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Computations Underlying the Execution of Movement: A Biological Perspective

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To execute voluntary movements, the central nervous system must transform the neural representation of the direction, amplitude, and velocity of the limb, represented by the activity of cortical and subcortical neurons, into signals that activate the muscles that move the limb. This task is equivalent to solving an "ill-posed" computational problem because the number of degrees of freedom of the musculoskeletal apparatus is much larger than that specified in the plan of action. Some of the mechanisms and circuitry underlying the transformation of motor plans into motor commands are described. A central feature of this transformation is a coarse map of limb postures in the premotor areas of the spinal cord. Vectorial combination of motor outputs among different areas of the spinal map may produce a large repertoire of motor behaviors.

THE CENTRAL NERVOUS SYSTEM (CNS) CONTROLS THE events from the planning to the execution of movements. To specify a plan of action, the CNS must first transform sensory information into motor goals such as the direction, amplitude, and velocity of the intended movement. In higher vertebrates, these motor goals are represented by the activity of populations of neurons in different cortical and subcortical areas (*1*). Recordings of the electrical activity of single neurons from the parietal and frontal cortices of monkeys show a correlation between neural activity and the direction of the movement of the arm (*1*). Furthermore, on the basis of these recordings, a number of investigators have argued that the activity of cortical cells is represented in spatial coordinates without any specification about how muscles are to be engaged to

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produce the forces necessary for the movement (*1*). If actions are planned in spatial or extrinsic coordinates, then for the execution of movement the CNS must convert the desired direction, amplitude, and velocity of the limb into signals that control the muscles. A large number of muscles are simultaneously active during the execution of even the simplest kind of limb trajectory.

To convert a planned movement from extrinsic to muscle (intrinsic) coordinates, the CNS must perform a number of transformations. Consider the simple task of writing one's name on a blackboard. The planned motion in this case is completely specified by a set of coordinates that define the position and the pressure of the chalk on the blackboard. These coordinates are sufficient to describe the final result of the action. However, they are not sufficient to specify how this final result can be achieved by a coordinated motion of the arm. To this end, the CNS must convert the trajectory of the hand into the corresponding motion of each joint of the arm. Only after the desired motion of each joint is defined is it possible to establish the torque that must be generated at each joint in order to provide the motion. The final step of this computational process consists of deriving the control signals to be delivered to each muscle so that the appropriate joint torques can be generated.

Researchers of motor control have become increasingly aware of these computational problems in the last decade, because the same problems have become a focus of investigation in the field of robotics (*2*). The simplest artificial manipulators are open chains of rigid bodies interconnected by rotational or translational (or "prismatic") joints. For this class of mechanisms, the task of finding a motion of the joints from the desired motion of the end point is known as an "inverse kinematics" problem. Similarly, the task of deriving the forces to be delivered by the actuators in order to achieve a desired motion has been called an "inverse dynamics" problem.

Both of the inverse problems mentioned above may be "ill-posed"; that is, an exact solution may be either not available or not unique. Ill-posed problems arise frequently in different domains of biological information processing (*3*). A well-known example in the study of vision is the task of recovering shape, location, and orientation of a surface from its image over the retina. This problem is ill-posed because an infinite number of possible solutions exist for the same image. In the study of motor control, ill-posedness arises from the imbalance between the degrees of freedom of a limb and the number of variables that are sufficient to specify a task. In our blackboard example, any chalk location can be reached by a variety of joint angles. By the same argument, because there are several muscles acting upon any articulation, the same joint torque can be generated by a variety of different patterns of muscle forces.

