Cerebral Cortical Mechanisms of Reaching Movements

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Because reaching movements have a clear objective—to bring the hand to the spatial location of an object—they are well suited to study how the central nervous system plans a purposeful act from sensory input to motor output. Most models of movement planning propose a serial hierarchy of analytic steps. However, the central nervous system is organized into densely interconnected populations of neurons. This paradox between the apparent serial order of central nervous system function and its complex internal organization is strikingly demonstrated by recent behavioral, modeling, and neurophysiological studies of reaching movements.

THIS ARTICLE ADDRESSES TWO QUESTIONS: (i) WHAT PLANning steps intervene between the decision to make a reaching movement and its initiation? and (ii) how are those steps implemented in the central nervous system (CNS)? Functions such as motor control have often been approached as computational problems amenable to serial analytical solutions expressed in the activity of single cells. Motor control theory has long been dominated, in fact, by motor-program models that describe planning as a serial hierarchy of instructions, rules, decision trees, or computational algorithms that progress from more abstract or general features of a movement to its more specific details (*1–3*). However, these models present major conceptual problems with respect to causal mechanisms (*2, 3*): how are the instructions, algorithms, and Boolean logic of motor programs implemented by neurons? In this article, we survey new insights into biological mechanisms that address this conceptual cul-de-sac of traditional motor control theory.

Behavioral Studies

To produce a visually guided reaching movement, the CNS must convert information originating primarily in the occipitoparietal visual system (*4*) about the spatial location of a target into a pattern of muscle activity that moves the hand toward the target. Thus, movement planning can be viewed analytically as the process of transforming movement-related signals from the reference frame of the hand in space to that of arm muscle activity. The experimental problem, therefore, is to identify the intervening coordinate frameworks and transformations used by the motor system. Multiarticular reaching movements are computational problems with no unique solution; many different hand paths, joint motions, and muscle activities can accomplish the same goal. Nevertheless, behavioral studies have shown that unobstructed reaching movements have stereotyped features, such as approximately straight hand paths with bell-shaped velocity profiles, tight phase-coupling of the motions of the shoulder and elbow joints, and consistent patterns of muscle activity (*5*). These invariant features are presumed to reflect the movement attributes, coordinate frames, and transformations by which the CNS represents and plans movements (*5, 6*).

Many current models for reaching movements, influenced in part by robotic controller studies, recognize three general hierarchical levels of coordinate reference frames (*5–7*) (Fig. 1A). The highest level is a reference frame of extrinsic kinematic attributes that describe the motion of the hand through space, such as target location, movement hand path, and direction. Indeed, introspection suggests that we "think" of arm movement in terms of the motion of the hand through space; the goal of reaching movements—to place the hand at a spatial location—is defined in such terms. An intermediate level involves intrinsic kinematic attributes, such as the joint angles or muscle lengths that define a limb's geometry during movement. The lowest level concerns dynamics, namely, the causal forces and muscle activity required for motor behavior, whether at equilibrium (statics) or varying with time (kinetics) (*8*). These reference frames are described in terms of Newtonian mechanics, and one can plan every moment-to-moment detail of a reaching movement by using the laws of motion to solve the coordinate transformations (Fig. 1B). However, this is an inefficient approach even for robots (7). Not only are the equations of multijoint motion complex, but the subsequent conversion of joint torques to muscle activation patterns is problematic, given the complexity of musculoskeletal anatomy and biomechanics. Moreover, the fact that limb movements must obey the laws of motion does not mean that the CNS contains an explicit representation of those formalisms or that it controls the musculoskeletal system by applying such arbitrary first principles and engineering operations (*2, 3, 9–11*).

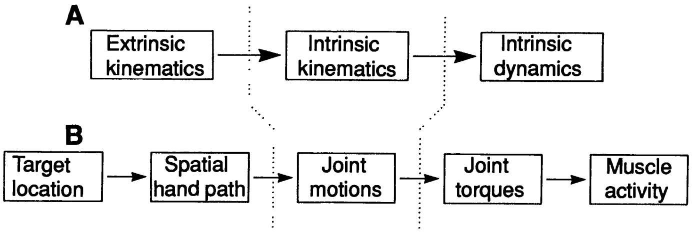

Fig. 1. Reaching movement hierarchies. (**A**) A general three-step planning hierarchy. Each arrow represents a coordinate transformation. (**B**) A robotics planning hierarchy that treats motor control as a problem in mechanics. The movement is planned explicitly by first defining the hand path and velocity profile from the current hand position to the target, then solving equations that define the moment-to-moment transformations from hand path to joint motions (inverse kinematics) and from joint angles to joint torques (inverse dynamics), and finally parceling out the joint torques among the many muscles acting across each joint. The dotted lines signify equivalent hierarchical levels between (A) and (B).

