

many cases the least important. What are required are detailed, quantitative descriptions of the behaviour of the overall system and its components. The availability of models of important components (e.g., muscle-spindle afferents) will make possible the development of comprehensive simulation models of the overall system for use in testing structural hypotheses and possible modes of system operation. Systems with multiple feedback pathways and extensive dynamics cannot be analysed intuitively but require solid, quantitative investigations of the type that cannot be accomplished without a combination of careful experimental design, quantitative analysis, modelling of data, and simulation.

Our answer to Stein's hypothetical multiple-choice question is therefore (H): the question cannot be answered on the basis of current knowledge. We agree with his remarks regarding the potential value of control theory but feel that they should be extended to include the sister disciplines of systems identification, modelling, and simulation.

Motor control: Which themes do we orchestrate?

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When we are confronted with a living system, whose design is mysterious and whose optimizations are obscure, it is no easy task – as Professor Stein reminds us – to arrive at an answer to the question he posed in his target article. The paper is an important contribution chiefly for two reasons. The first, which we shall mention only in passing, is that it is likely to provide much debate on what the controlled variables might be; moreover, it will force those who find this a burning issue to put their cards on the table. The second reason, and, we feel, the more important one, is that the paper poses a question, "What muscle variable(s) does the nervous system control . . . ?" whose very nature raises questions about the strategies neuroscience uses to investigate problems of control and coordination of movement. In our commentary we will focus on some of the (not so) implicit assumptions behind the question posed by Stein; if nothing else, we hope to heighten sensitivity to some of the issues involved and (perhaps) to force neuroscientists to consider their epistemology.

There are a couple of questionable assumptions in Stein's approach—at least as reflected in this article. The first is that control is the province of the nervous system; the second is that it is muscle variable(s) that are controlled. We shall examine in turn each assumption and its consequent ramifications for elucidating principles of coordination and control. In addition, we shall point to one notable omission in the author's list of candidates for control, and in our final remarks we shall take up Stein's invitation to advance, albeit briefly, an alternative to the control theoretic stance he advocates here. Although it may seem to the author "natural to assess . . . performance in terms similar to those applied to motors or other devices that produce movement," we assert that there are certain fundamental differences between living systems and machines (apart from structure) that render such a strategy not only dubious but highly unnatural. Most so-called machine theories regard biological control as a technical or engineering problem in which the many degrees of freedom to be regulated are a "curse" (Bellman 1961). In contrast, there are contemporary physical theories yet to be explored fully in the domain of movement that consider many degrees of freedom and nonlinearities to be a *requisite* (not a source of "complication") for the emergence of coherent phenomena. The physical strategies being uncovered

(principally in the form of Iberall and colleagues' homeokinetic theory [Iberall 1977; 1978], Prigogine and colleagues' dissipative structure theory [Nicolis & Prigogine, 1979; Prigogine, 1980], Haken's synergetics [Haken 1977], and Morowitz's bioenergetics [Morowitz 1968]; see also Kugler, Kelso & Turvey 1982 for contrasts among these theories and their application to control and coordination) stress autonomy, self-organization, and evolution of function as system attributes – attributes that already appeal to some neuroscientists (cf. Katchalsky, Rowland, & Blumenthal 1974; Llinas & Iberall 1977; Szentagothai 1978). Though we can classify ourselves as at best informed amateurs in this area, we believe that these system attributes will prove difficult for the student of movement to ignore. A consideration of the assumptions behind the question posed by Stein may allow us to ground this claim more firmly.

