Solving Bernstein's Problem: A Proposal for the Development of Coordinated Movement by Selection

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SPORNS, OLAF, AND EDELMAN, GERALD M. *Solving Bernstein's Problem: A Proposal for the Development of Coordinated Movement by Selection.* CHILD DEVELOPMENT, 1993, 64, 960–981. In recent years, many established concepts in the theory of human motor development have undergone profound change, and our knowledge has increased greatly. Nevertheless, some outstanding problems remain unsolved. A central problem concerns the redundancy of effective movements, first pointed out by N. A. Bernstein. The human motor system is mechanically complex and can make use of a large number of degrees of freedom. The controlled operation of such a system requires a reduction of mechanical redundancy, effectively by reducing the number of degrees of freedom. More recent work has shown that this problem is hard to solve explicitly by computing solutions to the equations of motion of the system. Equally challenging to traditional computational approaches is the fact the motor systems show remarkable adaptability and flexibility in the presence of changing biomechanical properties of motor organs during development and when faced with different environmental conditions or tasks. Solutions to these problems would have a large impact on a variety of issues in child development. In this article, we stress the importance of the somatic selection of neuronal groups in maps for the progressive transformation of a primary movement repertoire into a set of motor synergies and adaptive action patterns. We present results from computer simulations of a simple motor system that works according to such selectional principles. This approach suggests a provisional solution to Bernstein's problem and provides new parameters to guide experimental approaches to the development of sensorimotor coordination.

A major function of animal and human nervous systems is the coordinated control of limb and body movements. Coordinated motor activity enables an animal to explore its environment and to sample and attend to sensory stimuli, and it is essential for its survival within its econiche. Initially, however, the motor capabilities of newborn higher vertebrates are generally inadequate to accomplish any of these vital tasks, and these capabilities undergo profound changes over an extended period of postnatal development. This period is of particular interest in human infants, many of whose motor abilities at birth appear to be among the least developed when compared to those of other vertebrate species. A child's continued progress in achieving precise control of motor functions is an obvious prerequisite for its further behavioral, cognitive, and social development (Cratty, 1979; Thelen, 1989a).

A satisfactory understanding of early human development can only be achieved within the context of a global theory of brain function. Several theories based on information processing have been proposed. In such theories, motor function is largely viewed as dependent upon cybernetic control mechanisms and feedback loops of a more or less intricate nature. In this article, we consider a number of issues related to biological movement that pose several serious challenges to the formulation of an adequate theory in terms of conventional information processing. Some of these challenges are:

a) *Evolutionary changes* in the structure and function of the musculoskeletal apparatus must be compensated for by accompa-

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nying changes in the nervous system. During evolution, genetic changes may affect the biomechanics of limbs or the morphology of muscles and tendons in many different ways. In order to maintain adequate control by corresponding circuits in the nervous system, these circuits must be adjusted in a coordinated manner (for examples, see Edelman, 1987). Coordinated mutations affecting both body mechanics and brain structure are, however, unlikely to occur simultaneously in the same individual (although the two domains obviously co-evolve on a larger time scale). This evolutionary problem demands a theory of motor function that permits for the possibility of rapid alterations of neural circuits (involving mechanisms of neural plasticity) in response to peripheral biomechanical change.

b) All but the most stereotypic movements exhibit high degrees of *variability*, can be executed in a large number of possible ways, are *redundantly* specified by neural signals, and seem to involve widespread and mutually overlapping parts of the nervous system. While motor learning generally increases the precision of movements, even fully matured motor systems can execute movements in a large number of unpracticed ways. The key point is that the number of executable solutions to a given motor task always far exceeds the small number of learned examples. As we have mentioned, the problem posed by motor redundancy was first clearly recognized by N. A. Bernstein (Bernstein, 1967; Turvey, 1990; Whiting, 1984).

c) Motor coordination (particularly in humans) is not innately specified but *develops gradually during postnatal life*. For example, reaching movements in human infants are initially highly imprecise and variable and lack the characteristic patterns of organization found in the adult (see, e.g., Fetters & Todd, 1987; Thelen & Fisher, 1983; Trevarthen, 1974; von Hofsten, 1982). In the course of its development, an individual is able to accommodate great individual variations in neural and biomechanical structures. Moreover, many motor systems remain plastic throughout adult life, ready to compensate for metric and dynamic changes in the biomechanics of motor organs, including even the loss of entire limbs.

Although some promising advances have been made in the framework of ecological psychology and nonlinear systems theory, these challenges have not been met adequately by cybernetic, kinematic, or information-processing models. We will consider an alternative view that appears to deal more effectively with all these challenges. After briefly discussing the historical origins of some key problems of motor development (especially the problem of redundancy in the specification of motor commands), we will consider Bernstein's notion of motor synergies as functional units of the motor system. We will then explicitly discuss some limitations and inconsistencies in viewing motor function as governed solely by feedback control loops, algorithms, or computations. In contrast to these approaches, we propose that successful developmental coordination between neuronal activity and the biomechanics of the musculoskeletal system is based on variation and is the result of *somatic selective processes* within brain circuits. Selection acts to match possible motor commands to constraints posed by neural structure and kinematics. We will contrast our proposals with previous ideas based on information-processing models and briefly discuss some computer simulations that exemplify the proposed approach and demonstrate its self-consistency.

Bernstein's Problem

Bernstein, in 1935, pointed out that "the relationship between movements and the innervational impulses which evoke them is extremely complex and is, moreover, by no means univocal" (quoted in Whiting, 1984, p. 77; see also Turvey, 1990). Bernstein recognized that an "unequivocal relationship between impulses and movements does not and cannot exist" (Whiting, 1984, p. 82), partly because any movement is defined by greatly varying interactions of centrally synthesized motor signals and the external force field acting on the moving part of the body at the periphery. He noted that the design of the vertebrate motor apparatus creates a problem in the control of body movements, largely because of the many sources of indeterminacy between central command and peripheral movements. The motor organs of animals or humans, composed of multiple linkages and joints and an even greater number of muscles, can attain a large number of degrees of freedom. This number will in general be far greater than the dimension of their workspace, defined as that region of space within which the motor organ can move. This leads to what Bernstein termed redundancy: more than one motor signal can lead to the same trajectory of a given motor system; moreover, identical motor signals can lead to different movements under nonidentical initial conditions or in the presence of variations in the external force field. Indeed, Bernstein defined motor coordination itself as "the process of mastering redundant degrees of freedom of the moving organ, in other words its conversion to a controllable system" (Bernstein, 1967, p. 127). Determining how this conversion process takes place is what we will refer to as *Bernstein's problem.*

Bernstein proposed that the motor apparatus is functionally organized into synergies or classes of movement patterns. He emphasized the "gestalt" character of individual movements, finding it difficult to decompose them into constitutive atomic parts, such as the activities of individual muscles or rotations around a single joint: "A movement never responds to detailed changes by a change in its detail; it responds as a whole to changes in each small part" (in Whiting, 1984, p. 84). Quite naturally, repetitions of movements produce a class of similar but not identical trajectories. An example of how the gestalt character of a movement is preserved under complete reconstruction of its accompanying muscle activities is given in Figure 1A. Many different circles can be described with the hand as the arm extends in various directions from the body; these movements (forming a functional synergy) can be performed without further specific training. In related experiments, Lashley and others noticed that "when habitually used motor organs are rendered nonfunctional by removal or paralysis, there is an immediate spontaneous use of other motor systems which had not previously been associated with or used in the performance of the activity" (Lashley,

