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# Neural basis of motor control and its cognitive implications

Emilio Bizzi and Ferdinando A. Mussa-Ivaldi

**It has recently been demonstrated that human subjects and nonhuman primates adapt their arm movements when subjected to complex patterns of disturbing forces. The presence of aftereffects following the removal of the disturbing forces indicates that adaptation takes place through the development of an internal model of the disturbing force. The experimental evidence described in this paper has identified some important properties of this internal model: (1) it is limited to a region surrounding that part of the space where the disturbances had been experienced; (2) there is an enhancement of the internal model that depends only on the passage of time; and (3) there is a process of consolidation of the internal model, which takes a minimum of four hours.**

**Anatomically, the substrate of the internal model is distributed; the motor cortex, basal ganglia, and cerebellum are interconnected structures that are active to different degrees during the acquisition of motor skills. Recent investigation of the spinal cord has suggested the existence of modules that organize the motor output in a discrete set of synergies. The outputs of these modules combine by addition, and might thus form the building blocks for the internal models represented by supraspinal structures.**

In a number of recent studies investigators have shown that when networks of artificial neurons are repeatedly exposed to examples of input–output associations, learning of fairly complex motor tasks occurs<sup>1</sup>. The learning results from a change of the internal structure of the artificial network, specifically a change in the connectivity among the

elements of the artificial network. On the basis of these results, scientists have proposed that processes similar to those occurring in the artificial networks might be present in the central nervous system (CNS) during learning of a motor task. The hypothesis is that human subjects learn a new task as the result of repeated exposures to sensory signals

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### Box 1. Experimental procedures

Each subject participated in a preliminary training phase where the task was to move a cursor to a target. The cursor was a square of size  $2 \times 2 \text{ mm}^2$  on a computer monitor and indicated the position of the handle of the manipulandum. Targets were specified by a square of size  $8 \times 8 \text{ mm}^2$ . The task was to move the manipulandum so as to bring the cursor within the target square. Starting from the center of a workspace, a target at a direction randomly chosen from the set  $\{0^\circ, 45^\circ, \dots, 315^\circ\}$ , and at a distance of 10 cm was presented. After the subject had moved to the target, the next target, again in a random direction and at 10 cm distance, was presented. In some trials, the cursor position during the movement was blanked, removing visual feedback during the reaching period.

After the training phase, forces were applied to the moving hand. With practice, the subjects' hand trajectories converged to the trajectory observed before the application of this force field. This convergence was gradual but monotonic in all subjects, consistent with an adaptive process whose goal was to compensate for the forces imposed by the field and to return the hand's trajectory to that produced before the perturbation. This finding suggests that the kinematics observed in reaching movements are not merely a consequence of arm dynamics but reflect the presence of a plan; that is, a desired trajectory<sup>a</sup>.

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coming from their moving limbs while they interact with the environment. These repeated sensory signals are funneled to the motor areas of the central nervous system where signals that activate the muscles are produced.

This iterative process leads to the establishment of an internal model of the controlled dynamics – the body and its environment – through the gradual change of the synaptic strength of the neurons of cortical and subcortical motor areas. The internal model, according to this view, is embedded in the newly formed connectivity of a group of neurons. The activity of this group of neurons generates the neural impulses necessary for the execution of the learned motor task. Motor learning and the control of dynamics are thus two facets of the same process. In the next section we describe the formation of a relatively simple internal model.

#### Formation of an internal model: description of the motor task

A task where a subject makes a reaching movement while the hand interacts with a field of external forces is a relatively simple visuo-motor task. In general, in a task such as this, the first problem involved in reaching the hand towards a target is one of transforming information regarding the target position, as presented in the visual domain, into a force to be applied by the muscles to the skeletal system in order to move the hand. Initially, the solution of this problem involves a set of co-ordinate transformations. The work of Andersen *et al.*<sup>2</sup> suggests that the image of the target is transformed sequentially from retinocentric to a head-centered, and finally a body-centered co-ordinate system.

