

9

Preliminaries to a Theory of Action with Reference to Vision

M. T. Turvey

University of Connecticut
and
Haskins Laboratories

Of the distinction which his own efforts had done much to foster, Magendie commented in 1824:

The organs which concur in muscular contraction are the brain, the nerves, and the muscles. We have no means of distinguishing in the brain those parts which are employed exclusively in sensibility, and in intelligence, from those that are employed alone in muscular contraction. The separation of the nerves into nerves of feeling and nerves of motion is of no use: this distinction is quite arbitrary [cited in Evarts, Bizzi, Burke, DeLong, & Thach, 1971, 111-112].

More recently this viewpoint has been expressed in a different but closely cognate fashion by Trevarthen (1968): "Visual perception and the plans for voluntary action are so intimately bound together that they may be considered products of one cerebral function [p. 391]."

In the light of such remarks, it is curious that theories of perception are rarely, if ever, constructed with reference to action. And, while theories of perception abound, theories of action are conspicuous by their absence. But it must necessarily be the case that, like warp and woof, perception and action are interwoven, and we are likely to lose perspective if we attend to one and neglect the other; for it is in the manner of their union that the properties of each are rationalized. After all, there would be no point in perceiving if one could not act, and one could hardly act if one could not perceive.

Of course, history has not been remiss in comments on the relation between perceiving and acting. From the time of Aristotle it has been taught that the

motor system is the chattel of the sensory system. Nourished by the senses the motor system obediently expresses in automaton and relatively uninteresting fashion the cleverly contrived ideas of the higher mental processes, themselves offshoots of the sensory mechanisms. In this view, action is interpretive of the sensory mind and thus, in principle, problems of coordinated activity are secondary to and (if we assume an associative link between sensory and motor) independent of problems of perception. It has also been taught, usually with less fervor, that perception is a disposition to act: to perceive an event is to be disposed to respond in a certain way. Modification of this view leads to a constructive theory of mind in which it is argued that higher mental processes in addition to perception are skilled acts that reflect the operating principles of the motor system. In short, experience is constructed in a fashion intimately related to the construction of coordinated patterns of movement. So far as action assumes primary importance in this approach to mind, we would expect its proponents to put great store by the analysis of coordinated motions. However, where motor-theoretic interpretations have been forwarded to account for perception and the like, statements of how acts are actually produced have been either absent or trivial (e.g., Bartlett, 1964; Festinger, Burnham, Ono & Bamber, 1967; Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967; Sperry, 1952). Curiously, action-based theories of perception and of mind in general have been advanced on a nonexistent theory of action.

Thus, it seems that the theory of action deserves more attention than it has received and that the interlacing of the processes of perceiving and acting is a problem we can perhaps no longer afford to ignore. This chapter is a preliminary and speculative response to these reproofs. Its purpose is twofold: first, to identify a set of basic principles to characterize the style of the action system in the production of coordinated activity; second, to describe, in a rough and approximate way, how the contents of vision may relate to the processes of action. To a significant degree, the ideas expressed in this chapter derive, on the one hand, from the work of Nicolai Bernstein (1967) and Russian investigators who have followed his intuitions, and on the other hand, from the analysis and amplification of the Russian views by Peter Greene (1971a, b). We begin our inquiry by illustrating an equivalence between problems of action and problems of perception and cognition (cf. Turvey, 1974).

THE CONSTANCY FUNCTION IN ACTION, AND ACTION AS CONSEQUENCE

A visually presented capital letter A can occur in various sizes and orientations and in a staggering variety of individual scripts. Yet in the face of all this variation, the identification of the letter remains, for all intents and purposes, unaffected.

This phenomenon of constancy is not limited to the domain of perception, but is equally characteristic of action. Thus, the letter A may be written without moving any muscles or joints other than those of the fingers. Or, it may be written through large movements of the whole arm with the muscles of the fingers serving only to grasp the writing instrument. Or, more radically, one can write the character without involving the muscles and joints of either arms or fingers, by clenching the writing instrument between one's teeth or toes. It is evident that a required result can be attained by an indefinitely large class of movement patterns.

On examination of the phenomenon of constancy in action we might raise the query: How can these indefinitely large classes of possible movement patterns be stored in memory? The answer is that they are not. Clearly, I do not have on record in memory all possible temporal sequences of all possible configurations of muscle motions that write A; indeed, I have yet to perform them and by all accounts I never will. The essential question about our A-writing task, therefore, can be stated more fundamentally: How can I produce the indefinitely various instantiations of A without previous experience of them?

In response to this question let us turn our attention to linguistic theory. A departure point for transformational grammar is that our competency in language is such that we can produce and understand a virtually infinite number of sentences. As Weimer (1973) has pointed out, there are echoes of Plato's paradoxes in Chomsky's (1965) claim that our competence in language vastly outstrips our experience with it. Chomsky's claim is motivated by the observation that experience with a limited sample of the set of linguistic utterances yields an understanding of any sentence that meets the grammatical form of the language. To explain this competency is, for Chomsky (1966), a central problem in the theory of language. But, given the points advanced above, the constancy function in action is likewise indicative of a competency that exceeds prior learning. The child, we may note, learns to write A under conditions that restrict her to a small subset of the very large set of A-writing movements. But she is able subsequently to write A with practically any movement pattern she chooses, that is, she can write A in novel ways. A writing is creative in the sense that language is creative.

The search for a workable account of the creativity manifest in language has led transformational grammarians to what can be aptly described as "the explanatory primacy of abstract entities" (Hayek, 1969). The idea is that the speak-listener has at his disposal an abstract system of rules or principles, referred to as the deep structure, that allows him to generate and to understand an indefinitely large set of sentences, referred to as the surface structure. This distinction, drawn in linguistic theory, between deep and surface structure will prove relevant to our analysis of action in two important respects. The first is the idea that deep structure is far removed from surface structure; grammarians argue that although the deep structure determines the surface structure, it is not

manifested in the surface structure. The second is that the child must come to determine the nature of the underlying deep structure from a limited experience with surface structures. Chomsky and his colleagues assume that the child essentially "looks through" the utterances she hears to the abstract form behind those utterances. The child is said, therefore, to construct a theory of the regularities of her linguistic experience. Similarly, our hypothetical child learning to write the letter A must determine from her limited experience with the set of A-writing movements a theory of how to write A. Thus, we may conclude that the ability to write A in indefinitely various ways is based on procedures that are abstract and generative, like the grammar Chomsky has in mind for language. Others have sought similar parallels between action and grammar (e.g., Lenneberg, 1967).

There is an interesting upshot to this discussion of action constancy. We generally say that an abstract representation, a concept, underlies our ability to recognize indefinitely various As. Let us call this the perception concept of A. Now clearly we may propose that there is an action concept of A underlying our ability to write A in indefinitely various ways. So in general are there two different kinds of structures, two different classes of concepts—one specific to perceptual events, the other specific to action events? In short, is the constancy function in perception achieved in ways fundamentally different from the constancy function in action? If it is, then the construction of theories of how we identify events (see Neisser, 1967)—theories of the perception concept—can proceed virtually independent of the construction of theories of the action concept. On the other hand, if the constancy function is treated in the same way in both perception and action, that is, if there is only one class of appropriate structures or only one class of appropriate procedures for achieving constancy, then the theory of identification and the theory of production ought not to be considered separately. In this view, which I suspect is the more viable, any account of constancy in perception must also be an account of constancy in production—a perceptual account of constancy must be potentially translatable into an action account of constancy. If such a translation is in principle implausible then we may suppose that the account is incorrect.

The reader's attention is drawn in this preamble to one other important aspect of action—its relation to "consequence." An act modulates environmental events, but philosophers have found that they cannot conceptually distinguish between occurrences that are actions and occurrences that are consequences (see Care & Landesman, 1968). A typical argument from language usage might go like this: George kicks the football (of the round kind) and scores the goal that wins the championship. Now we could say that George kicked the football and that a consequence of his action was that a goal was scored. Or we could say, just as appropriately, that George scored a goal with championship-winning consequences. "Scored the goal," therefore, can be viewed either as consequence or as action. We may wish for criteria to determine which occurrences should

receive an action label, and which occurrences should receive a consequence label. Unfortunately, the criteria that have been advanced have not met with any degree of universal approval.

The failure to distinguish conceptually between action and consequence is understandable from the viewpoint of Bernstein (1967). He comments:

Whatever forms of motor activity of higher organisms we consider . . . analysis suggests no other guiding constant than the form and sense of the motor problem and the dominance of the required result of its solution, which determines, from step to step, now the fixation and now the reconstruction of the course of the program as well as the realization of the sensory correction [p. 133].

The implication is that an action plan as a statement of consequences is not a static structure but a structure that is by virtue of processes we will discuss below, continually becoming. Yet in all of its phases of change, phases that constitute a tailoring of the plan to the current kinematic and environmental contingencies, the essential character of the action plan remains invariant. What is to be achieved, what is to be consequence of the evolving pattern of motions, persists from the conception of an act through its evolution to its completion.

The arbitrariness of distinguishing between action and consequences parallels the arbitrariness of distinguishing between perception and memory. As William James (1890) observed and as others concur (e.g., Gibson, 1966a), the traveling moment of present time is not a razor's edge and no one can identify when perception ends and memory begins. The distinction between action and consequence is as much a will-o'-the-wisp as the distinction between perception and memory.

THE DOMAIN OF ACTION CONCEPTS

For present purposes we will entrust ourselves to the view of concepts as functions (Cassirer, 1957). Thus, we may represent an action concept such as that for A writing as $A(x)$ and explore the nature of the variable x that enters into this function. We perform this exercise in order to identify some fundamental characteristics of the action system. Let us assume that the elements entering into $A(x)$ are a proper subset of the set of elements that enter into any rule for coordinated activity. And, in addition, that coordinated activity is under the management of an "executive system" and that the character of the elements entering into $A(x)$ and any other action function are mirrored in the character of (or constraints on) this system.

One view of the executive is that expressed in the traditional piano or push-button metaphor. In this metaphor muscles are represented cortically in keyboard fashion, one muscle per key, and central impulses to the muscles are held to be unequivocally related to movement. The essence of the view is that

the executive instructs each muscle individually. At the outset we may question the worth of this metaphor simply on the ubiquity of reciprocal innervation: The intricate and extensive interrelation among muscles makes it both arduous and wasteful to instruct them singly. But more importantly, we can argue (as did Bernstein, 1967) that there cannot be an invariant relation between innervational impulses and the movements they evoke.

Consider the movement of a single limb segment in relation to a fixed partner and under the influence of a single muscle. The differential equation describing this situation is of the form

$$I d^2\alpha/dt^2 = f(E, \alpha, d\alpha/dt) + g(\alpha),$$

where I is the inertia of the limb segment, α is the angle of articulation, E the innervational level of the muscle, and f and g are the functions determining respectively, the muscle force and gravitational force acting on the limb segment.

If we take $E = E(\alpha, d\alpha/dt)$, that is, independent of time and simply a function of position and velocity, then the equation reduces to that for a movement of a limb indifferent to central influences; in brief, an instance of central paralysis. If, for contrast, we assume that the excitation of a muscle is solely a function of a centrally predetermined sequence and independent of the peripheral variables of position and velocity, that is, $E = E(t)$, then the equation is that of a system insensitive to, or ignorant of, changes in local conditions. Obviously, it is more judicious to argue that $E = E(t, \alpha, d\alpha/dt)$, in which case the fundamental equation can be written

$$I d^2\alpha/dt^2 = f [E(t, \alpha, d\alpha/dt), \alpha, d\alpha/dt] + g(\alpha).$$

Solutions to equations of this kind depend on the initial conditions of integration. The implication, therefore, is that in order to obtain the same movement for various values of α and $d\alpha/dt$, different innervational states E will be needed. In a word, the relationship existing between impulses to the muscle and the movement of the single limb segment is equivocal: same impulses may produce different movements and different impulses the same movement.

We continue Bernstein's argument by noting that in the temporal course of moving a limb segment changes occur in the force of gravity (which is related by a function $g(\alpha)$ to the angle of articulation) and in other external forces operating on the limb and that these changes affect E . Now suppose that the limb segment traces out a rhythmical motion. This rhythmical motion can be identified with a function relating the required forces at the joint to time. However, another function can be identified relating forces at a joint to time, and the forces in this case correspond to the changes in the external force field. As a result, the sequence of impulses to the muscle can be interpreted as determining a mapping of the function generated by the variations in the external field over time to the desired function. Now suppose that the same

rhythmical motion is traced out with the hand holding on separate occasions (a) a hammer, (b) a baton, and (c) a can of beer. The function relating the changes in the external force field to time will differ in each instance even though the pattern of the rhythmical movement is unchanged. In each of the three instances a different mapping would be required from the function generated by the external force field to the desired function specifying the rhythmical pattern. The import of this, as Bernstein (1967, pp. 20-21) points out, is that the sequence of impulses to the muscle "cannot maintain even a remote correspondence" to the factual form of the movement.

A third criticism of the push-button metaphor is that if the executive behaved in the fashion suggested, instructing each muscle individually, then it would be called upon to manage the enormous number of degrees of freedom that the motor apparatus attains

... both in respect to the kinematics of the multiple linkages of its freely jointed kinematic chains, and to the elasticity due to the resilience of their connections—the muscles. Because of this there is no direct relationship between the degree of activity of muscles, their tensions, their lengths, or the speed of change in length [Bernstein, 1967, p. 125].

Herein lies a fundamental principle which simply states that the number of degrees of freedom of the system controlling action is much less than the number of mechanical degrees of freedom of the controlled system (Kots, Krinsky, Naydin, & Shik, 1971). A homely example illustrates the point: try writing a letter, for example, *W*, while simultaneously making circular motions with a foot. An experimental illustration is provided by Gunkel (1962): when one makes movements of different rhythms simultaneously with the two hands, the amplitude of the movements performed by one of the hands is modulated by the frequency of the movements performed by the other. Thus, it is not difficult to demonstrate that the number of degrees of freedom of the executive is very small; on the push-button metaphor it would have to be very large. We can conclude, therefore, on three counts, that the executive does not, or indeed cannot, control individually each motor unit or even each muscle participating in a complex act.

One consequence of the conclusion that in the course of performing a coordinated pattern of movements the executive system does not control muscles singly is that it need not be apprised of peripheral details, since such information would be irrelevant. In this light let us take another look at the equation for the movement of a single-limb segment. In that equation the innervational impulse is expressed as a function of time, angle of articulation (muscle length), and velocity, that is, $E = E(t, \alpha, d\alpha/dt)$. But if the executive is stripped of the responsibility for instructing individual muscles and if it is ignorant of the current, precise details of the external force field then clearly executive instructions are not written in the form relevant to that field, that is, in the form $E(t, \alpha, d\alpha/dt)$.

Moving a single-limb segment rhythmically requires an action plan and we may suppose that executive instructions spell out that plan (in the sense of defining the contours and timing of the movement) through a sequence of impulses of the form $E(t)$. The action plan and impulses of the form $E(t)$ must correspond, or so it would seem, to the factual form of the movement, in contrast to impulses of the form $E(t, \alpha, d\alpha/dt)$, which on the above account bear no such relationship to the movement. Thus, we see that the action plan (the deep structure) is dissimilar to the innervational signals issued to the muscles (the surface structure) and these signals in turn are dissimilar to the movement that evolves: "... it is as if an order sent by the higher center is coded before its transmission to the periphery so that it is completely unrecognizable and is then again automatically deciphered" (Bernstein, 1967, p. 41). In general, if impulses of the form $E(t)$ are close to the action plan and hence close to the actual form of the movement, then those impulses of the form $E(t, \alpha, d\alpha/dt)$ are close to the muscles and to the actual forces operating at the joint complexes. On this view, the mapping of $E(t)$ to $E(t, \alpha, d\alpha/dt)$ identifies the evolution of an act; in particular, it identifies the adaptation of an action plan to the prevailing field of external forces.

But if the executive does not control individual muscles, then what does it control? In response to this question, students of action (e.g., Bernstein, 1967; Gelfand, Gurfinkel, Tsetlin, & Shik, 1971) propose that the executive charge is to control the modes of interaction of lower centers. These, it is argued, are capable, through the systems that they govern, of producing a coordinated movement pattern in a relatively autonomous fashion.

Consider a commonplace, coordinated activity such as running. There are lower centers that control individual limbs, with each center asserting particular relations among the components of the limb that it controls. Thus, the interaction between these centers determines the coordinate motion of the limbs, and the problem of coordination in running becomes for the executive a problem of intercenter coordination (Shik & Orlovskii, 1965). Let us pursue this example in more detail because it is representative of a mode of organization that we will entertain as characteristic of the action system.