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Thus, many recent studies have searched for biological processes that do not presuppose formalisms such as Newtonian mechanics (*11*). For instance, Soechting and Flanders have studied the transformation from extrinsic to intrinsic kinematics by analyzing errors made by subjects in a variety of pointing tasks (*12*). Their results suggest that the spatial location of the target is first transformed from head-centered to shoulder-centered spatial coordinates. The location is then redefined in an intrinsic kinematic framework by two separate channels that convert target azimuth (horizontal direction) into the intended yaw angles of the upper arm and forearm in the sagittal plane when the hand is at the target, and target elevation and distance into arm segment elevation angles (*13*). The difference between current and intended arm angles is then transformed into a motor command signaling the direction of hand movement. The error patterns suggest that the CNS uses linear approximations of the exact nonlinear relation between limb segment angles and target location. Alternatively, others propose that the extrinsic to intrinsic transformation is realized by learning a mapping between target location and intended muscle lengths (*14*). Visual input about hand position relative to the target also plays a key role in this transformation (*15*).

Because the dynamics of multiarticular movements are very complex (*7, 11*), how the CNS determines appropriate multimuscle activity patterns is a major problem in motor control theory. Some have proposed that the CNS can ignore dynamics if it controls muscles like tunable springs to exploit the inherent relation between muscle length and tension (*16*). In these controversial models (*11*), reaching movements are planned in terms of equilibrium points, the muscle lengths or joint angles at which net joint torques are zero. Centrally generated shifts in equilibrium points cause the limb to move along a trajectory to a new posture with zero net torque. Muscle activation patterns and output forces result from the springlike response of muscles to the equilibrium-point signals (*14, 16*).

Two insights generated by these various studies are that many features of reaching movements may not be explicitly planned by supraspinal systems and that the motor system may use simplifying rules to generate close but inexact approximations of an intended movement. For instance, specification of a hand's path may not be an obligatory early planning step but could result indirectly from the transformation of target location to intrinsic kinematics (*12, 14*). Similarly, spinal cord circuitry and the mechanical properties of a limb could convert simple central control signals into complex time-varying responses [such as bell-shaped velocity profiles and triphasic electromyogram (EMG) patterns] without overt planning (*14, 16*). Indeed, cervical propriospinal and segmental locomotor circuits may play critical roles in organizing reaching movements (*17*). Therefore, it is still not possible to distinguish the features of reaching movements that are arbitrarily imposed by supraspinal planning processes from those that are due to spinal circuitry or are an inevitable consequence of musculoskeletal mechanics.

Furthermore, all of these models have limitations, and their frequent assumption that a single unifying principle governs the planning of all movements is probably simplistic (*6, 11, 12*). Thus, although there is extensive circumstantial evidence that reaching movements are planned by a serial hierarchy of coordinate transformations, there is still no consensus on the intermediate reference frames by which motor plans for a reaching movement through space are converted to muscle activity.

Neurophysiological Studies

A distributed cerebral control system. Just as hierarchical planning models predict that the CNS should contain multiple representations of movement in different reference frames, several separate cerebral cortical areas are now implicated in the control of arm movements (Fig. 2). Lesions in each area cause distinct motor deficits, ranging in nature from spatiomotor discoordination and misreaching (parietal cortex), deficits in learning or retrieval of motor strategies and sequences (prefrontal and premotor cortex), to paralysis [primary motor cortex (MI)] (*18–20*). This suggests that each area is concerned with motor planning at a different level of abstraction, as if they form a serial cascade of structures that terminates in MI from which the final motor command is issued.

However, the complex pattern of serial, reciprocal, and parallel interconnections among these arm-related areas does not lend itself readily to a simple unidirectional hierarchy (*18–22*). For instance, several of them project to MI as if serially antecedent to it but in parallel to one another; they are also extensively interconnected (*19–21*). Moreover, a number of them have their own descending corticorubral and corticopontine outputs, and their corticospinal projection now appears to be more substantial than previously thought (*21*), showing that their motor function is not mediated only by means of their projections into MI. Although MI may be the principal cortical access to the spinal motor apparatus, it is clearly not the final common path for cerebral control of movement (*21*).