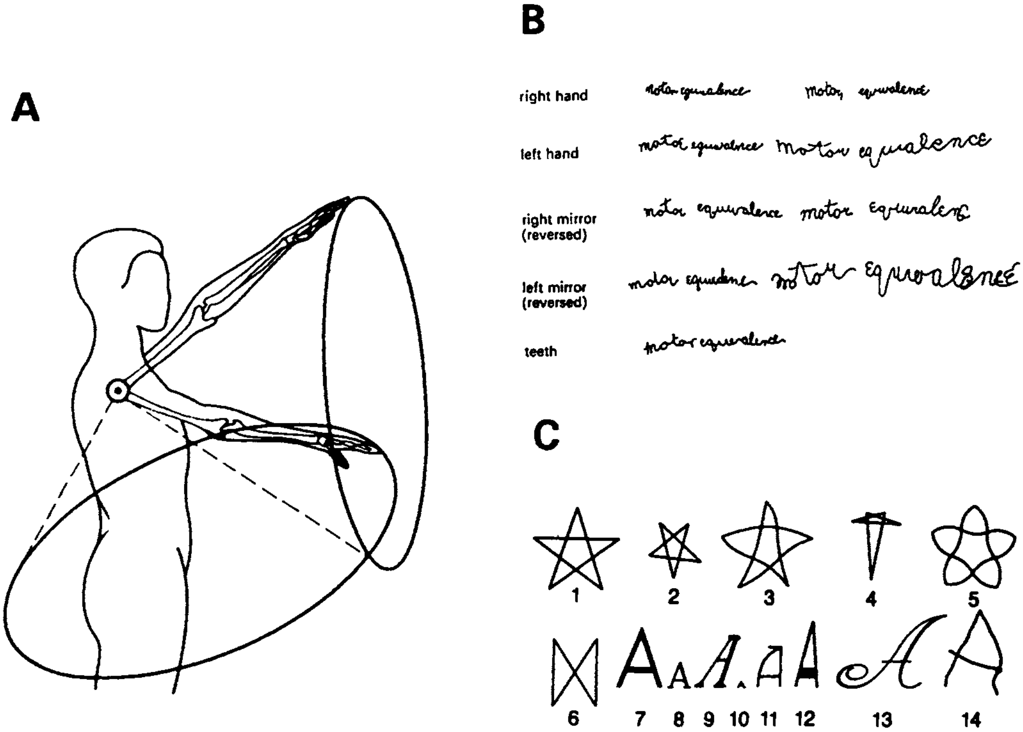

FIG. 1.—*A*, An equivalence class of movements according to N. A. Bernstein. Movements with topologically identical trajectories are executed by different sets of motor commands and under participation of different muscle groups. From Bernstein (1967), reproduced with permission. *B*, Motor equivalence according to K. Lashley. This Figure shows "the writing of two individuals, blindfolded, using right and left hands in various positions, as well as other muscle groups, unpracticed. In spite of clumsiness, the general features of the writing, individual differences in the forming of letters, and the like, are characteristically maintained. The mechanics of writing is a sequence of movements in relation to body position, not a set pattern of special groups of muscles" (Lashley, 1942, quoted after Pribram, 1969, p. 248). From Pribram, 1969, reproduced with permission. *C*, "Topology" according to Bernstein (1967). This term is adopted for all qualitative aspects of spatial configuration or forms of movements, in contrast to quantitative metric aspects. Examples include 1–5, topological class of five-pointed stars; 6, topological class of figure eights with four angles; 7–14, topological class of letters A. From Bernstein (1967), reproduced with permission.

1933, quoted in Beach, Hebb, Morgan, & Nissen, 1960, p. 239). In other words, "motor acts . . . may be executed immediately with motor organs which were not associated with the act during training" (p. 240; see also Fig. 1*B*). These reflections gave rise to the concept of *motor equivalence*, referring to the variety of specific muscle contractions and joint revolutions that produce the same end result (Hebb, 1949).

Synergies and the Structure of Movements

Synergies are classes of movement patterns involving collections of muscle or joint variables that act as basic units in the regulation and control of movement. Bernstein was the first to propose that synergies are used by the developing nervous system to reduce the number both of controlled parameters and of afferent signals needed to generate and guide an ongoing movement. According to Bernstein, certain synergies are often associated with a particular muscle group and can therefore be at least partially defined by morphology and anatomy. Other synergies can be more clearly related to a given task and provide a basis for "motor equivalence." Bernstein also proposed that synergies capture the "topological" rather than metric features of movements (see Fig. 1*C*). The temporal structure of motor programs emerges through their parallel or sequential activation. These ideas have been elaborated by others. In closely related formulations by Gelfand (Arshavsky, Gelfand, & Orlovsky, 1986; Gelfand, Gurfinkel, Tsetlin, & Shik, 1971, 1973), syngergies are identified with central motor programs that can be triggered by simple commands. Saltzman (1979) distinguishes between functional synergies and muscle synergies operating at different levels in a hierarchical control structure (Turvey, 1977). Functional synergies give rise to, or consist of, a set of motions produced across a given set of joints. Muscle synergies are defined by groups of muscles that act as units and can span many joints. The activation of a functional synergy produces a pattern of joint velocities characterized, for example, by relatively fixed ratios across multiple joints. Most synergies emerge after sensorimotor training during postnatal development and underlie such well-practiced actions as walking or reaching for objects. Even after such fundamental synergies have emerged, however, additional problems must be confronted, such as the selection of the appropriate functional synergies in a given situation and the ordering and timing of muscle contractions and joint angle changes in ongoing motor activity.

The study of synergies in humans and animals has led to the identification of many kinds of invariant movement features. Although, in principle, many different strategies to execute a movement can be pursued, certain kinematic variables exhibit mutual dependencies and patterned changes. Kinematic variables have been studied in different systems and including fixed joint velocity ratios, time profiles of spatial movement parameters, and the relative timing of articulator movements during speech production. Examples of fixed joint velocity ratios have been described for hand movements (Kots & Syrovegin, 1966) and pointing movements (Soechting & Laquaniti, 1981) in humans. Laquaniti, Soechting, and Terzuolo (1986) showed that, although individual variations occur, shoulder and elbow motions are generally tightly coupled. The hand trajectories of humans drawing geometrical figures like ellipses and circles in free space (Soechting, Laquaniti, & Terzuelo, 1986) have the same overall shape independent of the starting position or orientation of the figure (compare Fig. 1*B*). In summary, many of the defining characteristics of synergies (e.g., the invariance of kinematic or muscle variables and the fact that they cannot be unequivocally dissociated into independent elementary components) have been demonstrated in a wide variety of motor systems (Buchanan, Almdale, Lewis, & Rymer, 1986; Ganor & Golani, 1980; Greene, 1982; Lee, 1984; Nashner & McCollum, 1985; Shik & Orlovsky, 1976; Soechting & Laquaniti, 1989; Viviani & McCollum, 1983).

Vigorous efforts to understand these issues have been made by workers who have adopted computational formulations of the kinematics of motion. A brief discussion of these approaches will help to identify some of the current problems in this area and set the stage for a contrasting treatment of these problems by selectional theories.

Kinematic Concepts and Computational Strategies

Kinematics.—The variability and flexibility of movements reflect the mechanical redundancy of the musculoskeletal system. A redundant system can be defined as one in which the number of degrees of freedom is larger than the number of independent spatial variables of the mechanical components. In a mechanically redundant system, there is more than one way to generate a given trajectory through the motion of the joints involved. According to Saltzman (1979), "the degrees of freedom for a given system are the least number of independent coordinates required to specify the positions of the system elements without violating any geometric constraints." In the case of an open kinematic chain consisting of multiple links with joints that revolve around a single axis of rotation (hinge joints), the number of degrees of freedom simply equals the number of joints. Some joints of animal and human limbs have more than 1 degree of freedom; for example, the wrist joint is biaxial, the shoulder joint triaxial. The number of independent spatial variables depends also in part on the dimension of the workspace. In a two-dimensional (planar) workspace, the position of each link in a kinematic chain can be specified by its Cartesian coordinates. Thus, in a two-dimensional workspace, kinematic chains with more than two links are redundant. In a three-dimensional workspace, six coordinates must be specified for a given link, three for position and three for orientation. Typically, the human arm (in its three main joints—wrist, elbow, and shoulder) contains 7 mechanical degrees of freedom and thus represents a redundant system in three-dimensional space. If one also takes body motion or motion of the shoulder girdle into account, the effective number of degrees of freedom grows significantly (up to 100, according to Turvey, 1990).

Roughly speaking, kinematics deals with the interconversion of joint and spatial variables. Joint variables may comprise, for example, a set of joint angles, angular velocities, or angular accelerations, and are often expressed in a polar coordinate system centered at the base of the kinematic chain. Spatial variables are, for example, the course of a movement path or the position or velocity of an environmental target and are often expressed in Cartesian coordinates. The *direct kinematic transform* describes the translation of a given set of joint coordinates into a geometric path of the kinematic chain. While this transform always exists uniquely, the inverse operation (called the *inverse kinematic transform*) is indeterminate if the system is redundant. This means that any given path can be produced by a variety (potentially an infinity) of sets of joint angle changes. A typical example (easily reproduced by the reader) is a pointing movement of the arm along a given path. For each configuration of start point, end point, and path, an infinite number of solutions can be carried out (see also Fig. 1A). Cybernetic theories of motor control and robotics hold that computing the inverse kinematic transform for a given desired movement path is the key problem that motor systems face. Because of its indeterminacy, the problem is mathematically "ill-posed."

In principle, two different strategies can be adopted to compute a set of joint angle changes for the inverse kinematic transform:

a) Decrease the number of independent joint variables. The number of degrees of freedom that are used in the movement of a multilink chain can be reduced, for example, by freezing one or several of the joints. Another possibility is to introduce constraints that allow the expression of one joint variable as a function of another. For example, if elbow movements can be expressed as a function of shoulder movements, the number of degrees of freedom has effectively been reduced by one. This strategy is related to the formation of *synergies* of joint or muscle ensembles.

b) Increase the number of specified spatial variables. In addition to specifying desired spatial coordinates for the end point of the kinematic chain (usually carrying the effector, e.g., a gripper), spatial coordinates for other links of the chain may be introduced (e.g., as criteria for optimization of the movement path in terms of length or minimal energy consumption). For example, such criteria could involve the requirement that individual joints rotate as little as possible or that distal joints move more than proximal ones.