We have evidence that mechanisms inherent in the segmental apparatus of the mammalian spinal cord can initiate and maintain flexion-extension or stepping movements of the limbs in the absence of afferent participation (Eldred, 1960). Apparently, these segmental pattern generators determine the fundamental form of flexion-extension activity, but they do not specify in detail the actual spatial and temporal characteristics of the motion (Engberg & Lundberg, 1969). It is the role of afferent information, enumerated through autonomous (reflex) structures (and of tuning influences from above, as we shall see later) to supply the requisite spatial and temporal details and thus to tailor the basic pattern to the field of external forces. A small leap now takes us to the assertion that

walking and running can be attributed to a relatively simply executive instruction which sets into characteristic motion the entire segmental apparatus and which, in itself, is deficient in information about the actual strategic order of necessary muscle contractions (cf. Evarts *et al.*, 1971).

This mode of organizing action achieves the following. First, it resolves the degrees of freedom problem noted above by apportioning relatively few degrees to the executive level but relatively many to the subsystems whose activities the executive regulates. (Since it is the subsystems that must deal with the vagaries of kinematic linkages and muscles). Second, and related, it reduces the detail required of the executive instructions, for with autonomous lower centers those instructions do not have to be coded for the individual muscle contractions that will ultimately occur.

In overview, what has emerged is the understanding that the element entering into the design of an act is typically not an individual muscle but a group of muscles functioning cooperatively together. We have good reason to speculate that the reflexes may well comprise the "basis" of the set of all such functional groupings and hence of the infinitely large set of all acts (Easton, 1972a). A "basis" is a mathematical structure found in the theory of vector spaces. It is defined as a linearly independent (nonredundant) set of vectors that under the operations of addition and scalar multiplication spans the vector space. Essentially, a "basis" contains the minimum number of elements that are required to generate all members of the set.

We have several reasons for identifying the set of reflexes as the "basis" for action. First, reflex systems are not independent entities that function in isolation. On the contrary, there are a multiplicity of functional relations among reflexes and other structures. Second, virtually every reflex observed experimentally and clinically is an instance of a reasonably complex configuration of motions often elicitable by a single stimulation. Third, reflex systems are under very effective and often complex control by supraspinal structures (cf. Eccles & Lundberg, 1959; Evarts *et al.*, 1971; Kuno & Perl, 1960). And fourth, reflexes are obviously purposeful and adaptive, and they may be organized and modulated flexibly by means of the operations of ordering, summing, fragmentation, and through their "local sign" properties (Easton, 1972a). Collectively, these characteristics of reflexes suggest that

... the neuronal mechanisms which have been studied as reflex arcs can be utilized in a variety of ways by virtue of the interaction between reflex pathways and by the action of control systems that are present, even at the level of the spinal cord segment. The dichotomy between reflex control and central-patterning control of movement may in this sense be artificial [Evarts *et al.*, 1971, p. 62].

Through the provision of reflexes, evolution has supplied a partial answer to the degrees of freedom problem. We might now suppose that a further reduction in the burden of control is achieved ontogenetically through the gathering

together of reflexes into larger functional units (cf. Gelfand *et al.*, 1971; Paillard, 1960; Pal'tsev, 1967b). We will refer to reflexes and functional combinations of reflexes as "coordinative structures" (a term borrowed from Easton (1972a) but used here with greater latitude).¹ Of cardinal importance to this chapter is the assumption that a closely knit functional combination of reflexes performs as a relatively autonomous unit; by this assumption, relative autonomy is a fundamental property of coordinative structures, at any level of complexity.²

In sum, we have seen that the executive does not construct acts from individual muscle contractions. What we now infer is that acts are synthesized from a set of coordinative structures for which the reflexes constitute a basis.

We return now to the question of the variable entering into action concepts of the form $A(x)$. The executive does not deal in muscles, so muscle properties (length, tension) can be ruled out. The executive does deal in coordinative structures (at least so we may argue), but these similarly cannot be the elements we seek. An action concept such as that supporting A writing is indifferent to functional groupings of muscles in the same way that it is indifferent to individual muscles. However, the analogy drawn above between the set of reflexes and a "basis" in vector space theory provides a clue to the answer. To reiterate: A basis is a subset of a set of elements which when acted upon by suitable operations generates the entire set of elements. We assume, therefore, a repertoire of operations that modify and relate the coordinative structures so as to produce any and all acts. Thus, we may conjecture that the elements entering into an action concept are the operations defined over the set of coordinative structures. In this sense an action concept is analogous to a mathematical operator, a function whose domain is a set of functions, of which differentiation is a classical example.

¹ One motivation for bringing reflexes and functional combinations of reflexes under the single heading "coordinative structures" is the assumption that for the activation of either a single reflex or a single functional combination of reflexes, one degree of freedom of the control system is enough (see Kots *et al.*, 1971). In regard to functional combinations it is important to recognize that new tasks may often require the discovery of new combinations and their establishment as single functional units. In very large part acquiring a skill is, as Bernstein (1967) would have expressed it, a problem of reducing the degrees of freedom in the action structures being regulated (see Kots & Syrovagin, 1966).

² Consider insect flight. The evidence suggests that it is not due to a built-in structural system of simple segmental reflex loops nor to any flight center, yet identified. Rather, it seems that there is a functional system of distributed oscillators—autonomous pattern generators—which on receipt of the appropriate *nonphasic* input are coupled together as a unit which then operates autonomously in a preset fashion (Weiss-Fogh, 1964). Walking may use some of the very same oscillatory structures as flying, but for locomotion on the ground they would be mutually coupled in a different way (cf. Wilson, 1962) to form a different autonomous unit.

THE ORGANIZATION OF THE ACTION SYSTEM

The foregoing account identifies two particularly important properties of the action system. First, acts are produced by fitting together structures each of which deals relatively autonomously with a limited aspect of the problem. Second, the action plan is stated crudely "in three-dimensional kinematic language" (Gelfand *et al.*, 1971), yet the actual pattern of motions is precise in displacement, speed, and time of occurrence. To achieve this measured performance the differentiation of an action plan must proceed through multiple stages of computation in which needed details emerge gradually. Patently, a computation of details over time is inelegant and inefficient for a system that has a limited repertoire of skills, but it is preferred for a system called upon to solve novel action problems posed by ever-varying kinematic and environmental conditions.

We commonly classify a system that behaves in this fashion as hierarchic, a classification that is certainly suggested by the unqualified use of the term "executive" in the preceding discussion. By a hierarchy we understand that an executive at the highest level of a decision tree makes the important decisions and spells out the fundamental goals. Decisions on the details are left to the immediately subordinate structures which in turn leave decisions that they cannot make, for whatever reason, to even lower structures. This general strategy is repeated until the final remaining decisions are made by the lowest structures in the decision tree.

The crucial property of a substructure in a hierarchy is that in the perspective of a higher level it is a dependent part, but in the perspective of a lower level it is an autonomous whole. Koestler's (1969) term "holon" expresses this whole-part personality of hierarchic substructures; a holon is defined as "a system of relations which is represented on the next higher level as a unit, that is, a relatum" (Koestler, 1969, p. 200). We may question, however, the notion explicit in the concept of a hierarchy that the *direction* of the whole-part personality of substructures is immutable. Certainly from the viewpoint of the "geometry" of anatomical arrangements certain structures may appear as dependent parts of other structures, and a compelling argument may well be made for the immutability of this relation in the peripheral reaches of the neural mechanisms supporting action and perception. Yet from a computational viewpoint in which we emphasize "knowledge" structures rather than anatomical structures the relation between any two structures need not be fixed; either may treat the other as a relatum, or subprocedure, depending on the problem to be solved at a given moment. This commutability of "subordinate" and "executive" roles; of "lower" and "higher," is expressed in the related interpretations of biological systems as "coalitions" (Reaves, 1973; Shaw, 1971; von Foerster, 1960) or "heterarchies" (Minsky & Papert, 1972). In these interpretations, management

of the action system would not be the prerogative of any one structure; many structures would function cooperatively in the framing of action plans and desired consequences, although not all structures need participate in all decisions (Reaves, 1973). Furthermore, while it is certainly the case that the action system has very definite and nonarbitrary (anatomical/computational) structures, in these interpretations the partitioning of these structures into agents and instruments and the specification of relations among them is arbitrary. Any inventory of basic constituent elements and relations is equivocal (Reaves, 1973). Decentralization of control and arbitrariness of partitionings are not alien notions to students of action theory (e.g., Berstein, 1967; Greene, 1971b) as evident from Greene's apologia:

The 'executive' and 'the low-level systems' will occur frequently . . . These terms are simply abbreviations for what I really mean: any two subsystems, one of which, at the moment, in respect to the task under consideration, is behaving like an executive relative to the other. The systems are not unique, and their relation is not immutable: a 'lower' part of the nervous system might, for instance, at some time behave like an executive relative to some higher part [Greene, 1971b, pp. 2-3].

ACTION AS HETERARCHIC

Perception and action contrast in that the tasks of the former are to digest, abstract, and generalize, while the tasks of the latter are to spell, concretize, and particularize (Koestler, 1969). One is the mirror image of the other. For the sake of argument and to facilitate comparisons with perception, let us say that the "input" to the action system is an intention (e.g., to pick up a cup, to write one's name). (We respectfully ignore the problem of how an intention is determined and in addition we give due recognition to the likelihood that some of the structures responsible for determining an intention may also be responsible for its translation into an action plan and for the plan's subsequent differentiation). Therefore, an intention is an "event" for the action system in the way that, say, a scene is an event for the visual, perceptual system.

Taking a leaf from artificial intelligence research on visual perception, we may say that action involves knowledge domains or abstract representations—where a representation is defined as a set of entities, a description of the relations among them, and a description of their attributes (Minsky & Papert, 1972; Sutherland, 1973). Thus, for the perception of scenes portrayed in two dimensions we may identify, as examples, (1) a Lines Domain in which "bars, picture-edge, vertex, end, midpoint" are the entities; "join, intersect, collinear, parallel" are the relations; and "brightness, length, width, orientation" are the attributes; and (2) a more abstract Surfaces Domain where "surface, corner, edge, shadow" are the entities; "convex, concave, behind, connected" are the relations; and "shape, tilt, albedo" are the attributes (see Sutherland, 1973). From a hierarchical view

we might think of perception as an ordered sequence of unidirectional mappings from less abstract to more abstract representations and the differentiation of an intention as the successive mappings of the intention onto a series of progressively *less* abstract representations. But the argument from the coalitional/heterarchical interpretations of organization is that the conversation between abstract representations (domains, knowledge structures) is not one way. A fundamental result in artificial intelligence research on scene analysis is that while it is necessary to construct descriptions in many different domains, a procedure that exploits only unidirectional mapping from a lower domain to the next and higher domain is significantly limited in its capability to interpret a scene successfully (Sutherland, 1973). Success in scene interpretation is greatly enhanced by allowing a more flexible strategy in which processing in lower domains can use, as subprocedures, hypotheses generated about structures in higher domains (e.g., Falk, 1972).

Let us comment briefly on entities that in theory could be gathered together to form domains in action. On the basis of what has already been said it would be logical for us to identify the entities in a representation with coordinative structures. In this regard it is important that reflexes can be arranged on a scale from complex and wide-ranging to simple and local. The organization of reflexes reveals "parallel hierarchies of complexity whose regularity and order leave little to be desired: local spinal reflexes, such as the flexion reflex, appear to be subsumed by reflexes requiring an intact spinal cord such as the scratch and long spinal reflexes, and these in turn are subsumed by pontine and medullary reflexes, such as the tonic neck and labyrinthine reflexes, and, at still higher levels, by locomotion and righting" (Easton, 1972a, p. 593). This suggests that we might equate the entities in *each* abstract representation of an act with coordinative structures, remarking that in higher domains an action plan is represented by functions defined over a relatively small number of large and complex coordinative structures and in lower domains by functions over a relatively large number of small and simple coordinative structures. We are thus provided with the following description of the evolving act: *an act evolves as the mapping by a coalitionally/heterarchically organized system of an intention onto successively larger collections of increasingly smaller and less complex coordinative structures, with each representation approximating more closely the desired action.*

There are many other ways we might conceivably characterize the entities of a representation in the building of a theory of action, but I hope the arguments that follow will pinpoint the special advantages conferred on a system in which the entities at all levels of representation are relatively autonomous structures. At all events, let us simply note at this juncture two contrasts between action as hierarchy and action as coalition/heterarchy. In one, the contrast is between the hierarchic strategy of a detached higher level dictatorially commanding lower levels and the heterarchic strategy of procedures constructing a representation in

a higher domain entering into "negotiations" with lower domains in order to determine how the higher representation should be stated. In the other, the contrast is between the hierarchic principle of low-level structures unquestioningly responding to high-level instructions and the heterarchical principle of procedures establishing a representation in a lower domain reprocessing higher representations from the perspective of the special kinds of knowledge available to the lower domain.

The anatomical and neural structure of mechanisms related to movement suggests quite strongly that the fluidity called for by coalitional/heterarchical organization, the constant shuttling back and forth between domains, is not without basis. Consider, for example, the notion of internal feedback. Most generally the idea of feedback in behaving organisms is identified in two senses. In one sense, it is information that arises from the muscles as a direct consequence of their being active; in the other sense, it is information originating outside the organism as an indirect consequence of muscular contraction. The latter is often dubbed "knowledge of results." These senses of the concept of feedback are not exclusive, for they omit the afferent information that arises from structures within the nervous system in the course of an act's emergence. We refer to this feedback from the nervous system to itself as internal (Evarts *et al.*, 1971) and it plays a central role in the evolution of coordinated activity.

In reference to internal feedback from spinal centers, Oscarsson (1970) has remarked on the fact that a number of ascending pathways (at least six spinocerebellar tracts) are not especially well equipped to provide information about muscle contraction. Rather, the organization of these ascending paths suggests that they monitor activity in spinal motor centers, which in turn provide an abstracted account of the relation between themselves and other lower centers. This property of ascending paths fits the character of descending paths: most descending fibers terminate in interneuronal pools rather than passing directly to motor neurons. The basis for this arrangement may lie in the fact that the coordination of movement rests on the patterning of groups of motor neurons rather than on instructions to individual units, and the mapping between domains consists of predictions of how functional groupings of muscles (coordinative structures) will behave (cf. Arbib, 1972). Spinal centers thus provide a means for checking predictions against the current status of lower centers. Therefore, interneuronal pools may function as "correlation centers" (Arbib, 1972) reporting the degree to which an action plan is evolving as desired or indeed capable of evolving in the desired manner from a particular representation. At all events, there are probably many such internal feedback loops broadcasting the state of each level of the actor from executive to muscle (Taub & Berman, 1968), a highly desirable state of affairs from the perspective of a strategy in which executive procedures draw rough sketches and low-level procedures furnish needed details.

Our appreciation of the flexible relations between neuroanatomical structures supporting action is fostered further by recognition of the fact that signals from

above can bias the abstracted accounts supplied by spinal centers. Many supra-spinal mechanisms exert influences on the first synapse in ascending systems, that is, the synapse between the peripheral afferent neuron and the second order neuron which crosses the spinal cord to the tracts projecting to the brain (Ruch, 1965a). These influences from above are exerted mainly by motor areas and motor tracts, including the classically defined principal motor tract, the pyramidal (corticospinal) tract.

Current deliberations on the interrelations among the motor cortex, basal ganglia, and cerebellum may well be resolved on the acceptance of the coalitional formulation (see Kornhuber, 1974). We know that before the first signs of muscle innervation relevant to a particular movement significant changes occur in the activities of the cerebellum and basal ganglia, in addition to the motor cortex (Evarts, 1973; Evarts *et al.*, 1971). This contrasts sharply with more traditional interpretations of basal ganglia-cerebellar processes operating as movement control and error-correcting devices coming into play only after the innervation of muscles. Rather, it would seem that these mechanisms gang together in the constructing and differentiating of action plans—they incorporate different procedures, each using the others as subprocedures as the situation demands. The structure of the cerebellum and its relations with other structures exemplifies the flexibility of neural computation in action. The cerebellum receives inputs from the entire cerebral cortex, projects to the motor cortex. (Evarts & Thach, 1969), and is in two-way communication with the segmental apparatus of the spinal cord and thus with the structures that will actually execute the intended configuration of motions.

Thus the cerebellum can operate as a comparator, relating information about cerebral events to information about spinal events. The argument has been made that the cerebellum carries out a speeded-up differentiation of representations of the action plan, thereby providing a projection of their outcome and a basis for their modification. On this argument the cerebellum plays a significant role in tailoring action plans to prevailing environmental and kinematic conditions prior to their realization as muscle events and thus prior to feedback from muscle contraction (see Eccles, 1969; Kornhuber, 1974).

