# Modular Organization of Motor Behavior*

E. Bizzi, P. Saltiel, M. Tresch

Massachusetts Institute of Technology, Department of Brain and Cognitive Sciences,
77 Massachusetts Avenue, Cambridge, MA 02139-4307, USA

Z. Naturforsch. **53c,** 510–517 (1998); received May 20, 1998

Convergent Force Field (CFF), Spinal Cord, Spinal Interneurons, Vector Summation of CFF, Modules, Muscle Synergies

The issue of translating the planning of arm movements into muscle forces is discussed in relation to the recent discovery of structures in the spinal cord. These structures contain circuitry that, when activated, produce precisely balanced contractions in groups of muscles. These synergistic contractions generate forces that direct the limb toward an equilibrium point in space. Remarkably, the force outputs, produced by activating different spinal-cord structures, sum vectorially. This vectorial combination of motor outputs might be a mechanism for producing a vast repertoire of motor behaviors in a simple manner.

## Introduction

To specify a plan of action the central nervous system must first transfer the sensory inputs into motor goals, such as the direction, the amplitude, and the velocity of the intended movement. Then, to execute movements, the CNS must convert the desired goals into signals that control the muscles that are active during the execution of even the simplest kind of limb trajectory. Thus, the CNS must transform information about a small number of variables (direction, amplitude and velocity) into a large number of signals to many muscles.

Any transformation of this type is "ill-posed" in the sense that an exact solution might either not be available or not unique. For instance, if the goal is to move the hand from an initial position [A], to a point [B] in space, then, clearly there are a number of possible hand trajectories that could achieve this goal: the solution of this elementary motor problem is not unique. Even after the central nervous system 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: potentially the nervous system must specify the activation level of each motor unit.

Recently, a way to transform motor goals into the muscle synergies that subserve a limb's movement has been described. Electrical and chemical (NMDA) stimulation of the interneuronal circuitry of the spinal cord has been shown to impose a specific balance of muscle activation leading to a convergent force field.

## Description of Convergent Force Fields (CFFs)

In this section, we describe the results we obtained through microstimulation of the lumbar region of the spinal cord in spinalized frogs. Bizzi *et al.* (1991) and Giszter *et al.* (1993) elicited the activation of the leg's muscles by microstimulating the lateral and intermediate neuropil zone (300 to 1000 μm in depth and 200 to 500 μm from the midline). Each stimulus consisted of a train of anodal current impulses. Typically, the train lasted 300 msec. The peak current's amplitude ranged between 1 and 8 μA. This peak magnitude corresponded to an estimated stimulation volume of less than 100 μm radius. Enough current was used so as to elicit measurable mechanical responses

---

* This communication is a contribution to the workshop on "Natural Organisms, Artificial Organisms, and Their Brains" at the Zentrum für interdisziplinäre Forschung (ZiF) in Bielefeld (Germany) on March 8–12, 1998.

Reprint requests to Prof. E. Bizzi.
Fax: 617-2585342.
E-mail: emilio@ai.mit.edu.

0939–5075/98/0700–0510 $ 06.00 D

while remaining close to the threshold of EMG activations.

To measure the mechanical responses of the activated muscles, Bizzi *et al.* attached the right ankle of the frog to a six-axis force transducer, as shown in Fig. 1. The transducer held the ankle approximately level with the acetabulum. The transducer was mounted on a two-axis Cartesian manipulator, and the Cartesian location of the frog's ankle was set using this manipulator. The $x$-$y$-plane corresponded approximately to the horizontal plane. The output of the transducer was a set of three forces and three torques. In the experiments described here only the $x$ and $y$ components were considered. Following the microstimulation of the spinal cord, Bizzi *et al.* observed a change in the forces at the ankle after a latency of between 30 and 150 msec. (Most response latencies were at about 100 msec.) The forces rose to a plateau level, and then declined to the baseline level after a variable period (300 msec to 2 sec) following the termination of stimulation. At each ankle location, the net force vector, $\boldsymbol{F}$, obtained in response to stimulation, was expressed as the sum of two components – the "resting" force vector, $\boldsymbol{F}_r$, and the "active" force vector, $\boldsymbol{F}_a$:

$$\boldsymbol{F} = \boldsymbol{F}_r + \boldsymbol{F}_a. \tag{1}$$

The resting force vector corresponded to the force measured before the onset of the stimulus. The active force vector, $\boldsymbol{F}_a = \boldsymbol{F} - \boldsymbol{F}_r$, represented the additional forced induced by our stimulus. The active field was generated only by those muscles directly or indirectly activated in response to stimulation.