Both of these strategies work by introducing additional constraints, either on the motor apparatus itself or on the workspace. Let us see how these kinematic concepts can be put to use in computational approaches.

Computational strategies.—Most computational approaches to the problem of guidance and control of a kinematic chain follow a number of defined steps. We choose as an example a robot arm. First, the desired trajectory (in Cartesian coordinates) of the effector attached to the arm is computed. Second, the inverse kinematic transform is computed, resulting in a set of joint angles and joint angle changes that correspond to the desired effector path. If real motors are involved in moving the robot arm, the adequate motor torque for each joint must be computed in a third step.

The second and third steps involve computing inverse transforms. In principle, there are two computational strategies that will produce solutions for these steps (Hollerbach, 1982; see also Loeb, 1983):

a) The joint angle changes and torques producing a desired movement path can be found by directly solving the set of dynamical equations that describe the behavior of the multijointed arm. For realistic motions of a robot arm, it is important to solve these equations in real time, that is, all computations have to be done at least as fast as incoming signals arrive. Computational strategies of this class are hampered by the fact that a large number of (often nonlinear) terms has to be taken into account. These include inertial forces such as link interaction, centripetal and Coriolis forces, and a variety of other effects due to gravity. The dynamical equations for a multijointed arm in three-space can thus become extremely complicated, and computations of even simple trajectory fragments tend to take significant computational time. A complete set of Newtonian equations for position and joint velocities of a three-jointed arm in three-space contains 1,600 terms and requires 13,000 multiplications for its solution (after Raibert, 1978). The equations to compute the inverse dynamics of motions for a model with five degrees of freedom of the upper arm alone can themselves occupy two entire pages of closely spaced text (after Hogan, 1988). Attempts have been made to simplify the systems of equations and associated algorithms sufficiently, to allow fast and reliable computation (Hollerbach, 1980; Luh, Walker, & Paul, 1980). The continual increase in computer power is likely to make this strategy more feasible for many applications, but its biological relevance remains marginal.

b) A second class of solutions to the inverse dynamics problem involves the retrieval from memory (in the form of a "lookup table") of the desired joint torques for a given desired movement of the multijointed arm (first introduced by Raibert, 1978; Raibert & Horn, 1978). However, the amount of memory needed is very large and increases dramatically with the dimensionality and complexity of the task. Furthermore, a precise index is needed for retrieval, and the stored items may have to be updated instantly, particularly if the mechanical configuration or mass of a kinematic chain changes abruptly (as happens when a load is picked up).

What both approaches have in common is that they attempt to solve the inverse kinematics problem *directly by computation*. Neither strategy makes use of synergies as functional components of the motor ensemble or of the dynamic and associative properties of neural architectures in order to constrain the number of possible solutions. Neural network models have been claimed to take some of these issues into account in their approach to the inverse kinematics problem.

Neural network models.—Computational approaches to motor control have been enriched by a recent resurgence of interest in neural network models (e.g., Berkinblit, Gelfand, & Feldman, 1986; Bullock & Grossberg, 1988; Hinton, 1984; Kawato, Furukawa, & Suzuki, 1987; Kawato, Isobe, Maeda, & Suzuki, 1988; Kuperstein, 1988; Massone & Bizzi, 1989). Much of the appeal of these models appears to have arisen from their resemblance to real brain structures, a resemblance that is nonetheless often only superficial. Most network models share a common feature with more conventional computational approaches. The movement of a kinematic chain is determined by a "desired trajectory." This is either precomputed and presented to the model as a desired output vector to which network behavior must converge (Kawato et al., 1987, 1988), or it is represented internally (computed from sensory input) and then serves to guide an ongoing movement to its goal (Bullock & Grossberg, 1988; Hogan, 1988).

Hinton's (1984) iterative model for the generation of reaching movements contains representations of joint angles and positions in addition to a "desired vector" from the tip of the arm to the target. Joint angles are updated in a parallel fashion while the desired vector is minimized or shortened. Hinton notes that elimination of interactions between individual joints will frequently lead to grossly suboptimal trajectories. To remedy this situation, he proposes that, under certain conditions, synergies act as computational subroutines.

Bullock and Grossberg (1988) have described a model of arm movements called the vector-integration-to-end-point model. A target position command specifies where the arm is intended to move, and an independently generated second command specifies the movement speed. An arm trajectory is then computed from a present position vector and a difference vector that is continuously updated and that specifies the difference between present and target position. The present position vector (in connection with the difference vector) determines an outgoing motor signal leading to motion. The model essentially depends on the continuous updating of the difference vector, presumably by sensory feedback signals sampled during motion. A model requiring constant updating may be inadequate for rapid movements such as saccades or ballistic reaching.

Ritter, Martinetz, and Schulten (1989) have constructed a model containing neural maps that learns to position an arm under visual feedback. Ultimately, the arm moves with high accuracy to a target position. The authors found that, if some subregions of space are covered more frequently than others, the sensorimotor map adapts by recruiting more neuronal units in that area. Another model of sensorimotor coordination has been developed by Kuperstein (1988; see also Grossberg & Kuperstein, 1986; Kuperstein, 1991). The arm used in their model has 5 degrees of freedom and operates in three-dimensional space. During reaching, the arm travels instantly from one equilibrium position to another (that is, joint angles are linearly proportional to muscle activity). During the first stage of training, the "eyes" of a robot are fixed on the target by an unspecified mechanism. The arm is allowed repetitively to position itself by random motions from a standard starting position. During these movements, kinesthetic eye position signals and target vision are sampled and correlated with the random motor signal in simulated neural networks. The discrepancies between actual postures and the ones computed from the sensory information are split into respective components for individual sets of muscles and the synaptic weights in the networks are changed in order to minimize this discrepancy. After training of the system, the random generator is removed and a visual target can then drive the individual joints, using the maps constructed in the first stage.

In summary, most of the existing network models require both the setting of a desired path and the specification of fairly elaborate feedback signals, such as difference or error vectors, in order to converge to a desired mode of action. However, these feedback signals are often not specified in biological terms. While it has certainly been shown in many experiments (e.g., Bauer & Held, 1975; Held & Bauer, 1974) that sensory input is essential for ongoing purposeful movement as well as motor learning, the predominant view of learning as convergence to a previously determined or prescribed state, and thus the *instructive* nature of such inputs, is far from proven.

Dynamic systems theory.—Recently, attempts have been made to link the emergence of coordinated movements to concepts of nonlinear systems theory. This approach was originated by Kelso (for review see Kelso & Tuller, 1984; Schöner & Kelso, 1988), as well as Kugler and Turvey (1987; see also Kugler, Kelso, & Turvey, 1982). According to this approach, coordinated movement is produced by many interacting elements with potentially many degrees of freedom, constituting a nonlinear system which can attain a certain number of dynamic states. For example, rhythmic swimming motions can be described by relatively few parameters (such as frequency and amplitude), that is, are characterized by only a few degrees of freedom, even though many neurons, muscles, and bones may be involved in their generation. The interest in rhythmic movements of this kind dates back to Erich von Holst (1937); recent work on rhythmic movements in animals and humans viewed in the context of dynamic systems theory includes the studies by Schmidt, Beek, Treffner, and Turvey (1991); Schöner and Kelso (1988); Thelen, Skala, and Kelso (1987); and Ulrich (1989). More recently, Thelen has proposed that development might be understood as a temporal sequence of coordinative modes or attractor states (Thelen, 1990). The transition from one state to another would be under the control of relatively few developmental control parameters; the emergence of coordinated leg movements in infants has been investigated from this perspective (Thelen, 1989b).

Many basic concepts (such as the importance of nonlinear self-organizing interactions within a complex system) of these dynamical theories are consistent with selectionism (see Kelso & Tuller, 1984). Like selectionism, dynamical systems theory rejects instructionism and an algorithmic treatment of learning and motor development. However, selectionism differs in that it is explicitly based on neuroanatomy and neurophysiology and explicitly recognizes the importance of analyzing the interactions of multiple levels of organization (such as neural circuits or limb biomechanics). In particular, dynamical systems theory by itself does not identify specific neural mechanisms of developing and mature motor systems.

The next section contains a broad outline of our proposal to abandon the instructive or computational paradigm and look at the problem from a new selectional perspective.

An Approach to Solving Bernstein's Problem by Selection

There is overwhelming evidence that the emergence of coordinated movements is intimately tied both to the growth of the musculoskeletal system and to the development of the brain. Thus, neural development and learning cannot be considered outside of their biomechanical context. A key theoretical issue is how changes in brain circuitry controlling muscles and joints become matched to simultaneously occurring developmental changes at the periphery (the interface between the musculoskeletal system and the environment of the organism). How can coordination emerge from the many components and interactions of such a system? A promising approach is to consider various aspects of this question in terms of population thinking (Mayr, 1959). The theory of neuronal group selection (Edelman, 1978, 1987, 1989, 1993) is a consistent attempt to apply population thinking to the functioning of the nervous system and provides the basis for the present proposal.