Neuronal recording studies. Three cortical areas—MI, parietal area 5 (PA5), and the dorsal premotor cortex (PMd)—have been the most intensely studied for neuronal correlates of a planning hierarchy during controlled reaching movements. Cells in all three areas have several response properties in common. When monkeys reach from a common start position to targets in different locations, cells in all three areas show similar directional tuning. Single-cell activity varies approximately as a cosine function of movement direction, centered on one preferred direction that varies from cell to cell (Fig. 3) (*23–26*). Each cell, therefore, emits a graded signal for a broad range of movements. Conversely, each movement evokes a complex pattern of graded activation in each area that varies with movement direction (Fig. 4). The tonic activity of many cells also varies with stable arm posture at different targets (*23–26*). Although important differences also exist among the three cortical areas, they are relative and not absolute. Correlates of several putative hierarchical levels of movement representation can be found to different degrees in each cortical area by manipulation of different task variables (*27–29*), and

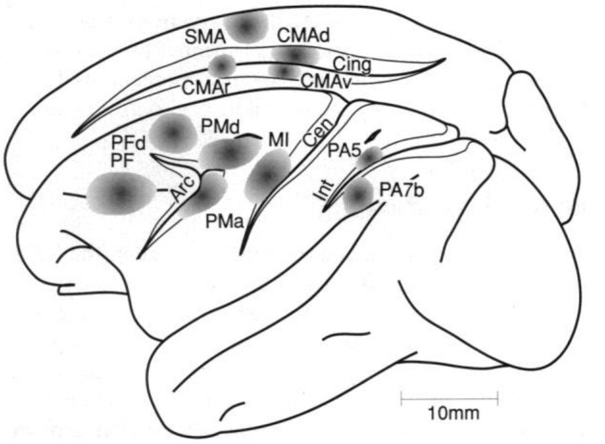

Fig. 2. Several arm-related neuronal populations in the cerebral cortex of a macaque monkey. MI, primary motor cortex; PMd and PMa, dorsal and postarcuate premotor cortex; SMA, supplementary motor cortex; PF and PFd, prefrontal and dorsal prefrontal cortex; PA5 and PA7b, posterior parietal cortex areas 5 and 7b; CMAr, CMAd, and CMAv, rostral, dorsal, and ventral cingulate motor areas. Cingulate areas are on the medial surface of the hemisphere and are shown as if reflected in a mirror. Major sulci are shown as if opened up (thin lines) to expose their banks. Cen, central sulcus; Arc, arcuate; Cing, cingulate; Int, intraparietal sulcus.

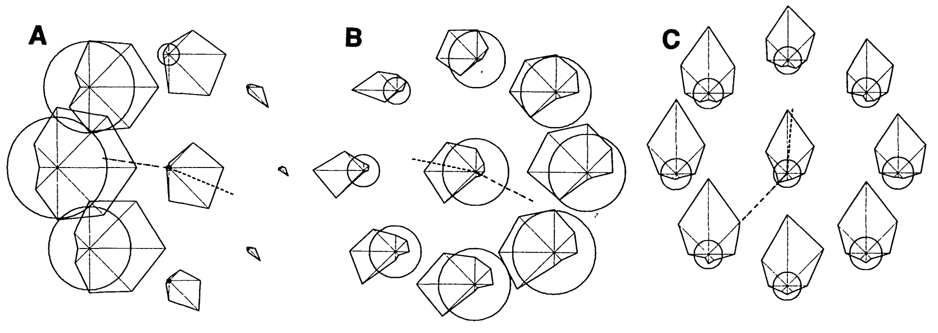

Fig. 3. The responses of three MI cells during reaching movements under different load conditions. The central polar plots in (**A**), (**B**), and (**C**) show the directional tuning of a neuron during unloaded arm movements in eight directions. The radius of each circle is the tonic activity with the arm at the central start position. The eight polar plots around each central plot illustrate the change in the cell's activity during the same arm movements, with external loads that pull the arm in eight different directions. The position of each polar plot corresponds to the direction in which the load pulled the arm. Responses ranged continuously from (A) cells that were very sensitive to loads to (C) relatively insensitive cells. [Adapted from (*30*) with permission, *Journal of Neuroscience*]

the correlates of any given level are distributed across all three areas.

