temporal sequence of positions.

To investigate the structure of $C(\circ)$, we have developed a paradigm exploiting the mechanism of motor adaptation to perturbing force fields (Shadmehr and Mussa-Ivaldi 1994; Conditt and Mussa-Ivaldi 1999). Specifically, if the dynamics of the limb are altered by a perturbation that depends explicitly on time, $E(t)$, and

whose time course is not in a predefined temporal relation with the planned motion, $q_d(t)$, then the only way for the control system to recover the planned motion over a repeated set of trials is by developing a new control function that exhibits an explicit time dependency:

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

The time-varying force $\hat{E}(t)$ is a prediction – or internal model – of the external perturbation. With a perfectly accurate prediction of $E(t)$, the perturbed form of the limb's dynamics (Eq. 2) admits $q_d(t)$ as a solution.[1] In the rest of this section we briefly present a formal definition of time representation that is needed in order to construct the internal model $\hat{E}(t)$.

A dynamic system is described by means of a set of state variables and the following differential equation:

$$\dot{x} = f(x, u(t)) \text{ with initial condition } x(t = 0) = x_0 \tag{3}$$

The vector x contains all the states that determine the behavior of the system. In the case of a biological control system, x may include information about joint angles and velocities (q and $\dot{q}$ of Eq. 2), the state of the muscles, and the state of the nervous system. The vector of signals $u(t)$ represents all the external influences on the system. When the system is isolated from the environment, it is called an autonomous system. In this case, the variable t does not explicitly appear in the dynamics equation, but some of the state variables may still provide an external observer with a representation of time. If it is possible to deduce the time from the current value of the state variables, the system is said to be capable of representing time. More formally:

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[1] Recent studies have shown that the equilibrium-point hypotheses could be used to explain motor adaptation (Weeks et al. 1996; Gribble and Ostry 2000). In this framework, the modifier $\hat{E}(t)$ in Eq. 2 above would be called not an internal model but the internal representation of the external perturbation generated by modification of the virtual trajectory and/or the R and C parameters of the λ-model. The question would then be: could the system that generates the equilibrium trajectory employ time representation?

Definition 1: A system (Eq. 3) with n state variables is said to be *capable of representing time* if there exists a deterministic function $h : \Re^n \to \Re$ such that $t = h(x)$ for any $u(t)$.

This strict definition can be relaxed by limiting the accuracy of the function h and the time span over which the time representation is possible.

Definition 2: A system (Eq. 3) with n state variables is said to be *capable of representing time for up to T seconds with accuracy ε* if there exists a deterministic function $h : \Re^n \to \Re$ such that $|t - h(x)| \leq \varepsilon$ for $t \leq T$ and for any $u(t)$.

The basic idea is the existence of a subsystem from which time information can be extracted and which could be used thereafter for the purpose of modeling the external perturbation. Note that according to the above definitions, h must not depend on the input, u. This property implies that the time representation must not be affected by influences that are external to the system.

For example, consider a pendulum moving freely without friction. The linearized dynamic equation is $\dot{x} = \begin{bmatrix} 0 & 1 \\ -\alpha & 0 \end{bmatrix} x$. The state vector $x = (x_1, x_2)$ has two components, representing the pendulum position and velocity, respectively. The solution for an initial condition $x_0 = (x_1, x_2) = (1, 0)$ is $x_1 = \cos(\alpha \cdot t)$. During the first cycle, time can be extracted as follows: $t = h(x) = \frac{1}{\alpha} \cos^{-1}(x_1)$. Actual clocks typically use such a basic dynamic system with an additional counter that keeps track of the number of cycles to obtain a time representation. It is legitimate to hypothesize the existence of similar mechanisms in the nervous system based on some form of periodic dynamics that is isolated, at least for substantial periods of time, from external influences.

Sequence representation is a special case of time representation. A sequence implies the existence of a discrete variable, $n \in N$, that is monotonically increasing with time and takes values from the set of natural numbers ($n = 1, 2, 3, \ldots$). The above discussion can be extended to the case of sequence representation, where a discrete time variable n replaces the extracted time variable. Once the variable n is extracted, any sequence $S(n)$ can be represented.

Introducing the above definitions in Eq. 2, it becomes:

$$D(q, \dot{q}, \ddot{q}) + E(q, \dot{q}, \ddot{q}, t) = C(\circ) + \hat{E}(x) \qquad (4)$$

We assume that the dynamics of the variables (x) are described by an equation of the form of Eq. 3. This study was aimed at exploring the structure of the internal model $\hat{E}(x)$ when the external field depends explicitly on time. In previous studies, it was demonstrated that the motor control system is able to adapt to perturbations that depend on or correlate with the dynamic state of the limb (Shadmehr and Mussa-Ivaldi 1994; Flash and Gurevich 1997; Flanagan and Wing 1997; Lackner and Dizio 1998; Wolpert and Ghahramani 2000). Therefore, we know that the state vector x includes representations of $q, \dot{q}, \ddot{q}$ and that $\hat{E}(x)$ can be modified in order to estimate various functions of these variables. If the adaptive motor control system were capable of representing time, then it could compensate for time-dependent fields as well. In this case, the function h in definition 1 or 2 could be employed to extract time so that the internal model could provide an approximation of the external force, that is $\hat{E}(x) \approx E(h(x))$.