Control as the province of the nervous system. It was surely one of Bernstein's (1967) most significant contributions (and he has made many that have still to be appreciated) that control and coordination are not reducible to the orchestration of neural signals to and from the motor apparatus. Stein appears to recognize this fact in several places (e.g., in his discussions of stiffness and his awareness of the possibility that energy fluxes may shape control), but his paper as a whole shows little appreciation of it. In fact, the predominant methodology in the studies cited by Stein dictates that the organism and its parts are quiescent until mechanically or electrically stimulated. Obviously, we do not wish to be interpreted as saying that such a methodology has not proved useful in many cases or that the effects observed are not real. But control involves more than *reactivity*, and its analysis goes far beyond the deterministic input/output approach espoused in Stein's paper. One wonders to what extent the results of the studies cited by Stein, many of which involve single muscles, in nonintact preparations, can be generalized to normal movements in organisms continually interacting with their environments. There are a number of grounds for expressing skepticism on this issue (cf. Bernstein 1967). To be blunt, an unequivocal relation between neural impulses to muscles and resulting movement does not, and cannot, exist (see Benati et al. 1980; Boylls 1975; Kelso & Holt 1980; Saltzman 1979; and Turvey, Shaw & Mace 1978 for anatomical, mechanical, and physiological sources of functional nonunivocality or indeterminacy).

Consider, for example, the task of maintaining the elbow at a steady-state angle of 180 degrees (i.e., the elbow in full extension). The orientation of the arm in the gravity field determines not only the relative contributions of muscle and gravity torques at the desired elbow angle, but also the stability properties of this equilibrium configuration. When the arm is in a downward vertical orientation, the elbow angle is stable; if the elbow is perturbed (flexed) it will return to equilibrium due to the stable restoring torque of gravity. No muscle activity is required in this case. If, however, the arm is in an upward vertical orientation, the elbow angle is unstable since gravity plays a destabilizing role in this configuration. If the equilibrium angle is to be restored, muscle activity is required to provide the stabilizing restorative torque. Thus, the relative contributions of gravity and muscle stiffnesses for a stable equilibrium angle vary with the arm's orientation in the gravity field. In short, the nervous system "controls" only to the extent that it complements the force field of the environment. Its role is better envisaged as exploitative rather than injunctive.

On the selection of analytic units. In the target article, Stein has attempted to pinpoint the variables used by the nervous system to control muscular activity during the performance of sensorimotor tasks. Such tasks may involve a limb that moves, remains stationary, or exerts forces and torques at the limb–environment interface. It is important to recognize, however, that such controlled variables are defined only in the context of the organizational structure(s) comprising the system to be controlled. These organizational structures are defined

functionally at a higher level of description than that of single muscles or joints. Specifically, they are defined at the relatively abstract *task* level and, as mentioned in the section above, span the dynamic system comprised of both organism and environment. In solving the problem posed by a task, the nervous system is the indispensable medium through which the requisite limb organization can emerge. The limbs (or any set of articulators) thus become different types of functionally defined, special-purpose devices for different types of tasks.

Although the foregoing statements may seem trivial at first glance, they reveal a perspective that has decidedly nontrivial implications for how we approach the problem of controlled variables. More specifically, this perspective leads us to place significant constraints on our selection of analytic units of behavior. Stein, for example, limits his analysis to "simple physical variables appropriate to single muscles or groups of muscles acting normally around a joint." Few scientists would disagree that some decomposition of the system is necessary for analytic purposes. However, the unit of analysis should not be casually or arbitrarily chosen, at least if the ultimate goal is to understand control in animals (not simply in a single joint). Our point can be made through an example from physics (cf. Rosen 1978).

It is well known that the three-body problem defies an analytic solution in closed form: whether the earth-sun-moon system is truly stable is an open question. Although it is possible to decompose the system into one body and two body subsystems that are completely tractable analytically, such a strategy does not facilitate obtaining a solution to the three-body problem. The reason is that the physical decomposition itself destroys the original dynamics. In order to solve the three-body problem, a new set of analytic units must be discovered that are defined by new observables such that the partitioning of the system does not annihilate the original dynamics. As Rosen (1978) remarks, this partitioning will seem strange to us because we are used to selecting so-called simple units that correspond to some physical fractionation of the system. The point is that when we reduce or decompose the system the greatest care must be taken in selecting the proper unit of analysis. It is most likely that "simplicity" (a term with an exceedingly slippery definition) will be neither the only nor the chief criterion involved.