EXECUTIVE IGNORANCE: EQUIVALENCE CLASSES AS INSTRUCTIONAL UNITS

Clearly, coalitional/heterarchical organization is far more flexible than hierarchical organization. Yet this flexibility is constrained in important ways. For example, in action there would be limits on the depth to which procedures constructing a representation on a higher domain may go in search of useful hypotheses. For any given higher abstract representation of an intention the utility of knowledge about any lower domain would be inversely related to the degree of abstraction separating the two domains. Hypotheses about individual

alpha-gamma links (the smallest coordinative structures) regulating muscle contraction, for example, would not be useful to the determination of relevant large coordinative structures and related functions. And this, of course, is no more than a restatement of the degrees of freedom problem noted above. It then follows that while a representation of an intention in a higher domain is mapped into an immediately lower domain, the particular form that the representation will actually take in the lower domain cannot be known in advance, for the procedures operating in the lower domain have access to knowledge that is immaterial, in principle, to the procedures in the higher domain.

This form of "ignorance" has been duly recognized by students of action. We recall the earlier comment that the role of the executive (which is understood to be not a single neuroanatomical structure but a set of procedures engaging a number of neuroanatomical structures) is to modify the mode of interaction among elements at a lower level (Bernstein, 1967; Gelfand *et al.*, 1971). As a general rule, however, it is argued that the executive does not have advance knowledge of which particular state, out of a set of possible states, a lower level will arrive at after a mode of interaction has been specified (Greene, 1971b; Pyatetskii-Shapiro & Shik, 1964). In this perspective Greene (1971a) asks: "Can there be units of information that behave deterministically, even though the executive can rarely specify control functions more narrowly than to place them within broad classes of possible realizations? [p. 22]." Consider a situation in which the executive specifies a function transferring a given system into a "model" state. Now we may say that the "model" state serves not as a binding decree to be followed dogmatically by the system but rather as the identifier of a "ballpark," that is, an equivalence class of states convertible into the "model" state. For the system two states are defined as equivalent if they differ by a transformation that is realizable by the system. To Greene's (1971a, b) way of thinking the interconverting of states or functions is characteristic of low-level systems, so that a state or function specified by the executive (or for that matter any higher domain) may be substituted for by one from the same equivalence class but one which is more attuned to the current conditions operating within and around the system and to the system's privileged knowledge of the capabilities of other low-level structures. Similarly, executively specified functions determining the switching from one structure to another form another "ballpark," and low-level systems may autonomously interconvert transition functions of the same equivalence class as the need arises. By this reasoning the units of information that behave deterministically are not functions but equivalence classes of functions. (The reader should refer to Greene, 1971a, b, for a more detailed and formal account of the various kinds of possible equivalence classes.)

In both of the above instances (specification of model states and transition functions) the executive instructions would be judged as satisfactory by the executive even though the instructions (functions) specified were not those actually carried out by the instructed systems. However, executive ignorance about which functions or states actually arise in the lower levels, implies a high

degree of uncertainty in executive commands, since for any given system the executive is specifying an unknown member of a family of possible functions or states. "This uncertainty introduces ambiguities and errors in an executive system's memory, commands, and communications to other executive systems" (Greene, 1971b, pp. 4-11). And we must expect these ambiguities and errors to be propagated through the action system during an act's evolution. The question arises, therefore, of how a configuration of motions is coordinated with precision and finesse? Indeed, in the face of this apparent chaos we should ask how coordination can be achieved at all? We can only assume that the action system is so constructed and its procedures so related that these ambiguities and errors are immaterial to the differentiation of an action plan (cf. Pyatetskii-Shapiro & Shik, 1964).

For Greene (1971a, b) the answer lies in the relations among the various equivalence classes: even though errors induced in one class may lead to erroneous specification in another, that specification would still be confined within the equivalence class of the desired function. Thus the equivalence classes as invariant units of information provide a means for specifying instructions in terms that are reliable and intelligible, even though an executive system is ignorant of the desultory character of low-level systems. We may summarize with Greene (1971a):

Roughly speaking the equivalence classes serve as ballparks into which it is sufficient for the executive to transfer the state: once the state enters the ballpark it will be automatically brought to the correct position without further attention—although ambiguities inevitably lead to erroneous signals, these signals will never be moved outside their correct ballparks or equivalence classes. Hence the equivalence classes seem to be systematically behaving units of information in situations in which the individual elements themselves will behave in haphazard fashion [pp. 24-25].³

THE ACTION PLAN AND THE ENVIRONMENT

Taking stock of our analysis thus far, we may draw a rough sketch of how an action plan is represented in the highest domain, namely, as the specification of a subset of large coordinative structures that almost fits what is intended, and a set of functions on that subset (identifying the necessary equivalence classes) that

³From what has already been said, it is evident that the derivation of a pattern of motions from its underlying representation is the cumulative result of the application of a long series of "rules." We should suppose, therefore, that there are regularities in the representation of an act in the highest domain that are obscured at the movement level by the application of these rules. In part, Greene's (1971a) equivalence classes are an attempt to recover the regularities, and the rules of the action system are defined by the conditions underlying the change in identity of functions and states, that is, interconverting of elements within a class. Obviously the enterprise undertaken by Greene has much in common with current approaches to problems in linguistics.

will relate its elements both adjecently and successivly in a particular way. Thus, the serial nature of an act is said to arise not from the extemporaneous linking of component motions but rather from the differentiation of an already formed plan (cf. Bernstein, 1967; Evarts *et al.*, 1971; Lashley, 1951; Pribram, 1971). We have not, however, made any comment on the relation between the action plan and perception. To rectify this omission we return once again to the nature of an action concept, more precisley, $A(x)$. We do so on the following rationale: If some common ground between the action *concept* $A(x)$ and its perceptual counterpart can be identified, then perhaps we can gain some perspective on the relation between the action *plan* and the perceived environment in which the action plan is to unfold.

Consider, much as we did before, a sample of As written by the same individual using different muscle combinations, that is, one A may have been written by small motions of the fingers, another by large motions of a leg with the writing instrument grasped between the toes. Members of the sample will differ metrically: They will probably be of different sizes, of varying orientations, and of differing degrees of linearity, that is, some will be written in curved strokes, while others will be virtually straight. And supposedly all members of the set will differ spatially in that they will occupy different locations on the page. On inspection we would probably have little difficulty identifying each members as an instance of capital A. But in what sense are they equivalent? In geometry, figures are defined as equivalent with respect to a group of transformations. We say that two figures are equivalent if and only if the group contains a transformation that maps one figure onto the other. The group of transformations relevant to this discussion, that is, relevant to our sample of As, is clearly nonmetrical and, by elimination, must be topological. It is nonmetrical properties rather than metrical properties (which would be left undisturbed by the metric groups: the group of motions, the similarity group, and the equiareal group) that are of significance to the perceptual determination of membership in the class of capital A.

But the same token, the action concept supporting A writing is determined by nonmetrical properties rather than metrical properties. After all, the sample of As we are considering was the product of an actor, and the sample, as we have noted, is indifferent to metrics. Since this is no more than a paraphrase of an argument by Bernstein (1967) we should let Bernstein draw the relevant conclusion concerning the action concept of A:

The almost equal facility and accuracy with which all these variations can be performed is evidence for the fact that they are ultimately determined by one and the same higher directional engram in relation to which dimensions and position play a secondary role . . . the higher engram, which may be called the engram of a given topological class, is already structurally extremely far removed . . . from any resemblance whatsoever to the joint muscle schemata; it is extremely geometrical, representing a very abstract motor image of space [p. 49].

In short, the action concept of writing A and the perception concept for identifying A share common ground in their dependence on nonmetrical properties, and it is not difficult to imagine an isomorphic relation (of some degree) between them (Turvey, 1974). But this is a very special case and we may ask: Does the action plan in general relate in similar fashion to the perceived environment? Bernstein (1967) hazards the guess that it does. For him the high-level abstract representation of an action plan may be construed as a projection of the environment relevant to the intention, where this projection relates to the environment topologically but not metrically.

Owing to the vagueness of this argument we may feel that we have not really acquired any new insights (after all, what does it mean to talk about an isomorphism between action plans and environmental events?) Yet honoring our eccentricities for the present we may acknowledge that we have reinforced our respect for the action plan and the action coalition/heterarchy. In earlier arguments we established the fact that the high-level abstract representation of an action plan was not a projection of muscles and joints. In the current argument we maintain that an action plan may be usefully construed as a projection of the environment. Therefore, we view the task of the action coalition/heterarchy as that of translating an abstract projection of the environment into joint-muscle schemata.

Some research by Evarts (1967) is of special relevance to these speculations. Evarts showed that when a monkey makes a movement of the wrist to counteract an opposing force (in a task in which the direction of force and the direction of displacement are varied orthogonally) recordings from unit cells in the motor cortex are related to the amount of force needed rather than to the degree of displacement. Moreover, this activity in the motor cortex is manifest prior to evidence of muscular contraction. As Pribram (1971) points out, Evarts' observation suggests that the representation at the motor cortex is a mirror image of the field of external forces. But by our account this "image" must represent the action plan at a fairly late stage in its differentiation and, in terms of the earlier analogy with linguistic theory, is more closely related to the surface structure of art than to the deep structure. Indeed, Evarts (1973) has claimed recently that the representation of movement at the motor cortex, rather than identifying the highest level of motor integration (a classical point of view), is, on the contrary, much closer to the muscles and hence much lower in the organization of the action system than representations in other (traditionally lower) anatomical systems such as the cerebellum and the basal ganglia.

Accepting the proximity of this motor cortical representation to the act's surface structure we can see that by this level the action heterarchy has transformed a projection of topological properties of the environment into a projection of environmental contingencies (e.g., forces). According to Bates (cited by Evarts, 1973) force is the logical output for the motor cortex; velocity is the single integral of this quantity and displacement is the double integral, and

both of these quantities are theoretically more difficult to specify than force itself. Yet ultimately acts call for accurate displacements, and accurate displacements, in turn, call for a projection of metrical properties of the environment. We are led, therefore, by this reasoning to another description of the evolving act, namely, that *the action plan unfolds as a series of progressively less abstract projections of the environment.*

THE PROBLEM OF PRECISION AND THE CONCEPT OF TUNING

The realization of an action plan as a coordinated pattern of motions requires its translation from the crude language of coordinative structures to the precise language of muscles. Commerce between animal and environment reduces ultimately to the regulation of pairs of antagonistic muscle groups coupled together at joints. In the translation from abstract action plan to mechanical response the alphasomatomotorneuron stands as the penultimate component. The central question now is how can alphasomatomotorneurons specify to muscles the needed lengths and tensions when these terms, length and tension, are not in the lexicons of higher domains and hence, by definition, cannot be ingredients in an action recipe. In short, we seek to understand more fully the mechanisms through which the action system generates precise commands to muscles from crude commands to coordinative structures.

An instructive portrayal of the problem in limited form follows from the concluding comments of the preceding section—that a suitable output for the motor cortex is force. Suppose that subsequent processes, metaphorically speaking, integrate this quantity. Then, as already noted, the single integral will yield velocity and the double integral will yield displacement. But the particular velocity and the particular displacement obtained for any given force will depend on the end-points or limits of integration. Thus, specification of force alone is insufficient for the achievement of a desired velocity or displacement—the limits of integration must also be identified. How such “end points” might be supplied in the relating of action to environment is the kernel of our problem.

We now proceed to consider and illustrate properties of the spinal cord that will aid our inquiry. Earlier we remarked that the role of higher levels of the nervous system is to pattern the interactions within and among coordinative structures. Let us now recognize that, in the main, coordinative structures have their origins in the spatially divided and relatively autonomous subsystems of the spinal cord. And let us modify our terms slightly to read: the role of the higher levels of the nervous system is to modulate interactions within and among neural mechanisms at the spinal level (cf. Gelfand *et al.*, 1971; Obituary: Tsetlin, 1966).⁴

⁴This viewpoint is also expressed by students of motor control in insects (e.g., Rowell, 1964; Weiss-Fogh, 1964; Wiersma, 1962).

The segmental apparatus of the spinal cord is a functional entity well suited to the organization of coordinated activity. Its component structures are richly interconnected by a variety of horizontal and vertical linkages, providing an intrinsic system of complex interactions which is no less essential for the evolving act than supraspinal influences. The spinal cord is an active apparatus that does not passively reproduce instructions from above (Gurfinkel, Kots, Krinskiy, Pal'tsev, Fel'dman, Tsetlin, & Shik, 1971) and, indeed, may regulate its degree of subordination to supraspinal mechanisms (Sverdlov & Maksimova, 1965; Verber, Rodionov, & Shik, 1965). Several properties of spinal cord architecture and dynamics provide the basis for this interpretation. We take note of some of them here. First, of the great many interneurons in the spinal cord relatively few are afferent neurons. Second, interneurons rather than motor neurons are the terminal points for the majority of descending fibers from the brain. Third, the majority of synapses in the spinal cord are formed by connections between spinal neurons, and relatively few are formed from axons coming from the brain and spinal ganglia. And fourth, reciprocal facilitation and inhibition, and myotatic reflex action are all processes at the segmental level (see Gurfinkel *et al.*, 1971).

The integrity of the spinal cord rests on the fundamental servoprocess manifest in the alpha-gamma link regulating muscle contraction. Upon this servoprocess are built the intra- and intersegmental reflexes. We suppose that the modus operandi for integrating reflexes (the basis of the set of coordinative structures) in coordinated action exploits rather than disrupts the fundamental servomechanism. Indeed, this will prove to be the key notion for unraveling the problem of how precise instructions are formulated at the level of alphaservomotorneuron activity.

But before examining the evidence for this view we observe that in the unfolding of the action plan on the segmental apparatus the responsibility for demarcating coordinative structures and for the parsing of those structures may devolve on separate neuroanatomical systems. Greene (1971b) cites a series of experiments by Goldberger in which the corticospinal and brainstem spinal paths in monkey were interrupted. With corticospinal interruption the animal can no longer inhibit unwanted components of a coordinative structure such as the group of muscle contractions that extend joints of the same limb. Thus, for example, when presented with food that he must stretch for the monkey reaches out with extended limb but cannot then close his fingers to grasp the food. If with the joints flexed the animal grasps food placed close to him and raises it to his mouth he cannot then let go. In contrast, brain-stem spinal interruption appears to impede the animal's ability to restrict the evoked coordinative structures to those relevant to the task. When extending an arm to reach for food at a distance the group of contractions that rotate the limb, or those that raise the limb, may come into play in addition to the task-relevant group of limb extensors.

In short we see that the delimiting of coordinative structures and the manner of their decomposition are effected in the segmental apparatus by instructions from separate mechanisms. But now we must pass from this gross differentiation of the action plan at the segmental level to the finer differentiation afforded by the fundamental servomechanism (or, more aptly, the fundamental coordinative structure).

The main body of a muscle consists of extrafusal fibers that on contraction alter the relative positions of the bones to which they are attached. The innervation of extrafusal fibers is supplied by alphas motoneurons. Within the main body of the muscle are intrafusal fibers which are wrapped around the middle by the terminals of sensory fibers. These sensory fibers and the intrafusal muscle fibers to which they attach are referred to collectively as a muscle spindle. Muscle spindles connect to the extrafusal fibers at one end and to a tendon at the other and are therefore "in parallel" with the extrafusal fibers. Two functionally distinct spindle components can be identified: a static component that is sensitive to the instantaneous muscle length and a dynamic component that is sensitive to the rate of change of muscle length (Matthews, 1964). On contraction of the intrafusal fibers, the spindle receptors register the difference in length and the difference in rate of change of length between the intrafusal and extrafusal fibers. The induced receptor excitation is communicated to the linked alphas motoneurons which respond by recruiting more extrafusal fibers until the discrepancies in length and velocity have been annulled. Thus, in a situation in which a load is applied to a muscle extending it beyond its resting length, the spindle feedback provides an autonomous means of tailoring the muscle response to the new conditions. This negative feedback system identifies the fundamental servomechanism; it is now incumbent upon us to show that this servomechanism is biasable in ways of considerable importance to the theory of action.

Intrafusal fibers, like extrafusal fibers, have a source of innervation, the gammamotoneurons. These motoneurons fall into two relatively independent classes, the gammastatic and the gammadynamic, regulating respectively the static and dynamic components of muscle spindles (Matthews, 1964). Again, gammamotoneurons, like alphas motoneurons, are under high-level control but the motor nerves that project from brain to gammamotoneurons and those that project from brain to alphas motoneurons are largely separate and thus it is optional whether the spindles and the main body of a muscle contract and relax together. "The spindles could therefore be activated while the main muscle remained passive, and vice versa" (Merton, 1973, p. 37).

We see therefore that the gamma system allows for the modulation of the fundamental servomechanism. The gamma-static motoneurons can control the equilibrium state of the servomechanisms while the gamma-dynamic motoneurons can control the "damping" of the servomechanism, that is, the rate at which it achieves equilibrium. Thus, the servomechanism is not only informed of what it has done, but more importantly it can be informed of what it must do.

This completes the elementary description of the biasable nature of the fundamental servomechanism; but one or two points remain to be considered.