Neuronal group selection.—The theory of neuronal group selection places great emphasis on the structural variability of brain circuitry. During development, neuronal circuits are not precisely wired at the level of microanatomy. Thus, the brain contains *repertoires* of variant circuits (structural variability) that can give rise to many different outputs (dynamic variability). Those variant circuits form *neuronal groups,* local collectives of several hundreds to thousands of more strongly interconnected neurons that tend to share functional properties and to discharge in a temporally correlated fashion. The postulated neuronal groups are considered to be the basic functional units or units of selection. They have recently been experimentally identified in several cerebral cortical regions (Gray & Singer, 1989).

In the cortex, neuronal groups are arranged in neural maps, representing, for example, visual space or the body surface. While these neural maps are often functionally segregated and occupy circumscribed regions of the cortex, they are anatomically coupled through long-range connections. Virtually all of these connections are reciprocal. Recursive reciprocal signaling (called *reentry*) between neuronal groups in distant sensory and motor regions gives rise to new dynamical properties, including temporal correlations (Sporns, Tononi, & Edelman, 1993; Tononi, Sporns, & Edelman, 1992a, 1992b). In general, reentry is the key operation that serves to integrate the activities of the multiple sensory and motor areas of the brain.

How do these ideas relate to population thinking? Repertoires of variant neuronal groups are subject to *somatic selection* (i.e., selection occurring during the lifetime of the organism). This selection occurs for particular groups when their activation in a given context matches given environmental and internal constraints as compared to competing groups. For example, particular groups may be selected for their contribution to perceptual categorization or to motor tasks. The mechanism of selection in the nervous system is synaptic change (by a variety of detailed mechanisms) leading to the selective amplification or diminution of neuronal group responses. The selection of neuronal groups ultimately allows the discrimination and categorization of sensory inputs and the integration of sensory and motor processes to yield adaptive behavior. This integration depends upon higher-order relationships. For example, dynamically coupled sets of neuronal groups in a variety of functionally segregated maps linked by reentrant connections that are active for a given sensorimotor task can constitute a *global mapping* (see Edelman, 1989). By its nature, a given global mapping involves widespread and distributed regions of the brain.

Neuronal group selection by no means relies purely on mechanisms of elimination or regression, as has been implied by others (Purves, 1988). Simple regression (i.e., overproduction of neural connections and subsequent elimination of "inappropriate" ones in development) may occur in some isolated instances, but is not general enough to account for either somatic or evolutionary selection (Edelman, 1987, 1989). Instead, the theory of neuronal group selection stresses the importance of both stabilization of selected neuronal circuitry (including the possibility of generating new connections, under favorable circumstances) and balanced competition.

Selection in sensorimotor development.—How do these notions apply to Bernstein's problem? We propose that the development of sensorimotor coordination proceeds in three concurrent steps: (*a*) the *spontaneous generation* during development of a variety of movements forming a basic movement repertoire; (*b*) development of the *ability to sense* the effects of various movements in the environment, eventually allowing neural selection to be guided by *adaptive value* (for a discussion of *value,* see below); and (*c*) the *actual selection* of movements in various global mappings under the constraint of adaptive value. Selection in the nervous system is mediated mainly via synaptic change, resulting (on average) in the stabilization of those brain circuits that support adaptive (or goal-directed) movements. Somatic selection in the nervous system and motor action at the periphery are thus subtly intertwined through the action of global mappings. Successive selection events will result in a progressive modification of a given movement repertoire and will thus shape the ongoing motor activity of the organism. On the other hand, an emerging movement repertoire (occurring as a result of changes in biomechanics or environmental demands) will also drive selection to yield consistent and adaptive coordination.

A natural consequence of selection is the emergence of synergic relationships between members of the motor ensemble. Indeed, the formation of synergies by selection effectively replaces the need to solve the problem of inverse kinematics by computational means. Instead of having explicitly and accurately to compute a desired trajectory in order to reach a goal, animals select those purposeful movements from a diverse repertoire that fulfill adaptive constraints. After selection, synergies will emerge *that are formed by the amplification of movements that are favored in a given task and context.* Thus, a model based on somatic selective processes eliminates the need *explicitly to compute* systems of nonlinear differential equations containing many kinematic and dynamic terms. Rather, we suggest that, through spontaneous and exploratory motor activity, the organism *discovers* possible "solutions" that satisfy the task constraints as well as internal value. The variability and degeneracy that are so vexing in computational or kinematic approaches are in fact a necessary prior condition for successful selection. The synergic, "topological" and "gestalt" character of movements emerge under a given set of mechanical and neural constraints because movements are selected as *whole patterns,* without being decomposed into parts that are subject to separate analysis and adjustment by instructive learning algorithms.

A selectional scheme also allows preexistent or preferred movement patterns to be readily integrated with subsequent motor learning and adaptation. There is ample evidence that organisms are born with a considerable set of intrinsically specified motion patterns (presumably the result of evolutionarily selected circuits in certain parts of the brain). Such characteristic movement patterns can even be observed at embryonic stages (Bradley & Bekoff, 1990; Smotherman & Robinson, 1988); indeed, prenatal motility may be important for the anatomical specification of neuromuscular connection patterns (Coghill, 1929; Hamburger, 1970). Preexistent patterns impose considerable constraints on the basic movement repertoire of an organism and on subsequent motor development. The selective history of an organism is critically influenced by such preexistent patterns which can guide the transformation of the primary movement repertoire into a set of adaptive action patterns. These issues bear upon that of value.

Value.—Inasmuch as a selectional system operates upon preexistent diversity and does not have a specific program for most refined movements, the question of constraints upon selection arises. According to the theory of neuronal group selection (Edelman, 1989), these constraints are provided by value systems already specified during embryogenesis as the result of evolutionary selection upon the phenotype. In the case of movements, such constraints appear in neuroanatomy as specific circuitry signaling via particular neurotransmitters. Such value circuits are prespecified by evolutionary selection rather than derived from experience. The crucial features of such value schemes are their anatomical simplicity and the diffuseness of their effects on their target networks; these features sharply distinguish value schemes from the instructive agents and error feedback employed in most learning algorithms. In general, value circuits cannot themselves lead to the variety of highly articulated movements necessary for development and survival. In this view, in contrast to instructive views, the coordination of movement occurs *ex post facto* as a result of somatic selection upon value that has been established by evolutionary selection.

Value systems involved in sensorimotor development receive sensory inputs that enable them to respond to actions or events in the environment by increasing or decreasing their level of neuronal activity. Due to their evolved anatomical structure, the level of response of such value systems is related to simple criteria of saliency or adaptiveness. For example, a reaching movement establishing tactile contact with an object may result in increased neuronal firing in the value system, thus signaling the adaptiveness of the movement. This value system might receive sensory inputs from tactile receptors located in the skin.

In order to be effective on sensorimotor development, value systems must be able differentially to affect synaptic changes in circuitry controlling movement. For example, increased activity in a value system can influence synaptic changes involving a large majority of those neurons that participated in a successful (adaptive) reaching movement. As a result of a positive change (given positive value) in the underlying circuitry, this adaptive movement is more likely to be executed in the future. It is important to stress that the action of value systems is both diffuse and probabilistic. Because output fibers of value systems branch widely over extended regions of the cerebral cortex, they influence synaptic modification in large parts of the nervous system. Given this diffuse effect of value, there can be no local determination of the contribution of individual neurons or synapses to a given movement; instead, value acts on whole populations of neurons. Therefore, value does not act deterministically but probabilistically. While on average (over time) selection upon value will lead to increasingly adaptive behavior, on individual trials some members of the neuronal populations may exhibit "undesirable" synaptic changes (driving the system away from a more adaptive state). Such ongoing effects may serve an important function in maintaining variability as a basis for further selection. We will give a specific and detailed example of how a value system acts in the section on computer simulations.

An important issue concerning value has to do with the specificity or generality of value systems. It seems unlikely that a separate value system exists for each motor task that an organism might carry out during its lifetime. Many different levels of phenotypic constraints act to define value systems. These include morphology itself, the acquisition of new neurotransmitters, interactions between cortical and midbrain homeostatic systems, and hormonal changes. There is no simple relation between the mapping of motor control systems and combinations of these different constraints on value. Given the fact that value is evolutionarily selected for in the species and varies with different species, no simple one-to-one correspondence between value and a given motor system would be expected. Clearly, since motor responses are achieved differently in different individuals during ontogeny, their possible patterns are much more numerous than could be arranged by evolutionary selection. We would expect that different value systems are activated for a variety of functionally interrelated tasks, that different value systems might interact, or that hierarchies of specificity might exist. It is consistent with this general view that, as compared to specific acquired cortical responses and their interactions, there seem to be relatively few value-related "saliency" systems in the brain and that these systems project to very widespread and diverse regions of the cerebral cortex. Examples are the hypothalamus, the locus coeruleus, the raphe nuclei, and the cholinergic basal forebrain system. How specificity of learning is achieved through the combined action of such systems with the cortex is a deep problem that requires more attention. We believe that the issue of value constraints and their number presents one of the greatest future challenges to selectional theories of brain function. A possible insight may be gained by considering different combinatorial arrangements of systems of value as they act on different motor arrangements.