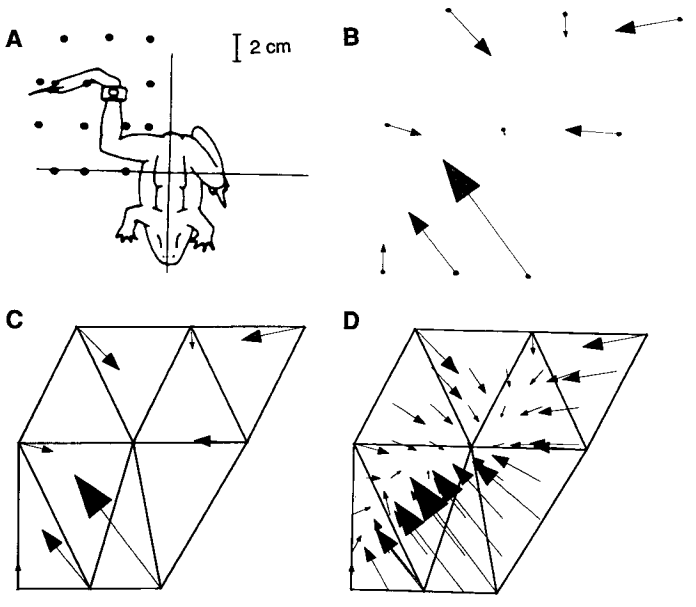

Fig. 1. Procedure used to estimate a force field. (**A**) Locations in the workspace at which we recorded forces at the ankle after microstimulation of a site in the premotor spinal cord. (**B**) Force vectors recorded at nine locations in the frog's workspace. (**C**) Partitioning of the tested workspace into a set of nonoverlapping triangles. Each vertex of a triangle is a tested point. Force vectors that were measured at each point at the same latency are displayed as solid arrows. (**D**) Interpolated field.

The excess or "redundancy" of degrees of freedom is not only a source of complex computational problems but also the basis of the versatility of biological systems—that is, their ability to perform different tasks in a wide range of environmental conditions. For this reason, the design and control of redundant manipulators is attracting increasing interest in robotics research (*4*). In this article we present a theoretical and experimental framework that describes the way in which the CNS takes advantage of a limb's biomechanical properties to transform planned movements into muscle activations. To illustrate how the CNS achieves this transformation, we consider three points: (i) the key role played by the mechanical properties of the muscles; (ii) the way in which the circuits of the spinal cord exploit muscle properties to express motor outputs; and (iii) the spatial organization of the circuits of the spinal cord.

Mechanical Properties of Muscles

The mechanical properties of muscles are important because the features of the CNS have probably evolved as a result of its need to both control and take advantage of the viscous and elastic properties (*5*) of the musculoskeletal apparatus. The tension developed by a muscle depends on its length in a way that is reminiscent of a spring; if we stretch a stimulated muscle, there exists a restoring force that depends on the amount of stretch (*5*). In addition, many muscles are arranged about the joints in opposition to each other. Hence, the position of a limb is maintained when the torques exerted by opposing muscle groups are equal and opposite.

The elastic behavior of the muscles implies that when the limb is perturbed by an external force, the limb will be displaced by an amount that varies with both the external force and the stiffness of the muscles. When the external force is removed, the limb returns to its original position. When small displacements are applied in several directions to the hand, elastic restoring forces are observed (*6*). These forces are organized as a field, because a single force vector is consistently associated with each position of the limb. The point in the field at which the force vector is zero is an equilibrium point.

The observation that posture derives from the interaction between the springlike properties of opposing muscles led to the formulation of the equilibrium point hypothesis. According to this hypothesis, first proposed by Feldman (*7*), limb movements result from a shift in the neurally specified equilibrium point. Studies on the movements of a single joint have provided experimental evidence that supports the equilibrium point hypothesis (*8*). This evidence shows that arm trajectories of moderate speed are generated by neural signals that specify a series of equilibrium positions for the limb.

The equilibrium point hypothesis has implications both for the control and for the computation of movements. With respect to control, the elastic properties of the muscles provide instantaneous correcting forces when a limb is moved away from the intended trajectory by some external perturbation. With respect to computation, the same elastic properties offer the brain an opportunity to deal with the inverse dynamics problem. Once the brain has achieved the ability to represent and control equilibrium postures, it can master movements as temporal sequences of such postures. In

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this context, a representation in the CNS of the inertial, viscous, and gravitational parameters contained in the equations of motion is no longer necessary. The competence of the equilibrium point model in dealing with multijoint, goal-directed movements has been established by the simulation studies of Flash (*9*), who reproduced the kinematic features of human multijoint movements with such a model.

A set of experiments performed in frogs with spinal cords that were surgically disconnected from the brainstem has provided neurophysiological support for the equilibrium point hypothesis (*10*). By microstimulation of the spinal cord, we have shown that this region is organized to produce the neural synergies necessary for the expression of equilibrium points. These experiments have indicated 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 toward an equilibrium point in space.

