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Motor learning by field approximation

(arm trajectories/adaptation/generalization of learning/regularization/intrinsic coordinates)

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ABSTRACT **We investigated how human subjects adapt to forces perturbing the motion of their arms. We found that this kind of learning is based on the capacity of the central nervous system (CNS) to predict and therefore to cancel externally applied perturbing forces. Our experimental results indicate: (*i*) that the ability of the CNS to compensate for the perturbing forces is restricted to those spatial locations where the perturbations have been experienced by the moving arm. The subjects also are able to compensate for forces experienced at neighboring workspace locations. However, adaptation decays smoothly and quickly with distance from the locations where disturbances had been sensed by the moving limb. (*ii*) Our experiments also show that the CNS builds an internal model of the external perturbing forces in intrinsic (muscles and/or joints) coordinates.**

How does the motor control system adapt to new mechanical environments? When we move the arm in a novel environment (for example, when we hold a hammer for the first time), we encounter unexpected forces as the arm goes through a temporal sequence of states (i.e., positions and velocities). As we adapt to this environment, the motor control system must learn to predict the perturbing forces that the limb will encounter so as to cancel them out while carrying out the desired movement. There are at least three ways for the motor control system to achieve adaptation. One is by representing the perturbing forces as a lookup table—that is, as a map that associates these forces to the states (positions and velocities) where perturbations have been experienced. An alternative is that the adaptation is not strictly limited to the visited states but to a small region around them. In this case, we would say that adaptation is local to the visited states. A third hypothesis is that the pattern of forces experienced locally generalizes over the entire arm's workspace. To find which alternative is most likely to be implemented by the motor control system, we investigated how subjects change their performance after prolonged exposure to a novel mechanical perturbation.

The protocol we used was designed by Shadmehr and Mussa-Ivaldi (1). Subjects were asked to execute arm movements toward visually specified targets. Once a baseline was established, force perturbations proportional to the movement velocity were applied to the subject's hand. Initially, the trajectories were significantly distorted by the applied forces. But after a period of practice within this altered mechanical environment, subjects recovered the original performance to a remarkable degree. In addition, when the mechanical perturbations were removed, the resulting trajectories displayed a compensatory response, which was a mirror image of the perturbed trajectory. This compensatory response has been termed aftereffect (1). The presence of aftereffects is an indication that subjects adapted to the novel environment not by a generic strategy, such as by making their limb more rigid, but by generating endpoint forces that exactly compensate for the applied perturbation. Accordingly, the sudden removal of the perturbation resulted in an equal and opposite unbalanced force that gave rise to the observed aftereffects.

Our experiments demonstrate that the motor control system builds a model of the environment as a map between the experienced somatosensory input and the output forces needed to counterbalance the external perturbations. In addition, our results indicate that this map is local; it smoothly decays with distance from the perturbed locations.

METHODS

We tested 15 right-handed individuals, ranging in age from 18 to 35 years and with no known history of neuromotor disorders. Subjects were seated on a chair and instructed to grasp the handle of a robot manipulandum with their right hand (see Fig. 1*A*).

They were asked to execute arm movements to targets displayed on a computer screen. They used the manipulandum to guide a cursor on the screen to the targets. Full visual feedback (target and cursor) was given during the experiment.

In the first part of each experiment, subjects practiced movements until they achieved a stable performance (baseline) and the desired timing. Subsequently, the torque motors of the robot generated a programmed pattern of force perturbations. The programmed forces were proportional to the subject's hand velocity. An example of a perturbation pattern is shown in Fig. 1*B*, where the force exerted by the manipulandum is plotted as a function of the hand's velocity. Initially, the subjects' trajectories were highly distorted by this perturbation (Fig. 1*D*), but as training progressed, they recovered the baseline pattern (Fig. 1*E*). On random trials, no perturbation was applied, and compensatory trajectories, referred to as aftereffects, were observed (Fig. 1*F*).

A quantitative study of the distortions in the trajectories was performed by analyzing the velocity profiles. We defined our measure of similarity, or correlation coefficient, as the inner product between the velocity profile of the baseline trajectory and the trajectory itself. The baseline trajectories were chosen among the unperturbed trajectories as those having the highest mean correlation coefficient with the other unperturbed trajectories. The average score for the trajectories in Fig. 1*C* was 0.97. Each trajectory during the experiment was then compared with the typical trajectory (1).

RESULTS

To estimate the generalization of motor learning, we trained subjects over a region of the workspace and tested for evidence of adaptation by observing the aftereffects inside and outside this region.