In addition to the biasable feedback loop signaling length and velocity through spindle receptors, there is another which signals muscular force through tendon organs. The signals conveying force feedback converge on interneurons on their way to alphamotorneurons. As before, interneurons can be manipulated by higher-level instructions so that the inhibitory effects of force feedback on alphamotorneuron activity can be modulated. The biasable feedback loops conveying length, velocity, and force are inextricably linked in the regulation of the servomechanism. So we may expand on our comments above. While higher level control signals to alphamotorneurons set the servomechanism going, the higher level control signals to the gamma system and to the interneurons transmitting force information from the tendon organs function less as instigators of movement than as modulators of the gain of the feedback loops, that is to say, they serve to adjust the ratios of the outputs of feedback loops to their inputs. This principle of higher-level modulation of spinal reflexes is generalized to the segmental mechanism of reciprocal inhibition by which we understand that spindle activity not only impinges upon an alphamotorneuron of its own muscle but also via inhibitory motorneurons upon an alphamotorneuron of the antagonist muscle. Spindle output contributes both to agonist contraction and to antagonist relaxation in the regulation of pairs of muscles controlling a joint. Clearly, from all that has been said the reflex interplay between agonist and antagonist is biasable.

We are now in a position to identify the property of the spinal cord that is central to our current concerns (and for which we will shortly provide evidence), namely, that the system of segmental interactions is biasable and as a general strategy the activating of coordinative structures occurs against a background of spinal mechanisms already prejudiced toward executive intentions. Thus, it may be argued that the control of movement is in many respects the reorganization or *tuning* of the system of segmental interactions and that this attunement precedes the transmission of activating instructions to coordinative structures (Gelfand *et al.*, 1971; Gurfinkel *et al.*, 1971).

Before we pass from this elementary discussion of tuning to take up the topic in earnest let us glance at two examples of how alpha-gamma linkage might embellish a relatively simple instruction. For the first, consider the previously discussed action of stepping, recognizing the fact that a double joint flexor of the hip also produces extension at the knee. The high-level representation of stepping can be said to specify crudely a general "flexor plan" for the limb (Lundberg, 1969). The knee flexors innervated on this plan are strong enough in the early phases of the movement to prevent extension but as flexion proceeds the double-joint muscle will become stretched inducing an intense discharge of spindle activity. The spindle feedback will impinge upon hip-flexor alphamotorneurons and also produce reciprocal inhibition of the motor units belonging to knee flexors. Thus during the swing the knee flexors originally innervated on the

flexor plan will suffer inhibition from the spindle activity of the double-joint muscle. The upshot of this interplay is the differentiation of the broadly stated flexor plan into coordinate stepping (Lundberg, 1969).

For the second example, consider a sudden change in the loading on an outstretched arm: a heavy object is placed into the hand, in a task where the arm's inclination to the ground is to be kept constant. We may suppose that instructions to the appropriate coordinative structures quickly bring the arm back into a close approximation to the desired position, with spindle feedback coming into play to finely tune the terminal point of the trajectory (cf. Arbib, 1972; Navas & Stark, 1968) and to maintain the arm in its desired position under the new conditions. In this sense we construe the alpha and gamma systems as participating in a "mixed ballistic-tracking strategy" (Arbib, 1972, p. 134) with the alpha system determining the ballistic component which gets the limb quickly into the right ballpark and the gamma system determining the superimposed tracking component which supplies the needed refinements.

From what has been said about the segmental apparatus and its pretuning we understand that the alpha-gamma processes of the two examples cited above do not take place in a vacuum. Rather, they occur against a backdrop suitably colored by supraspinal influences. It can be demonstrated that in the final 30 msec or so preceding a movement there is a pronounced enhancement of the effect of reciprocal inhibition on the future antagonist of that movement (Kots & Zhukov, 1971, see below). What this suggests is that a motion like stepping or raising the arm is anticipated through the supraspinal tuning of the segmental mechanisms of reciprocal inhibition. We should also recognize that the backdrop for a voluntary act is not limited to adjustments in spinal reflexes. Thus, for example, when an arm is raised voluntarily by a person standing upright it is possible to observe in the period immediately prior to the first signs of arm muscle activity, anticipatory activity in a number of muscles of the lower limb and trunk (Belen'kii, Gurfinkel, & Pal'tsev, 1967). Figuratively speaking, when one moves an arm in a standing position one first performs "movements" with the legs and the trunk and only then with the arm.

In summary, we have considered in preliminary but sufficient fashion the kinds of mechanisms that effect significant variation in the behavior of low-level holons without infringing upon their autonomy. These mechanisms suitably controlled from higher domains allow for the precise regulation of muscular contraction. The gist of the whole matter is given in a short paragraph by Pribram (1971):

When reflexes become integrated by central nervous system activity into more complex movements, integration cannot be effected by sending patterns of signals directly and exclusively to contractile muscles, playing on them as if they were a keyboard. Such signals would only disrupt the servoprocess. In order to prevent disruption, patterns of signals must be transmitted to the muscle receptors, either exclusively or in concert with those reaching muscle fibers directly. Integrated movement is thus largely dependent on changing the bias, the setting of muscle receptors [p. 225].

To this we need only add that the modulation of interneuronal pools must also play a significant part in the biasing of servomechanisms.

MOVEMENT-RELATED SEGMENTAL PRETUNING

Our task now is to view evidence for segmental pretuning in voluntary movements. But before we do so we must acknowledge that the available evidence comes from experiments in which the performers on cue are required to flex a knee, bend an elbow, extend a foot, and in general to execute movements whose trajectories, velocities, degrees of displacement, etc., are indifferent to the environment. To my knowledge there are no experiments on segmental pretuning for acts that depend on the detection of environmental properties for their performance. As a precautionary measure, therefore, we will distinguish between movement-related and environment-related pretuning. The former will refer to the changes in the segmental apparatus preceding the execution of a simple voluntary motion that is unrelated to the environment, in the sense that neither the actor's position with respect to the environment nor the position or orientation of objects with respect to each other and to the actor are altered by the motion. The latter, environment-related pretuning, will refer to segmental changes that precede actions or, more precisely, components of actions which are environmentally projected, in that their purpose is to displace the actor with respect to the environment or to displace (or rotate, or reflect) objects with respect to the actor, or both.

The goal we are approaching slowly is that of understanding, in a rough and approximate way, how seeing enters into doing. To this end we will need to extrapolate from movement-related pretuning to a general picture of how environmental properties control action. At all events, our immediate concern is with movement-related pretuning and we begin with some general comments.

The methodology for investigating movement-related pretuning has much in common with the methodology that characterizes the information-processing approach to visual perception (cf. Haber, 1969) which seeks to determine how visual "information" is modified in the course of its flow in the nervous system. Thus, techniques of masking, delayed partial-sampling, and reaction time are used to assess the correlation between stimulus and response at varying delays after visual stimulation.

In a similar if less sophisticated vein the tuning experiments that we will consider in this section judiciously apply the principle of probing the nervous system, in particular the spinal cord, in the interval elapsing between a warning signal and a cue to respond, or (more especially) between a cue to respond and the first signs of activity in the agonists executing the motion. The probes are simple reflexes elicited during the interval, with the latency and amplitude of the reflexes (recorded by the electrical response of the corresponding muscles) taken as indicants of the state of the segmental apparatus prior to the movement. The

reflexes used for this purpose have generally been tendon reflexes elicited by a tap and the Hoffman or H reflex, which is a monosynaptic reflex in the gastrocnemius-soleus muscle group and elicited by electrical stimulation of the tibial nerve in the popliteal fossa (Hoffman, 1922).

As an introduction to the procedure and to the observations that will be of interest to us we consider two exemplary experiments. In the first (Gurfinkel *et al.*, 1971) the participant is seated with legs flexed and on command extends one leg, the responding leg remaining constant throughout the experiment. Surface electromyographic (EMG) recording of activity in the quadriceps femoris muscle reveals that the tibia extension occurs at a latency of 160-180 msec. If the patellar reflex is evoked in the same leg within 100 msec or so of the cue to respond the amplitude of the reflex is unaffected (compared to the control condition in which no command to extend is given). However, if the patellar reflex is elicited beyond this period then its amplitude is enhanced the closer to the command that it is elicited. We infer, therefore, that the state of the segmental apparatus has been altered prior to activation of the muscle group extending the knee. In the second example (Gottlieb, Agarwal, & Stark, 1970), the participant is again seated normally but with the right leg extended, knee slightly flexed, and the foot firmly strapped to a plate to which he transmits an isometric force through either plantar flexion or dorsiflexion. The task of the participant is to match the level of his foot torque with a target level specified by the experimenter in what is, essentially, a continuous tracking task in which the varying target level of torque and the level of the participant's matching torque are displayed on a scope viewed by the participant. The H reflex is elicited at different delays subsequent to the target adopting a new level, and both the H reflex and the activity in the gastrocnemius-soleus muscle group (agonist in plantar flexion) and the anterior tibial muscle (agonist in dorsiflexion) are measured. Summarized briefly, the results are that the amplitude of the H reflex is distinctly augmented if elicited in the period 60 msec prior to the initial signs of voluntary motor unit activation in plantar flexion and is generally inhibited in approximately the same interval before the first signs of voluntary dorsiflexion. Again we infer that there are changes in the spinal cord that precede agonist activation.

How specific is segmental pretuning? Consider initially some further experiments reported by Gurfinkel *et al.* (1971). In one, two movements are executed by the subject on separate occasions: flexing the leg at the hip joint and extending the knee. Measures are taken of the tendon reflex of the rectus head of the quadriceps femoris muscle, which spans two joints, and of the lateral head of the same muscle, which spans only one joint. When the hip is flexed a pre-movement increase is observed only in the amplitude of the tendon reflex elicited by stimulation of the rectus head. But it is important to note here that while the rectus head of the quadriceps femoris is involved in hip flexion the lateral head is not. By contrast, when extension of the knee is called for, a

movement that involves both heads of the quadriceps femoris, both reflexes are significantly increased in amplitude prior to signs of voluntary motor neuron activity. In another experiment Gurfinkel *et al.* (1971) observed that in the 70–80 msec prior to flexing the leg at the knee the patellar reflex is amplified, but they also observed that the patellar reflex is amplified (although not to the same degree) prior to flexing the elbow of the arm ipsilateral to the leg in which the patellar reflex is elicited. We may conclude therefore that both specific and nonspecific changes in the segmental apparatus of the spinal cord precede voluntary motor unit activation.

This conclusion is buttressed by some other experiments that examine the changes in the spinal cord during the period intervening between a warning signal and the signal to execute a given movement. We take, as examples, experiments reported by Requin and Paillard (1971) and by Requin, Bonnet, and Granjon, (1968). In these experiments the movement is extension of the foot (plantar flexion), and both tendon and H reflexes are recorded from both the participating leg and the nonparticipating leg. Following the warning signal there is evidence of an increase in the amplitude of the reflexes measured in both legs, an increase which persists for the reflexes of the nonparticipating leg but is progressively depressed in the participating leg with greater proximity to the cue to respond. In short, these experiments provide evidence that after a warning signal and before a signal to execute a movement there occur both a nonspecific change in spinal sensitivity and a specific change related to the motoneuron pool—the servomechanisms—about to be involved in the forthcoming movement. In the view of Requin and his colleagues the depression of the reflex amplitude in the participating leg is due, under the conditions of the warning signal procedure, to central (supraspinal) influences that selectively “protect” the direct participants in the movement from irrelevant influences exerted upon them prior to their activation.

Evidently in the premovement period specific changes occur in the feedback loops related directly to agonist regulation. But can we demonstrate similar effects in the more extended feedback loop relating the state of an agonist to its antagonist? Two experiments by Kots (Kots, 1969; Kots & Zhukov, 1971) provide an answer.

Kots (1969a) wanted to know whether the enhancement in the H-reflex excitability of the motor neurons of the gastrocnemius evidenced in the latent period of a voluntary movement depended on the role the gastrocnemius was to play in the forthcoming movement. To this end the H-reflex amplitude was measured in the gastrocnemius when it was the future agonist of the movement, that is, in plantar flexion, and when it was the future antagonist of the movement, that is, in dorsiflexion. It was observed that following a command to move, the amplitude of the H reflex was significantly enhanced in the period beginning 60 msec prior to the first signs of voluntary motor unit activation only when the gastrocnemius was future agonist. When the antagonist role was

assumed, the H reflex was neither enhanced nor depressed in the latent period but was found to decline sharply immediately following the first myogram signs of motor unit activity in the agonist muscle, the anterior tibial.

It would appear, therefore, that the effect of tuning was specific to agonistic activity and that the failure to detect a depression in the H reflex when the gastrocnemius was the antagonist suggests that the "positive" priming of agonist centers is not paralleled by a "negative" priming of antagonist centers. The absence of antagonist depression in Kots' (1969a) experiment contrasts with the evidence of such depression in the experiment of Gottlieb *et al.* (1970), described above. While not stating it explicitly, the report of the latter experiment implies that plantar flexion and dorsiflexion were mixed randomly in the course of an experimental session; in Kots' experiment the two response modes were examined separately and this difference in procedure may account for the difference in results. At all events, taken together, the two investigations suggest that depressing the motor neurons of antagonistic muscles in the latent period of voluntary movement is not a necessary concomitant of tuning agonists. However, as we shall see in the second experiment of Kots (Kots & Zhukov, 1971), there is indeed an adjustment made in the inhibitory influences on the antagonists of a movement during the latent period that is not manifest as a depression in motor neuron excitability.

The Kots and Zhukov (1971) experiment made use of paired stimulation, a procedure that is comparable to the forward masking procedure commonly used in visual information-processing experiments (e.g., Turvey, 1973); essentially, a leading stimulus is used to impede the response to a lagging stimulus. For Kots and Zhukov the leading member of the stimulus pair was electrical stimulation of the peroneal nerve and the lagging member was electrical stimulation of the tibial nerve. Peroneal nerve stimulation elicits a direct response (the M response) in the motor neurons of the anterior tibial muscle without accompanying M and H responses in the gastrocnemius-soleus muscle group. Tibial nerve stimulation, as we have already seen, elicits the monosynaptic H reflex of the gastrocnemius-soleus group. The H response in the gastrocnemius-soleus group is significantly depressed when elicited very shortly after peroneal stimulation, say 2-4 msec. The brief latency of this effect implies that it is realized by the "spinal apparatus of reciprocal inhibition" (Kots & Zhukov, 1971). We can therefore exploit this paired-stimulation procedure to monitor the state of reciprocal inhibition mechanisms during the latent period of a voluntary movement. Thus, Kots and Zhukov sought to determine whether the impairment in the H reflex induced by prior peroneal stimulation was intensified in the latent period of voluntary dorsiflexion. In more general terms, they sought to determine whether there is pretuning of the mechanisms of reciprocal inhibition. During dorsiflexion, reciprocal inhibition would protect the anterior tibial muscle from the antagonistic response of the gastrocnemius-soleus muscles; Kots and Zhukov looked to see if this mechanism was primed for its task before voluntary activation of the

anterior tibial motor neurons. The experiment showed that in the final 30 msec prior to dorsiflexion the paired-stimulation effect was significantly enhanced and, moreover, that this enhancement could not be due to a reduction in excitability of the motor neurons of the gastrocnemius-soleus group, since the H response in the absence of preceding peroneal stimulation was unaltered during the latent period. Of course, this is what Kots (1969a) had found before.

Collectively, the experiments we have discussed suggest that a profound reorganization of the spinal cord precedes movement.⁵ There are both nonspecific and specific components of this reorganization, and the latter have been shown to include the mechanisms of reciprocal inhibition in addition to the servomechanisms regulating agonist activity. Moreover, the reorganization of the interaction among neural mechanisms at the spinal level follows the pattern of initially diffuse becoming more localized the closer in time to the manifestation of the desired movement (Gelfand *et al.*, 1971). It is evident, therefore, that in the differentiation of an action plan the realization of instructions to coordinative structures is determined by the state of these structures on receipt of the instructions (cf. Gurfinkel & Pal'tsev, 1965).⁶ Since the argument is that coordinative structures when activated perform in a relatively autonomous fashion, it follows that the details of their performance are very much determined by the state of the segmental apparatus at the time of activation.

TUNING AS PARAMETER SPECIFICATION

The elegance of tuning as a control process is that it permits the regulation of an autonomous system without disrupting the system's autonomy. So far we have illustrated this principle only in the control of servomechanisms at the level of muscle contractions. But this should not blind us to the likelihood of tuning as a general principle fundamental to all domains of the action heterarchy. We recall the comment that actions are produced by fitting together substructures, each of

⁵While we have chosen to discuss only experiments using simple, single movements we should note that other experiments have examined patterns of segmental pretuning in the performance of sequential and rhythmic movements (e.g., Kots, 1969b; Surguladze, 1972). Thus, Kots (1969b) showed that in the sequential performance of two movements opposite in direction in the ankle joint the segmental organization for the second movement is realized during the execution of the first.