With this theoretical framework in mind, we have designed a set of experiments to explore the capabilities of the internal model $\hat{E}(x)$ and, more specifically, to test the hypothesis that asserts that sequence, time, and state representation are all equally available for adaptation by the motor control system.

3 Methods

Eleven subjects, seven male and four female ranging in age from 30 to 47, gave their informed consent and participated in this study. Each subject was assigned a unique identifying letter (Subject A–Subject K). Each experiment lasted about 50 min and included five or six parts with a short rest of a few minutes between parts. In each part, the subjects performed 120–170 reaching movements according to the detailed description provided below. We report here four experimental protocols. Four subjects performed Experiment 1 (time-varying force field), six performed Experiment 2 (sequence of force fields with four targets,) and six performed Experiment 3 (sequence of force fields with three targets). In addition, as a control to Experiment 1, three subjects performed an experiment with velocity-dependent forces.

3.1 Experimental setup

Subjects were comfortably sitting and held the handle of a two-degrees-of-freedom robotic manipulandum (Fig. 1a). They looked at a screen that displayed the location of the hand and the location of the target. Arm movements were performed in the horizontal plane. The robotic manipulandum exerted forces on the subject and recorded the trajectory of the hand. For further details about the manipulandum see Shadmehr and Mussa-Ivaldi (1994).

3.2 Experimental protocol

Subjects were asked to perform 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 and size according to the following three rules: (1) if the target was reached after 633 ms from its presentation, the rectangle turned blue, indicating that the movement was too slow; (2) if the target was reached within 533–633 ms, the rectangle

exploded (it expanded and disappeared over a period of 200 ms); and (3) if the target was reached quicker than 533 ms, the target turned red, indicating the movement was too fast or that the subject started to move before the target presentation. Subjects were instructed to start moving as soon as the target appeared and to try to explode the targets. Targets appeared at random locations to avoid anticipatory behavior. When the subjects were provided with timing feedback, time was measured from the appearance of the target instead of the motion initiation to prevent the subjects from synchronizing motion initiation to some feature of the time-varying force field. Experimental data verified that movement initiation was indeed uncorrelated to the time initiation of the force field (Fig. 1e). The timing feedback to the subjects was designed to induce movement durations similar to other related experimental studies (Conditt and Mussa-Ivaldi 1999).

Targets could only appear in three or four possible locations, and the distance between consecutive targets was 10 cm (the length of diagonal movements in Experiment 1 and 3 was 14.1 cm, but these movements are not reported directly). The set of targets was randomly generated for each protocol, and the same set was presented to all the subjects performing the same protocol. The first part in all the experiments was the null condition, in which no forces were applied. The following parts were carried out in the presence of a force field as described below for each experiment. Catch-trials (i.e., force field in the first part and null field in other parts) were introduced in at most 10% of the movements. It has been demonstrated that catch-trials interfere with learning (Thoroughman and Shadmehr 2000). Therefore, in the analysis of regular trials, we excluded catch-trials and the trials immediately following catch-trials.

3.3 Experiment 1 (time-dependent force)

The force (in Newton) was:

$$f_x = 3 \cdot (1 - \cos(6 \cdot \pi \cdot t))$$
$$f_y = 0 \tag{5}$$

The application of this force field was uncorrelated with the movements and was sustained throughout the experiment (also between movements and not only during the movement; see Fig. 1). In order to verify that the subjects were sufficiently perturbed, two subjects repeated this experiment with a maximum magnitude of 9 N instead of 6 N.

There were four possible targets on the vertices of a rectangle (Fig. 1d). The first part of the experiment was in the null condition, in which no forces were applied and movements were generated on the sides of the rectangle and diagonally (diagonal movements are not drawn in Fig. 1d since we do not report their analysis for this experiment). Each movement was performed ten times, for a total of 120 movements. The subsequent parts were carried out in the presence of a force field,

and only movements on the sides of the rectangle were performed (Fig. 1d). Each movement was performed 20 times for a total of 160 movements. A similar part with a different random order of the movements was repeated three times. Since no learning occurred in this experiment, no after-effects in catch-trials and no generalization were expected or observed, and therefore we do not report these trials.

3.4 Control experiments (velocity-dependent force)

To investigate adaptation in similar conditions, three subjects performed the same protocol of Experiment 1 in the presence of the following velocity-dependent field: $f_x = (-b) \cdot v_y$; $f_y = (+b) \cdot v_x$, where b equals 7, 10, or 15 Ns/m. The purpose of this control experiment is to verify that even when the deviation from a straight line is small, there is still adaptation in the case of velocity-dependent force. This would allow us to conclude that absence of adaptation with time-dependent forces (Experiment 1) is not due to a floor effect, the presence of small initial errors. This velocity-dependent force field is similar to the one used by Brashers-Krug et al. (1996) and many other studies showing evidence for adaptation.

3.5 Experiment 2 (sequence of two fields with four targets)

In this experiment, a sequence of two velocity-dependent fields was applied as follows:

$$\begin{bmatrix} f_x \\ f_y \end{bmatrix} = \sigma \begin{bmatrix} 0 & -15 \\ 15 & 0 \end{bmatrix} \cdot \begin{bmatrix} v_x \\ v_y \end{bmatrix} \tag{6}$$

where $\sigma = \{+1, -1, +1, -1, +1, -1, ...\}$ causes the field to reverse its direction after each movement. For both fields the magnitude of the force is proportional to the velocity, and the direction is perpendicular to the direction of motion. The direction (right and left relative to the direction of movement) alternates after each movement.