Returning to the domain of movement, the identification of appropriate units of analysis has long been a thorny issue, going back at least to Sherrington's reference to the reflex as "a simple, if not a probable fiction" (Sherrington 1906). More recently, Greene (1971), in echoing Nicolai Bernstein, has remarked that much of our confusion in studying problems of coordination has arisen "from our limited ability to recognize the significant informational units of movement." However, there are signs (although they are only considered in passing in the target article) that some consensus may be drawing near. There has been a growing appreciation that individual muscles (or muscle variables) are *not* the proper units of analysis for discussing coordinated movements; rather, such movements are partitioned more naturally into collective functional units defined over groups of muscles and joints, within which component elements vary relatedly and autonomously (e.g., Boylls 1975; Fowler 1977; Kelso, Southard & Goodman 1979; Lestienne 1979; Nashner 1977; Saltzman 1979; Szentagothai & Arbib 1974; Talbott 1979; Turvey 1977). The Soviet school (e.g., Bernstein 1967; Gelfand & Tsetlin 1971; Shik & Orlovskii 1976) refers to such muscle-joint groupings as *linkages* or *synergies*. These terms reflect an appreciation of the fundamental problem of control and coordination, namely that of constraining a complex system with many degrees of freedom to behave in a regular and orderly manner.

Synergies (or coordinative structures; cf. Easton 1972; Kelso, Southard & Goodman 1979; Turvey et al. 1978) are by definition functionally specific units defined over groups of muscles and joints, units which constrain the component elements to act

together in a manner appropriate to the task at hand. Such muscle collectives are thought to share a common efferent and afferent organization and are deployable as relatively autonomous units in sensorimotor tasks (e.g., Boylls, 1975; Gelfand, Gurfinkel, Tsetlin & Shik 1971). Coordinative structures as functional units of control are currently undergoing rigorous analysis in a number of laboratories; they have been identified in various tasks and at different levels of analysis (cf. Kelso 1981; Kelso, Tuller & Harris, in press; Kugler, Kelso & Turvey 1980 for recent examples). Their chief feature rests in a mutable partitioning of component variables into those which preserve the structural ("topological") organization of movement (e.g., the relative timing and relative force properties of muscular events) and those which are capable of effecting scalar transformations on these qualitative structures. A theoretical rationale for coordinative structures has been offered (cf. Kugler et al. 1980; 1982; Kelso 1981), focusing on those properties which distinguish movement patterns that exhibit structural stability from those which do not.

There are indications in the target article that Stein prefers to sidestep the issue of functionally specific units of movement as not germane to his interests, and as one that pertains only to "multijoint movements" or the "large behavioral literature on complex patterned movement." However, he does not hesitate to negate arguments for length and stiffness control on the basis of "complex patterned movements" like speech or piano playing in the case of length, and walking in the case of stiffness. We welcome the functional argument in each case, although we note that for Stein it involves jumping rather precariously between muscle-joint levels (e.g., stiffness and length) and task levels of analysis (such as skiing and needle threading). Though aware of the problem, Stein seems to apply a single muscle-joint unit of analysis generally to all types of complex multijoint tasks. Such an approach is at the same time too powerful and too arbitrary. It is too powerful because it allows descriptions of movement control that fail to distinguish between those acts which do occur and those acts which are physically possible but never occur. It is too arbitrary because single-joint actions will rarely relate unequivocally to particular task functions. In short, when we deal with coordinated activity we are dealing with task-specific functional units whose degrees of freedom are constrained according to task demands, or more generally, according to the mutual relationship between organism and environment.

Contrasting views on the origins of order. Whenever we observe a regular and orderly phenomenon, it is always a temptation to assign responsibility to some device that is antecedent to, and causally responsible for, the said phenomenon. The device has available to it "representations" that have characteristics very much like the phenomenon we are trying to understand. As philosophers have often told us, "representations" require users with goals and interests (much like the animal itself), and so, when we assume their presence, we take out a loan on intelligence that must ultimately be paid back (cf. Dennett 1978; Searle 1980). We can bury our heads in the sand on this issue or we can approach the problem in a different way — one that asks not how control can be explained according to some a priori prescription for the system (such as the central representations and the cybernetic, negative-feedback paradigms favored by Stein), but rather how control arises as an a posteriori consequence of the system's dynamic organization.