We asked subjects to execute movements to targets placed as shown in Fig. 1*A*. Fig. 2*A* shows the baseline trajectories

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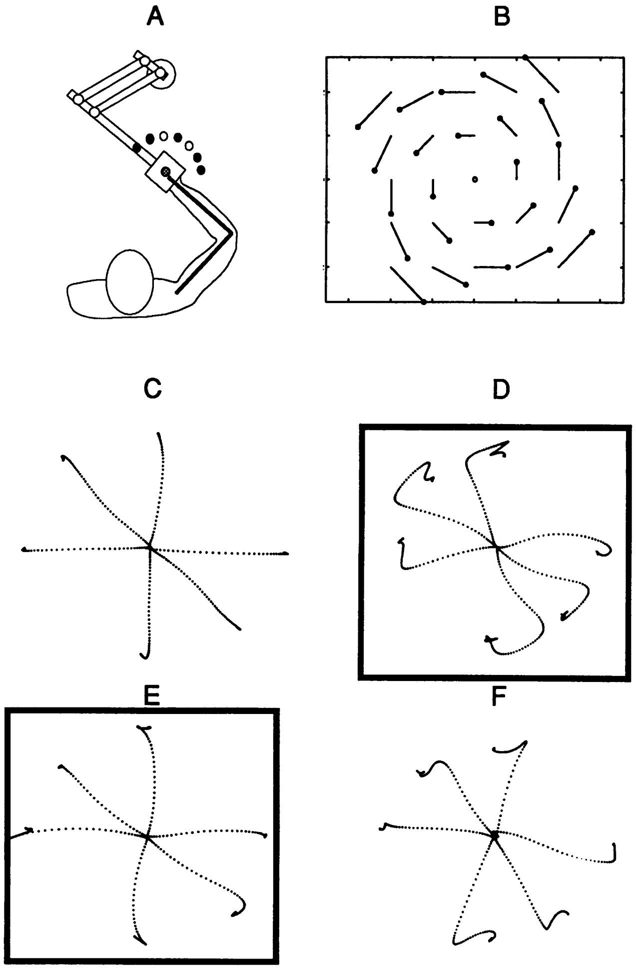

FIG. 1. Experimental procedure. (*A*) Subjects sit in front of a manipulandum and execute reaching movements to visual targets. (*C*) Their trajectories are initially straight, and a prototype for each direction is computed. When exposed to a field (*B*), their trajectories are initially perturbed (*D*). With training, they resume the prototypical shape (*E*). If the field is removed after learning, subjects display aftereffects (*F*) as overcompensation for the expected perturbation.

(correlation coefficient = 0.95) obtained in the absence of perturbations. Once a stable performance was reached, subjects moved the cursor back and forth from the center to the targets at 45° and 90°, indicated in Fig. 1*A* by open circles. During the execution of these movements, identified in Fig. 2*A* by a thick broken line, a clockwise perturbation was applied to the moving hand, resulting in distortions of these trajectories (Fig. 2*B*). However, after ≈400 movements, the original, nearly straight trajectories reappeared (Fig. 2*C*). At this point, our test session started. Subjects continued to move to the training targets, but test targets (located at 0°, 22.5°, 67.5°, 112.5°, or 135°) appeared randomly, and subjects moved to those targets. No perturbation was applied during the movements to test targets. We found that aftereffects were present (see Fig. 2*D*) not only along the trained directions but also along the directions of the test targets.

The magnitude of the aftereffects, though, decayed smoothly with increasing distance from the trained locations. (ANOVA shows a directional effect; $F_{(11,108)} = 5.3$; $P < 0.001$; F test shows a statistical difference between a new trajectory within the training region and the trajectory that was farthest away from this region.) To rule out systematic factors associated with particular movement directions, we repeated the experiment using different training directions. Regardless of the training direction, we found a decay of the aftereffects outside the training region. This finding is consistent with a local model for adaptation and not consistent with either a lookup table or a global model.

Having found that learning is local, we searched for the presence of interference that could arise if two training configurations are not sufficiently far apart. We asked subjects to execute a series of movements, some with wrist posture *A* (shown in Fig. 3*A*), some with wrist posture *B* (see Fig. 3*B*). These grips induced wrist rotation, defining two distinct sets of joint configurations. Note that the endpoint trajectory is the same for both postures. Only one posture (*B*) was associated with a perturbation, while the other (*A*) was associated with a no-perturbation condition.