As the electrode penetrated deeper into the cord, the orientation of the "active," above-baseline force vector recorded at a given leg position generally remained constant. Its magnitude usually varied, reaching a peak at the site of lowest threshold. Normally, as long as a single electrode penetration remained in the lateral neuropil, the

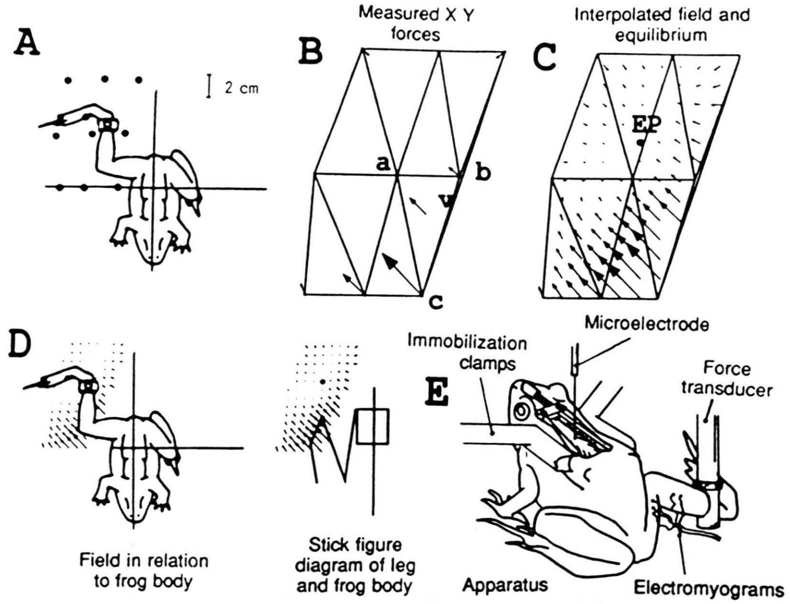

Fig. 1. The apparatus and method of construction of a force field. A, A collection of forces recorded at several different spatial locations (circles). B, A minimum perimeter (Delaunay) tessellation of the nine points is constructed. Within each triangle, vectors are estimated using an exact linear interpolation based on the three corner vectors. Thus, vector v is calculated using vectors at vertices a, b, and c. C, The interpolated field is used to find any equilibria (EP). D (Left), The interpolated force field is shown in relation to the frog in the apparatus. (Right), This reduced to a stylized construction that is used to express the relation of frog body axis and leg to the interpolated force field in the remaining figures. E, The apparatus. The spine is clamped. The pelvis is held clamped by restraints (not shown). With an elec-trode in the spinal gray, the mechanical response to stimulation is recorded at the force sensor that is attached to the limb at the ankle. The limb configuration is fully constrained by the pelvis restraint and the force sensor (from Bizzi *et al.* (1995) TINS **18,** 442–446).

same force orientation was maintained at depths ranging from 400 to 800 μm, and the same collection of muscles was activated.

To record the spatial variations of forces generated by the leg muscles, Bizzi *et al.* followed a three-part procedure. First, they placed the frog's leg at a location within the leg's workspace. Second, they stimulated a site in the spinal cord and recorded the direction and amplitude of the elicited isometric force at the ankle. Third, they repeated the stimulation procedure with the ankle placed at each of 9–16 locations. These locations sampled a large portion of the region of the horizontal plane that could be reached by the frog's ankle (i.e., the leg's workspace). At each location, they stimulated the same site in the spinal cord and recorded the force vector, $\boldsymbol{F} = (\boldsymbol{F}_x, \boldsymbol{F}_y)$ at the ankle. Although the site of spinal cord stimulation was constant throughout, they found that the elicited force vector varied as they placed the leg at different locations. These changes in force throughout the workspace resulted from a variety of mechanical factors such as the length, moment arms, and viscoelastic properties of the muscles. In addition, reflex modulation of the muscles' activations played a role in the development of the forces at the ankle.