Moreover, it is not yet possible to make conclusions about the specific attributes of movement and the reference frames signaled by neuronal activity in each area. For instance, when movements converge on one target from different start positions, discharge still varies with direction, as if signaling information about the movements themselves and not their common endpoint (*25*). The time-varying pattern of total population activity varies with the instantaneous direction and velocity of movement (*23, 24*), which is strongly suggestive of an extrinsic representation of movement trajectories. However, it is also compatible with an intrinsic representation because of the stereotypical coupling between hand path and joint motions during reaching (*26, 28, 29*). When reaching movements are made with parallel hand paths but different start and end positions to dissociate extrinsic movement direction from intrinsic variables, cell-preferred directions in MI and PMd rotate with the starting shoulder joint angle (*26*). Although this supports a shoulder-centered intrinsic framework for single-cell activity during movement, population activity still varies with trajectory (*26*), suggesting that important differences exist between movement representation at the level of single cells and at the level of populations.

The models in Fig. 1 predict that high-level planning stages represent movement in kinematic reference frames, whereas stages that are closer to movement execution transmit information about movement dynamics. This can be tested by making the same movement trajectories (constant kinematics) with different loads applied to the arm (variable dynamics). Studies have shown that cell discharge varies to different degrees in all three areas as a function of external loads (*27–33*) (Fig. 3). Load sensitivity forms a continuum; cells cannot be sorted into two distinct populations processing only kinematics or dynamics. Cells most sensitive to load are in MI, but even there, some cells are relatively insensitive (*26–33*) (Fig. 3). Sensitivity to load may depend on the structure to which each MI cell projects: corticospinal neurons may transmit more dynamics-level information than corticorubral or corticostriatal neurons (*32*). Total MI population discharge during movements with a load does not always correspond to movement direction (Fig. 4), and so cannot be transmitting only kinematic information about trajectory (*28–31*). The load-induced change in MI population activity acts as a signal appropriate to compensate for the loads (*30, 31*). Whether such changes are best correlated to output forces at the hand, shoulder joint torques, equilibrium points, multimuscle activation patterns, or other possible reference frames is not yet certain (*28–31*). In contrast, most single cells in PA5 are only modestly sensitive to loads, and the net PA5 population response is an unambiguous signal about arm movement kinematics under all load conditions (*28–31*). Sensitivity to load in PMd falls between that of MI and PA5 (*33*).

Another way to see whether cell activity is related to movement planning or execution is to test its temporal coupling to movement initiation. For instance, one can give monkeys prior information about the direction of intended movement but delay movement initiation for several seconds. Activity changes during the delay period are presumed to be involved in planning the upcoming movement (*34*). Tasks that use instructed delay periods again reveal a continuum of response patterns within and across areas without a sharp segregation of cells implicated in either movement planning or execution. During a delay period, many cells show directionally tuned activity; these cells are most common in PMd, less so in PA5, and least common in MI (*35*). Although some cells discharge only during the delay period, others discharge during both the delay period and the subsequent movement; still others, including the majority of MI cells, discharge only in relation to movement execution.

Consistent with the hierarchical scheme, activity during a delay period appears to signal kinematic attributes of movement (*27*). The highest level in the hierarchical represention of movement (Fig. 1) concerns extrinsic kinematic attributes, and there is some evidence of its existence, particularly in PMd. For instance, delay-period activity

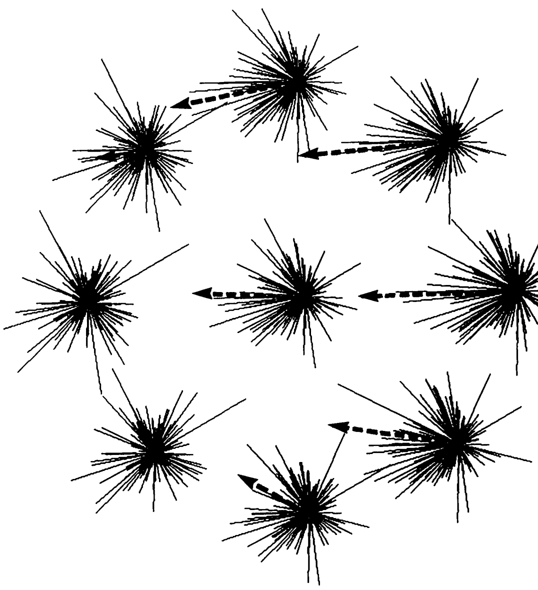

Fig. 4. Vectorial representation of the activity of a population of MI neurons during arm movements toward the left. The response of each cell is represented by a vector along its preferred direction, whose length is proportional to the cell's discharge rate for that movement. The central vector cluster is the population response without external loads applied to the arm; the other eight vector clusters are the responses of the same cells during the same movements, with static loads that pull the arm in directions corresponding to the position of each vector cluster relative to the center. Each dotted arrow is the population vector sum, which points in the direction of movement. [Reprinted from (*28*) with permission, John Wiley and Sons, Ltd.]