⁶To demonstrate this point Gurfinkel and Pal'tsev (1965) examined the effect of eliciting a tendon reflex subsequent to a cue for voluntary movement (extension of the knee) on the latency of the voluntary movement. They found that the latent period of voluntary extension was linearly dependent on the time at which the reflex was elicited. In addition they showed that this effect held even when the reflex was elicited in the leg contralateral to that executing the voluntary leg extension. It is assumed that the reflex induces a change in the segmental apparatus and that the realization of commands for leg extension is therefore dependent on the prevailing state of the system of spinal relations.

which deals relatively autonomously with a limited aspect of the action problem. In addition, we recall that each domain may be construed as a representation in which relations are defined on a set of autonomous structures with the size of these structures becoming progressively smaller and their number progressively larger as the action plan is mapped into progressively less abstract representations. We now hypothesize that into each representation tuning functions may enter as modulators of coordinative structures.

Miller, Galanter, and Pribram (1960), discussing the acquisition of typing, suggest that the student typist learns to put feedback loops around larger and larger segments of her behavior. We might well suppose that this notion applies beyond typing to skilled acts in general, and with internal feedback loops in addition to the more commonly understood forms of feedback. We can imagine tuning functions of a more abstract kind related to the modulation of feedback between action segments that collectively behave as relatively autonomous units in the performance of any given skilled behavior. Again tuning would permit appropriate variation without disrupting, in these instances, the *acquired* self-regulating procedures.

To extend our usage of tuning, we will adopt a most important and provocative hypothesis, namely, that tunings parameterize the equivalence classes of functions specified by executive procedures. This follows from Greene's (1971a, b) contention that the smallest units of information available to an executive are probably not functions but families of functions parameterized by possible tunings.

Although we are here attempting to pass beyond the idea of tuning limited to the fundamental servomechanism we may profitably exploit our earlier discussion of that mechanism to illustrate the notion of tuning as parameter specification. We take as our departure point the experimental and mathematical analysis supplied by Asatryan and Fel'dman (1965) and Fel'dman (1966a, b) of the maintenance of joint posture and of the simple voluntary movement needed to achieve a desired angle of joint articulation. Consider a simple mass-spring system defined by the equation $F = -S_0(l - \lambda_0)$ where F is the force, S_0 is the stiffness of the spring, l is the length of the spring and λ_0 is the steady-state length of the spring, that is, the length at which the force developed by the spring is zero. This simple mass-spring system is controllable to the degree that the parameters S_0 and λ_0 are adjustable. Changing λ_0 with S_0 constant generates a set of nonintersecting characteristic functions, $F(l) = -S_0(l - \lambda)$, and changing both parameters generates a set of functions $F(l) = -S(l - \lambda)$ that will pass through all points in the plane defined by the cartesian product $F \times l$.

Let us now suppose that a joint-muscle system is analogous to our simple mass-spring system, in which case we can argue that the problem of controlling a joint-muscle system reduces to that of fixing certain characteristics of the system, that is, of setting mechanical parameters of the muscles, or more precisely, of setting biases on the fundamental servomechanisms. In the analogy

the characteristic functions of a joint-muscle system are of the form $M(\phi)$ where M is the total muscular moment and ϕ is the joint angle. And each $M(\phi)$, therefore, is determined by the mechanical parameters of the muscles regulating the joint:

$$\lambda = (\lambda_1, \lambda_2, \dots, \lambda_n), \quad S = (S_1, S_2, \dots, S_n),$$

where n is the number of muscles.

Given the foregoing comments let us now consider experiments using the technique of partial unloading—a technique (which we will shortly describe) that would assay the characteristic properties of an ordinary spring. These experiments (Asatryan & Fel'dman, 1965) sought to demonstrate that for a given situation the variations of muscular moment as a function of joint angle (or vice versa) are defined by an initial setting of the parameters, that is, by a characteristic function. For purposes of analysis we will refer to the state of the joint-muscle system as α , where α is defined by the vector (M, ϕ) . When M and ϕ are constant for some period of time then α is a steady state of the system.

The experimental methodology may be described briefly. The participant's forearm is fixed on a horizontal platform whose axis of rotation coincides with the axis of flexion and extension of the forearm. The horizontal platform is attached to a simple pulley system supporting a set of weights which can be selectively unloaded. At the outset of a trial the participant establishes a steady state, α_s , of the joint-muscle system: given a specified angle of articulation the participant must establish a muscular moment to compensate for the effect of the moment of external forces—determined by the weights and their direction of pull on the horizontal platform—opposing flexion (or extension) of the joint. Thus for a standard initial opposing force, different steady states, α_s , can be established for different joint angles, ϕ_s . Once the steady state is established at a given ϕ_s the participant is then asked to close his eyes and the weight is unloaded, with the amount of unloading varying across trials. The new angle of articulation—the new steady-state α'_s —to which the arm briefly moves following unloading (and before the participant can make compensatory adjustments) is recorded. From a series of experiments such as the one we have described Asatryan and Fel'dman (1965) demonstrated that for all possible initial states α_s of the joint-muscle system a set of *nonintersecting functions*, $M_s(\phi)$ (or $\phi_s(M)$), are generated relating muscular moments to the new steady-state angles of the joint. Moreover they showed that the form of the function $M_s(\phi)$ does not depend on the external moments but is determined unambiguously by the parameters of the initial state of the system. (This was demonstrated by using a set of external moments that were rising functions of joint angles, and a set that were diminishing functions of joint angles.) So we conclude that the function $M_s(\phi)$ for each α_s is an invariant characteristic of the joint-muscle system: If the system is perturbed it will follow a trajectory of states leading to a new state of equilibrium, where both the trajectory and the equilibrium state are defined by

the parameters fixed in the initial steady-state α_s . And since the curves are nonintersecting, the transition from one $M(\phi)$ to another requires changing λ_i with little, but preferably no change, in S_i (Asatryan & Fel'dman, 1965). It would seem, therefore, that a joint-muscle system does behave like a spring, that is, like a vibratory system, and that the action structures can choose parameters for this "spring" in accordance with the prevailing conditions. For a brief period of time following perturbation, until new parameters of the spring can be specified, the joint-muscle system behaves in the way that we would expect the chosen "spring" to behave.

We now proceed to develop this theme through the experiments of Fel'dman (1966b). These were conducted with a slight variation on the apparatus described above. The pulley-weight system was replaced by a detachable spring that opposes flexion of the joint but is insufficiently taut to prevent flexion. At rest the joint is flexed at an angle ϕ_0 , and on the occurrence of an auditory cue the participant must establish as rapidly as possible and without the aid of vision the steady angle ϕ_1 . (The participant is given a practice session so that he can achieve ϕ_1 with a minimum of error). During a series of trials the spring is occasionally detached within the period subsequent to the auditory cue and prior to movement. Now suppose that at the outset of a trial a fixed invariant characteristic $M(\phi)$ has been determined for the attainment of a steady-state α_1 , corresponding to the desired angle ϕ_1 . In the steady-state α_1 , $\phi = \phi_1$ and $M = M_e$, where M_e is the moment of force provided by the spring attached to the platform. But when the spring is detached, a new steady-state $\alpha_1' = (0, \phi_1)$ is required to achieve the same angle of articulation ϕ_1 , which means, of course, that a new invariant characteristic $M'(\phi)$ is needed. The question is: Can the transition from one invariant characteristic to another be effected during the execution of the movement? If it cannot, then when the spring is detached the joint will move to the angle ϕ_2 determined by the characteristic function $M(\phi)$. In the space (M, ϕ) , ϕ_2 will be at the intersection of $M(\phi)$ with $M = 0$ (since $M_e = 0$). The results of the experiment reveal that during the rapid establishment of a desired steady angle in the joint, correction of the invariant characteristics of the joint-muscle system (correction of the parameters defining the projected steady state) does not occur. The correction is made only after the achievement of the new steady state (corresponding to ϕ_2) when the error becomes obvious.

Now we wish to prove that the joint-muscle system truly behaves in this situation like a mass-spring system; although the movement of such a system as a whole is determined by the initial conditions, the equilibrium position does not depend on them and is determined only by the parameters of the spring and the size of the load. Using the paradigm described above we attach a pulley-weight system opposing extension such that release of the weight induces passive extension in the joint. Thus there are two external moments operating on the

limb: a spring-opposing flexion and a weight-opposing extension. The participant becomes acquainted with the situation in which the spring is detached in the latent period before movement to the intended angle ϕ_1 , bringing about passive flexion of the joint. But on some occasions the weight is also detached, leading additionally to passive extension before the voluntary movement. The results show that these rather radical and unpredictable changes in the initial conditions do not alter the behavior of the joint-muscle system: The trajectory of the system is still determined by the initial setting of parameters; that is, it moves to the state defined by the characteristic function $M(\phi)$ established at the outset of the trial. In brief, the equilibrium position is independent of the initial conditions (Fel'dman, 1966b).

In further analyses, this time of rhythmic movements of the joints, Fel'dman (1966b) was able to demonstrate that there is an independent parameter setting for the dynamics of the joint-muscle system. We may, therefore, envisage the set of fundamental servomechanisms (the alpha-gamma links together with the tendon feedback loops) regulating joint flexion and extension as collected together into a single vibratory system for which "static" and "dynamic" parameters can be specified. Choice of static parameters for the system determines the aim of a movement (the final steady state) independently of initial conditions; choice of the dynamic parameters determines (to a large extent) the rate and acceleration of the movement and also its form (aperiodic, oscillatory, etc.) (Fel'dman, 1966b).

This analogy between systems controlling action and vibratory systems suggests that *we may usefully conceive of coordinative structures in general as biasable, self-regulating vibratory systems*. In their simplest forms such systems might be modeled by the following second-order homogeneous linear differential equation with constant coefficients:

$$mX''(t) + kX'(t) + sX(t) = 0,$$

where $X(t)$ is the function relating the displacement of the system from a steady state to time.⁷ In such a system the setting of the parameter s defines the "stiffness" of the system and thus its equilibrium state, and the setting of the parameter k defines the friction or damping constant which determines the rate at which the system achieves equilibrium and the form of its behavior, that is, whether it oscillates or not. By way of summary, we have seen that the functional tuning of the segmental apparatus of the spinal cord may be likened to the specification of the parameters s and k for vibratory systems. On the

⁷This simple linear differential equation is given only to illustrate a principle. It is not meant to model (although it might) an actual coordinative structure. If we were to make the illustration more realistic and more general we would need to consider forced vibration in addition to free vibration, and to concern ourselves with equations in which the applied force varied with time or acted in an arbitrarily short interval.

assumption that all coordinative structures behave as vibratory systems, then tuning as parameter specification emerges as a viable procedure for adjusting the behavior of selected coordinative structures at all levels of abstraction of the action heterarchy. Thus, while some coordinative structures coordinate autonomously a greater number of pieces of the action apparatus than other coordinative structures (compare, for example, two classes of basic coordinative structures, the long spinal reflexes and the flexion reflexes), the manner of their attunement is fundamentally the same.

We now address the important question of whether the tuning and activation of autonomous systems are governed by the same mechanisms. Again, we will proceed on the assumption that the regulatory principles for large systems follow very much the pattern of small systems. This permits us the latitude of extrapolating from the tuning of small systems, that is, the fundamental servomechanism, about which we know something, to large systems, about which we know very little. The evidence of segmental pretuning suggests, among other things, that the nervous system has available a means of selectively raising and lowering the gain of spindle and tendon organ feedback loops. Indeed, the comment was made earlier that the control of the alpha and gamma systems is largely separate so that it is optional whether the two systems be concurrently active. But in the experiments we have taken as evidence for segmental pretuning, can a case be made for the selective modulation of servoprocesses independent of instructions sent specifically to activate alphas motorneurons, either directly or indirectly through gammamotorneurons? In experiments exploiting the H reflex and plantar flexion, such as those of Gottlieb *et al.* (1970), we might suppose that changes in the reflex during the latent period reflect nothing more than the increasing excitability of gastrocnemius-soleus motor units brought about by direct supraspinal signals to the alphas motorneurons. Or, in a similar vein, the increase in the H reflex represents the increased excitability in the alphas motorneuron pool of the gastrocnemius-soleus group in response to stimulation from the gamma system, which is in turn responding to directions from above. In these accounts the variation in the reflex is not an independent event but an epiphenomenon of alpha system innervation; that is to say, the voluntary EMG and the H-wave variations are manifestations of the same controlling input. Against this argument, however, Gottlieb *et al.* (1970) point out that changes in the wave form and amplitude of the H reflex are not correlated with changes in the agonist or antagonist EMG and, in addition, that the time courses of the recordings are clearly different. From their point of view it is much simpler to propose that for their particular form of voluntary movement there is a means for modulating the H reflex (and by inference, the fundamental servomechanism) that is separate from the means for activating alphas motorneurons. In more general terms we may conjecture that the mechanisms of tuning and activating coordinative structures are largely separate.

THE RELATIONSHIP BETWEEN THE EXECUTIVE AND TUNING

Let us summarize briefly our thinking thus far. The executive specified action plan identifies the relevant subset of coordinative structures and a set of functions on that subset (identifying the necessary equivalence classes) that will modulate its elements and relate them in a certain fashion. In the course of spelling out the action plan through successive procedures within the action heterarchy the functions identified by the executive may be substituted for by functions more suited to the current low-level conditions of the system. The interconverting of functions, however, leaves the equivalence classes invariant. Of these interconversions and of the low-level realization of the details of the action plan, the executive remains virtually ignorant.

The eventual activation of coordinative structures takes place against a background of prearranged interactions within the segmental apparatus of the spinal cord. We say that the segmental apparatus has been pretuned, or simply, tuned, and that the detailed performance of coordinative structures is determined by the extent interactive state of the segmental apparatus. The tuning of coordinative structures and the activation of coordinative structures appear to be governed by separate mechanisms.

We now ask: If it is the case that the activation and tuning of coordinative structures are separately controlled events, at what level is the separation first evident? More precisely, we are keenly interested in the issue of whether tuning is the responsibility of the executive, and thus part of the initial representation of the act, or whether this responsibility lies outside the executive's domain.

For a given movement such as plantar flexion we may suppose that the executive specifies a tuning function to the servomechanisms for the (possibly) separate alpha and gamma instructions to follow. The independence of movement-related tuning would arise, on this account, because the tuning function is effected by substructures different from those responsible for motor neuron activation, much along the lines that the delimiting of coordinative structures and their decomposition are controlled separately. In this view the family of possible tunings defines just another equivalence class, another invariant unit of information for the executive specification of solutions to action problems.

Alternatively, we may propose that *segmental tuning is not specified in the action plan but is determined by other structures on acknowledgment of the executive's intention* (cf. Greene 1971a, b). There would be special advantages accruing to a devolution of responsibility for specifying action plans and segmental tuning, advantages that would be especially pronounced when actions are related to environmental events. For example, it would mean that the executive could develop a repertoire of plans appropriate to frequently occurring classes of environmental events, so that when confronted with an event of a certain class the executive issues a standard set of instructions and leaves to

relatively independent tuning systems the responsibility for achieving the appropriate variant. Indeed, the largely invariant species-specific behavior of animals documented in the now celebrated works of ethologists (e.g., Tinbergen, 1951) strongly suggests that evolution has thoroughly exploited the principle of separating action-plan specification from tuning. The instinctive rituals are released by stimulation of a simple kind—the red belly of the stickleback, the spot under the herring gull's beak—but the unfolding stereotypic behavior is flexible: it relates to the lie of the land, to the contingencies of the local environment. We should suppose that these species-specific action plans are adjusted by the pickup of information about the environment, that is to say, their tuning is environment related.

Visual Control of Locomotion

Locomotion provides an instructive example of this viewpoint, for although locomotion propels an animal through its cluttered, textured environment, the basic locomotion pattern generator is independent of local conditions (Everts *et al.*, 1971). The necessary adaptive modifications are effected by feedback from the peripheral motor apparatus (the muscles and the joints), from changes in tactual motion, from the basic orienting system (Gibson, 1966b), and most significantly, from the perceptual pickup of information about surfaces and objects, about the relations among them and the moving animal. Visually detected information about the environment plays a fundamental role in permitting anticipatory changes in the basic locomotion pattern through "feed forward"; appropriate changes in coordination may be induced before the animal confronts a certain kind of surface irregularity or a certain kind of object. To manipulate the locomotion plan by touch or kinesthetic feedback alone would be unsatisfactory, since this form of regulation would often occur after an ill-adjusted movement and thus would specify compensatory changes for states that are no longer current. It is far better to have the low-level realization of the plan adjusted beforehand through patterns of feed forward related to properties of the optic array and to leave to touch and joint-muscle feedback the task of achieving small, final adjustments. At all events, the locomotion illustration raises the important issue in the present context of how the visual detection of environmental properties relating to the modification and control of locomotion is realized in the language of the action system.