As expected, we found that trajectories performed with posture *B* displayed aftereffects (Fig. 3*F*). However, quite surprisingly, even the trajectories with *A* postural configuration, which had been performed with no disturbing forces, appeared to show aftereffects (Fig. 3*E*). This finding indicates that there is interference between the two conditions.

As learning progressed, the interference subsided, and no aftereffects were detected when subjects produced trajectories with the wrist in the *A* posture (see Fig. 3 *G* and *I*). In contrast, as shown in Fig. 3*J*, we continued to observe clear aftereffects when the subjects moved the manipulandum with the *B* posture.

We conclude that during adaptation, the motor-control system carries out a reconstruction of the dynamical environment by following a process similar to the way in which a statistician could approximate an unknown function from a set of noisy data. The approximation technique known as "regularization" consists in deriving a function that minimizes the sum of two distinct cost components (2, 3). One cost component is the approximation error, which measures the distance between the approximating function and the data. The other cost component reflects what is known *a priori* about the function to be approximated. Typically, this cost component is a measure of smoothness; the unknown function is supposed to minimize the amount of oscillation between data points. The data shown in Fig. 3 *E* and *F* indicate that at the beginning of the experiment, the motor system assumes that the same pattern of forces may be present in the two hand postures. This working hypothesis corresponds to a smoothness criterion. However, as learning progresses (Fig. 3 *G* and *H*), the subject explores the mechanical environment of each posture and recovers the correct movement pattern by producing two distinct compensatory responses.

Is the environment encoded in intrinsic or extrinsic coordinates? To help answer this question, we asked subjects to grasp the manipulandum using two postures, *A* and *B* (see Fig. 3 *A* and *B*) and to alternate between the two postures by switching from one to the other every 48 movements. A clockwise field was presented whenever the subject grasped the handle in the *A* posture, and a counterclockwise field was presented in the *B* posture. As expected, the movements were at first perturbed (Fig. 4 *C* and *D*); however, subjects were eventually able to learn how to compensate for both perturbations (Fig. 4 *E* and *F*). We then removed the forces, and subjects continued to move the cursor switching between the two hand postures.

We observed that the aftereffects were specific to the field to which subjects had been exposed in each posture (Fig. 4 *G* and *H*). For example, if they adopted the *A* posture in the absence of forces, the observed aftereffects were consistent with the field experienced in *A*. Moreover, once the aftereffects disappeared in posture *A*, subjects displayed strong specific aftereffects as a result of switching over to posture *B*, even in the absence of further exposure to forces.

There are two possible interpretations of this result. In the first interpretation, the motor control system adapts to the imposed disturbances in a joint-based configuration. The two different configurations of the arm correspond to two different patterns of joint angles, and the two force fields correspond to