varies with both target location and degree and intended curvature of the hand path (*36*). Moreover, PMd cells often generate delay-period activity with similar directional tuning before reaching movements made with either arm, as if processing information about spatial attributes of the ensuing movement independent of its intrinsic biomechanics (*37*). In tasks in which reaching movements are made in arbitrary directions away from a stimulus, transient changes in cell activity occur in all three areas between cue appearance and movement onset, which may contribute to the visuomotor transformation of cue direction to movement direction (*38*).

Another important feature of cell discharge is conditionality. The response of many cells, especially those outside MI, depends not only on the form of the movement but also on its context (*39*). Some cells discharge during reaching movements to grasp food but not during aversive reaching movements to push away an undesirable object. Similarly, cells in some areas may respond preferentially when movements are controlled by external stimuli rather than by self-generated motor strategies, or vice versa (*40*).

Hierarchies and heterarchies. The neurophysiological studies just described reveal neuronal correlates of several putative hierarchical planning stages for reaching movements, distributed across three cortical areas. The different combinations of response properties in each area imply that each cortical area has primary but not exclusive responsibility for certain representations or transformations and that each may be involved to varying degrees in planning several aspects of movement. Thus, the findings do not support an absolute segregation of response properties within a strict serial hierarchy of areas but are more consistent with a distributed hierarchy or heterarchy of nested interconnected cortical populations (*3, 6, 41*). In a heterarchy, there is no fixed chain of command or direction of information flow; instead, the flow of information is flexible and dependent upon the context of an event (*6, 41*), allowing different movement attributes or cortical areas to take priority under different behavioral circumstances (*6, 41, 42*). This concept is strongly supported by the conditionality of cell discharge. Representations of various movement attributes evolve concurrently in different interacting parts of the heterarchy (*3, 27–29, 41, 43*), so that from moment to moment there can be a net serial flow of information across the intermeshed representations although its direction may vary with task conditions. Indeed, differences in the timing of movement-related activity in different areas are routinely observed (*20, 24, 44*) (Fig. 5). When a reaching target abruptly appears, many prefrontal (PF) and PMd cells begin to discharge before MI neurons, consistent with their close anatomical coupling to the occipitoparietal system (*20, 44*). Paradoxically, although many PA5 cells have response properties that seem to place them hierarchically antecedent to MI, PA5 is activated later than MI in visually initiated reaching tasks (*24, 43*). PA5 is a major component of the somatosensory system but also projects to MI and PMd. Thus, the signal it generates about arm kinematics could contribute simultaneously to kinesthetic perception and to motor control, as if both "downstream" and "upstream" of PMd and MI (*43*). This example illustrates how difficult it is to determine functional relations among components of a distributed system.

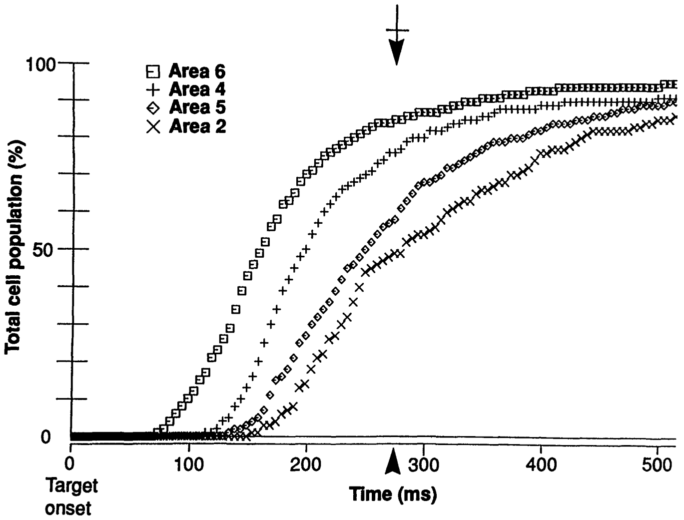

Fig. 5. Cell recruitment curves illustrating the sequential but overlapping activation of four different arm-related cortical populations in one monkey during a reaching task (*65*). Each curve is a cumulative frequency histogram of the time of the first change in activity of each cell for eight different directions of movement from a common central starting position. Targets of movement appeared at time 0; the mean time of arm movement initiation is indicated by the arrows. Area 6, PMd; area 4, MI; area 5, PA5; area 2, primary somatosensory cortex immediately anterior to PA5.