Selection from a movement repertoire.—It is evident from the above outline of a selectional model that the formation of synergies requires not only the interaction of the organism with the environment but also a means by which the adaptive value of a movement can be assessed and in turn influence future movements. A schematic diagram illustrating the selectional principle for coordination of movement is given in Figure 2. We assume for simplicity that a movement such as a simple gesture is characterized by values of a set of n joint variables ϕ_n. The set of all possible combinations of these n joint variables thus forms an n-dimensional movement space $\mathbf{M}$ (for simplicity $n = 2$ in Fig. 2). Initially, the subset of movements that are available to the organism is only constrained by the mechanics of its motor ensemble and preexistent movement structures, but is basically unconstrained by experience in the environment.

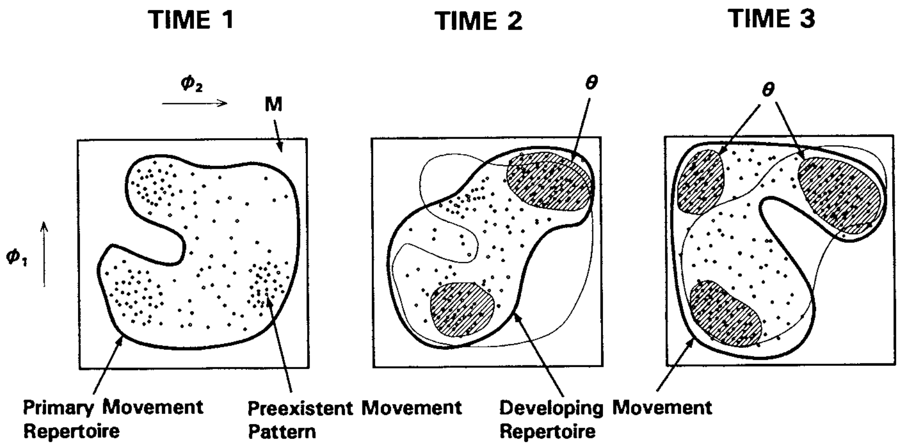

FIG. 2.—Schematic diagram of a developing movement repertoire contained in a movement space **M**. A single movement within the space is specified by a combination of the movement variable ϕ_1 and ϕ_2; it is represented as a small dot. The dot density represents the frequency with which movements are executed in a particular region of **M**. The three frames depict different temporal stages. At the left is the primary movement repertoire containing several preexistent (or "innate") movement patterns. The shape of the movement repertoire evolves with time to include previously unoccupied regions of **M** or to exclude others. Hatched regions define movement patterns that correspond to a given task. Movements within these regions θ meet with positive adaptive value. As a result, their frequency increases. With time, due to changing environmental and biomechanical constraints, both the movement repertoire and the regions θ will continue to change shape (see middle and right).

This primary movement repertoire is thus largely unstructured—with the exception of preexistent synergic relationships between the relevant movement variables ϕ_n. At the onset of sensorimotor experience, the organism is confronted with demands from the environment, while at the same time it is subject to its own value systems. For example, during spontaneous motor activity, some movements will help to accomplish a task better than others. In our scheme, such movements, often primarily defined by constraints in the environment (as in a spatial reaching task), but also by constraints imposed by the geometry of the kinematic chain, might form one or more subsets θ within the movement space **M** (Fig. 2). Because of mechanical redundancy for each given task, these subsets may span extensive regions in **M**.

Somatic selection in the nervous system results from the competitive strengthening of neural connections (synapses) involved in the generation of "successful" movements (e.g., those involved in touching an object or bringing it to the center of the visual field). Those giving rise to other movements are weakened or left unchanged, depending on the particular synaptic mechanism that is invoked. As a result of selective synaptic change, movements that help to accomplish the task become more probable on average than others. Because of individual variations in the biomechanics of motor organs, their progressive structural and dynamical change during development, and the unpredictable nature of environmental demands, these "desirable" subsets θ will appear quite different, not just for different species, but also for different coexisting individuals of the same species. Thus, there are narrow limits for "preprogrammed" or "hard-wired" neural control of movements; the organism must rely both on spontaneous (though not necessarily random) motor activity and the subsequent selection of those movements that simultaneously match environmental demand and internal value.

In this scheme, synergies control movements, forming different task-related subsets θ. The set of movements comprising functional synergies is often degenerate (Edelman, 1987) in that it contains movements that are functionally related (they all accomplish the same task) but are structurally nonisomorphic (they utilize different joint variables or muscles groups to different extents, and are controlled by different sets of neuronal groups). The degenerate structure of functional synergies provides a basis for motor equivalence. By allowing flexibility (Partridge, 1986) and by forming a diverse substrate for further selective events, a rich degenerate structure yields evolutionary advantages to an organism.

Experiments in many areas of neuroscience and psychology are needed to substantiate and refine the key points of the proposal briefly described here. But it is also important to show how the proposed mechanism actually can work. One way to show its overall feasibility and self-consistency is to simulate on a supercomputer a structurally and functionally realistic motor system working on selectional principles.

Computer Simulations

For several years, we have pursued an approach to the understanding of higher brain functions called synthetic neural modeling (for a review, see Reeke, Finkel, Sporns, & Edelman, 1990; Reeke, Sporns, & Edelman, 1990). This approach attempts to address the complex problem of integrative brain function by using computers to carry out large-scale simulations of neuronal circuits acting together with phenotypic organs that are embedded in an environment. In the simulations discussed in this section, we require that afferent sensory signals (coming from visual or kinesthetic receptors) be sampled both during and after the occurrence of a movement. A second requirement is that an intrinsic bias or value must exist favoring modes of behavior that are more adaptive than others; an example of such a favored action might be reaching out and touching an object. The first instantiation of an autonomous "artificial creature," Darwin III, consists of a complex nervous system, an arm, and an eye. It behaves in a two-dimensional environment containing sensory stimuli. Darwin III is able to track objects visually and reach for them; visual and tactile sensory inputs are combined to allow complex perceptual categorizations of a large variety of stimulus objects. For more detailed descriptions of all of Darwin III's components, see Reeke, Finkel, Sporns, and Edelman (1990) and Reeke, Sporns, and Edelman (1990). Here we focus exclusively on its motor functions.

Darwin III contains a four-jointed arm moved by four sets of independent agonist-antagonist muscle pairs operating in two-dimensional space. The system thus has surplus degrees of freedom and is mechanically redundant. The basic idea behind the model is that, through experience, gestures or gestural components (corresponding to synergies) are selected from a relatively unstructured primary repertoire of movements. The model has two main functional components (see Fig. 3): a module corresponding roughly to the cerebral cortex, where motor signals eventually leading to gestural motions are generated, and a module corresponding roughly to the cerebellum, which correlates these motor signals with current sensory inputs and smooths the responses by eliminating components that are inappropriate. Hand and object vision as well as a simple form of kinesthesia and light touch provide the sensory signals utilized by the system. The different signals from these modalities are transformed through mapped and unmapped interactions of separate neuronal networks present in the two modules into motor signals that move the arm to new positions. It must be understood that, while components of the model perform functions similar to those in real brains (and are named analogically), they are not modeled in explicit detail. The model is simple as compared to real vertebrate brains; Darwin III essentially contains a total of 50,000 neurons and 620,000 connections, organized in about 50 neuronal repertoires.

The "motor cortex" generates patterns of activity corresponding to primary gestural motions through a combination of spontaneous activity (triggered by a component of Gaussian noise) and by responses to sensory inputs from vision and kinesthetic signals from the arm. This activity pattern is selectively remodeled ("sculpted") under the influence of inhibitory connections coming from the "cerebellum." Ultimately, the "cortical" module sends out connections to four sets of motor neurons (one for each joint) organized in extensor/flexor pairs.

The "cerebellar" networks receive sensory inputs (vision and kinesthesia) as well as activity driving the current primary gesture emanating from the "motor cortex." The networks respond to specific combinations of the actual positions of the arm and target and to combinations of activity patterns corresponding to primary gestures. Their inhibitory influence (negative selection) on primary gestures as they are generated in the motor cortex serves to select or "filter out" those gestures that are appropriate.