This experiment included four possible targets (Figs. 2a and b). In the first part, no forces were applied and movements were generated on the sides of the rectangle and diagonally (see Fig. 2b without the forces). In this first part, each movement was performed ten times, for a total of 120 movements. The following parts were carried out in the presence of the force field (Eq. 6), and only movements on the sides of the rectangle were performed (Fig. 2a). Each movement was performed 20 times for a total of 160 movements. A similar part with a different random order of the movements was repeated four times, and then in the sixth part diagonal movements were added again (Fig 2b). We call this sixth part a *generalization part* since it contains the same force field with different sets of movements. The movements in the generalization part were similar to those in part 1 (i.e., included diagonal trajectories). However, in contrast to
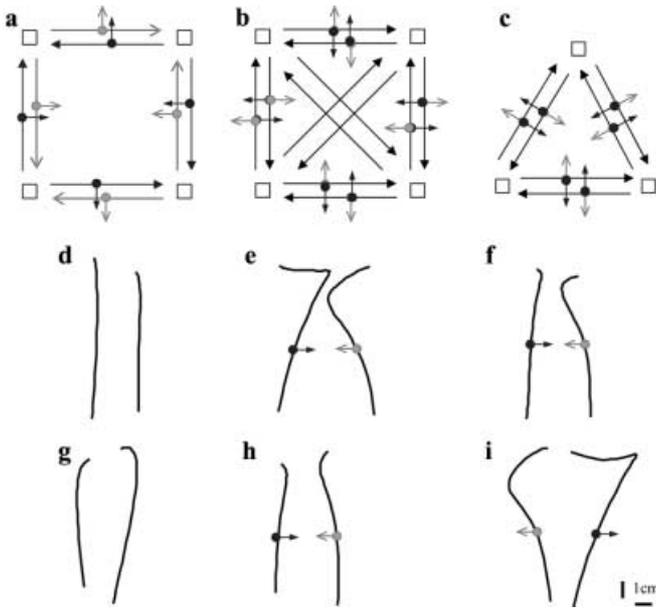
Fig. 2. The sequence of force fields. **a** The targets, the eight movements, and the direction of the force applied during the learning phase of Experiment 2. Note that although the force alternated its direction after each movement, the field could also be perceived as being a function of the particular movement being executed. **b** The targets and the 12 movements in the last part of Experiment 2 (part 6). Note that in this phase, each movement was executed in both force fields on different occasions according to the sequence. **c** The targets and movements in Experiment 3. The *curved lines* in **d–i** describe representative hand trajectories of Subject A. The trajectory in the left of each picture represents movement from the bottom-left to the upper-left target, and the trajectory in the right of each picture represents movement from the bottom-right to the upper-right target. **d** Part one, null field. **e** Part two, early training. **f** Part five, late training. **g** Part five, catch-trial. **h** Part 6 trials with field that is consistent with state generalization. **i** Part 6 trials with field that is consistent only with the sequence

part 1, the force field was present in this generalization part. Note that in the training parts (parts 2–5), there was a correspondence between the direction of the force field and the position of the hand. Since there were four targets and no diagonal movements and the sequence was an alternation between two force fields, when a specific movement with given start and end targets was executed, the subjects always experienced the same force field. For example, in Fig. 2a the movement from the bottom left to upper left was always performed in the same field that pushed the hand to the right, while the movement from bottom right to upper right was always in the field that pushed the hand to the left. In the generalization part, the same sequence of forces was applied. However, since diagonal movements were introduced, subjects could repeat the same movement after an odd number of intervening movements. In this case, they would execute the same movement with opposite force fields, and the correspondence between state and force would cease to exist (Fig. 2b). Catch-trials were introduced in 10% of the trials in parts 1, 2, 5, and 6 (12 movements with a force field in part one, 16 without a force field in parts 2 and 5, and 12 without a force field in part 6). This allocation of catch-trials was designed to minimize the number of catch-trials while equally distributing them among all the possible directions.

3.6 Experiment 3 (sequence of two fields with three targets)

In this experiment, the same sequence of force fields was used as in Experiment 2, but only three targets were presented (Fig. 2c) to eliminate the possibility of matching the force fields to the state of motion of the arm (see Results). In the first part, with the null field, 120 movements were performed (20 in each direction). In the other parts, 168 movements were performed (28 in each direction). Since no learning was observed, the last generalization part was dropped from the protocol of this third experiment. Catch-trials were introduced in a few random trials in parts 1, 2, and 5 (12 movements with a force field in part 1, and 12 without a force field in parts 2 and 5).

4 Data analysis

To quantify learning and after-effects, we measured the deviations of hand trajectories from straight-line paths joining initial and target positions. We used two different measures. One is the maximum distance between the actual path and a straight line, and the second measure, the direction error (DE), was developed for the sequence learning of the second and third experiments. The DE was calculated as follows: at the point of maximum velocity, which is well before possible corrective movements (Smith et al. 2000), the euclidian distance from the actual position to its projection onto a straight-line trajectory was measured. Distance to the left (in the direction of movement) was assigned a positive value, and distance to the right was assigned a negative value. This error was multiplied by the sign of the sequence $(+1, -1, +1, \ldots)$ both for regular trials, where the sign represented the direction of the applied field, and for catch-trials, where the sign represented the direction of the expected field. Positive DE indicates yielding to the force field (wrong or underestimation). Negative DE indicates overestimation of the force field (correct estimation of the field direction but extreme reaction, or absence of force in a catch-trial).