To specify a trajectory of limb towards a target, the CNS must not only locate the position of an object with respect to the body, but also the initial position of the arm. The conventional wisdom is that proprioception provides information about arm configuration to be used in the programming of the trajectory of the arm. Gordon *et al.*<sup>3</sup> have demonstrated, however, that directional errors are present during reaching when subjects rely upon proprioceptive cues only. It is of interest that these errors disappear when static vision of the hand or of the target, or both, is allowed. It is not known where in the CNS the visual and somatic information combine. However, this combination of the

afferent inputs is reflected in the activity of neurons in the motor cortex and parietal cortical area 5 (of Brodmann). Georgopoulos *et al.*<sup>4</sup>, Kettner *et al.*<sup>5</sup>, and Caminiti *et al.*<sup>6</sup> have shown that when a monkey holds its hand at various positions in two-dimensional space, the activity of neurons in cortical areas 4 and 5 (of Brodmann) varies with the position of the hand in space.

It is important to stress that the task of moving the hand to a target position is an 'ill-posed' problem in the sense that an exact solution might either not be available or not be unique. For instance, if the goal is to move the hand from an initial position to a point in space, then there are a number of possible hand trajectories that could achieve this goal; the solution of this motor problem is not unique. Even after the CNS has chosen a particular path for the hand, its implementation can be achieved with multiple combinations of joint motions at the shoulder, elbow and wrist – again the solution is not unique. Finally, because there are many muscles around each joint, the net force generated by their activation can be achieved by a variety of combinations of muscles. The situation is even more complex at the level of individual muscles; eventually the nervous system must specify the activation of each motor unit.

In the particular experiments that are described here, a key feature of the task to which subjects were exposed involved a change in the mechanical environment with which their hand interacted. Because of this change, the internal model of the arm had to adapt to the new dynamics of the environment. In these experiments (see Box 1 for details of the experimental procedure), subjects grasped the handle of a robot manipulandum – a two degrees of freedom, lightweight, low-friction robot with a force–torque transducer mounted on the handles. Two torque motors were mounted on the base of the robot. The manipulandum was programmed to produce forces on the hand of the subject as the subject performed reaching movements. These forces were computed as a function of the velocity of the hand. When the manipulandum was producing a force field, there were forces that acted on the hand as it made a movement, effectively changing the dynamics of the arm. The force field initially caused a significant divergence from the trajectory that was normally observed for a reaching movement. The results of these experiments suggest that the

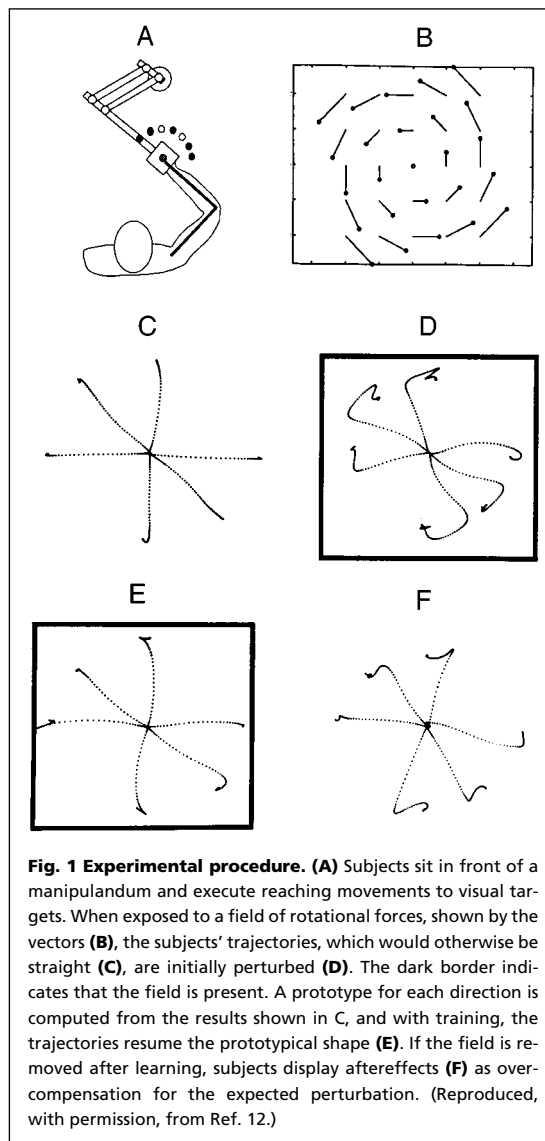
kinematics observed in reaching movements are not just the consequence of arm dynamics, but reflect an underlying plan – a desired trajectory<sup>7</sup>.