The collection of the measured forces corresponded to a force field (Fig. 1). Remarkably, in most instances (80%), the spatial variation of the measured force vectors resulted in a field that was at all times both convergent and characterized by a single equilibrium point (i.e., a point at which the amplitude of the $\boldsymbol{F}_x$ and $\boldsymbol{F}_y$ force components was zero). This equilibrium point represented the locus at which the leg would have been at steady state if it were free to move. The temporal evolution of the total force field caused a smooth movement of the equilibrium point from its position at rest to a new position at peak force magnitude and then back to the resting position. This motion of the equilibrium point constitutes what has been called the "virtual trajectory." The virtual trajectory is defined as the trajectory of positions at which the leg would experience no net force.

Bizzi *et al.* and Giszter *et al.* found that the interpretation of the force field data was simplified when the baseline forces (representing the resting field) were removed. Following a division of the total field into active and resting fields, they found there were important distinctions between the active and the total fields. The equilibria of the total recorded fields were spread across the workspace. However, they found that the active-field data fell into a few classes or force field types (Fig. 2). When they varied the duration and amplitude of stimulation, they found that the structure of the peak active field remained constant. (In other words, the orientation, the relative proportions of force vector magnitudes, and the equilibrium location were stable.)

## Different Types of Force Fields

After mapping most of the premotor area of the lumbar cord, Bizzi *et al.* (1991) and Giszter *et al.* (1993) reached the conclusion that there are at least four areas from which four distinct types of CFFs are elicited. Within each region, a qualitatively similar set of *x* and *y* forces were produced. This map of postures is shown in Fig. 2.

Recently, Giszter *et al.* (1998) performed another series of mapping experiments of the lumbar spinal cord, and used a measurement grid at a finer grain. They examined the spatial variations of force production and muscle activity across the

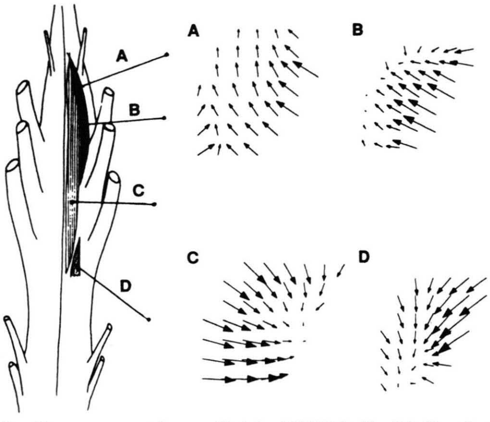

Fig. 2. Convergent force fields (CFFs) (Left) Regions of the lumbar spinal cord that contain the neural circuitry that specifies the force fields (A through D). Within each region, similar sets of CFFs are produced. The diagram is based on 40 CFFs that were elicited by microstimulation of premotor regions in three frogs with transected spinal cords. (Right) Four types of CFFs. To facilitate comparison among CFFs that were recorded in different animals, the passive force field was subtracted from the force field that was obtained in steady state (from Bizzi *et al.* (1991) Science **253,** 287–291).

entire lumbar spinal cord in six frogs at 200 micron intervals mediolaterally and dorsoventrally, and 1 μm intervals rostrocaudally. The recorded data represent a three dimensional map of the lumbar cord. In order to generate these maps, they focused on measurement of force samples at a fixed limb configuration. This restriction of data collection to single force vectors rather than fields was done to make the mapping experiments feasible. Full force field collection at the density of sampling used in this study would not be possible because of the data explosion of at least an order of magnitude that would be required for force field description.

By normalizing individual force samples and using kernel smoothing, they obtained probability distributions for force directions in the total data set. They observed that only a few directions were very strongly represented. This result confirms previous results. In the course of these experiments, they recorded the electromyographic (EMG) patterns from 11 of the legs' muscles in six frogs. The analysis of these indicated that a few (one or two) EMG patterns may be associated with a given force direction.

## Control Experiments

A priori, there are a number of structures in the spinal cord whose activation might give rise to CFFs. For instance, CFFs might derive (A) from stimulation of the intraspinal components of sensory and descending fibers; (B) from current spreading to the motoneurons and to the afferent fibers ending upon them, either randomly or in accordance with their topographic organization; or (C) from activation of long and short propriospinal INs. The following experiments were designed to explore these alternatives.

### *CFFs are elicited in chronically transected frogs*

Giszter *et al.* (1993) kept chronically transected frogs alive up to six weeks before performing microstimulation. Under these circumstances, all descending tracts and their synaptic arbors have degenerated. In these chronically transected animals, fields were essentially unchanged compared to fields recorded in acutely transected animals.