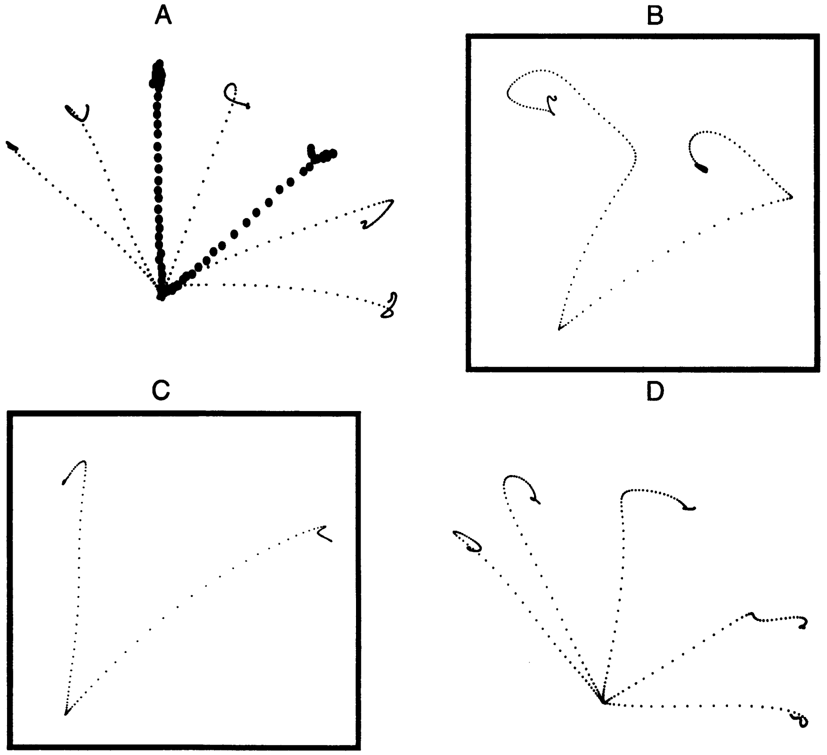

FIG. 2. (*A*) Baseline trajectories in the absence of perturbations. Darkened lines identify the trajectories that were subsequently exposed to perturbating forces (training targets). Lighter traces indicate trajectories that were never exposed to perturbations (testing targets). (*B*) Trajectories due to early exposure to the perturbation. (*C*) Trajectories after adaptation. (*D*) Aftereffects on trajectories that were not exposed to perturbations (testing targets).

two separate mappings between joint angles and joint torques. These mappings do not interfere with each other because the two sets of joint angles are separate. In the second interpretation, the motor control system is capable of learning different endpoint force fields and is able to switch among them by using a sensory cue, such as the arm configuration. We tested this second hypothesis by requiring our subjects to use sensory cues other than the joint angles for switching between two different endpoint fields.

We first tried classical conditioning with a visual cue. The two perturbations were no longer associated with different postures but with the color of the room light. When the first perturbation (clockwise force field) was on, the room was flooded with green light. As the perturbation changed (counterclockwise force field), the room was flooded with red light. We used exactly the same protocol as in the previous experiment, alternating blocks of 48 movements. When we tested for aftereffects, we found a dependence on the field that was experienced last and not on the field corresponding to the current light color. Furthermore, after the aftereffects were extinguished, no aftereffects could be elicited by a change in illumination.

Since a visual cue did not induce adaptation, we modified the experiment once more by asking the subjects to use two different thumb postures (horizontal and vertical) when moving in the fields. In this case, the overall arm posture was not altered. As with the light experiment, it was not possible to elicit aftereffects by changing the thumb position.

Both the experiments with the visual cues and with the different thumb positions strongly suggest that motor adaptation can be affected only by factors that are physically involved in compensating for the changes of the environmental mechanics. Clearly, both the visual cues and the thumb orientation had no mechanical relation to the forces experienced by the motor control system. In this regard, they were abstract and symbolic cues. In contrast, the change in arm configuration associated with switching from position *A* to position *B* had a direct effect on the pattern of joint torques induced on the limb by the force perturbations. Therefore, our experiments are consistent with the hypothesis that the internal model of the environmental mechanics is represented in intrinsic coordinates. In this system of coordinates, the two experimental conditions (field A associated with posture *A*, and field B with posture *B*) can be regarded as a single mapping between torque and limb configuration.

DISCUSSION

Whereas many investigators have studied the adaptation of the visual and auditory systems (4, 5), the motor control system has received little attention, and most of the observed sensorimotor recalibration (for example, in the vestibuloocular system) has been attributed to reorganization of a visuomotor map (6–8). The most important finding reported in this paper is that local motor adaptation occurs. Furthermore, it is best represented in intrinsic coordinates (1, 9). The motor system apparently builds a model of the environment that is constantly updated to account for the experienced perturbations. The update of the model is consistent with the results obtained using a regularization scheme that trades off smoothness for accuracy around the experienced data points.

Our finding that motor adaptation is local is consistent with the results reported in the visual system (10–12). In addition, studies by Held and Bauer (13) found that monkeys deprived of the sight of their body during infancy showed poor visuomotor coordination. Training on a restricted area of the workspace led to little generalization to the rest of the workspace.

We found that subjects were able to associate different postures to different perturbation patterns while preserving the same endpoint trajectory. Both visual and overlapping somatosensory cues failed to help subjects make correct predictions of the expected perturbation. Instead, subjects