Generation of Force Fields

When the spinal cord of the frog is surgically disconnected from the brainstem, the cord still retains significant motor skills (*11*). For example, a frog that has been treated in such a manner is able to remove a noxious stimulus from the skin by the coordinated motion of multiple limb segments. We used these surgically altered frogs to explore the organization of the spinal circuitry through microstimulation of a number of spinal cord structures. We sought primarily to determine the field of static forces associated with the stimulation of a spinal cord site. To this end, we measured the isometric force produced by the muscles of the leg at different ankle locations when subjected to the same spinal stimulation. Typically, we recorded the force vectors at the ankle in a set from 9 or 16 locations forming a grid (three by three or four by four) in the workspace of the limb. Here the term "workspace" indicates the range of movement of the ankle in the horizontal (x-y) plane. At each grid location, we recorded the force vector elicited by the stimulation of the same spinal cord locus. The force vector varied as we placed the leg at different workspace locations, denoted as $\mathbf{r} = (x, y)$. The change in force through the workspace resulted from the interaction of a number of factors, such as the lengths, moment arms, and elastic properties of the muscles and stretch reflexes.

The data recorded in our microstimulation experiment can be described as a collection of samples from a time-varying force field, $\mathbf{F}(\mathbf{r}, t)$, obtained at a number of tested sites. We set the instant of stimulation as $t = 0$. Hence, $\mathbf{F}(\mathbf{r}, t)$ denotes the force vector at the location r after a latency t from the onset of the stimulus. The field at $t = 0$, $\mathbf{F}_0(\mathbf{r})$, is the "resting" field that characterized the mechanical behavior of the frog before the stimulation. The field at steady state, which we indicate as $\mathbf{F}(\mathbf{r})$, was measured when the forces induced by the stimulation had reached maximum amplitude at all the test points. This "peak" field often persisted for some time (100 to 500 ms, depending on the stimulus duration) before the measured forces returned to their resting values. At given latency, we used the measured force vectors to estimate the force field across a broad convex region of the ankle's workspace. To this end (Fig. 1), we implemented a piecewise-linear interpolation procedure according to the Delaunay triangulation algorithm (*12*). The algorithm partitions the workspace into triangles as close to equilateral as possible. The vertices of each triangle were the tested grid points. Within each triangle, we applied a linear interpolation to the force vectors measured at the corners. Thus, within each interpolation triangle the force components were given as:

$$F_x = a_{1,1}x + a_{1,2}y + a_{1,3} \quad (1)$$

$$F_y = a_{2,1}x + a_{2,2}y + a_{2,3} \quad (2)$$

The above expressions have six unknown parameters, $a_{i,j}$. Therefore, the interpolation problem with three data vectors (that is, six data components) has a unique solution.

In most instances, the spatial distribution of the forces induced by the stimulation was structured in a well-defined pattern that we refer to as a convergent force field (CFF) (Fig. 2). The field was characterized by a single equilibrium point to which the force vectors converged. This point is indicated by a filled circle in Fig. 2, B and D, and represents the locus at which the leg would be at steady state if it were free to move. The CFFs were qualitatively similar for a variety of stimulus parameters. For instance, when we changed the duration of the train of stimuli from the standard 250 ms to 500 ms, we found that a similar CFF was maintained for a longer period. Similarly, the expression of a CFF was not substantially dependent on a specific frequency of stimulation. The area of the spinal cord from which such single, well-defined equilibria were observed was centered on the lateral neuropil region (Fig. 2).