5 Results

5.1 Experiment 1 (time-dependent force)

Figure 3 depicts the training curves of two subjects in two conditions. We measured the performance by the distance of the actual movement from a straight line over repeated execution of perturbed movements. In the first condition, the control experiment, a velocity-dependent field was applied. In the second condition, a
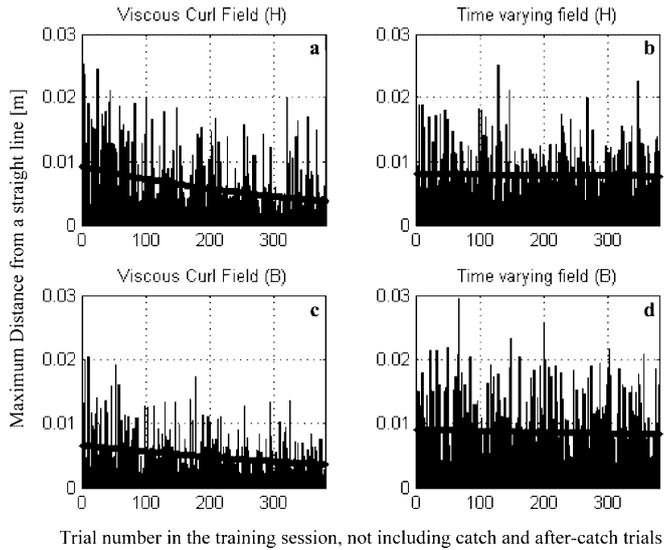
Fig. 3. Maximum distance from a straight line (in meters) during repeated execution of movements in velocity-dependent field (*left*) and in time-dependent field (*right*). The *bold line* is an exponential fit to the data. **a** Subject H, velocity-dependent force field $f_x = -10v_y, f_y = 10v_x$. **b** Subject H, time-dependent force field $f_x = 3(1 - \cos(6\pi_t)), f_y = 0$. **c** Subject B, velocity-dependent force field $f_x = -10v_y, f_y = 10v_x$. **d** Subject B, time-dependent force field $f_x = 4.5(1 - \cos(6\pi_t)), f_y = 0$ (the force unit is Newton)

time-varying force perturbation was applied. The lack of adaptation to the time-varying force perturbation is in striking contrast to the clear adaptation to a perturbing force that depended on the instantaneous velocity of the hand. The force field was in the *x* direction, changing its amplitude according to a sinusoidal function of time at 3 Hz (Fig. 1). The field was applied continuously, without interruption. Subjects were instructed to start the movement as soon as the target appeared. It would have been impossible for a subject to associate the force with the state of motion of the arm because the hand movement started at different phases of the force perturbation. However, if subjects had access to some time representation, they could have anticipated and counteracted a force that varied as a simple and predictable function of the time. The four subjects who participated in this experiment showed no significant learning of the task, compared to clear learning in the case of the velocity-dependent field. To verify that the lack of learning was not due to the presence of a small initial error (floor effect), we conducted the experiment also with larger force perturbations and a few control experiments with various force amplitudes (Figs. 3 and 4). A *t*-test comparing the deviation from a straight movement at the beginning of the training to that at the end of the training yielded a *p*-value larger than 0.1 for all the subjects that performed the time-varying force experiment in all conditions, compared to a *p*-value smaller than 0.01 for all the control (velocity-dependent force) experiments. Since no learning occurred, no after-effect was observed. This experiment was carried out in conditions similar – with respect to movement velocities and frequency content of the perturbing force – to those
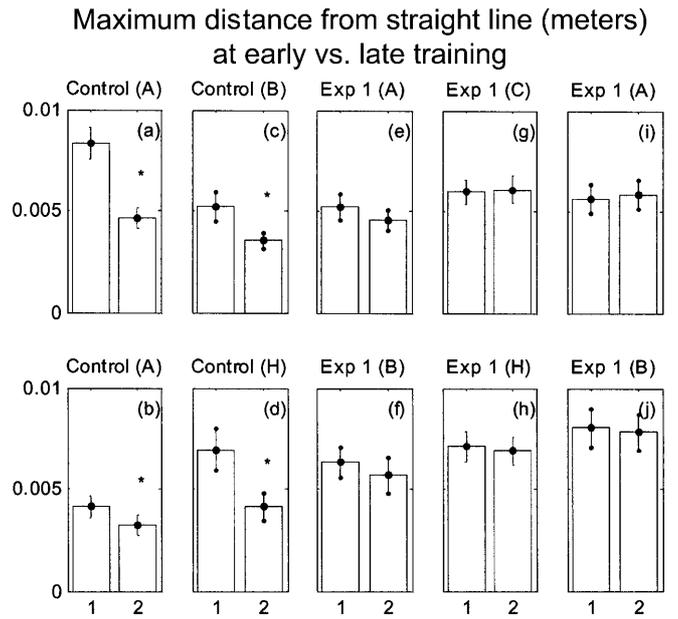