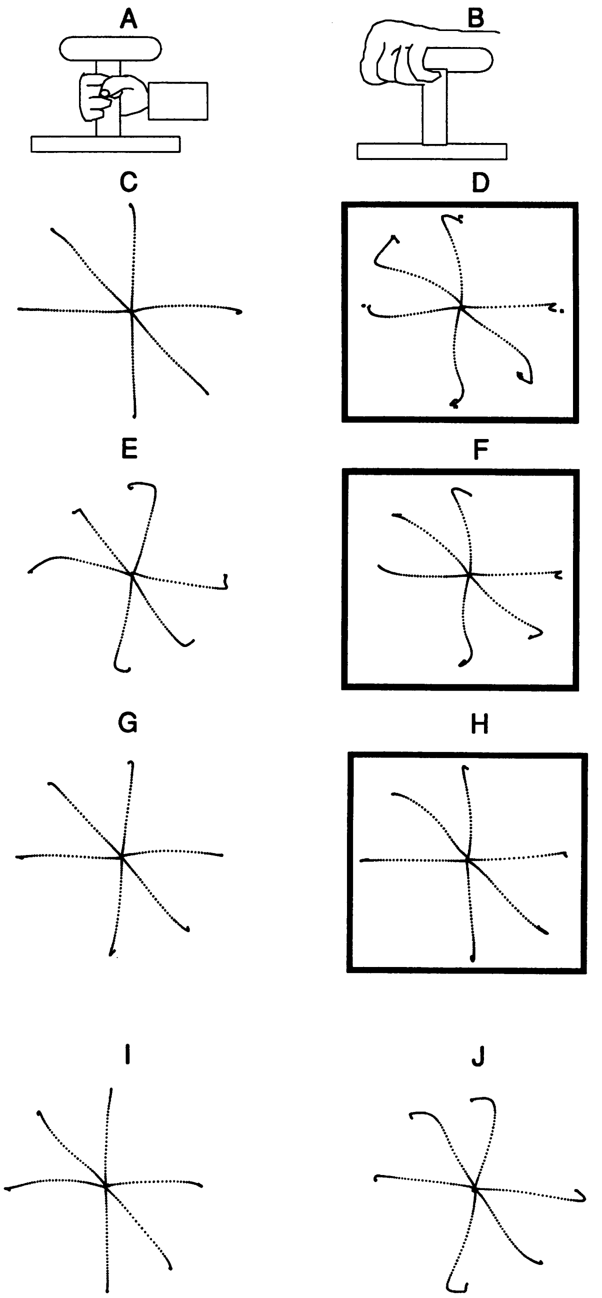

FIG. 3. Interference between representations. (*A* and *B*) Grips used by the subjects. Left column shows trajectories (*C*) performed with posture *A* in the no-perturbations condition. Right column shows trajectories (*D*) performed with posture *B* and exposed to a counterclockwise field. (*E*) Aftereffects while moving with posture in *A*. As training progresses, there is adaptation while moving in the perturbing field (*H*). Aftereffects (*G* and *I*) are not present in the nonexposed posture (*A*). Aftereffects are present (*J*) when subjects move without perturbations with posture in *B*.

could always correctly predict the nature of the incoming perturbations on the basis of full somatosensory input. We therefore argue that distinct postures allow the central nervous system to represent different perturbations as a single field, eliminating prediction ambiguity.

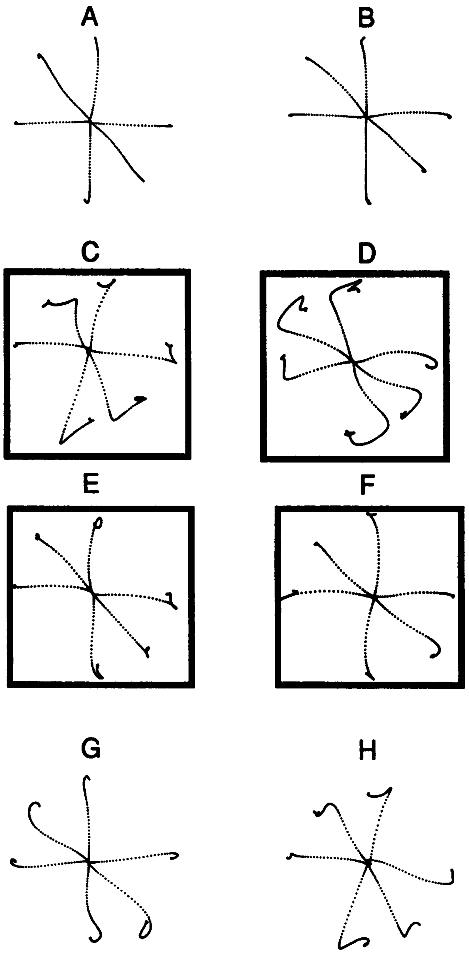

FIG. 4. (*A* and *B*) Baselines obtained in each posture. (*C* and *D*) Trajectories distorted by exposure to perturbations (clockwise for one posture and counterclockwise for the other). As learning progresses, trajectories straighten out (*E* and *F*). (*G*) Aftereffects consistent with the field and posture in *A*. After washout of the aftereffects, if the posture is changed to that in *B*, aftereffects arise (*H*) that are once again consistent with the expected field.

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