Both "motor cortex" and "cerebellum" in Darwin III are topographically ordered in that they contain groups of units that primarily connect in an ordered sequence to single

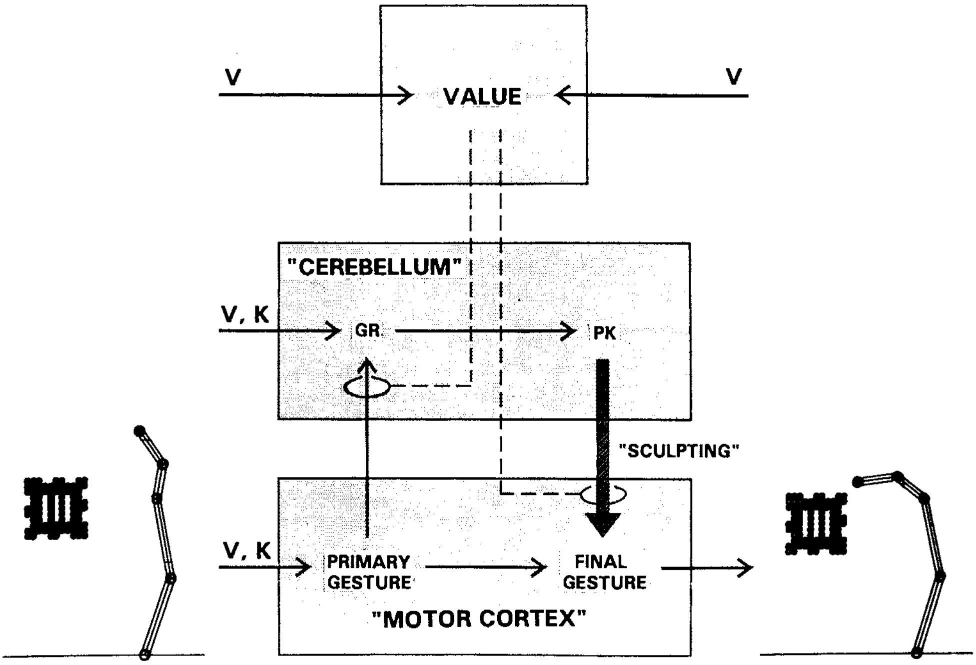

FIG. 3.—Schematic diagram of the neural circuits controlling Darwin III's four-jointed arm system. For detailed explanation see text. Main modules are labeled "MOTOR CORTEX, CEREBELLUM" (with GR = granule cells and PK = Purkinje cells), and VALUE. Inputs to modules are visual (V) and kinesthetic (K). Value-dependent modification of connections to and from the cerebellum is indicated by dashed lines.

joint extensors or flexors. This arrangement is consistent with anatomical and physiological evidence for such motor maps. Intrinsic connections in the "motor cortical" network (not shown in Fig. 3) are biased to favor the spread of activity from units representing proximal to more distal joints. Gestural motions therefore tend to unfold proximodistally, a useful preexistent characteristic for the large-amplitude reaching movements under study in the simulations. Although a certain degree of topography is present in the system from the beginning, there is no explicit representation of either "movements," "muscles," or "joints" within the motor cortex. (What is represented in actual motor cortex is still an open and much debated question; see Humphrey, 1986; Lemon, 1988.)

Initially, the connectivity of the reaching system of Darwin III is uninstructed with respect to appropriate directions and amplitudes of movement. Coordinated motions of sets of joints occur only later, *after* gestural components have been selected from spontaneous movements by amplification of those synaptic populations that give rise to such gestures. To detect and signal the *consequences* of such successful motor activity, neuronal circuitry instantiating an intrinsic value scheme is required. In Darwin III's reaching system, this circuitry consists of a set of neurons responding more strongly as the moving hand approaches the vicinity of the visually foveated target object. These neurons receive topographically mapped visual inputs from two separate neural repertoires responsive, respectively, to objects in the environment and to the hand of the automaton itself. Each of these inputs arborizes in an overlapping fashion over the surface of the value network, and thresholds are arranged such that correlated activity in both inputs is required for a vigorous response. The responses of the value units thus increase, independent of the absolute position of the target, as the hand approaches the target and as the degree of overlap in the topographically mapped inputs increases.

The activity in the value repertoire is transmitted to parts of both the "motor cortical" and "cerebellar" networks and serves selectively (but only probabilistically) to strengthen or weaken populations of synapses. After repeated amplification, appropriate activity patterns in the cerebellum will arise as soon as a target appears in the visual field and before a gesture is initiated. Its inhibitory connections terminating in the motor cortex are thus available for "filtering" and "sculpting" gestures as they happen.

As a biologically based system, Darwin III's reaching system offers several distinct advantages over neural network models, such as that described by Kuperstein (1988, 1991): (*a*) No instructive learning algorithm is used to adjust synaptic weights. Instead, Darwin III's networks are subject to selective amplification depending on a value scheme (no error vector is used), and synaptic changes simultaneously affect neurons related to all components of the movement. On the other hand, Kuperstein's model requires the determination of an error vector and the splitting of this vector into components used to adjust synapses related to specific joints. While Kuperstein's calculation of the error vector is accomplished by a computational subroutine, value schemes in Darwin III are implemented as specialized networks that are anatomically and functionally integrated with the rest of the model. (*b*) Kuperstein's model operates as a look-up table of movements arranged in a sensorimotor map; it does not use synergies to reduce the number of degrees of freedom. In fact, its 5-degrees-of-freedom arm is nonredundant in three-dimensional space. The network architecture does not allow for interactions between individual joints. (*c*) Each individual reaching movement in Darwin III evolves and changes in time and is elaborated over multiple time steps. This allows the evaluation of the shape of arm trajectories, a very important characteristic of human reaching movements. In contrast, a reaching movement in Kuperstein's model consists of only one step from the initial position to the end point; this excludes the possibility of characterizing trajectories. (*d*) In contrast to Kuperstein's model, Darwin III does not operate in distinct training and performance modes. Instead, the development of synergies by selective amplification and actual performance of the arm are concurrent processes; it is not necessary (as in Kuperstein's model) to connect or disconnect components of the model when switching from training to testing.

Darwin III's reaching movements may be examined by looking at a short sequence of simulation cycles (Fig. 4) or by considering diagrams showing plots of bundles of trajectories (Fig. 5). The large variance among individual motions that exists initially (Fig. 5A) is progressively reduced to a narrow envelope of motions, most of which point toward the object (Fig. 5*B*). This result resembles data shown by Georgopoulos, Kalaska, and Massey (1981, see especially their Fig. 3), who have studied the geometry of pointing movements in rhesus monkeys during learning. (Of course, this resemblance does not by itself indicate that the underlying neural processes are identical.)

More detailed observation of single joints in Darwin III (e.g., "elbow" and "shoulder") reveals that, after training, changes in joint angles are no longer independent of each other (Fig. 6). Instead, joints act together in more or less stable ratios and, as a result of this synergic interaction, the effective number of degrees of freedom is reduced. Such relationships exist only in trained movements (Fig. 6*B*), but are absent before training and selective amplification (Fig. 6*A*). We have observed linkages between proximal as well as distal joints and between joints that are not immediately adjacent to each other (data not shown). Joint relations may be linear or nonlinear, varying from example to example, reflecting the different requirements of parts of the workspace, of arm geometry and neural structures, as well as differences in the individual history of selectional events.

The complex anatomical organization of the system does not allow precalculation of the relevant neural pathways for a given "desired" movement. Given the mechanical redundancy of Darwin III's arm, there are multiple degenerate means for each trajectory to reach a given end point. We have pointed out above that one way to solve Bernstein's problem (and to reduce the number of degrees of freedom in a multilink kinematic chain) is to group muscles or joints together to form synergies. In the present model, *selection* constrains the envelope of possible motions; as a result, synergies *emerge*. Thus, selection guarantees execution of *one or another* of the numerous solutions that lead to a successful outcome. Note that Darwin III's reaching system does not work by *determining* a desired trajectory; in fact, trajectories are not explicitly represented anywhere within the system. Thus, the model embodied in Darwin III may serve as a first working example to illustrate the benefits of a selectional strategy in creating synergies.