Fig. 4. The performance during the training phases in the presence of time-dependent force fields (Experiment 1, six right panels **e–j**) vs. control experiments of velocity-dependent forces (four left panels **a–d**). The mean of the maximum distance (in meters) from a straight line in the beginning of training (part 2 of the experiment, *left bar* in each plot) is compared to the late phase of training (part 4 of the experiment, *right bar* in each plot). The error bars depict the 95% confidence interval. A *t*-test was performed to check whether the late training error was significantly different than the early training error. The *star* describes *p*-values that are smaller than 0.01. The *capital letter* in the brackets is unique for each subject. **a** Subject A, $f_x = -15v_y, f_y = 15v_x$. **b** Subject A, $f_x = -7v_y, f_y = 7v_x$. **c,d** Subjects B and H, $f_x = -10v_y, f_y = 10v_x$. **e–h** Subjects A, C, B, and H, $f_x = 3(1 - \cos(6\pi_t)), f_y = 0$. (i-j) Subjects A and B, $f_x = 4.5(1 - \cos(6\pi_t)), f_y = 0$ (the force unit is Newton)

in other experiments where significant adaptation was easily obtained (Conditt and Mussa-Ivaldi 1999; the control experiments reported here; and Figs. 3 and 5). Therefore, the lack of adaptation with the time-varying field cannot be attributed to incidental factors such as the amplitude or rate of change of the force. This result is inconsistent with the null hypothesis that time and state representations are equally available for adaptation by the motor control system. In contrast, the finding suggests that the system, which is responsible for adaptation to changes in the external force field, may be incapable of coping with forces that depend explicitly only on time and are otherwise uncorrelated with the state of motion of the arm.

5.2 Experiment 2 (sequence of two fields with four targets)

A simple temporal sequence of two velocity-dependent force fields was applied. The fields had the same magnitude but opposite directions. Each field was present for the entire duration of one movement, then the opposite field was activated during the movement to the next target, and so on. We refer to these alternating
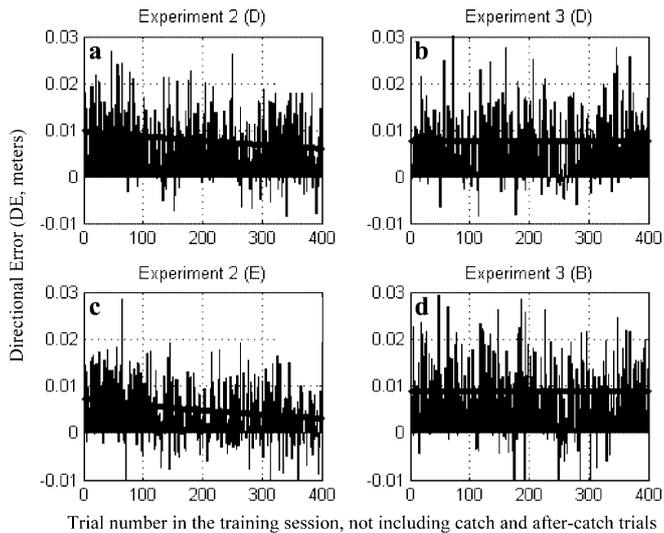
Fig. 5. Directional error (DE), in meters, during repeated execution of movements in the sequence for force field with four targets (Experiment 2, left) and with three targets (Experiment 3, right). The bold line is an exponential fit to the data. The capital letter is unique for each subject

force fields simply as "the sequence." Figure 2a shows the four targets and the eight possible movements that were performed during the training phase. Note that in this protocol, although the force was generated as a sequence, each movement of a given direction and starting point was always executed in the presence of the same field (the small arrows in Fig. 2a represent the direction of the perturbing force). This particular combination of movements and fields allows for successful adaptation either by learning the temporal structure of the sequence or by learning the spatial mapping depicted in Fig. 2a (that is, learning the dependence of the force on the state of motion, where the state of motion consists of the instantaneous position and velocity of the hand.)

All subjects adapted to the perturbations applied in this experiment (see the left side of Fig. 5 and the first two rows of Fig. 6). At the first exposure to the perturbation, subjects exhibited a clear deviation from a straight line (see Fig. 2e and compare to the typical movement without a force field in Fig. 2d). After training, the deviation was reduced (Fig. 2f). When the perturbation was unexpectedly removed in catch-trials, after-effects were observed (Fig. 2g). Negative DE in the right (late-training) side of Fig. 7a indicates anticipation of the force (see Methods). A two-way ANOVA comparing the responses to catch-trials of the six subjects indicates significant change ($p = 0.003$) between the early and late training and no significant difference between subjects ($p = 0.398$). These results suggest that subjects developed an internal model of the perturbation. However, further analysis of generalization refutes the hypothesis that this was a correct model of the sequence and is consistent with the alternative hypothesis that subjects adapted to a state-dependent force field yielding the same forces as the field sequence during the training phase.
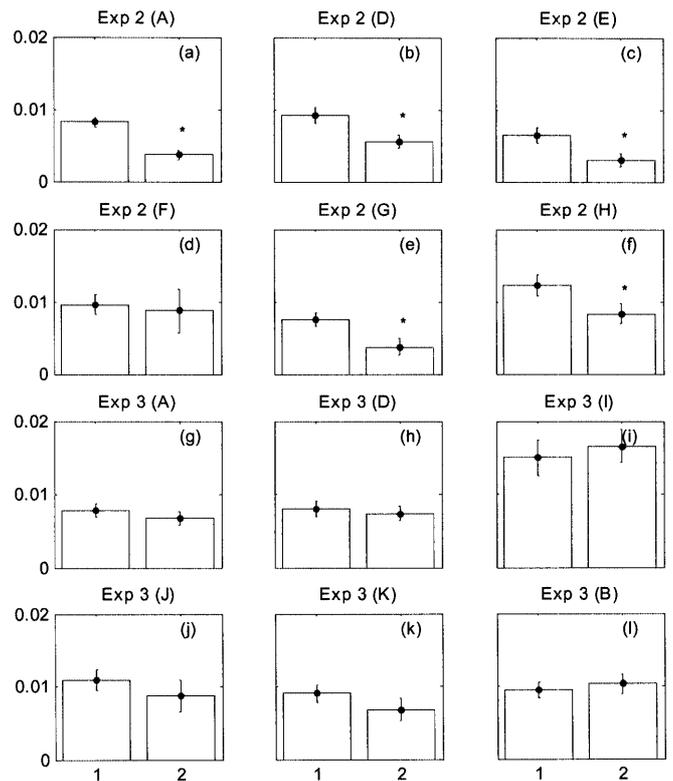