Recent results from Flash and Gurevich<sup>8</sup> have provided evidence suggesting that there is an invariant kinematic plan for reaching when a static load is placed on the hand. Similarly, Lacquaniti *et al.*<sup>9</sup> found that subjects who were asked to move a 2.5 kg weight did so, after some practice trials, along essentially the same trajectory as when moving without the weight. Our work has shown that even when the change in the dynamics of the limb is severe, the response is a convergence to the trajectory observed before the change. This convergence can take place over a fairly long practice period (500–1000 movements). This is similar to the conclusion reached for single degree-of-freedom movements by Ruitenbeek<sup>10</sup>, who found that when a subject interacted with a manipulandum with variable dynamics, practice led to a trajectory that was invariant with respect to the dynamics of the manipulandum.

Thus, the subjects' recovery of performance is due to learning. In order to investigate the neural changes underlying this type of motor learning, Shadmehr and Mussa-Ivaldi<sup>7</sup> devised a simple, but revealing, experimental manipulation. After the training had been established, they removed the force field unexpectedly for the duration of a single hand movement. The resulting trajectories, named aftereffects, were approximately mirror images of those that were observed when the subjects were initially exposed to the force field (see Fig. 1F). The magnitude of these aftereffects increased gradually with the practice period. The emergence of the aftereffects indicates that the CNS had composed an internal model of the external force field, which was generating patterns of force that effectively anticipated the disturbing forces that the moving hand encountered. The fact that these learned forces compensated for the disturbances applied by the robotic arm during the subjects' reaching movements indicates that the CNS programs these forces in advance. Thus, the aftereffects demonstrate that these forces are not the product of some reflex compensation of the disturbing field. Experiments by Condit *et al.*<sup>11</sup> have provided additional evidence that the internal model, learned by subjects during the exposure to a perturbing field, is a representation of the functional relationship between the velocity of the hand and the experienced force.

#### Will the internal model generalize beyond the training region?

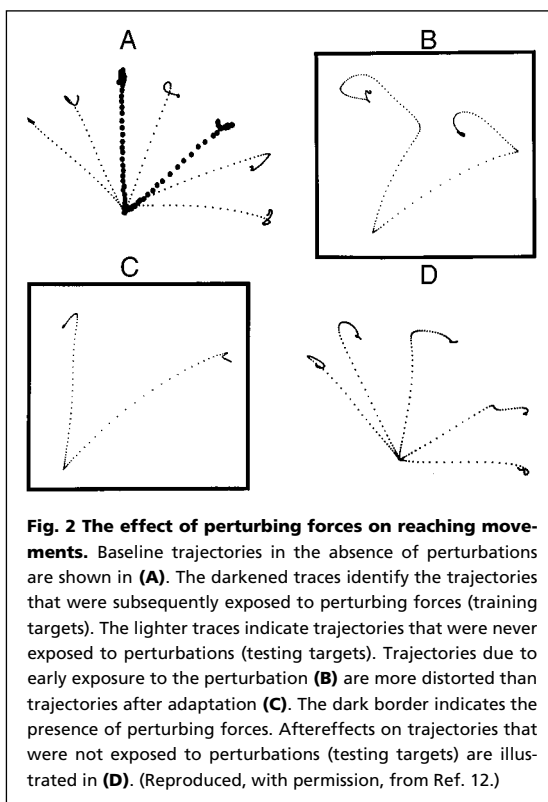
To estimate the generalization of motor learning, Shadmehr and Mussa-Ivaldi<sup>7</sup> asked subjects to adapt to a force field in a region of the workspace, and after adaptation was completed, they tested the subjects' performance in a different region. They found significant aftereffects in the second location, after training in the first. It should be noted that the perturbing field used in these experiments generated forces that depended only on the velocity of the hand. By showing generalization of learning in different locations of the workspace, subjects demonstrated that their adaptive system had captured an important feature of the external field: its relative independence on the operating position.