### *CFFs are found in acutely deafferented frogs*

Loeb *et al.* (1993) have demonstrated identity of force field patterns at a single spinal cord site both before and after acute deafferentation. Thus, the pattern of afferent impulses and the presence and topography of afferent terminals are not necessary for the generation of CFFs.

### *CFFs are found in chronically deafferented frogs*

Giszter *et al.* (1993) microstimulated chronically deafferented spinal frogs and found that the CFFs with equilibria persisted. To obtain complete degeneration of afferent fibers, they allowed a full three weeks after the bilateral section of roots 10, 9, 8, and 7. Microstimulation performed in these chronically deafferented, but acutely spinalized frogs showed that both the strength of the fields and their convergent tendency were preserved though some disorganization was seen in a few fields.

### *Direct stimulation of motoneuronal areas does not usually result in CFFs*

When Giszter *et al.* placed microelectrodes directly among the motoneurons' somas or in the ventral roots, they often obtained force fields with divergent or parallel patterns rather than convergent patterns.

### *CFFs and natural behaviors*

Gizster *et al.* (1993) and Tresch (1997) have shown that, qualitatively and quantitatively, force fields similar to those induced by microstimulation are elicited in spinal frogs by cutaneous stimulation.

## Conclusions Derived from Control Experiments

Taken together, the results indicate that the electrical and chemical stimulation of the premotoneuronal circuitry imposes a specific balance of muscle activations leading to a convergent force field. These muscles' activations cannot be established by current spread or random activation of motoneurons. Neither can they be the result of activating the fibers of passage belonging to the sensory and descending systems. On the basis of these control experiments, the conclusion was reached that the *intrinsic interneural circuitries* of the spinal cord must be the source of the specific types of convergent force fields.

## Convergent Force Fields Elicited by Chemical Stimulation

With electrical stimulation, it is not clear, even in chronically deafferented preparations at what level the interneuronal systems are being stimulated: somas, dendrites, axons and nerve terminals can all be depolarized by current. For this reason, Saltiel *et al.* (1998) induced force output from the spinal cord of the frog by using a compound that is known to activate only somas and dendrites (Saltiel *et al.*, 1996). NMDA microiontophoresis was used with current and duration parameters expected to produce a spread estimated at 150–270 μm radius.

This study confirmed that the spinal cord produces a limited number of discrete motor outputs, identified as five preferential directions of the isometric force vector recorded at the ankle in a single limb position. NMDA iontophoresis was applied to 229 sites of the lumbar spinal cord gray while monitoring the isometric force output of the ipsilateral hindlimb at the ankle. A force response was elicited from 69 sites. At 18 of these sites, tonic forces were generated, and at 44, rhythmic forces were generated. In the case of tonic forces, their directions clustered along four orientations: lateral extension, rostral flexion, adduction and caudal extension. For the entire set of forces (tonic and rhythmic), the same clusters of orientations were found with the addition of a cluster directed as a flexion towards the body. This distribution of force orientations was quite comparable to that obtained with electrical stimulation at the same sites, although they did not necessarily match at individual sites. The map of tonic responses revealed a topographic organization; each type of force orientation was elicited from sites that grouped together in zones at distinct rostrocaudal and depth locations. In the case of rhythmic sequences of force orientations, some were distinctly more common, while others were rarely elicited by NMDA. Mapping of the most common rhythms showed that each was elicited from two or three regions of the cord. These regions were close in location to the tonic regions which produced those forces that represented components specific to that rhythm. There was an additional caudal region from which the different rhythms could also be elicited. Taken together, these results support the concept of a modular organization of the motor system in the frog's spinal cord and delineate the topography of these modules. They also suggest that these modules are utilized by central pattern generators.

These results suggest that the different types of responses organized within the spinal cord, evoked either by NMDA or by microstimulation, might be combined together in order to create complex behaviors, such as those produced during rhythmic pattern generation. One mechanism by which these responses might be combined flexibly in order to create more complex behaviors is described in the next section.