Fig. 6. The performance during the training phase in the presence of sequence of force fields with four targets (Experiment 2, **a–f**) and with three targets (Experiment 3, **g–l**). The mean of the directional error (DE, in meters) in the beginning of training (part 2 of the experiment, *left bar* in each plot) is compared to the late phase of training (part 5 of the experiment, *right bar* in each plot). The error-bars depict the 95% confidence interval. A *t*-test was performed to verify whether the late training error is significantly different than the early training error. The *star* describes *p*-values that are smaller than 0.01. The *capital letter* in the brackets is unique for each subject

Subjects were able to associate the perturbation to the state of motion of the arm because of the unique structure of the targets and possible movements. During the training phase no diagonal movements were introduced, and therefore a correspondence between the state of the arm (position and velocity) and the disturbing force was established (Fig. 2a). Note that the appearance of the next target was randomly selected. However, since there were four targets and no diagonal movements and the sequence was an alternation between two force fields, the subjects always experienced the same force field when moving from specific start targets to specific end targets. For example, movement from the bottom left to upper left was always performed in the field that pushed the hand to the right, while movement from bottom right to upper right was always in the field that pushed the hand to the left. In the last part of the experiment, diagonal movements were occasionally introduced. The field sequence remained the same, but the unique correspondence that allowed state representation was no longer consistent (Fig. 2b). Movements that in the training phase were always performed with the same perturbing field were now occasionally performed in
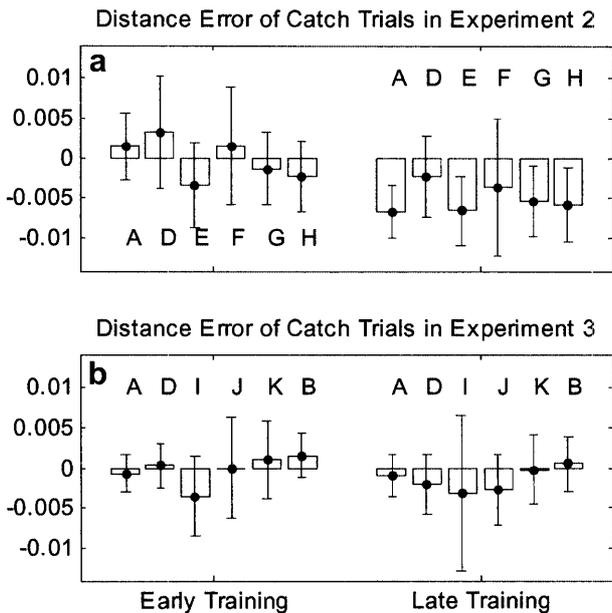
Fig. 7. Analysis of the catch-trial errors during the application of a sequence of force fields. **a** The upper bar plot describes the direction errors (DE, in meters) from a straight line during catch trials of Experiment 2 for the six subjects (A, D, E, F, G, H, from left to right). On the left side are the catch-trials in part 2 (the beginning of the training) and on the right side the catch-trials of part 5 (the last part of the training). One can see that the errors in the last part of the training are much more negative than the first part, which reflects expectation of the force field. **b** The lower bar plot describes catch-trials in Experiment 3 for the six subjects (A, D, I, J, K, B). Here one cannot find any evidence of expectation to the forces

Fig. 8. Generalization analysis in Experiment 2 for each subject. The *letter* is the unique label for each subject. The direction error (DE) is measured in meters. The first *bar* is the DE of the catch trials in the first part (the very first surprising encounter with the perturbation). The second *bar* is the DE of movements in the last part that are consistent with the sequence but inconsistent with a possible state-dependent force field. The third *bar* is the DE of movements in the last part that are consistent with the possible state representation. The errors in the second column are comparable to the error of the first column and demonstrate no generalization of the sequence. (Note that the temporal sequence was identical for the movements in columns 2 and 3). However, there was a clear adaptation to a state-dependent force field that coincides with the temporal sequence during the training phase