**Fig. 1 Experimental procedure.** (A) Subjects sit in front of a manipulandum and execute reaching movements to visual targets. When exposed to a field of rotational forces, shown by the vectors (B), the subjects' trajectories, which would otherwise be straight (C), are initially perturbed (D). The dark border indicates that the field is present. A prototype for each direction is computed from the results shown in C, and with training, the trajectories resume the prototypical shape (E). If the field is removed after learning, subjects display aftereffects (F) as overcompensation for the expected perturbation. (Reproduced, with permission, from Ref. 12.)

In subsequent experiments, Gandolfo *et al.*<sup>12</sup> asked subjects to execute movements to targets placed as shown in Fig. 1A. 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. 1A by open circles). Figure 2A shows the baseline trajectories obtained in the absence of perturbations. During the execution of these movements (identified in Fig. 2A by a thick, broken line), a clockwise perturbation was applied to the moving hand, resulting in distortions of these trajectories (Fig. 2B). However, after about 400 movements, the original, nearly straight trajectories reappeared (Fig. 2C). While subjects continued to move to the training targets, 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. However, aftereffects were found to be present (see Fig. 2D) not only along the trained directions, but also along the directions of the test targets.

However, the magnitude of the aftereffects decayed smoothly with increasing distance from the trained directions. The results of Gandolfo *et al.* together with those of Shadmehr and Mussa-Ivaldi indicate that learning is not confined to the particular states of motion, that is, positions



and velocities, explored during the training period. However, the evidence demonstrates that adaptation does not generalize globally across the entire workspace of a limb. Learning can be characterized as local because it affects a limited region that surrounds the positions and velocities experienced during training. The shape and extension of this region remain to be determined, although some data have been provided by the experiments of Gandolfo *et al.* Similar preliminary findings have been reported by R. Sainburg and C. Ghez (pers. commun.). The results of DiZio and Lackner<sup>13</sup> are also consistent with a local model of adaptation. These investigators have shown that adaptation to Coriolis force perturbations of reaching movements does not transfer to the non-exposed arm.

Having found that learning is local, Gandolfo *et al.* searched for the presence of interference that could arise whenever two training configurations were not sufficiently far apart. Subjects were asked to execute a series of movements, some with the wrist in posture A (Fig. 3A), some with the wrist in posture B (Fig. 3B). These grips defined 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, whereas the other (A) was associated with a no-perturbation condition. As expected, Gandolfo *et al.* found that, after training, trajectories performed with posture B displayed aftereffects both during the learning phase (Fig. 3D and F) and when the perturbing field was removed (Fig. 3J). However, quite surprisingly, even the trajectories with posture A, which were performed with no disturbing forces, appeared to show aftereffects during the early learning phase (Fig. 3E). This finding indicates that in the initial phases of learning 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 Figs 3G and 3I). By contrast, as shown in Fig. 3J, clear aftereffects were observed when the subjects moved the manipulandum with the posture B.

Gandolfo *et al.* concluded that during adaptation, the motor-control system carries out a reconstruction of the 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. A possible interpretation of this result is that 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 two separate mappings between joint angles and joint torques. At the completion of training, these mappings do not interfere with each other because the two sets of joint angles are separate. Therefore, the experiments by Gandolfo *et al.* 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 – the 'null' field – associated with posture A, and field B with posture B) can be regarded as mappings between torques and limb configurations.

Shadmehr and Mussa-Ivaldi<sup>7</sup> and Gandolfo *et al.*<sup>12</sup> have shown that subjects adapt to a new environment by forming a representation of the external force field that they encounter when making reaching movements. Does this representation form an imprint in long-term memory? Recently, Brashers-Krug *et al.*<sup>14</sup> investigated this question by exposing their subjects to perturbing force fields that interfered with the execution of reaching movements. After practicing reaching movements, these subjects were able to compensate for the imposed forces and were able to guide the cursor accurately to the targets, despite the disturbing forces. This group of subjects, which was tested 24 hours later with the same disturbing forces, demonstrated not only retention of the acquired motor skill, but also additional learning. Surprisingly, they performed at a significantly higher level on day two than they had on day one.