With this issue in mind let us proceed to examine in some detail the problem of how an animal moves about in a stable environment. We take as our orientation J. J. Gibson's (1958) analysis of locomotion and its control by vision. First, we recognize, following Gibson, two fundamental assertions: (1) the control of locomotion relative to the total environment is governed by transformations of the total optic array to a moving point; (2) the control of locomotion relative to an object in the environment is governed by transforma-

tions of a smaller bounded cone of the optic array—a closed contour with internal texture in the animal's visual field. Second, and again respecting Gibson, we recognize the following as aspects of locomotion requiring our attention: (1) beginning locomotion in a forward direction; (2) terminating locomotion; (3) locomoting in reverse; (4) steering toward a specific location or object; (5) approaching without collision; (6) avoiding obstacles; (7) pursuing and avoiding a moving object. Additionally, we recognize that locomotion must be adjusted to the physical properties of the surface—its convexities and concavities, its slants and slopes, its edges.

For each of the aspects of locomotion we can identify correspondences in the flow patterns of the optic array. Thus, to initiate locomotion in a forward direction is to activate and relate the coordinative structures that comprise the locomotor synergism (Gelfand *et al.*, 1971) in such a fashion as to make the forward optic array flow outward; to cease locomotion is to terminate the optic flow; and to locomote in reverse is to pattern the locomotor synergism in a manner that makes the optic array flow inward. To move faster or slower is to make the rate of flow increase and decrease respectively. As Gibson (1958) remarks: "An animal who is behaving in these ways is optically stimulated in the corresponding ways, or, equally, an animal who so acts to obtain these kinds of optical stimulation is behaving in the corresponding ways [p. 187]." Now during forward movement the center of the flow pattern is the direction in which the animal is moving, that is to say, the part of the array from which the optic flow pattern radiates corresponds to that part of the solid environment to which the animal is locomoting. If the animal changes direction then naturally the center of flow shifts across the array. Thus we can say that to maintain locomotion in the direction of an object is to keep the center of flow of the optic array as near as possible to that part of the structure of the optic array which the object projects.

In moving about a stable environment an animal will approach solid surfaces that it will need to contact or avoid as situation and history demand. Objects are specified in the optic array by contours with internal texture. Areas between objects are specified either by untextured homogeneous regions (that is, sky) or by densely textured regions (that is, sand, grass). In approaching an object the closed contour in the array corresponding to the boundaries of the object expands with the rate of expansion for a uniform approach speed, accelerating in inverse proportion to the animal's proximity to the object. If the animal is on a collision course with the object, then a symmetrically expanding radial flow field will be kinetically defined over the texture bounded by the object's contours. On the other hand, if the expansion is skewed, that is, if the pattern of texture flow is asymmetrical then this specifies to the animal that it is on a noncollision course. A translation of the center of the flow pattern laterally to the animal's right or to the animal's left specifies that the animal will bypass the object on, respectively, its right or left. In Gibson's (1958) account the guiding principle

for approaching an object without collision is to move so as to cancel the forward and relatively symmetrically expanding flow of the optic array corresponding to the object at the instant when "the contour of the object on the texture of the surface reaches that angular magnification at which contact is made [p. 188]."⁸ And to avoid objects, to steer successfully around them, the animal needs to keep the center of the centrifugal flow of the optical array outside the contours with internal texture and inside the homogeneous or densely textured surface areas.

Suppose now that the object to which movement is being directed is a moving object, as in the case of one animal pursuing another. We can again identify corresponding properties of the optic array. A prey fleeing a predator is specified by the fact that for the predator the overall optic array flows from a center, but a contour with internal texture within the overall flow pattern is not expanding; absolute expansion of the contour means that our predator is making good ground on its prey, contraction of the contour may mean that our prey will live to run another day. The principle of pursuit is summed up lightheartedly by Gibson (1958), "... the rule by which a big fish can catch a small fish is simple: maximize its optical size in the field of view [p. 188]."

We see, in short, that controlling locomotion calls for the detection of change, detection of rates of change, and detection of rates of rates of change in the flowing optic array. It also calls for the detection of changes in parts of the structure of the optic array with respect to the optic array as a whole. We assume that animals are sensitive to all of these properties of stimulation that vary over time and that they do indeed detect them (Gibson, 1966b; Ingle, 1968). We should also note that modulating the optic array through movement and modulating movement through changes in the optic array go hand in hand; thus the cybernetical loop of afference, efference, reafference is virtually continuous.

But we must now face up to a point that has been neglected thus far. In directing its locomotion to one object and weaving its way among others, and in pursuing one moving object and fleeing another the animal exhibits its capacity to make discriminative responses. But these responses must be based upon different properties of stimulation from those that determine the control of locomotion: they are responses that are specific to those properties of the optic array which do not change as opposed to those which do; importantly, they are properties of stimulation that do not result from the animal's locomotion. The animal must be able to detect permanent properties of its environment: it must be able to detect whether a surface affords locomotion and whether a contour with internal texture affords collision; it must be able to detect whether a moving textured contour affords eating or whether it affords being eaten.

⁸For an interesting experiment in insect behavior that is of some relevance to these comments and to the general theory of perception-action relations see Goggs (1972).

In respect to the surface supporting locomotion the terrestrial animal must detect the gradients of optical texture specifying slant and slope, the topological shearing of texture specifying edge, and the changes of texture gradient specifying convexities and concavities. As it moves rapidly across a rough terrain, it must adjust its footfall pattern, temporally and spatially; it must adjust its gait to the wrinkled surface. It must detect surface protuberances and surface breaks that require leaping over as opposed to those that require going round or avoiding; it will often need to make transitions between running and leaping. With respect to the permanent properties of the environment we concur with Gibson (1966b) that the animal can detect in the changing optical flux those mathematically invariant properties that correspond to the physically constant object or surface and which afford for the organism possibilities for action.

We are led, therefore, to a distinction between those properties of stimulation which afford approach, avoidance, pursuit, flight, changes in the footfall pattern of a gait, and transitions from running to leaping, and those properties of stimulation which control locomotion in each of these respects. It would seem that the former are those properties which do not vary over time while the latter are those properties which do. And the pickup of change and nonchange are concurrent perceptual activities.

Tuning Reflexes and Environment-Related Tuning

At this stage of our inquiry as to how vision enters into locomotion (and into action in general) we turn our attention to the concept of tuning reflexes. In addition to those reflexes that resemble parts of acts, such as the flexion and crossed extension reflexes, or are themselves simple yet self-sufficient acts such as the righting reflex and the scratch reflex, we can identify a further class of reflexes whose task it appears is to impose biases upon the action system. We can distinguish, therefore, between "elemental" reflexes and "tuning" reflexes (Greene, 1969). As illustrations of tuning reflexes we can take classically defined postural or attitudinal (Magnus, 1925) reflexes such as the tonic neck reflex, which biases the motor apparatus for movement in the direction of gaze, and the labyrinthine reflexes, which bias the musculature to resist motion on an incline or to resist rotation (Roberts, 1967). Quite recently evidence has been forwarded of low-level tuning resulting from movements of the eyes (Easton, 1971, 1972a). In the cat, stretching the horizontal eye muscles facilitates a turning of the neck and head from the direction of gaze and stretch of the vertical eye muscles influences the forelimbs. Indeed, it appears that the eyes looking upward might foster forelimb flexion and the eyes looking downward might foster forelimb extension (Easton, 1972a).

The principal function of tuning reflexes seems to be that of altering the intrinsic system of segmental relations rather than that of initiating configura-

tions of motions in components of the motor machinery.⁹ The impression is that tuning reflexes adjust the bias in the fundamental servomechanisms (cf. Gernandt, 1967). In general it may be argued that the main advantage of tuning reflexes, whether induced by prior motion or induced more directly, is a reduction in the detail required of high-level instructions (Easton, 1972a). Thus when a cat turns its head to gaze at a passing mouse, the angle of tilt of the head and the degree of flexion and torsion in the neck will elicit a reflex modulation of the segmental apparatus such that a broadly stated executive instruction to "jump" will be realized as a jump in the right direction (Magnus, 1925; Ruch, 1965b). Clearly, such modulation must precede the innervation of muscles or the cat would constantly miss its target; obviously the cat in flight cannot rely on corrective feedback.

How do tuning reflexes relate to the visual control of locomotion? Analysis of the biomechanics of walking and running in animals (e.g., Arshavskii, Kots, Orlovskii, Rodionov, & Shik, 1965; Shik & Orlovskii, 1965; Shik, Orlovskii, & Severin, 1966) reveals that with change in speed or gait the majority of kinematic parameters is kept constant, suggesting that adjustments in the locomotion plan require a relatively minimal change in coordination. The action problem posed by the need to change speed of running or gait may be solved in most instances by a change in only two parameters. May we suppose, therefore, that a change in a small set of parameters is all that is needed to control locomotion through a "wrinkled" and object-cluttered terrain? Movement in a forward direction calls for a particular organization of the basic coordinative structures. If an animal so moving detects an invariant specifying an object or surface in its path that is to be avoided, then it must alter the organization of the relevant coordinative structures in order to change direction. But change in direction need not actually require direct executive intervention in the low-level organization of the locomotion plan; a shift in the direction of gaze may be all that is needed. In theory at least the tonic neck reflexes and related tuning reflexes could effect the necessary reorganization of the segmental apparatus. Similarly, if the contoured texture in the optic array afforded

⁹The potential range of changes in the segmental system induced by postural changes, and their implications for the behavior of coordinative structures is suggested in the following paragraph from an address delivered by Magnus almost fifty years ago:

Every change in attitude, with its different positions of all parts of the body, changes the reflex excitability of these parts and in some cases changes also the sense of the reflex evoked, excitations being converted into inhibitions, reflex extensions into flexions and so on. One and the same stimulus applied to one and the same place on the body may give rise to very different reactions in consequence of different attitudes which have been imposed to the body before the stimulus is applied [Magnus, 1925, p. 346].

For further intriguing and provocative comments on tuning reflexes see Jones (1965) and Fukuda (1957).

jumping on, then the act of directing the eyes or eyes and head upward would facilitate the transition in segmental organization from that of running to that of jumping.

These examples suggest the following: in the course of locomotion the detection of invariants affording specific changes in locomotion may serve to activate singularly simple action plans such as a change in the direction in which the head and/or eyes are pointing. Often these adjustments in orientation—owing to the functional tuning link between head and eye movements and the segmental apparatus—are sufficient to produce the needed parameters for the segmental realization of change in locomotion.

As we have noted, the optical stimulation for a moving animal has components of both change and nonchange (Gibson, 1966b). If the components of nonchange, specifying the permanent entities in the animal's environment, relate to action plans and their activation, to what do the changing components of stimulation relate? We must suppose that they relate to the mechanisms of tuning; but how is this relation effected? The following considerations may help us to move toward an answer to this question.

To leap from object to object is to project the body in particular trajectories, with each trajectory requiring different horizontal and vertical vectors of extension thrust. Variations in force could be achieved either through variations in the degree of activation of coordinative structures or parts of coordinative structures as might be permitted by the local sign properties of reflexes (the dependency of reflex patterns on the origin of stimulation) or through direct facilitation of motor neuron activity, or both (cf. Easton, 1972a). In theory, both of these sources of force variation are plausible instances of tuning. We can say therefore that each leap calls for the specification of parameters to the intrinsic system of segmental relations where these parameters relate to the desired trajectory. Now we might ask whether trajectory-related parameters could be determined through tuning reflexes. But cursory analysis would suggest that mechanical modulation—spinal tuning elicited reflexively by a prior motion such as directing the eye-head system toward an object—is inadequate for the task. Consider a cat perched on a particular platform. At a distance of X feet from its perch is another, higher platform. Directing its gaze to the top surface of the higher platform yields, say, a particular angle of neck extension and hence a particular tuning of the segmental apparatus. Yet we observe that we could arrange any number of higher platforms of different heights at any number of reasonable distances either more or less than X feet from the cat's perch that would correspond to the same inclination of the neck and hence to the same tuning parameters and hence, supposedly, to the same degree of thrust if the cat chose to jump. In brief, reflex tuning induced by any particular orientation of the eye-head system is ambiguous with respect to distance. Mechanically induced tuning, therefore, cannot supply the tuning parameters relevant to a given trajectory. How then are they supplied? We are forced to conclude that they are

supplied by the properties of the optic array that specify relative distance and height in the cat's normal cluttered and textured environment, and that these optical properties are realizable as segmental tunings without the intervention of executive procedures and without mechanical mediation.

With this conclusion in mind consider what we might now say about the scenario that unfolds when a scampering mouse appears at a leappable distance from an interested cat. In the cat's field of vision the mouse is projected as changing patterns in the optic array. Concurrently, there is a pickup by the cat's visual system of those properties of stimulation that change over time and those properties that do not. The former specify how far away the mouse is, in what direction it is moving, at what rate it is moving, and where it will be in a following instant relative to the cat; the latter specify the mouse's identity as something that affords catching and eating. Orienting in the direction of the mouse adjusts the segmental apparatus through the tuning reflexes for a movement in that direction; as the direction of gaze shifts according to changes in the mouse's location the mechanically induced segmental tuning likewise adjusts appropos the new direction. On activation of the action plan to pounce, the tuning parameters for the needed trajectory specified by the transformations in the optic array are given to the segmental system of interactions. The activation of coordinative structures then takes place against a backdrop of segmental relations appropriately adjusted for the generation of a precise, on-target leap.

In this cat-and-mouse story there are two main themes: one is that the activation of crudely stated action plans and environment-related tuning are based on different properties of stimulation; the other is that the properties of visual stimulation that control movement and the family of possible tunings that effect the control are tightly linked. In Gibson's view, perception is direct. He has also remarked that: "The distinction between an S-R theory of control reactions and an S-R theory of identifying reactions is important for behavior theory" (Gibson, 1958, p. 190). On this distinction we might now comment that in control reactions the relation is between changing properties of stimulation and patterns of tuning, and in identifying reactions it is between nonchanging properties of stimulation and action plans.

Mittelstaedt (1957) describes a similar story about prey capture in the mantis. A mantis strikes its prey with pinpoint accuracy within a latency of 10-30 msec, a period too brief to allow for adjustments during the course of the strike trajectory. The problem is to account for how this accuracy is achieved when the prey appears at a strikable distance either to the left or to the right of the body axis at some variable angle; and when the head is oriented at some (different) angle to the prothorax with which the forelegs—the striking instrument—are articulated. Mittelstaedt's modeling of this situation implies that the visual and proprioceptive information specifying the relevant relations is conveyed not to the executive issuing the strike signal but to the segmental machinery of the forelegs. On our account we would say that the higher-order invariant specifying

"prey" triggers the strike command (the strike action plan) but the properties of optical stimulation specifying the coordinates of the prey with respect to the body axis, and its rate and direction of movement, do not enter into the executive decision, for most assuredly that would introduce undesirable delays. Rather, these properties are realized as segmental tuning parameters effecting needed adjustments in the centers controlling foreleg extension. We may say of the mantis' prey catching that the prey determines the ballistic component while the prey's location and movement determine the tuning component in a mixed ballistic-tuning strategy. Moreover, we recognize what might indeed be a general principle, namely, that different properties of stimulation enter into the unfolding act at different levels.

In respect to this last point let us make one final comment on the topic of locomotion, which began this particular phase of our inquiry. We have argued that environment-related tuning is relatively independent of executive procedures. For locomotion we can say that tuning is coupled to the pickup of information conveyed by continuous transformations in the optic array. While the detection of higher-order invariants (affordances) may inject gross adjustments in locomotor activity, the fine control of locomotion in an object-cluttered and wrinkled terrain is through environment-related tuning which adapts the activity to the conditions by modulating a relatively small set of parameters, and does so without involving the higher domains of the action coalition/hierarchy.

Pal'tsev (1967a, b) advanced a theory that is of special relevance to this account of locomotor regulation. First, Pal'tsev (1967a) recognizes that in respect to uniform movements an argument can be made that in addition to movement-related segmental pretuning there is another type of reorganization of the segmental relations that is brought about *during* the execution of the movements. This latter form of tuning is due in Pal'tsev's (1967a) view to the fact that to a very large extent the interactions among different structures of the spinal cord are reorganized by processes that are inherently spinal. The segmental apparatus tunes itself, as it were, in harmony with the main supraspinal influence. By comparing experimental results on the effects spinal reflexes induce in neighboring spinal reflexes with the general picture of locomotion Pal'tsev (1967b) is led to the supposition that following the first few locomotor cycles the strategic ordering of muscle events in locomotion can be determined solely by the segmental system of relations. As he sees it, the supraspinal patterns of feedforward serve only to identify and to "trigger" the particular locomotion plan: the continuation of the plan, the subsequent locomotor cycles in walking or running, is then the responsibility of spinal processes. Which is to say that control of locomotion is simply and elegantly transferred from supraspinal structures to spinal structures. Thus, locomotion exhibited in the pursuit by a predator of its prey could proceed with insignificant involvement of the highest sectors of the action system. If such is the case, then it would be

propitious for the nervous system to exploit the principle of conveying visually specified adjustments in locomotion relatively directly to the segmental apparatus in which locomotion control is invested. This conclusion is consonant with the often expressed point of view that the spinal cord is a system that during action serves to integrate different supraspinal influences (cf. Pal'tsev & El'ner, 1967).