the opposite field. Figure 2h shows movements performed in the presence of the same force that was applied in the training phase for that movement direction and start point. Figure 2i shows the same movements in the presence of the opposite force. Note that the temporal order of the sequence was retained. If the subjects were building an internal model of the alternating force fields (i.e., a model of the temporal structure of the sequence), they would have been expected to generalize and perform correctly in this last part. In contrast, we found that subjects were unable to predict and compensate for the disturbing forces. Large deviations from a straight path were observed when the force field was inconsistent with the force-movement association learned in the training phase (Fig. 2i). This error suggests that the subject adapted by creating an association between force and state of motion of the arm rather than by building an internal representation of the temporal sequence of alternating fields. The same result – adaptation according to the state rather than sequence – was found in all subjects: we excluded the diagonal movements from this analysis and examined separately the movements in this part that were inconsistent with the state-dependent forces experienced during training (Fig. 8, second bar) and the other movements that were consistent with these forces (Fig. 8, third bar). These errors should be compared with the errors in the very first exposure to the field (Fig. 8, first bar). The large error in the
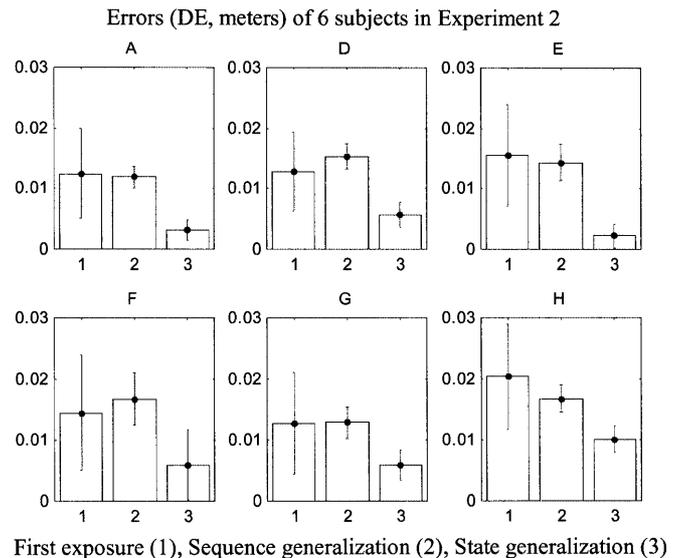
generalization trials where the previous state-force relationship did not apply (Figs. 2i and 8) strongly suggests that a representation of the correspondence between forces and movements and not of the temporal sequence of fields was the basis of the observed adaptation. Further evidence of the inability to adapt to the sequence of force fields is provided by the third experiment, where the tie between the sequence of movements and the two alternating fields was broken and learning was attempted in a configuration of movements that did not allow a state approximation to be used for adaptation.

5.3 Experiment 3 (sequence of two fields with three targets)

In this experiment, we used three targets (Fig. 2c). The sequence of two alternating fields thus generated different perturbing forces on different instances of the same movement. For example, subjects moving from the bottom left to the bottom right experienced both force fields ($\sigma = +1$ and $\sigma = -1$ in Eq. 6) at different trials during training. The subjects could not use a single state-based representation to compensate for these perturbations in different trials. Only strict sequence learning could account for adaptation in this case. The six subjects who participated in this exper-

iment showed no adaptation to the sequence (see two bottom rows in Fig. 6) over the same training period that was sufficient to see adaptation with four targets (as shown in upper two rows of Fig. 6, see also Fig. 7). This conclusion was supported by the analysis of the catch-trials that showed no after-effects (Fig. 7). A two-way ANOVA comparing the catch trials of the six subjects indicates no significant change ($p = 0.39$) between the early and late training and no significant difference among subjects ($p = 0.57$). This result is at odds with the results of Experiment 2, where learning was observed.

It is striking that evidence for learning over a sequence with four targets ceases to be present, with the same training time, in a simpler sequence of three targets. The only "complicating factor" in the smaller target set is the loss of coincidence between each starting point and the expected force, which makes it impossible to make predictions of force based on the current state of the arm. The only possibility for the subjects to adapt would have been to learn to anticipate the disturbance as a temporal sequence of force fields. But they were unable to do so.

6 Discussion

The experiments reported here demonstrate that learning to compensate for a force that depends predictably on time is, if not impossible, certainly harder than learning to compensate for a force that depends consistently on the state of motion of the arm. This conclusion applies not only to continuous time dependence but also to discrete temporal sequences of perturbing forces.

There are many strategies that subjects might develop to compensate for a time-varying disturbance while avoiding the use of time and sequence representation. For example, they can approximate the time-dependent force field by matching the experienced forces and motions with a state-dependent force field [see Conditt and Mussa-Ivaldi (1999) for a time-dependent force field and Experiment 2 here for a sequence of force fields]. Subjects could also build an internal state-dependent model of the external disturbance (Dingwell et al. 2002), which could be extended to an ad hoc time representation to specific task. In addition, since the system is redundant (Bernstein 1967), there are many possible combinations of motor command that could lead to the same measured kinematics. Therefore, there are many ways to explain adaptation to time-varying perturbations; however, the lack of adaptation to time-dependent perturbations observed in the kinematics clearly indicates that the use of time representation by the motor command is limited.