## Vector Summation of CFF Modules: Costimulation of Two Sites in the Spinal Cord

One of the most remarkable observations derived from the microstimulation of the frog spinal cord has been that the fields induced by the focal activation of the spinal cord follow a principle of vectorial summation. Specifically, Mussa-Ivaldi *et al.* (1994) have investigated vectorial summation with the following experimental paradigm. First, a focal electrical stimulation was delivered to a site, A, of the spinal cord and the subsequent active field $\Phi_A(x)$ was determined by measuring a set of force vectors at distinct ankle locations. Following the measurement of $\Phi_A(x)$, a second electrical stimulation was applied to a different site, B, and a field $\Phi_B(x)$ was derived. From these two fields their sum, $\Phi_\Sigma(x) = \Phi_A(x) + \Phi_B(x)$, was computed at all the sample points. Finally, another active field, $\Phi_\&(x)$, was measured by stimulating the sites A and B simultaneously. When Mussa-Ivaldi *et al.* compared the "costimulation fields", $\Phi_\&(x)$, with the corresponding "summation fields", $\Phi_\Sigma(x)$, they found that in 80% of cases the two fields were equivalent.

The observation that force fields sum vectorially suggests a way to relate natural movements to spinal cord microstimulation. Diverse neural signals conveyed by afferent inputs or descending tracts may gain access to the premotor areas described by Bizzi (1991) and Giszter (1993), and in this way specify the activation of a set of muscles. Physiological movements result from patterns of neural activity distributed by afferent fibers and/or by descending branching fibers throughout fairly wide regions of the spinal cord. The activity conveyed by these branches may stimulate local clusters of cells that in turn generate force fields. Our assumption is that these fields sum like the convergent force fields generated by our electrical or chemical stimulation, leading to the possibility that a wide range of behaviors can be created by the summation of these different force fields.

## The Mechanical Basis of Summation: Costimulation of Muscles and Kinematic Redundancy

Mussa-Ivaldi *et al.* (1994) also observed vector summation as a result of muscle costimulation. In this case, they repeated the procedure described above while stimulating two muscles instead of two sites of the spinal gray. The summation of endpoint force fields is not surprising when the limb is kept in a *non-redundant* kinematic configuration (i.e. when the number of endpoint coordinates does not exceed the degrees of freedom upon which muscles exert their action). Each endpoint position determines a corresponding set of joint angles; for each set of joint angles, each muscle generates a well-defined joint torque vector and a corresponding endpoint force; the net torque on the limb is the sum of individual torques (in effect, the muscles act "in parallel" on the limb) and hence the net endpoint force field is the sum of individual muscle fields.

However, Gandolfo and Mussa-Ivaldi (1993) were quite surprised to observe endpoint field summation when the frog's leg was connected to the force sensor in a kinematically redundant configuration. In these experiments, the foot was attached to the sensor through a gimbal which allowed the leg to assume a variety of configurations while the center of the foot was held at a fixed location of the plane. In particular, six joint angles (three at the hip, one at the knee and two at the ankle) were needed to define the configuration of the frog's leg. Consequently, each endpoint position does not uniquely define the limb configuration, which instead varies with the particular muscle or muscles that are activated. Straightforward analysis is sufficient to establish that the endpoint force fields, in this case, need not combine according to vector summation, even in the simple case in which independent muscles are coactivated.

Consider, for example, the fields of forces induced at the endpoint of the redundant limb by the activation of two distinct muscles, m and n, each one acting independently on different joint angles, $q_1$ and $q_2$. When muscle m is activated it induces a *torque field* $\tau_m(\theta)$. That is, for each setting of the joint angles, $q = (q_1, q_{2, \ldots})$, the muscle generates a well-defined joint torque vector. Similarly, a torque field $\tau_n(\theta)$ is induced by the activation of muscle n and costimulation torque field $\tau\Sigma(q)$ is induced by activating both muscles. However, in the experiment, only the location of the foot is fixed. When the muscles are activated separately and simultaneously, the limb assumes three *different* configurations qm, qn, and $\theta\Sigma$ corresponding to the three experimental conditions. Consequently, there is no guarantee that the net torque field $\tau\Sigma(\theta\Sigma)$ due to simultaneous activation of the muscles is the sum of the component torque fields $\tau m(\theta m)$ and $\tau n(\theta n)$ because the three functions have different arguments (the three different limb configurations). By the same reasoning there is no guarantee that the corresponding endpoint force fields will combine by vector summation.

While these mechanical considerations show that the endpoint fields of a redundant limb need not to combine vectorially, they do not rule out vector summation in particular cases, nor are they sufficient to establish the expected degree of non linearity. The surprising experimental results of muscle costimulation in the redundant limb indicated that vectorial summation is the predominant rule describing the effect of combining two stimuli.