The CFFs must derive at least in part from the activation of the interneurons. The branches of these interneurons make synaptic connections with different pools of motoneurons and activate groups of muscles. Because the motoneurons of the frog have

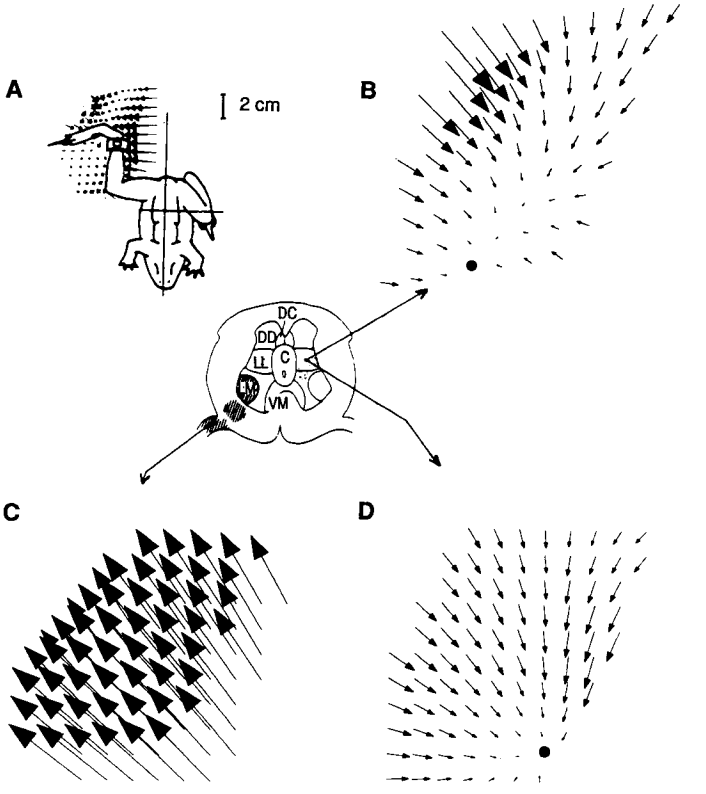

Fig. 2. Examples of force fields elicited by microstimulation. (**Center**) Transverse section of the spinal cord. DC, dorsal column nucleus; DD, dorsal neuropil region; LL, lateral neuropil region; C, central neuropil region; VM, ventromedial neuropil region; LM, lateral motoneuronal region. (**A**) Convergence force field (CFF) shown in reference to the frog's leg. (**B**) The CFF recorded from a chronically deafferented frog. The animal was prepared for microstimulation 3 weeks after bilateral section of dorsal roots 7, 8, 9, and 10. The equilibrium point is indicated by a filled circle. Stimulation parameters are similar to those in (D). (**D**) The CFF elicited by microstimulating a small area within the stippled region of the spinal cord with constant current pulses of 1 to 6 μA, applied at 40 Hz for 300 ms. The spread of current was ~100 μm in radius. Force vectors were recorded at each location of the four by four grid. At a given latency t from the onset of stimulus, we applied a piecewise-linear interpolation to the set of measured forces. The equilibrium point is indicated by a filled circle. (**C**) Parallel force field recorded from the region of the motoneurons. Parameters of stimulation are similar to those used in (B) and (D).

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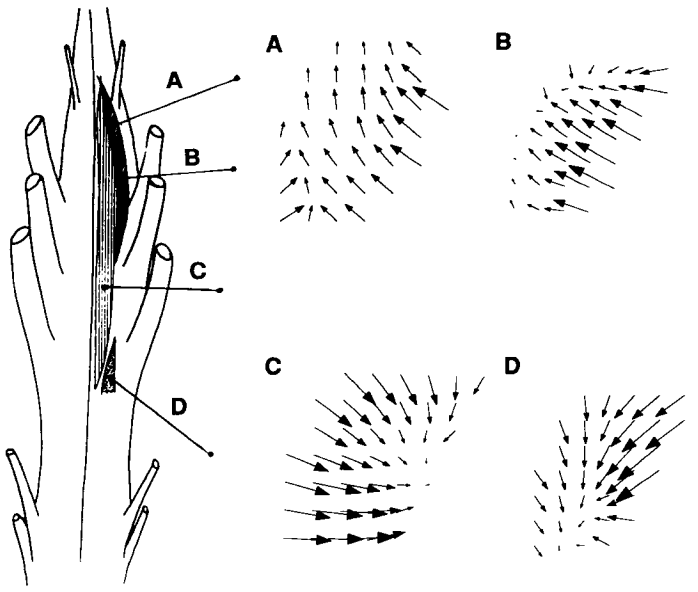

Fig. 3. (**Left**) Regions of the lumbar spinal cord containing the neural circuitry that specifies the force fields (**A** through **D**). Within each region, similar sets of CFFs are produced. The diagram is based on 40 CFFs elicited by microstimulation of premotor regions in three frogs with transected spinal cords. (**Right**) Four types of CFFs. To facilitate comparison among CFFs recorded in different animals, we subtracted the passive force field from the force field obtained at steady state. The passive field is the mechanical behavior generated by the frog's leg (recorded at the ankle) in the absence of any stimulation. The force field is at steady state when the forces induced by the stimulation of the spinal cord have reached their maximal amplitude.