Another important property of the motor system also appears to favor a distributed, or heterarchical, control system. In sensory systems, many features of a stimulus (form, size, color, texture) are independent attributes that theoretically could be analyzed by separate neuronal channels. In motor control, however, parameters of kinematics and dynamics such as direction, velocity, and forces, although individually controllable, are not truly independent. They are inextricably linked through the laws of motion, so that an intended change in one produces or requires changes in others. A heterarchy of interacting representations of different movement attributes may be the means by which the motor system can separately control many interdependent parameters of movement while successfully coping with the laws of motion, context-dependent changes in planning priorities, and the complexities of musculoskeletal biomechanics (*28, 29*).

Neuronal Implementation of Sensorimotor Transformations

What causal mechanisms could endow the motor system with the transcendent "intelligence" to perform sensorimotor transformations? Recent attempts to answer this question have modeled the motor system as interconnected matrix-like arrays of neurons (*2, 3, 45, 46*). The continuing development of network models, in particular, is attracting great interest for many reasons (*3, 47*). For one, networks are self-organizing; empirical trial-and-error learning rules cause them to converge on a solution to a computational problem by altering the weighting of interelement connections. Furthermore, certain temporal properties of network models such as membrane time constants, temporal facilitation, and conduction delays allow the motor system to produce signals varying in time without having to solve differential or integral equations (*14, 48*). Networks can be viewed as nonalgorithmic (*3*) information-processing mechanisms or as computational maps (*49*) that perform input-output transformations as determined by the topography and weightings of its connectivity matrix and the activation state of each element.

Motor control models based on these principles can find solutions to many problems concerning movement kinematics, dynamics, motor coordination, and sensorimotor transformations without a priori knowledge of the structure or mechanical properties of a limb or the external world (*14, 48, 50–52*). The optimal solution to such problems is often a hierarchical network with several layers of neurons between input and output. Recurrent connections among layers of the network, a prominent feature of biological motor systems, impart it with the ability to generate time-varying signals required for coordinated movement sequences (*51*). The success of these models suggests some important new perspectives on a number of biological motor control issues.

Sensorimotor transformations. The powerful effect of movement direction on cell discharge may reflect the need for accurate directional information at all stages of planning. The ubiquitous tuning curves could be produced by neuronal processes underlying sensorimotor transformations (*28, 29*). For instance, Lukashin (*53*) has described a simple network that learns arbitrary transformations between stimulus location and movement direction. The elements in the network show the same broad tuning curves, uniform preferred-direction distribution, and population-vector properties as motor cortex cells.

Andersen and co-workers (*54*) have been studying the hypothesis that a coordinate transformation occurs in parietal area 7 (PA7) between retinotopic and head-centered space. PA7 cells do not have explicit spatial receptive fields in head-centered space. Instead, the discharge of many PA7 cells varies with both stimulus position on the retina and orbital position of the eyes. Their modeling studies show that cells with this combination of properties can signal stimulus location in head-centered space at the neuronal population level. The transformation results when inputs in different reference frames (retinal and orbital) converge onto a population of neurons, each of which responds as if functioning simultaneously in both reference frames (or neither, if one prefers). The resulting head-centered representation is a distributed property of the population.

The role of eye position signals in PA7 emphasizes that proprioceptive input, often relegated to the feedback loop of servo-control mechanisms, may have a major role in sensorimotor transformations. Proprioceptive input modulates the activation state of cell populations throughout the motor system as a function of joint angles, muscle lengths, and muscle contractile states. This can contribute to extrinsic-intrinsic transformations by causing population output signals to vary with intrinsic parameters, even if other convergent inputs signal extrinsic information. Similarly, it could facilitate the transformation from kinematics to dynamics by altering input-output properties of cell populations to compensate for external loads and for biomechanical properties of a limb that change with its geometry, such as muscle length–tension properties.