Two Kinds of Vision

In some respects the ideas just expressed are reminiscent of the claim that there are two separate but interdependent visual systems related to action (Trevarthan, 1968). It appears that a distinction is drawn in the neuroanatomy of the brain "between vision of relationships in an extensive space and visual identification of things" (Trevarthan, 1968, p. 301). In its simplest form the distinction is demonstrated most straightforwardly by the experiments of Schneider (1969): a hamster with intact superior colliculus but no visual cortex can orient to objects but cannot distinguish between them; conversely, with intact visual cortex and no superior colliculus the hamster can successfully distinguish objects but cannot locate them and orient to them except through trial-and-error. In very general terms it appears that there is a functional differentiation between two kinds of vision that relates in part to forebrain-midbrain differences.

Let us remark briefly on the vertebrate midbrain. Suppose that we drew a map of the projections from the eyes to the midbrain tectum and suppose that we did so for two dissimilar vertebrates, the goldfish and the cat. The eyes of the goldfish are aligned roughly perpendicular to the body axis, while those of the cat are aligned parallel to the body axis. If one drew maps in the optical coordinates of the eye, one would find that for the two vertebrates the projection from the eyes to the midbrain differed considerably. But if the maps were drawn in the coordinates of the behavioral field, that is, with respect to the symmetry of the body, one would observe that the two maps were virtually identical. Indeed, if one went on to obtain such maps for other vertebrates, one would find that the mapping from eyes to tectum in the coordinates of the behavioral field is relatively invariant, and thus indifferent to the variation in alignment between eyes and body axis (see Trevarthan, 1968). One might conjecture that body-centered visual space is represented by a precise topographical mapping in the midbrain in very much the same way in all vertebrates.

This map of visual loci also maps a topography of points of entry into the action system. Stimulating points on the tectum produces orienting movements of eyes, head, and trunk to the corresponding visual location (cf. Apter, 1946; Ewert, 1974; Hyde & Eliasson, 1957). A singularly important feature of the midbrain is that in respect to the symmetry of the body it provides a precise topographical map of points in visual space and a virtually identical map of orienting movements to those points (Apter, 1946). Because of this feature the

midbrain serves to map object locations onto the set of movement-induced tunings. But there is reason to suppose that the capabilities of the midbrain extend beyond this and are concerned in a more general way with the control of locomotion.

Let us say that the two kinds of vision relating to forebrain-midbrain differences relate in turn to different kinds of acts performed in the animal's behavioral space. Discussing primates, Trevarthan (1968) conveys the tenor of this viewpoint as follows:

Orientations of the head, postural adjustments, locomotor displacements change the relationship between the body and spatial configurations of contours, surfaces, events, and objects. These movements occur in what I shall call *ambient vision*. In contrast praxic actions on the environment to use pieces of it in specific ways are performed with the motor apparatus of the body and the visual receptors oriented together so that both vision and the acts inflicted on the environment occur in one part of the behavioral space. The vision applied to one place and a specific kind of object, or deployed in a field of identified objects, I shall call *focal vision* [p. 302]."

Trevarthan builds his case upon facts found in the effects of surgically separating the cerebral hemispheres. This separation exhibits many instructive and curious phenomena, including that of central concern to Trevarthan's thesis—the capability of the split-brain primate to double perceive and learn for some types of visual stimulation but not for others and correspondingly to perform some aspects of visually defined acts chaotically and yet to perform others with no evident impairment. We note that the separated cortices may learn, independently and simultaneously, conflicting solutions to a visual discrimination problem when the stimuli are clearly of different identities, as in the example of cross versus circle, but not when the stimuli differ on a single dimension such as bright versus dim. In the former case, that of an identity difference, what is learned by one hemisphere is available to the other only if it in turn has the opportunity to learn the same thing; in the latter case, what is learned by one hemisphere is without practice available to the other. The inference is that differences in degree may be apprehended by visual mechanisms of the midbrain, while the apprehension of differences in identity is the responsibility of cortical visual mechanisms (Trevarthan, 1968). And Trevarthan emphasizes that it is the transformations relating the to-be-distinguished stimuli rather than the ease of distinguishing between them that is important to the dissociation.

Paralleling this dissociation in split-brain vision is a dissociation in split-brain action. If an object such as a peanut is presented to the commissurectomized primate both hands may reach forward with precision to grasp it; however, the activities of the two hands appear indifferent to each other, resulting often in collision. Given an object to manipulate and explore, the split-brain displays an inability to relate the activities of the two hands. The needed collaboration is replaced by redundant and conflicting movements.

In sharp contrast to these anomalies of voluntary movements of the hands in the field of focal vision, no such schism is witnessed in locomotion in which the hands play an important role. Locomotion-related movements of the arms and hands are properly coordinated to each other and to the motions of the hind limbs; and in terms of displacement, velocity and timing are finely attuned to the environmental structures supporting the action (Trevarthan, 1968).

While there are many more questions to be asked of these dissociations in vision and action and of the relation between them we can with some reasonable certitude draw the following conclusions. First, low-level sections of the visual system can effect the pickup of transformations in the optic array corresponding to changes in gross environmental properties such as texture and contour and to the detection of simple invariants such as solidity—in short, those properties of the optic array relevant to the control of locomotion. And in this regard it is of some import to note that electrical stimulation of the midbrain can bring about parameter changes in the segmental functions governing locomotion (Shik, Severin, & Orlovskii, 1966). Second, the higher-level sections of the visual system detect higher-order invariants specifying identity and more complex transformation that would be relevant to and indeed result from the skilled manipulation of objects. For it is evident that separating the hemispheres gives rise to two separate visual frames for the regulation of manipulative behavior and to a consequent breakdown in coordination between the two hands, but leaves intact the visual frame for the regulation of locomotion.

RELATING THE CONTENTS OF VISION TO ACTION: A SUMMING UP

We come now to a general summary of these speculations on how vision enters into action. We have provided two rather different descriptions of the unfolding act, and it will be helpful to collect them together at this time. In one we envisaged the act as evolving through the establishment of progressively less abstract representations, from the specification of relations among and within a few relatively large coordinative structures to the specification of relations among and within many relatively small coordinative structures, the fundamental servomechanisms. In the other we saw the action plan unfolding as ordered successions of progressively less abstract projections of the environment. What we must now attempt is a reconciliation of these separate views.

The kernel notion in this essay has been the idea of building acts through the fitting together of relatively autonomous units. This principle of operation reflects the fundamental argument that there are far too many degrees of freedom in coordinated activity for it to be controlled by a single procedure in a single instant. One consequence of this viewpoint is that the initial representa-

tion of an act in the highest domain must necessarily be crude in comparison to its ultimate representation in terms of instructions to muscles.

Similarly we saw that in view of the degrees of freedom problem the representation in the highest domain could not be constructed in respect to the details of skeletal space; the perception of the disposition of the limbs and branches of the body at any moment can only enter into the representation in the most general way as an abstracted account of the body's "pose" at that instant. Using very much the same rationale we are led to believe that in interactions with the environment not all the contents of vision can be involved in the determination of the initial representation of an act. Again we suppose that the executive procedure uses only the perceptual description that it can handle; the description cannot be detailed and by necessity must be fairly abstract. Earlier, following Bernstein (1967), we used the term "topological properties" to identify the description of the environment to which the initial representation of the action plan related. We may now regard these properties as invariants of a higher order, for example, those which specify the identities of objects and their possibilities of transformation. In any event, the manifestation of the action plan as motions finely attuned to the nuances of the environment's structure tells us quite plainly that the detailed contents of vision must be interjected into the act during its evolution. We have argued that tuning of coordinative structures is probably the mechanism through which the interjection of environmental details is brought about.

If these speculations are not too far off the mark, then we might further conjecture as follows. The determination of an act as an orderly pattern of motions is distributed across many structures. In the coalitional/heterarchical language used above, we say that it is distributed across different domains. But where the differentiation of an action plan requires information about the environment, we should suppose that the procedures operating at each domain incorporate optically specified environmental properties. It seems unlikely however that the entry of environmental properties into the various representations of an unfolding act is a haphazard affair. Rather, we hypothesize that the properties of the optic array interlace with the representation of an action plan in a systematic fashion: different properties map into different representations. We have, of course, already implied that this might be the case in arguing that the specification of action plans and the tuning of structures correspond to different properties of stimulation. But now suppose that the properties of stimulation relevant to the control of action may themselves be arranged from more complex to more simple; then perhaps we can imagine a natural mapping of these properties onto the unfolding act, a mapping that preserves their order. Of the properties of optical stimulation relevant to the control of action, those of a higher order are realized as tunings in higher domains and those of a lower order are realized as tunings in lower domains of the action heterarchy.

We conclude with some final thoughts on the general characterization of the perception-action relation. With respect to the representation of the action plan in the highest domain, it is not so much that the specification of a subset of large coordinative structures and functions defined on them relates to higher-order properties of the optic array but rather that the description of the plan in action terms and the description of the plan in perceptual terms are dual statements about the same thing. Earlier we described the action concept for A writing as an operator defined over a set of functions relevant to the manipulation of coordinative structures; but we have also referred to the action concept for A writing in geometrical terms consonant with the points of view expressed by Bernstein (1967) and Lashley (1951), and further suggested that the two descriptions were isomorphic. Similarly, with respect to tuning, we have implied that there is a relatively direct mapping of the properties of optical stimulation relevant to the control of action onto the set of tunings. To draw these concepts together, we can say that "detection of control-relevant optical properties" and "specification of environment-related tuning parameters" are descriptions of the same event: one is the dual of the other.

Perhaps we can gain a purchase on the duality of perception and action events by considering a problem drawn from a rather special domain of the perception-action relation—communication between members of the same species. For a variety of reasons it has been suggested that the perception of sounds of speech is achieved by reference to the mechanisms of articulation (see Galunov & Chistovich, 1966; Liberman *et al.*, 1967; Zinkin, 1968). One version of this action-based theory of speech perception suggests that the listener seeks to determine (tacitly and unconsciously of course) which phoneme articulation plans could produce the acoustic pattern; the listener uses the inconstant sound to recover the articulatory gestures that produced it and thereby arrives at the speaker's intent (Liberman *et al.*, 1967). Other students of speech, however, have argued against the articulatory matching explanation of the perception of speech sounds and have suggested that the explanation be sought in the sensitivity of the nervous system to higher-order properties of acoustic stimulation (e.g., Fant, 1967, Abbs & Sussman, 1971). There is growing evidence for neural mechanisms that selectively respond to complex acoustic invariants (e.g., Roeder & Treat, 1961, Frishkopf & Goldstein, 1963; Capranica, 1965), and it is becoming increasingly less venturesome to propose that the perception of phonological attributes of speech is direct rather than mediated (cf. Abbs & Sussman, 1971). However, viable descriptions of invariants in speech stimulation have been elusive.

Commendable as a direct perception interpretation is, we still must account for the evidently tight coupling between structures detecting speech sounds and structures producing speech sounds (see Chistovich, 1961; Chistovich, Fant, deSerpa-Leitaõ, & Tjernlund, 1966). Suppose, as Gibson (1966b) suggests, that vibratory patterns specify their source. Then we can say that a listener perceives

articulation because the invariants of vibration correspond to the invariants of articulation: the phonemes are present in the neural activity and vocal tract activity of the speaker and in the air between the speaker and the listener. Thus the linguistically relevant invariants on the input side are the same as the linguistically relevant invariants on the output side, and it is in this sense that perceiving and producing speech correspond (cf. Halwes & Wire, 1974). Now suppose that we were to describe an articulatory action plan as a set of relations defined over a collection of coordinative structures, then we would argue that our description is also a description of the relevant relations in the acoustic pattern. An appropriate analogy is the group concept in mathematics: given two different sets of elements, with a group structure defined on each, we might find that although the elements differ (even radically) in the two instances, their manner of inner interlocking is the same, in which case we say that they represent the same abstract group. Our hypothesis, therefore, is this: the structure that affords perception of a speech sound also affords its production; speech perception and speech production are related by abstract structures that are common to both but indigenous to neither (cf. Turvey, 1974). There is some evidence, though slight, that structures with this dual property may have been exploited in the evolution of intraspecies communication. For example, the calling song of male crickets is composed of stereotyped rhythmic pulse intervals. Cross breeding of two species of crickets with marked differences in the rhythmic structure of their songs produces hybrids whose calling song is distinctly different from either parental song. It has been shown that genetic differences that cause song change in males also alter song reception in the females: hybrid females prefer the song of hybrid males (Hoy & Paul, 1973). What intrigues is the speculation that the action plan for song generation in the male and the female's selective sensitivity to the male's song are coupled through a common set of genes (Hoy & Paul, 1973). Thus, at some level of abstraction the same structure may underlie song production in the male and song reception in the female.

Whether a stronger and more general case can be made for the dual representation notion remains to be seen. There is the possibility, of course, that the principle we have tried to describe has meaning, if at all, only in the communication mode: speaking and perceiving speech, reading and writing, and the primitive instantiations of signaling in animal and insect communication. On the other hand, when one considers the failure of schemes in which sensory input is routed through a central network into motor responses, the growing uneasiness over the application of the terms "sensory, motor, associative" to higher neural structures, the increasing usage of the bimodal term "sensorimotor" (see Evarts *et al.*, 1971, for comments on each of these points), and the arbitrariness of action-based theories of perception, then the notion of perceiving and acting as dual representations of common neural events may be a reasonable alternative to the sensory and motor views of mind.

ACKNOWLEDGMENTS

The preparation of this paper was supported by a Guggenheim Fellowship awarded to the author for the period 1973-1974. I thank N. S. Sutherland for kindly providing facilities and assistance at the Laboratory of Experimental Psychology, University of Sussex, Brighton, England.

REFERENCES

- Abbs, J. H., & Sussman, H. M. Neurophysiological feature detectors and speech perception: A discussion of theoretical implications. *Journal of Speech and Hearing Research*, 1971, 14, 23-36.
- Apter, J. T. Eye movements following strychninization of the superior colliculus of cats. *Journal of Neurophysiology*, 1946, 9, 73-86.
- Arbib, M. A. *The metaphorical brain: An introduction to cybernetics as artificial intelligence and brain theory*. New York: Wiley, 1972.
- Arshavskii, Yu. I., Kots, Ya. M., Orlovskii, G. N., Rodionov, I. M., & Shik, M. L. Investigation of the biomechanics of running by the dog. *Biophysics*, 1965, 10, 737-746.
- Asatryan, D. G., & Fel'dman, A. G. Functional tuning of the nervous system with control of movement or maintenance of a steady posture-1. Mechanographic analysis of the work on the joint on execution of a postural task. *Biophysics*, 1965, 10, 925-935.
- Bartlett, F. C. *Remembering*. Cambridge, England: Cambridge University Press, 1964.
- Belen'kii, V. Yi., Gurfinkel, V. S., & Pal'tsev, Ye. I. Elements of control of voluntary movements. *Biophysics*, 1967, 12, 154-161.
- Bernstein, N. *The coordination and regulation of movements*. London: Pergamon Press, 1967.
- Capranica, R. R. The evoked vocal response of the bullfrog: a study of communication by sound. *Research Monographs*, No. 33. Cambridge, Massachusetts: MIT Press, 1965.
- Care, N. S., & Landesman, C. *Readings in the theory of action*. Scarborough, Ontario, Canada: Fitzhenry and Whiteside, 1968.
- Cassirer, E. *The philosophy of symbolic forms*. Vol. 3. *The phenomenology of knowledge*. New Haven, Connecticut: Yale University Press, 1957.
- Chistovich, L. A. Classification of rapidly repeated speech sounds. *Soviet Physics-Acoustics*, 1961, 6, 393-398.
- Chistovich, L., Fant, G., deSerpa-Leitaõ, A., & Tjernlund, P. *Mimicking of synthetic vowels*. (STL-QPSR 2/1966) Stockholm, Sweden: Royal Institute of Technology, 1966.
- Chomsky, N. *Aspects of the theory of syntax*. Cambridge, Massachusetts: MIT Press, 1965.
- Chomsky, N. *Topics in the theory of generative grammar*. The Hague: Mouton, 1966.
- Easton, T. A. Patterned inhibition from horizontal eye movement in the cat. *Experimental Neurology*, 1971, 31, 419-430.
- Easton, T. A. On the normal use of reflexes. *American Scientist*, 1972, 60, 591-599. (a)
- Easton, T. A. Patterned inhibition from single eye muscle stretch in the cat. *Experimental Neurology*, 1972, 34, 497-510. (b)
- Eccles, J. C. The dynamic loop hypothesis of motor control. In K. N. Leibovic (Ed.), *Information processing in the nervous system*. Berlin and New York: Springer-Verlag, 1969.
- Eccles, R. M., & Lundberg, A. Supraspinal control of interneurons mediating-spinal reflexes. *Journal of Physiology*, 1959, 147, 565-584.