## Discrete Organization of Movements Evoked by Intraspinal Stimulation in the Rat Spinal Cord

The results described above were all found from examination of the frog spinal cord. Although the spinal cord of the frog shares many characteristics with the spinal cords of other vertebrates, there are also significant differences (Simpson, 1976). Because of these differences, generalizing the results found in the frog to other vertebrates can be difficult. There is also not as much known about the organization of the frog spinal cord as compared to the spinal cords of other vertebrated species, especially mammals.

For these reasons, Tresch and Bizzi (1995) examined the organization of movements obtained from applying microstimulation to the interneuronal regions of the spinal cord of a mammal, that of the rat. The motivation for these experiments was to test whether an organization similar to that of the frog could be observed in the rat spinal cord.

The results obtained from microstimulation of the rat spinal cord were very similar to those obtained from microstimulation of the frog spinal cord. First, microstimulation of interneuronal regions of the rat spinal cord evoked force fields similar to those found in the frog: i.e., they were convergent. Second, there were only a small number of different types of force fields observed from microstimulation of the rat spinal cord, as was described for the frog. Finally, stimulation simultaneously applied to two sites in the spinal cord produced a response which was a simple linear summation of the responses evoked from each site separately, a result also described for the frog. The consistency of these three features – convergence, modularity, and summation – in the responses evoked from microstimulation of the frog and the rat spinal cords suggest that these features might be general across different vertebrate species.

The experiments in the rat also suggested a link between the organization of the responses evoked from spinal microstimulation and known aspects of the physiological organization of the mammalian spinal cord. In particular, Tresch and Bizzi (1995) found that the anatomical organization of different types of movements within the rat spinal cord paralleled the somatotopical organization of spinal cutaneous systems. This relationship between the movement evoked from stimulating a site and the cutaneous receptive field of that site suggested a relationship between the movements observed from spinal microstimulation and the cutaneous systems organized within the spinal cord.

## Withdrawal Reflexes are Organized into a Small Number of Distinct Patterns of Muscle Activation in the Frog

This relationship between spinal cutaneous systems and the movements evoked from spinal microstimulation has been explored more extensively in a series of recent experiments (Tresch, 1997) These experiments examined the patterns of muscle activations underlying withdrawal reflexes and compared these patterns to those evoked from microstimulation of the frog spinal cord. The first observation Tresch and Bizzi (1995) made was that the withdrawal reflexes in the frog were organized in terms of a small number of discrete patterns of muscle activations. Each activation pattern was preferentially evoked from cutaneous stimulation of a particular region of the hindlimb skin surface: one from the back of the calf, one from the foot, and one from the front of the calf.

Tresch, in his thesis, then compared these distinct patterns of muscle activations to the distinct patterns of muscle activation evoked from spinal microstimulation of the frog spinal cord described previously (Bizzi *et al.,* 1991; Giszter *et al.,* 1993). He assessed the degree of similarity between these responses by using a number of different quantitative methods. He found that each method of comparison showed that the two sets of responses were, in fact, very similar to one another. This result suggests a relationship between the movements evoked from spinal microstimulation and the spinal neural systems underlying withdrawal reflexes. This relationship helps to place the results observed from spinal stimulation by Bizzi *et al.* (1991) and Giszter *et al.* (1993) in a physiological context. One of the main concerns with using microstimulation anywhere in the nervous system is the extent to which the effects of such stimulation reflect the normal physiological function of the stimulated substrate. By demonstrating the similarity between the responses from spinal microstimulation and withdrawal reflexes, Tresch concluded that the responses from spinal microstimulation are physiologically relevant. Given the nonspecific nature of microstimulation, this observation is important.

Despite the similarity between the two types of responses, Tresch and Bizzi (1995) consistently observed that the responses were not identical. These systematic differences might arise for a number of reasons. For instance, the difference might arise because the responses from spinal stimulation reflect the organization of both spinal cutaneous systems and some other, currently uncharacterized, spinal system, such as that activated by proprioceptive systems. Similarly, the difference could result from the fact that the only cutaneous behavior Tresch examined was withdrawal: other behaviors organized in the spinal cord, such as scratch reflexes, might also be expected to be related to the cutaneous somatotopical organization of the spinal cord. However, the similarity between the two types of responses does suggest that microstimulation of the spinal cord is reflecting the organization of spinal cutaneous systems to a large degree.