For example, imagine adopting the former, *prescriptive* strategy to a coherent biological phenomenon such as the schooling of fish. What we observe are individual fish behaving collectively in a highly coordinated manner. The "system" in this case has many degrees of freedom and exhibits an organized, seemingly holistic structure. Adopting a prescriptive strategy, we might search the system for a "reference value" or a "central representation" that regulates the individual fish or the collective of fish, but it would make little sense to do so. These would

be *special mechanisms* introduced by the unknowing observer to account for a poorly understood phenomenon. In fact, the highly coherent behavior of fish schooling can be accounted for with a fairly small set of key variables, such as "density" defined through the metric of fish length. When the average distance between nearest neighbors is less than one fish length (note that the metric is "intrinsic" and system-scaled; cf. Warren & Shaw 1981), spacing between fish is schooled, not random (cf. Okubo 1980 for an in-depth analysis).

Although the details of collective fish behavior may seem far removed from the issues raised by Stein, there is, we think, an important message for the neuroscientist or psychologist. It is that an understanding of a complex, organizational phenomenon such as fish schooling rests with articulating the necessary and sufficient conditions for that organization to occur. More generally, this approach entails a strategy that rejects the introduction of special mechanisms – as sources of explanation – before dynamics have been fully explored. Put another way, what can we, as students of movement, explain "for free" before we burden the nervous system with the onus of control?

In this regard, it is puzzling to us that Stein chooses to ignore a model whose dynamics obviate (or at least significantly reduce) the requirement for ongoing, computational control. If recent work is a guide, much may be gained through the identification of functional units of movement with nonlinear mass-spring systems. Although the model has received an uneven interpretation, its import for us is that it allows one to see the *qualitative* similarities between certain aspects of movement control (such as the ability to reach the same desired spatial location with different trajectories and from variable initial conditions) and the behavior of a mass-spring system. Following our arguments expressed above, the beauty of the mass-spring model lies not in the *literal* parallel between a single muscle and a spring, but in the recognition that particular behaviors share – to a first approximation – the same abstract *functional* organization as a mass-spring system.

The intuition that a muscle-joint system is dynamically similar to a mass-spring system with controllable equilibrium length is due to Feldman (cf. Feldman 1966, p. 771) and has undergone appropriate extension by a number of authors (e.g., Bizzi, Polit & Morasso 1976; Polit & Bizzi 1978; Kelso 1977; Kelso & Holt 1980; Schmidt & McGown 1980). The basic idea is that a given joint angle may be specified according to a set of muscle equilibrium lengths. Once these are specified, the joint will achieve and maintain a desired final angle at which the torques generated by the muscles sum to zero. Such a system exhibits the property of equifinality in that desired positions may be reached from various initial angles, and in spite of unforeseen perturbations encountered during the motion trajectory (see Kelso, Holt, Kugler & Turvey 1980 for review; but also Saltzman 1979 for some cautionary notes). Feldman (1966; 1980) has further noted that stiffness at a joint may be specified in terms of agonist and antagonist equilibrium lengths even if the stiffness of these muscles is not itself controllable. In the Feldman model, joint stiffness covaries with the degree of agonist-antagonist co-contraction.

Two points for Stein emerge from this discussion. One concerns a sin of omission in that he includes the spring property of stiffness as a possible control variable but neglects the related variable of equilibrium length. The other, perhaps more important issue warrants a little further development because of its theoretical consequences. It is that if one likens (to a first approximation) a constrained collective of muscles to a mass-spring system the need to introduce externally imposed measurement, comparison, and control operations is reduced. Though we could *describe* a dynamic system like a mass-spring in terms of externally imposed reference levels and though we could put it into canonical, mathematical feedback form, little would be gained by doing so (cf. Yates, in press). A muscle collective qua spring system is intrinsically self-equilibrating:

conserved values such as the equilibrium point emerge from the system's parameterization. More emphatically, in mass-spring systems (as in schools of fish and functional groupings of muscles?) there is no need to introduce a "representation" anywhere.