These ideas are central to models proposed by Jeannerod (*15*) and Burnod and co-workers (*55*) for sensorimotor transformations in reaching tasks. In these models, a signal about movement intent, such as a directional vector in space, projects onto a multilayer network of neurons. Each cell represents movement in a unique reference frame whose principal axis is defined by its preferred direction. Each neuron's output varies approximately as the cosine of the difference between the directional input signal and its own preferred direction. This tuning function is a result of the pattern of convergent inputs and the local activation state of the network; neurons do not know trigonometry. The net population signal of the different network layers contains information not explicit in any single cell about global features of the movement, such as its trajectory or the direction of its forces. Transformations between levels of movement representation are produced by introducing inputs in appropriate reference frames at appropriate points in the network.

The topography of interelement connections also is a critical aspect of the transformation mechanism. Several network robotics models predict that single output units form weighted connections that diverge onto different muscles (*14, 50*). In striking agreement, corticospinal axons that synapse directly onto spinal motor neurons branch into the motor neuron pools of several functionally related muscles (*56*). In this way, the transformation from the MI representation of movement to a single-muscle representation in the spinal cord is partly embedded in the spatial geometry of corticospinal terminations (*17, 28, 29*).

The motor system solves problems, not equations. The motor system does not control movement by solving algorithms derived from first principles. Rather, it might be more properly viewed as a system that develops empirical solutions to motor control problems: it "learns by doing" (*9, 57*). Developmental studies show that accurate reaching requires both practice and vision of the limb during movement, as if visuomotor experience is essential to learn the sensorimotor transformations (*58*). The learning occurs by successive approximation; repeated "perception-action cycles" (*14, 50–59*) use knowledge of reaching errors (provided by visual and proprioceptive input) to fine-tune the functional connectivity of the motor system to improve future reaching accuracy (*60*). In this way, empirical knowledge about planning transformations and musculoskeletal system properties becomes implicitly embedded in the synaptic connectivity matrix, from whose collective computational power emerges the intelligence of the motor system. Similar processes could account for the acquisition of any motor skill.

MI as a computational map for sensorimotor transformations: form follows function. An old question is how the role of MI is reflected in the organization of its topographic motor output map (*61*). This map is a complex mosaic of small clusters of corticospinal neurons which modulate the activity of one or more functionally related muscles, with extensive interdigitation of the different output clusters projecting to different muscle groups at the same or different joints (*61*). This reductionist view has yielded insights into how MI output modulates muscle activity (*56*). A different issue is how the map is used to control multiarticular movements. A simplistic hypothesis is that it functions as a reference table; the motor system determines which muscles to activate at what level and then locates and activates the appropriate output clusters scattered across the fragmented output map.

However, the motor command for reaching is a population code that implies graded modulation of the activity of many proximal-arm output clusters throughout the map. Therefore, it might be useful to view the map as a single functional unit whose seemingly chaotic arrangement of interdigitated output clusters is a computational map for the control of multiarticular acts, with the entire arm portion of the map implicated in any reaching movement. Although local aggregates of clusters may be optimally activated during specific reaching movements (*61*), functionally related output clusters throughout the map interact by means of a matrix of intracortical connections to coordinate different multiarticular movements (*62*). This also places great importance on the topographic distribution of inputs into MI in shaping the pattern of activity across the map (*9, 46, 61*).

The idea that MI is a computational map, rather than a map of muscles or movements, is further supported by recent findings of rapid changes in the MI output map (*63*), as if a considerable degree of flexibility exists between a given point on the map and musculature. These findings suggest that the input-output properties of the MI map can be continually altered during development and skill acquisition. Changes in local MI inhibitory circuitry (*63*) and in the efficacy of synaptic inputs into MI (*64*) may contribute to this reorganization.

Changing Perspectives on Motor Control

The material reviewed here indicates that the planning of reaching movements involves a distributed hierarchy, or heterarchy, of movement representations. Each cortical area has a specific role in the process, as reflected by the different combinations of cell response properties it contains. However, the neuronal correlates of a given movement attribute are distributed unequally across several cortical areas, and sensorimotor transformations result from the interactions among these distributed representations.