A second group of subjects was trained on day one with one pattern of forces (such as pattern B) immediately after learning a different pattern (A). Pattern B produced forces in a clockwise direction, but forces in the opposite direction were generated during exposure to pattern A. When this second group of subjects was tested for retention on day two on pattern A, Brashers-Krug *et al.*<sup>14</sup> found that the subjects did not retain any of the skills that had been learned in A. This phenomenon is known as retrograde interference. Next, Brashers-Krug *et al.* investigated whether or not the susceptibility to retrograde interference decreased with time. They found that retrograde interference decreased monotonically with time as the interval between pattern A and B increased. Thus, when four hours was allowed to pass before pattern B was learned, the skill learned during exposure to pattern A was retained; that is, the initial learning had consolidated. What is remarkable in these results is that motor memory is transformed with the passage of time and

in absence of further practice, from an initial fragile state to a more solid state.

Taken together these experiments indicate that: (1) the internal model is limited to a region surrounding that part of the space where the disturbances had been experienced, and the same external disturbances could not be handled outside this region; (2) there is an enhancement of the internal model that does not depend upon practice, but only the mere passage of time; and (3) there is a process of consolidation of the internal model that takes a minimum of four hours. The consolidation is not dependent on practice; it is an internally generated event.

### Some implications of these studies

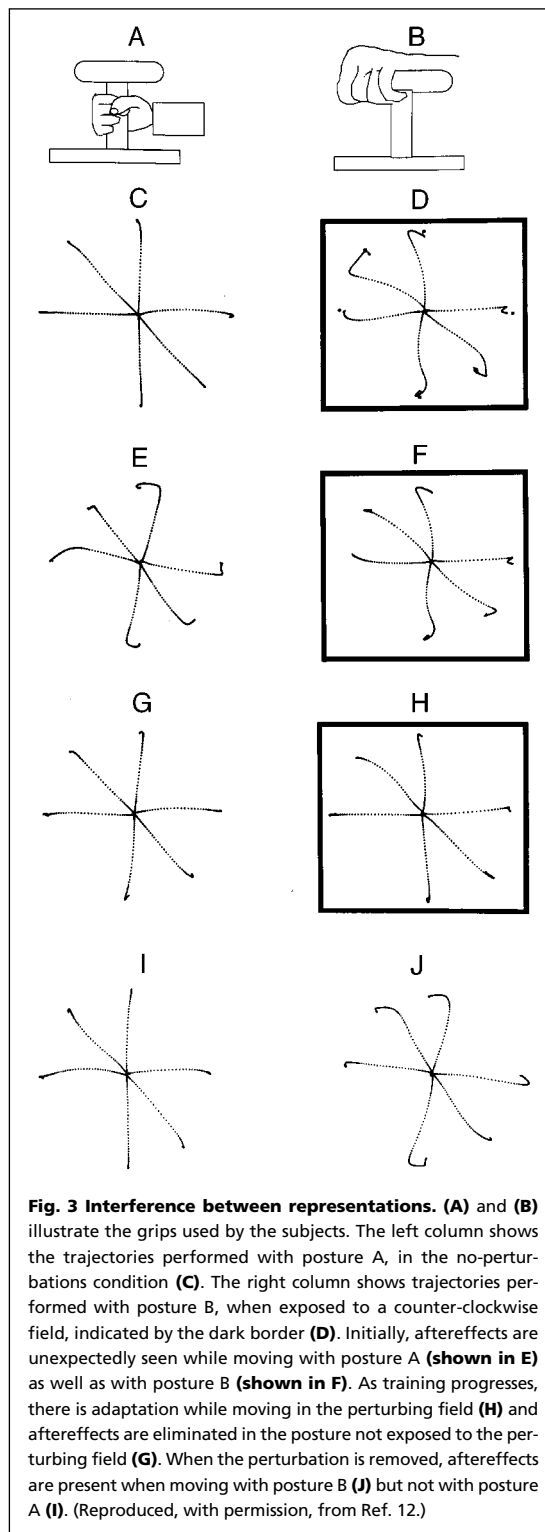
An implication of these studies is that there is an internal model for each of the tasks that we have learned throughout our life. This is a possibility in view of the fact that we conceive the internal model as a newly formed pattern of synaptic facilitations among a group of neurons. According to this view, it is possible that a given neuron may participate with a different synaptic weight in a number of assemblies, each supporting a different internal model.