Recent studies have demonstrated that subjects learn to compensate for two force fields after prolonged training with some contextual nontemporal cue that predicts which field will be present in the next movement. Rao and Shadmehr (2001) showed this in human subjects and spatial cue; Krouchev and Kalaska (2003) showed this with a monkey and color cue. A different

cue is a special catch-trial that was recently proposed by Korenberg and Ghahramani (2001). In that study, subjects were able to use feedback information from the very beginning of each movement. Here we designed experiments for testing adaptation to time-dependent and sequence-dependent force fields. In two of the experiments (1 and 3), we specifically designed the force perturbations so that each movement executed during training could not be uniquely associated with a single pattern of forces. Subjects were not given any cue or explicit information about the forces they would encounter. Therefore, they could only adapt their arm movements if they were able to detect and explicitly represent the time dependence of the external forces. We found that subjects were unable to adapt to these force fields.

In a restrictive interpretation, the validity of our results is limited to the adaptation of previously learned arm movements during a relatively short exposure to a perturbing environment. It is possible that time representation is available for other tasks. Perhaps time representation is not provided by one central clock but by different mechanisms for different tasks. This view is supported by the results of Hocherman and Ben-Dov (1979), which demonstrated that the ability to estimate time is affected by the modality of the stimuli (visual or auditory). It is also possible that a time representation could be developed either after extensive training or during the acquisition of a new motor skill. This distinction would refine the hierarchy of learning and adaptation so that the process of learning skills would refer to the acquisition of new movements and the process of adaptation to the transport of these skills into a modified environment (Karniel and Inbar 2000; Yom-Tov et al. 2001). If time representation were demonstrated in learning new skills, further questions would have to be answered about its mechanisms. For example, what would be the limits of accuracy and duration of time representation? How could the internal time synchronize with external inputs?

Our findings show no evidence for time representation, in contrast to prevailing notions of biological clocks and timekeepers. Our research suggests a strong tendency by the central nervous system to use motion-state information for adapting to limb or environment dynamics. In Sect. 2, we presented the mathematical form of the model for motor adaptation and some definitions of time and sequence representation. The essence of these definitions is that any internal time representation must rely on some mechanism *isolated from outside perturbations and the state of movement*. Our experiments failed to find evidence for this kind of representation. Instead, we found a clear tendency to approximate time-varying perturbations using the state of motion of the arm. These results call for a new interpretation of studies that make reference to time-keepers, either explicitly or implicitly. Recent imaging studies suggest that visual and auditory time perception involve some of the same brain areas that are responsible for movement coordination (Schubotz et al. 2000). This result does not support the idea of a timekeeper that is

isolated from movement. In another recent experiment, the spatial distribution of tactile learning was addressed (Harris et al. 2001). Subjects were trained to discriminate between two tactile stimuli in one finger, and their ability to generalize and perform the task in other fingers was tested. Subjects showed a clear ability to generalize to other fingers and to the other hand when the task consisted of discriminating pressure or roughness features in the stimuli. However, when the task required identification of vibration frequency, learning was observed but no generalization to other fingers was possible. The authors mentioned that these results rule out a cognitive strategy such as counting the number of deflections per unit of time.

One may speculate that the difficulty of our first experiment arose from a dual task: *performing the reaching movement and tracking a time-dependent force*. We do not object to this interpretation. However, our results suggest that this dual task is more difficult than *performing the reaching movement and tracking a velocity-dependent force*. This view is also consistent with our conclusion that the timing information is not readily available for the adaptive motor control system. Any robotic engineer with a clock would find the task of tracking the cosine function of time extremely easy. In contrast, with a poor representation of arm state, the task of adapting to complex velocity-dependent and position-dependent fields could be much more difficult. Observing the relative ease or difficulty of adapting to force fields is a valuable tool for understanding the structure of the biological motor control system.

Our results might appear at odds with our ability to generate rhythmic movements. This ability has been well studied (Pearson 2000; Sternad et al. 2000). Kugler and Turvey (1987) specifically discuss the structure of artificial clocks in this context. When one generates rhythmic movement and uses the arm or leg as a pendulum, the mechanical properties of the musculoskeletal system limit the range of possible frequencies and timing (see, e.g., Yu et al. in press). In addition, it is likely that an external perturbation would disrupt the timing of the movement. Therefore, the periodic motion of a limb does not satisfy a general requirement for an internal clock – to be insensitive to external perturbations (see also Definition 1 in Sect. 2). Our ability to generate rhythmic movements and other timely accurate tasks may be governed by ad hoc mechanisms that rely on delays and mechanical properties of the system rather than on a central representation of time as afforded by a clock.

It is possible that additional cues or longer practice might eventually lead to a representation of time-varying forces. The ability of musicians and dancers to synchronize and follow time patterns suggests the existence of internal representations of time (Palmer 1997). However, this is not the only way to account for such exquisite temporal skills. As an alternative to the use of some accurate representation of time it would be possible for the motor system to achieve accurate timing by synchronizing motor commands to sensory cues and using accurately coordinated motor patterns defined over short segments of time. After all, a representation of time can only originate by a device such as a clock that operates by virtue of some periodic dynamics. It is doubtful that actual neural circuits could implement such devices with sufficient precision, such as 10 ms over periods of several seconds (no robot designer would accept a lower standard for a clock). In contrast, the central nervous system is rich in sensory-motor structures capable of providing accurate state information for the control of movement such as muscle length, lengthening rate, and joint angles. Our evidence is consistent with the idea that the biological control system relies on state information rather than on timing information when constructing and adapting motor commands.

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