On networks and neurophysiology. We have emphasized some of the implications of network models for biological motor control. Such nonalgorithmic models are attracting considerable interest by demonstrating the capacity of self-organizing ensembles of simple elements, with limited individual information-processing power, to learn complex functions. Such models suggest that hierarchical movement representations are the product of iterative trial-and-error mechanisms that seek empirical solutions to the control problems arising in multiarticular acts and that sensorimotor transformations in the CNS are population functions to which single cells make only a fragmentary contribution. The resulting cell responses are a complex combination of signals that do not fit readily into any formal reference frame (*52*). Single-cell correlates of movement attributes, which we find convenient to describe in terms of such arbitrary formalisms as kinematics, dynamics, and coordinate frames, are the product of the activation state of that point in the network, as shaped at least partly by previous experience. Thus, we may never understand the causal relation of most cortical neurons to movement in the same formal sense that we can understand the role of each component of an electronic circuit (*52*).

If these implications of network models prove to be valid for biological systems, this will require a fundamental break from the strong reductionist tradition in motor control, which sought a deterministic understanding of how the CNS controls movement on a cell-by-cell basis (*52*). Traditional models (*1–3, 52*) implied that neurons perform definable logical or mathematical operations, or uniquely code the variation of a movement parameter along an axis of a coordinate system, so that one could reveal causal mechanisms by recording single-cell activity in behaving animals. Although the results of those experiments paradoxically helped reveal the inadequacies of traditional models, this does not invalidate behavioral neurophysiology as a research tool. On the contrary, properly designed neurophysiological studies will continue to be essential for elucidating the nature of neuronal correlates of movement in different parts of the motor system. Modeling approaches, such as networks, provide new ways to interpret those experimental data, new ways to test hypotheses, and new predictions to be tested in experiments. Thus, modeling studies complement recording experiments but cannot replace them, and the motor control field will only benefit from the interplay of the two approaches. Of course, networks are just the latest in a long line of motor control theories and models. There are as many network solutions to any given computational problem as there are arbitrary sets of network architectures and learning rules that force them to converge on the desired output. Ultimately, a critical test of any biologically plausible model of motor control, whatever its nature, will be how well it accounts for cell discharge patterns revealed by neurophysiological recordings, and not the other way around.

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Physics of the Granular State

H. M. JAEGER AND SIDNEY R. NAGEL

Granular materials display a variety of behaviors that are in many ways different from those of other substances. They cannot be easily classified as either solids or liquids. This has prompted the generation of analogies between the physics found in a simple sandpile and that found in complicated microscopic systems, such as flux motion in superconductors or spin glasses. Recently, the unusual behavior of granular systems has led to a number of new theories and to a new era of experimentation on granular systems.

> "To see a world in a grain of sand. . . ."
>
> —*Auguries of Innocence,* WILLIAM BLAKE

SAND IN AN HOURGLASS, SALT PILES ALONG THE SIDE OF A highway, screes at the bottom of a mountain, and sugar in a bowl are all examples of familiar granular materials. These materials show a number of easily observed phenomena that are immediate manifestations of exceptional properties (Fig. 1). As distinct from liquids, granular heaps are stationary as long as the top surface is at a slope less than the "angle of repose," θ_r. No avalanches spontaneously occur until the slope is increased above the "maximum angle of stability," θ_m. When the slope is increased slightly above θ_m, grains begin to flow and an avalanche of particles occurs (Fig. 1B). However, instead of uniform motion throughout the sample, as expected in ordinary fluids, all of the motion occurs in a relatively thin boundary layer near the surface, which appears blurred. Between θ_r and θ_m is a region of complex, bistable behavior in which the material can be either stationary or flowing depending on how the pile was prepared.

There is also unusual behavior in a second simple configuration: a container filled with granular material up to a height, h. In a normal liquid, the pressure at the bottom of a filled vessel is proportional to the height of the liquid. In the case of granular material the pressure at the bottom of a sufficiently tall structure is independent of h because the friction of the particles along the wall of the container is sufficient to withstand the weight of the extra mass placed on its top. For this reason, in an hourglass filled with fine sand there is an approximately linear relation between filling height and draining time. Granular materials also show a phenomenon known as arching (or vaulting). In the building of a cathedral, the careful placement of a keystone at the top of an arch enables the creation of a vast empty space. Likewise, in a random configuration of grains, there will be places where arches appear naturally, leaving empty regions below. Granular material is inherently inhomogeneous, and the force network providing the stability of the system is nonuniform.

We have long been accustomed to divide matter into gases, liquids, and solids. Granular materials cut across these predefined boundaries. An example is the transition from solid- to liquid-like

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