- Eldred, E. Posture and locomotion. In H. W. Magoun (Ed.) *Handbook of physiology: Neurophysiology*, Vol. II. Washington, D.C.: American Physiological Society, 1960.
- Engberg, I., & Lundberg, A. An electromyographic analysis of muscular activity in the hindlimb of the cat during unrestrained locomotion. *Acta Physiologica Scandinavia*, 1969, 75, 614-630.
- Evarts, E. V. Representation of movements and muscles by pyramidal tract neurons of the precentral motor cortex. In M. D. Yahr & D. P. Purpura (Eds.), *Neurophysiological basis of normal and abnormal motor activities*. New York: Raven Press, 1967.
- Evarts, E. V. Brain mechanisms in movement. *Scientific American*, 1973, 229, 96-103.
- Evarts, E. V., and Thach, W. T., Motor mechanisms of the CNS: Cerebrocerebellar interrelations. *Annual Review of Physiology*, 1969, 31, 451-489.
- Evarts, E. V., Bizzi, E., Burke, E. E., Delong, M., & Thach, W. T. Central control of movement. *Neurosciences Research Program Bulletin*, 1971, 9, No. 3.
- Ewert, J-P. The neural basis of visually guided behavior. *Scientific American*, 1974, 230(3), 34-42.
- Falk, G. Interpretation of imperfect line data as a three dimensional scene. *Artificial Intelligence*, 1972, 3, 101-144.
- Fant, G. Auditory patterns of speech. In W. Wathen-Dunn (Ed.), *Models for the perception of speech and visual form*. Cambridge, Massachusetts: MIT Press, 1967.
- Fel'dman, A. G. Functional tuning of the nervous system with control of movement or maintenance of a steady posture—II. Controllable parameters of the muscles. *Biophysics*, 1966, 11, 565-578. (a)
- Fel'dman, A. G. Functional tuning of the nervous system with control of movement or maintenance of a steady posture—III. Mechanographic analysis of the execution by man of the simplest motor tasks. *Biophysics*, 1966, 11, 766-775. (b)
- Festinger, L., Burnham, C. A., Ono, H., & Bamber, D. Efference and the conscious experience of perception. *Journal of Experimental Psychology Monograph*, 1967, 74(4, Pt. 2).
- Frishkopf, L., and Goldstein, M. Responses to acoustic stimuli from single units in the eighth nerve of the bullfrog. *Journal of the Acoustical Society of America*, 1963, 35, 1219-1228.
- Fukuda, T. *Stato-kinetic reflexes in equilibrium and movement*. Tokyo: Igaku Shoin, 1957.
- Galunov, V. I., & Chistovich, L. A. Relationship of motor theory to the general problem of speech recognition (review). *Soviet Physics-Acoustics*, 1966, 11, 357-365.
- Gelfand, I. M., Gurfinkel, V. S., Tsetlin, M. L., & Shik, M. L. Some problems in the analysis of movements. In I. M. Gelfand, V. S. Gurfinkel, S. V. Fomin, & M. L. Tsetlin (Eds.), *Models of the structural-functional organization of certain biological systems*. Cambridge, Massachusetts: MIT Press, 1971.
- Gernandt, B. E. Vestibular influence upon spinal reflex activity. In *Myotatic, kinesthetic and vestibular mechanisms: Ciba Foundation Symposium*, London: Churchill, 1967.
- Gibson, J. J. Visually controlled locomotion and visual orientation in animals. *British Journal of Psychology*, 1958, 49, 182-194.
- Gibson, J. J. The problem of temporal order in stimulation and perception. *Journal of Psychology*, 1966, 62, 141-149. (a).
- Gibson, J. J. *The senses considered as perceptual systems*. Boston: Houghton Mifflin, 1966. (b).
- Goggsall, J. C. The landing response and visual processing in the milkweed bug, *Oncopeltus fasciatus*. *Journal of Experimental Biology*, 1972, 57, 401-414.
- Gottlieb, G. L., Agarwal, G. C., & Stark, L. Interaction between voluntary and postural mechanisms of the human motor system. *Journal of Neurophysiology*, 1970, 33, 365-381.

- Greene, P. H. Seeking mathematical models for skilled actions. In D. Bootzin & H. C. Muffley (Eds.), *Biomechanics*. New York: Plenum Press, 1969.
- Greene, P. H. Introduction in I. M. Gelfand, V. S. Gurfinkel, S. V. Fomin, & M. L. Tsetlin (Eds.), *Models of the structural-functional organization of certain biological systems*. Cambridge, Massachusetts: MIT Press, 1971. (a)
- Greene, P. H. Problems of organization of motor systems. *Quarterly Report No. 29, Institute for Computer Research*, University of Chicago, 1971. (b)
- Gunkel, M. Über relative Koordination bei willkürlichen menschlichen Gliedbewegungen. *Pflügers Archiv für die gesamte Physiologia*, 1962, 215, 472-477.
- Gurfinkel, V. S., Kots, Ya. M., Krinskiy, V. I., Pal'tsev, Ye. I., Fel'dman, A. G., Tsetlin, M. L., & Shik, M. L. Concerning tuning before movement. In I. M. Gelfand, V. S. Gurfinkel, S. V. Fomin, & M. L. Tsetlin (Eds.), *Models of the structural-functional organization of certain biological systems*. Cambridge, Massachusetts: MIT Press, 1971.
- Gurfinkel, V. S., & Pal'tsev, Ye. I. Effect of the state of the segmental apparatus of the spinal cord on the execution of a simple motor reaction. *Biophysics*, 1965, 10, 944-951.
- Haber, R. N. Information processing analyses of visual perception: An introduction. In R. N. Haber (Ed.), *Information processing approaches to visual perception*. New York: Holt, Rinehart, & Winston, 1969.
- Halwes, T., and Wire, B. A possible solution to the pattern recognition problem in the speech modality. In W. Weimer & D. Palermo (Eds.), *Cognition and the symbolic processes*. Hillsdale, New Jersey: Lawrence Erlbaum Assoc., 1974.
- Hayek, F. A. The primacy of the abstract. In A. Koestler & J. R. Smythies (Eds.), *Beyond reductionism (The Alpbach Symposium)*. Boston: Beacon Press, 1969.
- Hoffman, P. *Untersuchungen über die Eigenreflexe (sehnreflexe) menschlicher Muskeln*. Berlin: Springer-Verlag, 1922.
- Hoy, R. R. and Paul, R. C. Genetic control of song specificity in Crickets. *Science*, 1973, 180, 82-83.
- Hyde, J. E., & Eliasson, S. G. Brainstem induced eye movements in cats. *Journal of Comparative Neurology*, 1957, 108, 139-172.
- Ingle, D. Spatial dimensions of vision in fish. In D. Ingle (Ed.), *The central nervous system and fish behavior*. Chicago: University of Chicago Press, 1968.
- James, W. *The principles of psychology*. New York: Holt, 1890.
- Jones, F. P. Method for changing stereotyped response patterns by the inhibition of certain postural sets. *Psychological Review*, 1965, 72, 196-214.
- Koestler, A. Beyond atomism and holism—the concept of the holon. In A. Koestler & J. R. Smythies (Eds.), *Beyond reductionism (The Alpbach Symposium)*. Boston: Beacon Press, 1969.
- Kornhuber, H. H. Cerebral cortex, cerebellum, and basal ganglia: An introduction to their motor functions. In F. O. Schmitt & F. G. Worden (Eds.), *The neurosciences third study program*. Cambridge, Massachusetts: MIT Press, 1974.
- Kots, Ya. M. Supraspinal control of the segmental centres of muscle antagonists in man—I Reflex excitability of the motor neurones of muscle antagonists in the period of organization of voluntary movement. *Biophysics*, 1969, 14, 176-183. (a)
- Kots, Ya. M. Supraspinal control of the segmental centres of muscle antagonists in man—II Reflex excitability of the motor neurones of muscle antagonists on organization of sequential activity. *Biophysics*, 1969, 14, 1146-1154. (b)
- Kots, Ya. M., Krinskiy, V. I., Naydin, V. L., & Shik, M. L. The control of movements of the joints and kinesthetic afferentation. In I. M. Gelfand, V. S. Gurfinkel, S. V. Fomin, & M. L. Tsetlin (Eds.), *Models of the structural-functional organization of certain biological systems*. Cambridge, Massachusetts: MIT Press, 1971.

- Kots, Ya. M., & Syrovegina, A. V. Fixed set of variants of interactions of the muscles of two joints in the execution of simple voluntary movements. *Biophysics*, 1966, 11, 1212-1219.
- Kots, Ya. M., & Zhukov, V. I. Supraspinal control of the segmental centres of muscle antagonists in man—III "Tuning" of the spinal apparatus of reciprocal inhibition in the period of organization of voluntary movement. *Biophysics*, 1971, 16, 1129-1136.
- Kuno, M., & Perl, E. R. Alteration of spinal reflexes by interaction with suprasegmental and dorsal root activity. *Journal of Physiology*, 1960, 151, 103-123.
- Lashley, K. S. The problem of serial order in behavior. In L. A. Jeffress (Ed.), *Cerebral mechanisms in behavior (The Hixon Symposium)*. New York: Wiley, 1951.
- Lenneberg, E. *Biological foundations of language*. New York: Wiley & Sons, 1967.
- Liberman, A. M., Cooper, F. S., Shankweiler, D. P., & Studdert-Kennedy, M. Perception of the speech code. *Psychological Review*, 1967, 74, 431-461.
- Lundberg, A. Reflex control of stepping. *Proceedings of Norwegian Academy of Science and Letters*. Oslo: Universitetsforlaget, 1969.
- Magnus, R. Animal posture. *Proceedings of the Royal Society of London*, 1925, 98 (Ser. B), 339-353.
- Matthews, P. B. C. Muscles spindles and their motor control. *Physiological Reviews*, 1964, 44, 219-288.
- Merton, P. A. How we control the contraction of our muscles. *Scientific American*, 1973, 288, 30-37.
- Miller, G. A., Galanter, E., & Pribram, K. H. *Plans and the structure of behavior*. New York: Henry Holt & Co., 1960.
- Minsky, M., & Papert, S. Artificial Intelligence. *Artificial Intelligence Memo*, 252. Artificial Intelligence Laboratory, M.I.T., Cambridge, Massachusetts, 1972.
- Mittelstaedt, H. Prey capture in mantids. In B. T. Scheer (Ed.), *Recent advances in invertebrate physiology*. Eugene, Oregon: University of Oregon Press, 1957.
- Navas, F., & Stark, L. Sampling or intermittency in hand control system dynamics. *Biophysical Journal*, 1968, 8, 252-302.
- Neisser, U. *Cognitive psychology*. New York: Appleton-Century-Crofts, 1967.
- Obituary: M. L. Tsetlin, *Biophysics*, 1966, 11, 1080.
- Oscarsson, O. Functional organization of spinocerebellar paths. In A. Iggo (Ed.), *Handbook of sensory physiology*, Vol. II *Somato-sensory system*. Berlin: Springer-Verlag, 1970.
- Paillard, J. The patterning of skilled movements. In J. Field, H. W. Magoun, & V. E. Hall (Eds.), *Handbook of physiology: Neurophysiology. Vol. 3*. Washington, D.C.: American Physiological Society, 1960.
- Pal'tsev, Ye. I. Functional reorganization of the interaction of the spinal structure in connexion with the execution of voluntary movement. *Biophysics*, 1967, 12, 313-322. (a)
- Pal'tsev, Ye. I. Interactions of the tendon reflex areas in the lower limbs in man as a reflexion of locomotor synergism. *Biophysics*, 1967, 12, 1048-1059. (b)
- Pal'tsev, Ye. I., & El'ner, A. M. Change in the functional state of the segmental apparatus of the spinal cord under the influence of sound stimuli and its role in voluntary movement. *Biophysics*, 1967, 12, 1219-1226.
- Pribram, K. H. *Languages of the brain: Experimental paradoxes and principles in neuropsychology*. Englewood Cliffs, New Jersey: Prentice-Hall, 1971.
- Pyatetskii-Shapiro, I. I., & Shik, M. L. Spinal regulation of movement. *Biophysics*, 1964, 9, 525-530.
- Reaves, J. M. The "coalition": A reaction to the machine metatheory in cognitive psychology. Unpublished manuscript, Center for Research in Human Learning, University of Minnesota, 1973.

- Requin, J., Bonnet, M., & Granjon, M. Evolution du niveau d'excitabilité Médullaire chez l'homme au cours de la période préparatoire au temps de réaction. *Journal de Physiologie*, 1968, 1, 293-294.
- Requin, J., and Paillard, J. Depression of spinal monosynaptic reflexes as a specific aspect of preparatory motor set in visual reaction time. In *Visual information processing and control of motor activity*. Sofia: Bulgarian Academy of Sciences, 1971. Pp. 391-396.
- Roberts, T. D. M. *Neurophysiology of postural mechanisms*. London: Butterworths, 1967.
- Roeder, K., & Treat, A. The reception of bat cries by the tympanic organ of Noctuid moths. In W. A. Rosenblith (Ed.) *Sensory communications*. Cambridge, Massachusetts: MIT Press, 1961.
- Rowell, C. H. F. Central control of an insect segmental reflex. I. Inhibition by different parts of the central nervous system. *Journal of Experimental Biology*, 1964, 41, 559-572.
- Ruch, T. C. Transection of the human spinal cord: The nature of higher control. In T. C. Ruch & H. D. Patton (Eds.) *Physiology and biophysics*. Philadelphia: W. B. Saunders, 1965. (a)
- Ruch, T. C. Pontobulbar control of posture and orientation in space. In T. C. Ruch & H. D. Patton (Eds.), *Physiology and biophysics*. Philadelphia: Saunders, 1965. (b)
- Schneider, G. E. Two visual systems. *Science*, 1969, 163, 895-902.
- Shaw, R. E. Cognition, simulation and the problem of complexity. *Journal of Structural Learning*, 1971, 2, 31-44.
- Shik, M. L., & Orlovskii, G. N. Coordination of the limbs during running of the dog. *Biophysics*, 1965, 10, 1148-1159.
- Shik, M. L., Orlovskii, G. N., & Severin, F. V. Organization of locomotor synergism. *Biophysics*, 1966, 11, 1011-1019.
- Shik, M. L., Severin, F. V., & Orlovskii, G. N. Control of walking and running by means of electrical stimulation of the mid-brain. *Biophysics*, 1966, 11, 756-765.
- Sperry, R. W. Neurology and the mind-brain problem. *American Scientist*, 1952, XL, 291-312.
- Surguladze, T. D. Functional changes in the segmental apparatus of the spinal cord on execution by man of rhythmic movements. *Biophysics*, 1972, 17, 141-145.
- Sutherland, N. S. Intelligent picture processing. Paper presented at Conference on the Evolution of the Nervous System and Behavior, Florida State University, Tallahassee, 1973.
- Sverdllov, S. M., & Maksimova, Ye. V. Inhibitory influences of efferent pulses on the motor effect of pyramidal stimulation. *Biophysics*, 1965, 10, 177-179.
- Taub, E., & Berman, A. J. Movement and learning in the absence of sensory feedback. In S. J. Freedman (Ed.), *The neurophysiology of spatially oriented behavior*. Homewood, Ill: Dorsey Press, 1968.
- Tinbergen, N. *The study of instinct*. Oxford: Clarendon Press, 1951.
- Trevarthen, C. B. Two mechanisms of vision in primates. *Psychologische Forschung*, 1968, 31, 299-337.
- Turvey, M. T. On peripheral and central processes in vision: Inferences from an information-processing analysis of masking with patterned stimuli. *Psychological Review*, 1973, 80, 1-52. (b).
- Turvey, M. T. A note on the relation between action and perception. In M. Wade & R. Martens (Eds.) *Psychology of motor behavior and sports*. Urbana, Illinois: Human Kinetics, 1974.
- Veber, H. V., Rodionov, I. M., & Shik, M. L. "Escape" of the spinal cord from supraspinal influences. *Biophysics*, 1965, 10, 368-370.
- von Foerster, H. On self-organizing systems and their environments. In M. C. Yovits & S. Cameron (Eds.), *Self-organizing systems*. New York: Pergamon Press, 1960.

- Weimer, W. B. Psycholinguistics and Plato's paradoxes of the *Meno*. *American Psychologist*, 1973, 28, 15-33.
- Weiss-Fogh, T. Control of basic movements in flying insects. In *Homeostasis and feedback mechanisms: Symposia of the Society for Experimental Biology*. No. XVIII. Cambridge, England: Cambridge University Press, 1964.
- Wiersma, C. A. The organization of the arthropod central nervous system. *American Zoologist*, 1962, 2, 67-68.
- Wilson, D. M. Bifunctional muscles in the thorax of grasshoppers. *Journal of Experimental Biology*, 1962, 39, 669-677.
- Zinkin, N. I. *Mechanisms of speech*. The Hague: Mouton, 1968.