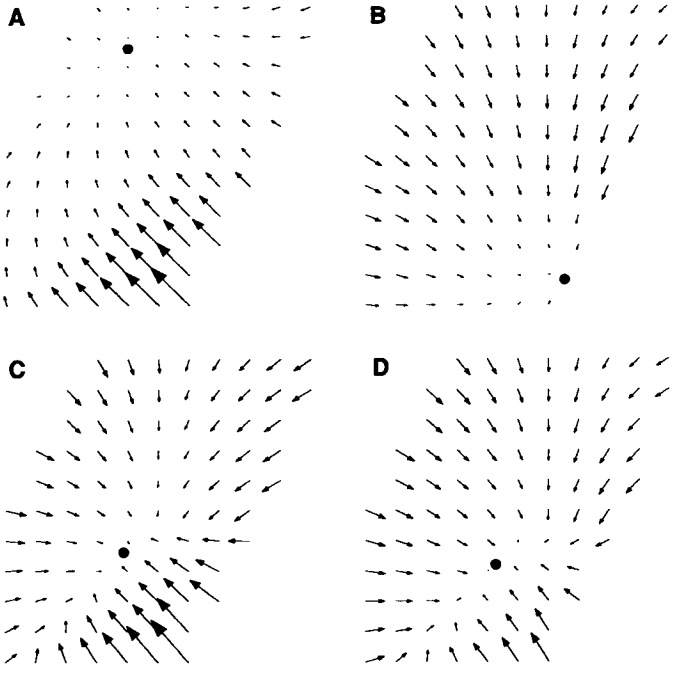

Fig. 4. Combinations of multiple stimuli. (**A**) and (**B**) show the individual fields resulting from stimulation at two different sites in the premotor areas of the lumbar spinal cord. The equilibrium of field (A) is in extension and (B) is in flexion. (**C**) The computed field <AB> is predicted by a simple vectorial summation of fields (A) and (B). (**D**) The actual field evoked by stimulation of (A) and (B) together. The equilibrium point is indicated by a filled circle.

extensive dendritic arbors and some degree of electrical connectivity, a CFF may result either from direct activation of the motoneurons or from random spread of excitation to a number of motoneural pools. Our experimental evidence is not, however, compatible with direct activation of the soma of the motoneurons. Our results indicate that direct stimulation in the motoneuron (MN) area generates fields that are different from the convergent fields elicited by the stimulation of the intermediate gray. When we placed our microelectrodes directly among the soma of the motoneurons, we obtained force fields with divergent or parallel patterns (Fig. 2C).

In a preliminary series of experiments, we also tested the hypothesis that CFFs may result from the random activation of several MN pools. We investigated this question by combining the isometric responses of individual muscles in a simulation. First, we stimulated individual leg muscles through a pair of implanted electrodes. We obtained muscle force fields by recording x and y forces at the ankle that were produced at each location of the workspace by the electrical activation of individual muscles (*10*). Second, we simulated random combinations of the measured muscle fields. We modulated each measured field by multiplying it with a randomly selected coefficient representing a certain amount of muscle activation. We obtained sets of combined fields by adding together all these modulated fields. We found that, in a set of 20,000 simulated combinations, the number of fields having an equilibrium point within the tested workspace was only 8.4%. Thus, random recruitment of motoneurons could not account for the CFFs observed in the majority of our experiments.

Another explanation of our results is that CFFs result from the activation of afferent fibers recruiting portions of reflex pathways. We investigated this issue in frogs that had been chronically deafferented bilaterally and in which all sensory fibers had degenerated. Microstimulation of the spinal cord in these animals still revealed the presence of CFFs (Fig. 2B).