A system designed to execute a number of different synergies must incorporate neural maps that allow the selection of the appropriate synergy for a given sensory context. Synthetic neural modeling allows one

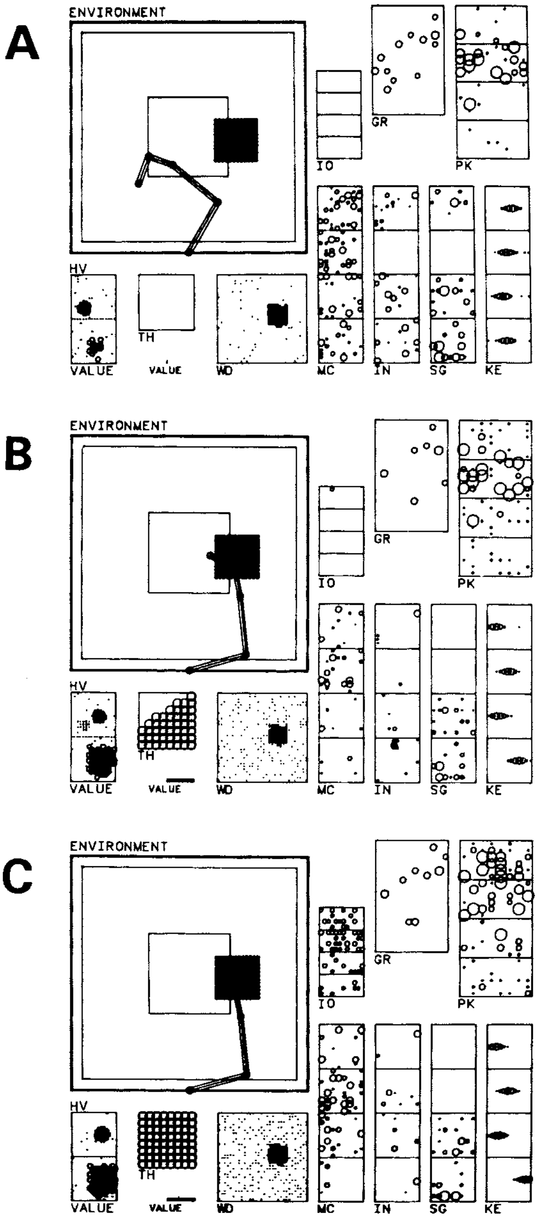

FIG. 4.—Display of Darwin III's four-jointed reaching system on three consecutive cycles *A*, *B*, and *C*. At each cycle Darwin III's environment and the state of its neuronal repertoires (with circles representing active neurons) are displayed. The neuronal repertoires, plotted as planar maps of neuronal units, are labeled as follows: VALUE, "value system"; HV, "hand vision"; TH, touch"; WD, "world"; MC, "motor cortex"; IN, "intermediate layer of the motor cortex"; SG, "spinal ganglia"; KE, "kinesthesia"; IO, "inferior olive"; GR, "granule cells"; PK, "Purkinje cells." In addition to object (dark square) and visual field, the environment display contains a four-jointed arm, anchored at the bottom of the environment. Repertoire WD reports the position of the target object to MC and GR, networks representing motor cortex and granule cells of the cerebellum, respectively. In addition to this visual input, MC and GR receive subthreshold inputs from KE, a network that reports kinesthetically the positions of the four joints. Notice how the activity in KE varies systematically with changing arm position. The pattern of activity in MC is transmitted to IO, which sends a number of strong excitatory connections to a repertoire, PK, representing Purkinje cells. Units in IO only fire if positive value occurred in the previous cycle (as happens in *C*); value acts as a modulatory signal that allows activity in MC to be transmitted to PK ("gating"). There are also a great number of initially weak

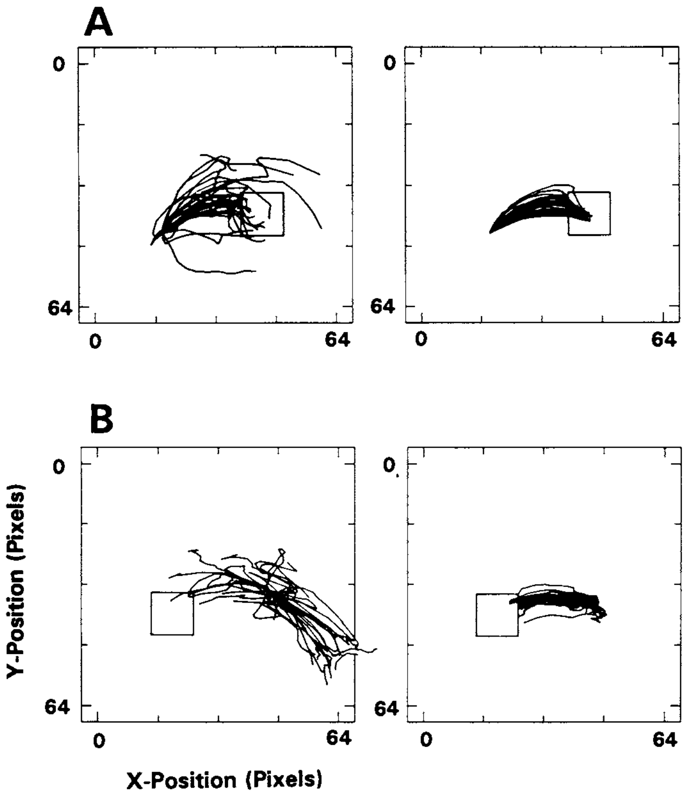

FIG. 5.—Examples of paths taken by the tip of the four-jointed arm as it reaches for square objects presented at the marked locations in the input array (compare Fig. 4). Left and right panels in *A* and *B* display data sampled before and after 1,440 cycles of training, respectively. Each panel displays 480 cycles (30 trials), recorded while synaptic amplification was frozen. *A* and *B* give examples of motions starting at different initial conditions. The initial set of joint angles was 60, 100, 200, and 90 degrees for *A*, and 25, 140, 200, and 90 degrees for *B* (see Fig. 6 inset). From Reeke and Sporns (1990), reproduced with permission.

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connections between GR and PK; these connections, as well as descending inhibitory fibers from PK terminating on IN, are modifiable. The PK inhibitory fibers act to select appropriate motor signals for gestures that are generated in MC and transmitted to the motor neurons, SG, through IN. Thus it is the pattern of active units in IN that determines which path the arm will describe. The IN activity pattern in *A* determines that the arm will move toward the target and is the result of a combination of excitatory influences from MC, as well as inhibitory action of PK units. PK units can be activated by strengthened connections from GR alone, and the IO network becomes unnecessary after training is completed. On impact on the target (*B* and *C*), touch-sensitive neurons in a sensory sheet tied to the tip of the arm, TH, become active and guide the subsequent tracing of the edges of the object (not shown). A value-sensitive network (VALUE) receives topographically mapped inputs from both the target visual area WD, as well as from a repertoire sensitive to the position of the hand (HV). VALUE fires more vigorously when the hand approaches the target (compare *A* vs. *B*); the global output of this repertoire is used to modulate activity in IO and amplify connections between WD and MC. The connections between GR and PK, as well as those between PK and IO, are modified without the participation of value, but modification can only occur if the IO network is active and fires PK units. The inhibitory action of PK units results in freezing of the second joint while the first joint flexes *A*. On impact gross arm motion is inhibited *B*, and an additional motion of the third and fourth joint establishes full contact *C* (for more complete information see Reeke, Finkel, Sporns, & Edelman, 1990). From Reeke, Sporns, and Edelman (1989), reproduced with permission.