Given the large number of synapses on the surface of neurons, this arrangement could sustain a very large number of internal models. However, it remains to be understood how the internal model, which (according to the experiments just reviewed) represents a specific mapping between sensory input and motor output, can include the flexibility that is needed in real life contingencies. As an alternative, entirely speculative view, internal models could be conceived, not as independent entities, but also as units that can be combined in bigger assemblies when more demanding motor tasks are faced by the body.

The studies based on recording the activity of individual cells and those that utilize imaging techniques have not yet provided an answer to these complex questions. However, these studies have demonstrated the involvement of cortical and subcortical neurons in the acquisition of motor tasks (Refs 15,16). Some of the most direct evidence for the development of new patterns of activity in the cells of the motor area of the frontal lobe, named M1, has been reported by B. Benda *et al.* (pers. commun.). Their most striking result was the gradual recruitment of previously silent cortical neurons in area M1; these neurons displayed activity related to the production of forces that compensated externally imposed disturbances. Similar results have been reported by S. Wise *et al.* (unpublished) with the same technique of single-cell recordings, but with different behavioral paradigms.

We assume that the patterns of activity that develop in the cortex during learning are conveyed by the cortico-spinal pathways to the spinal cord. Anatomical studies have clearly indicated that the descending fibers display considerable branching as they approach their main targets: the interneurons of the spinal cord. Hence, it is reasonable to speculate that the descending motor commands conveyed by the cortico-spinal pathways would make use of the circuitry of the spinal cord.

Recently we have investigated this circuitry and have proposed that the spinal-cord interneurons are organized in



**Fig. 3 Interference between representations.** (A) and (B) illustrate the grips used by the subjects. The left column shows the trajectories performed with posture A, in the no-perturbations condition (C). The right column shows trajectories performed with posture B, when exposed to a counter-clockwise field, indicated by the dark border (D). Initially, aftereffects are unexpectedly seen while moving with posture A (shown in E) as well as with posture B (shown in F). As training progresses, there is adaptation while moving in the perturbing field (H) and aftereffects are eliminated in the posture not exposed to the perturbing field (G). When the perturbation is removed, aftereffects are present when moving with posture B (J) but not with posture A (I). (Reproduced, with permission, from Ref. 12.)

functional modules to produce muscle synergies. We have shown that the spinal cord contains circuitry that, when activated, produces precisely balanced contractions in groups of muscles. These synergistic contractions generate forces that direct the limb towards an equilibrium point in space. Bizzi *et al.*<sup>17</sup> and Giszter *et al.*<sup>18</sup> have shown that microstimulation of the lumbar gray resulted in a limited number of force patterns. A number of regions of the spinal gray from which the same force pattern was elicited were identified.

Bizzi *et al.*<sup>17</sup> have shown that the simultaneous stimulation of two sites, each generating a force field, results in a

force field proportional to the vector sum of the two fields. Vector summation of force fields implies that the complex non-linearities that characterize the interactions both among neurons and between neurons and muscles are in some way eliminated. More importantly, this result has led to a novel hypothesis for explaining movement and posture based on combinations of a few basic elements. The limited force pattern could be viewed as representing an elementary alphabet from which, through superimposition, a vast number of movements could be fashioned by impulses conveyed by supraspinal pathways. Using mathematical modelling, Mussa-Ivaldi and Giszter<sup>19</sup> have verified that this novel view of the generation of movement and posture has the competence required for controlling a wide repertoire of motor behaviors. Recently, Lukashin *et al.*<sup>20</sup> have shown, using modelling, how the directionally tuned cortico-motor cells could converge upon the spinal motor neurons to produce force fields.

### Conclusions

We have briefly discussed evidence suggesting that the CNS is capable of learning and representing the dynamic properties of the limbs and of the environment with which they come in contact. This representation is an internal model. The internal model may be part of a control scheme in which the modules of the spinal cord are utilized by the supraspinal control signals. This view is in agreement with the results reported recently by Flanagan and Wing<sup>21</sup>. Anatomically, the neurosubstrate of the internal model is distributed; motor cortex, basal ganglia, and cerebellum are interconnected structures that are active to different degrees during the acquisition of motor skills. The modules of the spinal cord, which can act together, could provide a rich motor behavior when activated by supra-spinal commands.

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