A Coarse Map of CFFs

We investigated the spatial organization of the areas that specify different equilibrium-limb positions. After mapping most of the premotor area of the lumbar cord, we reached the conclusion that there are at least four areas from which four distinct types of CFFs are elicited. These regions form stripes that are oriented rostrocaudally. They extend dorsoventrally over a distance at least 300 μm in depth. Within each region, a qualitatively similar set of x and y forces are produced. This map of postures is shown in Fig. 3.

Preliminary experiments have shown that the simultaneous stimulation of two different points in some of the areas shown in Fig. 3 results in a force field proportional to the sum of the fields obtained from the stimulation delivered at each point (Fig. 4). This result is unexpected because of the complex nonlinearities that characterize the interactions both among neurons and between neurons and muscles. The superposition applies to the vectors of the fields. In contrast, the equilibrium points do not add vectorially. If one of the two fields has a stiffness larger than that of the other, the summed field has an equilibrium that lies closer to the equilibrium of the stiffer field. We view the superposition mechanism as the simplest way to explain how the spinal cord may generate a vast number of force fields from the limited variety of available fields (*13*).

The observation that force fields sum vectorially suggests a way to relate natural movements to the microstimulation results. Physiological movements result from patterns of neural activity distributed by branching fibers throughout fairly wide regions of the spinal cord. These branches may stimulate local clusters of cells that, in turn, generate force fields. If we assume that these fields sum like the CFFs generated by microstimulation, then a variety of motor patterns may result as a consequence of the terminal distribution of fibers.

Microstimulation of the premotor areas of the spinal cord has

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revealed a few zones that, when activated, produce distinct force fields. Through their mechanical and geometric properties, the activated muscles specify force fields with equilibria. These zones are ideal sites for the integration of signals coming from different sources. Diverse neural signals conveyed by afferent inputs or descending tracts may gain access to the premotor circuits, which, in turn, specify the activation of sets of muscles. The premotor zones with their afferent inputs may represent one of the substrates underlying transformation from extrinsic to intrinsic coordinates.

The idea that premotor spinal maps involving a few discrete types of movements are a key structure in sensory-motor transformations is consistent with investigations of the control of head movement in the owl. Masino and Knudsen (*14*) have postulated the existence of a few separate circuits for controlling horizontal and vertical head movements. These structures, which are located in the brainstem, receive inputs from the tectum and transform the tectal movement vectors into neck motoneural activation.

Our results described here imply that the spinal cord of the frog implements position control and equilibrium point mechanisms. In contrast, on the basis of electrophysiological recordings, planning at cortical levels is generally assumed to involve other types of variables and coordinates. Nonetheless, evidence has accumulated that position control occurs at the motor output stages of other CNS structures. This body of evidence is based on the use of stimulation techniques.

In oculomotor research, there is evidence that activation of certain circuits specifies the position of the eye in the orbit. Activation of a number of CNS structures brings the eyes to a unique orbital position irrespective of the starting position of the eyes. For instance, the stimulation of the posterior portion of the superior colliculus of the cat produces saccadic eye movements that bring the eyes to a particular position in the orbit (*15*). Also, stimulation of the most caudal portion of the colliculus in cats evoked head movements that bring the head to a particular location (*15*). In both cats and monkeys, goal-directed saccades can be evoked by stimulation of the internal medullary lamina of the thalamus (*16*), the posterior parietal cortex (*17*), and the supplementary eye fields (*16*). Although there is a superficial resemblance between the CFFs and equilibria and the final orbital position of the eye, we do not know whether these oculomotor areas and mechanisms generating final eye position are in any way equivalent to the zones in the spinal cord.

Within the spinal cord are a number of potentially autonomous functional units underlying motor behavior. Examples of these units include the spinal rhythm generators for locomotion (*18*) and scratching (*19*) and the propriospinal system for reaching (*20*). We do not yet know how the CFF units we have described relate to the spinal pattern generators or to the propriospinal system.

In conclusion, we have identified a discrete map of motor behaviors: the convergent force fields. We believe that this map may represent a mechanism whereby the CNS performs the transformation from movement planning to execution. The vectorial combination of motor outputs derived from activation across different areas of a very coarse map is a remarkable mechanism for producing a vast repertoire of motor behavior in a simple fashion.

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