Another observation Tresch and Bizzi (1995) made was that the responses from spinal microstimulation did not appear to be more simple or fundamental to the production of behavior than the withdrawal reflexes themselves. In both types of responses, there was a similar number of muscles activated. This observation suggests that the spinal responses are similar to withdrawal reflexes as a whole, and do not represent components of these behaviors.

## Conclusions

It is striking that all three methods of evoking movements from the spinal cord examined in these experiments: spinal microstimulation, NMDA iontophoresis, and of cutaneous stimulation, each evoked only a few types of movements. These observations have been previously characterized as reflecting a 'modular' organization of motor systems in the spinal cord. In this hypothesis, each spinal 'module' produces a distinct pattern of muscle activations. These results are therefore consistent with the idea that movements produced by the spinal cord are organized in terms of muscle synergies. The finding that the spinal cord organizes movements into only a small number of muscle synergies is surprising and begs the question of why this modularity arises.

One possible reason for a modular organization of spinal systems might be to reduce the degrees of freedom of the motor system in order to simplify the control of movements. By organizing the spinal cord into a small number of distinct muscle synergies, the nervous system can produce movements by specifying only a handful of variables. This hypothesis is similar to hypotheses previously proposed by other researchers (e.g. Sherrington, 1910; Grillner 1981; Stein 1986). In this context, the modularity of the spinal cord reflects an elegant solution by which the nervous system can produce a wide range of movements in a simple and flexible way.

Bizzi E., Mussa-Ivaldi F. and Giszter S. (1991), Computations underlying the execution of movement: a biological perspective. Science **253,** 287–291.

Gandolfo F. and Mussa-Ivaldi F. (1993), Vection summation of end-point impedance in kinematically redundant manipulators. In: IEEE/RSJ International Conference on Intelligent Robots and Systems, July 26–30, Yokohama, Japan.

Giszter S., Mussa-Ivaldi F. and Bizzi E. (1993), Convergent force fields organized in the frog's spinal cord. J. Neurosci. **13,** 467–491.

Giszter S., Loeb E., Mussa-Ivaldi F. and Bizzi E. (1998), Spatial maps of forces and muscle activity in lumbar spinal cord of the spinal frog elicited by microstimulation, in prep.

Grillner S. (1981), Control of locomotion in bipeds, tetrapods, and fish. In: Handbook of Physiology, The Nervous System, Motor Control (Brooks V., ed). Am. Physiol. Soc., Bethesda, MD, pp. 1179–1236.

Loeb E., Giszter S., Borghesani P. and Bizzi E. (1993), Effects of dorsal root cut on the forces evoked by spinal microstimulation in the spinalized frog. Somatosensory & Motor Res. **10,** 81–95.

Mussa-Ivaldi F., Giszter, S. and Bizzi E. (1994), Linear combinations of primitives in vertebrate motor control. Proc. Natl. Acad. Sci. USA **91,** 7534–7538.

Saltiel P., Tresch M. and Bizzi E. (1996), Modularity of the frog spinal cord motor system. Soc. Neurosci. Abs. **22,** 669.

Saltiel P., Tresch M. and Bizzi E. (1998), Spinal cord modular organization and rhythm generation: an NMDA iontophoretic study in the frog. J. Neurophysiol., in press.

Sherrington C. (1910), Flexion-reflex of the limb, crossed extension reflex and reflex stepping and standing. J. Physiol. **40,** 28–121.

Simpson J. (1976), Functional synaptology of the spinal cord. In: Frog Neurobiology (Llinas R. and Precht W., eds.). Springer, Berlin, pp. 679–706.

Stein P., Mortin L. and Robertson G. (1986), in: Neurobiology of Vertebrate Locomotion: Proceedings of an International Symposium Held at the Wenner-Gern Center, Stockholm, June 17th–19th, 1985 (Grillner S., Stein P., Stuart D., Forssberg H. and Herman, R., eds.). Macmillan Press, London, pp. 201–216.

Tresch M. (1997), A discrete organization of movements evoked by intraspinal and cutaneous stimulation in the frog and rat spinal cords. Ph.D. Thesis. Brain and Cognitive Sciences. MIT, Cambridge, MA.

Tresch M. and Bizzi E. (1995), Convergent force fields in the rat spinal cord. In: 5th Annual Meeting on Neural Control of Movement, Key West, FL.