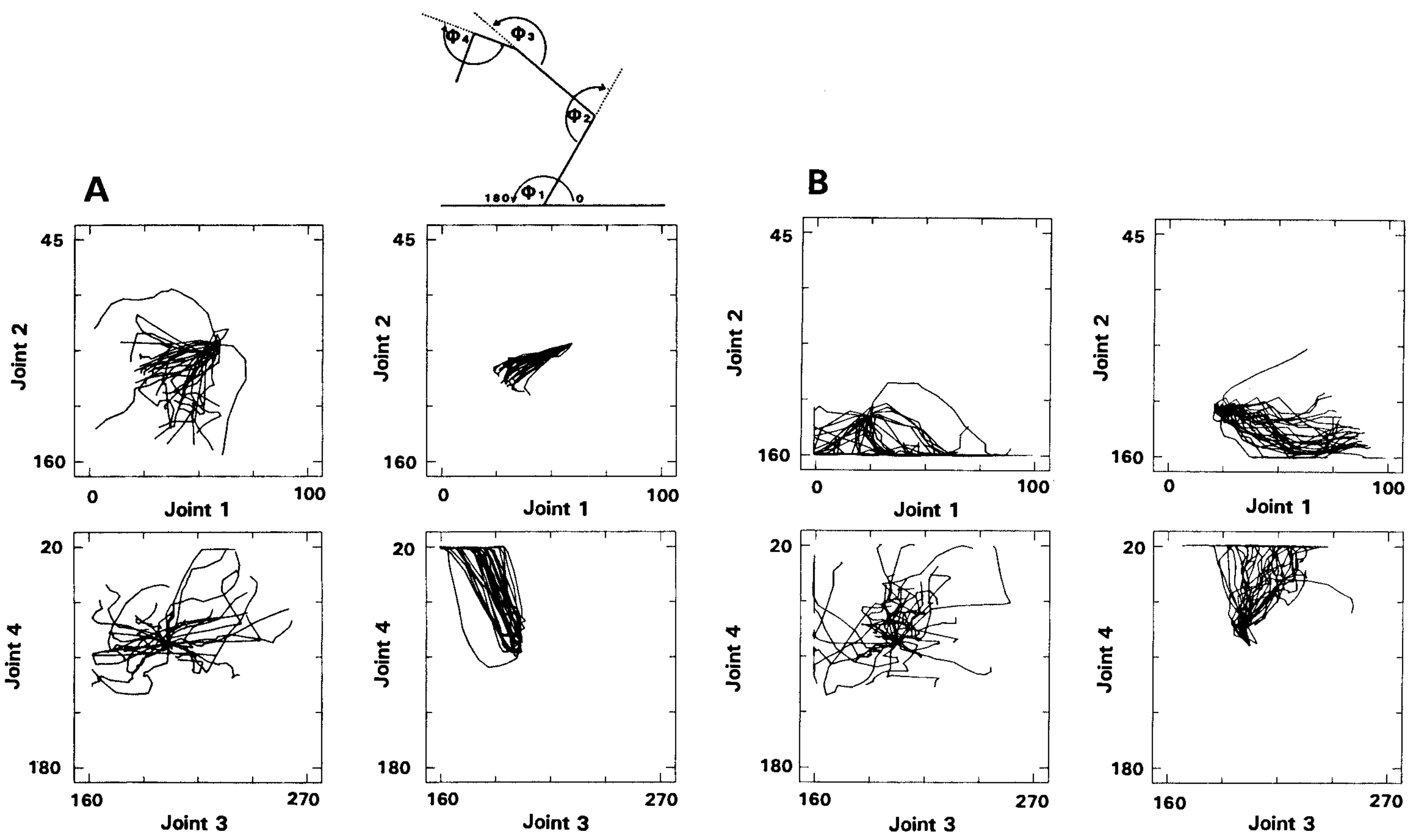

Fig. 6.—Plots of joint angles obtained from data on untrained and trained movements in Fig. 5 (Panels *A* and *B* correspond to each other in both figures). The inset illustrates the conventions for the measurement of joint angles. The half-arcs define the direction and origin of angular rotation around each joint and run from 0 to 180 degrees. Left panels in *A* and *B* show movements before training, characterized by widely dispersed distributions of combinations of joint angles. After training (right panels), these distributions are much narrower, and joint angles that were previously independent from each other have now established fixed relations. Such relations can be observed between proximal (upper panels in *A* and *B*) as well as distal joints, and can have more linear (*A*, upper right) or nonlinear (*B*, upper right) appearance. It should be noted that random initial variations in the neuronal structure of the system can lead to variations in the synergies selected by two different examples ("individuals"). From Reeke and Sporns (1990), reproduced with permission.

to explore the issue of mapping a sensory input space onto a map of synergies (or gestures) by incorporating different neural and phenotypic structures into any given model. Indeed, we have designed a second motor system for Darwin III with more sophisticated neural maps and have been able to achieve reliable and accurate reaching movements over the entire input space (for a detailed description, see Sporns, 1990). The mechanics of the arm were simplified by reducing the number of joints to two. While working according to the same selective paradigm used to create synergies in the model with the four-jointed arm, the model incorporating neural maps exceeded the performance of the previous model in several respects. The model was able to provide for accurate reaching movements from an arbitrary starting position to any target position within the workspace. Unlike the first model, such reaching movements could be performed at the same time the eye was moving, for example, while saccading to a visual object (Fig. 7). Furthermore, the model was able to perform over a wide range of changes in arm size or metric without *external* adjustments of structural or dynamic parameters in the nervous system. A sudden change in the biomechanics of the arm led to an initial decrease in performance accuracy. Continuing somatic selection of circuits, however, provided a sufficient basis for progressive adaptive change. This example provides a demonstration that developmental and evolutionary changes in the biomechanics of motor organs can be compensated for by accompanying somatic selective changes in the nervous structures controlling their action. This ability is one of the strongest arguments for somatic selection in the brain (Edelman, 1987).

In conclusion, the computer simulations presented in this article show the self-consistency of an approach based on selectional principles. Taken together with experimental evidence on sensorimotor development (e.g., Ulrich, 1989; see also the review by Thelen, 1989a), they make a case for the role of selection in the emergence of motor synergies. According to our hypothesis, selection provides the supervening principle that transforms a complex and heterogeneous system into one that is characterized by the coordinated action of its parts.

Discussion

Experimental evidence, theoretical considerations, and modeling studies suggest that somatic selection plays a key role in higher brain function and in the develop-

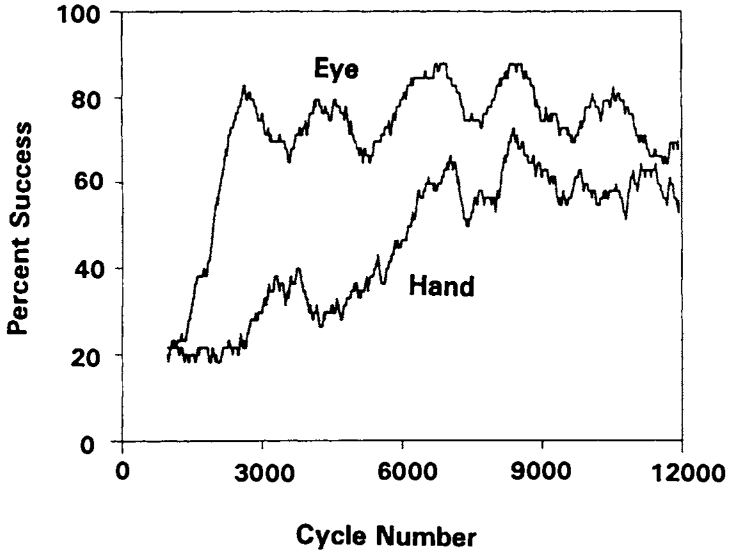

FIG. 7.—Training curves of oculomotor and reaching systems for a simultaneous simulation of a moving eye and two-jointed arm. Because of simultaneous training, visual signals used in the reaching system change constantly as the eye moves. As compared to simulations without simultaneous eye movements (data not shown), progress in training the arm is somewhat delayed, but eventually a high performance level is reached and maintained. This shows that the selective training paradigm is independent of the details of the simulation and the way sensory inputs are provided to the neuronal repertoires. Absolute performance limits are 100% for the oculomotor and about 80% for the reaching system. From Reeke, Sporns, and Edelman (1990), reproduced with permission.

ment of coordinated movement. In this article, we have reconsidered Bernstein's problem within the framework of a selectional theory of the brain. We have argued that an appropriate theory of selection appears closer to the biological data than a purely computational treatment of the inverse kinematics problem. Coordinated movement is possible without explicit computations of desired movement paths. A selectional theory also accounts for synergies as functional units of the motor ensemble and as active components in sensorimotor development. Synergies emerge from selective events as coordinative structures (Kelso & Tuller, 1984; Thelen, 1988; Thelen, Kelso & Fogel, 1987; Ulrich, 1989) that are able to reduce the numbers of degrees of freedom in a complex multicomponent motor system. The main advantage of a selectional theory is that it accounts for the instantaneous adaptability of the motor ensemble and its associated neural circuitry in response to biomechanical and environmental changes. This adaptability is not conferred upon the system by instructive procedures imposed from without. Instead, adaptation results from the dynamic interplay of the motor ensemble with the environment constrained by internal value systems. Such a view readily accounts for individual developmental change.

As we stated earlier, for selection to be effective in a motor system, three requirements must be met: (*a*) There must be a primary movement repertoire of sufficient richness and variability. (*b*) Movements must have differential effects in the environment which can be sensed by their originator. (*c*) Mechanisms must exist that allow sensory inputs reporting the consequences of movements to act differentially within the nervous system, such that (on average) those movements that simultaneously satisfy environmental constraints and evolved internal value constraints will become more likely than others. All of these requirements are easily met by actual biological motor systems. In contrast, there is little direct evidence that the nervous system precomputes desired trajectories, computes comparisons between actual movements and desired ones, or uses explicit error signals to adjust individual components of the motor control system and minimize future error.

Finally, several points that have not been considered in detail deserve at least some brief emphasis. The intricate interplay between sensory inputs and motor action in the formation of gestural components and synergies highlights only one aspect of the deep interrelation between action and perception. Motion is fundamental for perceptual categorization, one of the most basic of neural and cognitive processes (Edelman, 1987). For example, motion is crucial in the detection of spatially correlated object features, and it naturally ensures the continuity of successive sensory inputs referring to a single object. Body and eye movements are essential for the development of fundamental visual cognitive concepts such as the unity, boundedness, and persistence of objects (Spelke, 1990), and the construction during development of spatial maps of the environment. The importance of self-generated movements in such a variety of functions is recognized by the theory of neuronal group selection. Coordinated movement is taken to be not just peripheral output, but an active ingredient in perceptual and cognitive processes, both during development and in adult function.

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