Toward an alternative control scheme. In our final comments we take up – in rather condensed fashion because of space limitations – Stein's invitation to his critics to offer an alternative to the scheme he has put forward so authoritatively. We refer to an emerging theoretical view of movement control and coordination that has been expressed in two recent papers (Kugler, Kelso & Turvey 1980; 1982) and that has also undergone some as yet limited empirical scrutiny (Kelso, Holt, Kugler & Turvey 1980; Kelso, Holt, Rubin & Kugler, in press). Its origins (and to a large extent its appeal) lie in a unified treatment of cooperative phenomena at all scales of magnitude (cf. Haken 1977). Hence it speaks to the important issue raised by Stein at the beginning of his article, namely that of relating levels of analysis. Moreover, the perspective is consonant with some of the themes introduced above and may also interface with evolving oscillator theoretic views of neural control not considered by Stein in the target article (e.g., Delcomyn 1980).

A chief distinguishing feature of the view expressed here lies in the recognition that, first and foremost, living systems belong to a class of physical systems that are open to fluxes of energy and matter (in contrast, cybernetic systems are closed to energy-and-matter exchange with their surroundings). The principal theories addressing such systems are Iberall's homeokinetic theory (e.g., Iberall 1977; 1978; Soodak & Iberall 1978; Yates & Iberall 1973) and Prigogine's dissipative structure theory (e.g., Nicolis & Prigogine 1977; Prigogine 1980). The former, in particular, addresses systemic phenomena in biology and elaborates, among other things, the conditions for persistence of function, autonomy, and self-organization. It represents a concerted effort to apply irreversible thermodynamics to living systems. A fundamental tenet is that in steady-state systems the flow of energy through the system plays an organizing role and that, following Morowitz's theorem, energy flow from a potential source to a lower-order sink will lead to at least one cycle in the system (Morowitz 1968). Homeokinetic theory builds on the Bernard-Cannon principle of homeostasis (which contained no mechanism for preservation of conserved states); in the homeokinetic view, control is dynamically effected by means of coupled ensembles of limit-cycle oscillatory processes. Limit cycles represent the only temporal stability for nonconservative, nonlinear systems; they resemble "squirr" systems that by virtue of their design are capable of making up for dissipative losses that occur in the drift toward equilibrium (Yates & Iberall 1973). The system's conserved values or equilibrium operating points are thought to be specified in the loose coupling of limit-cycle processes. Limit cycles are manifestations of thermodynamic engines and quantize *action* (formally, the product of energy and time; Iberall 1978) at every level in the system.

As functional units of movement, ensembles of nonlinear limit-cycle oscillators offer a number of attractive features for a principled account of coordination and control. Among these are their self-sustaining properties, their ability to operate independently of initial conditions, their stability in the face of moderate perturbations, and, perhaps most important for the theorist of movement, the properties of mutual entrainment and synchronization (Minorsky 1962; Winfree 1980).

With respect to the issues raised by Stein, it is worth emphasizing that limit cycles are not special mechanisms per se. For spectrally distributed limit-cycle regimes to be observed and for new spatiotemporal organizations to emerge, certain necessary conditions must exist. Among these are the presence of many interacting degrees of freedom, nonlinearities, a relatively constant source of potential energy, and the requirement that energy be dissipated. Given such conditions, and subject to critical scaling influences, constraints emerge that are capable of

marshalling the free variables into coherent functions. Quadruped gait may be an example: when one stable movement pattern is driven beyond a critical value on a system-sensitive parameter, a bifurcation occurs and a new spatiotemporal pattern – a new stability – arises. In such a view, no explicit “gait selection” process is required (e.g., Gallistel 1980).

To reiterate our main point, however, in the perspective offered here, order (control and coordination) is functionally specified in the system’s dynamics. The radical claim, as Gibson (1979) once remarked, is that behavior is regular but there are no regulators. A less radical statement would be an affirmative answer to Yates’s (1980) question to the readers of the *American Journal of Physiology*: Do [you] know of a serious effort to discharge the homunculus?

The spirit of the foregoing discussion leads us to raise one final issue. It is the growing intuition – stemming from theoretical considerations raised here and elsewhere (cf. Anderson 1972) – that the problem of order in natural systems might be attacked more effectively by seeking out a single set of physical principles that can apply at all levels, rather than by positing different units of analysis at each level. One assumes that nature operates with ancient themes. In this commentary we have tried to provide the flavor of the ones that neuroscience in general, and the field of motor control in particular, might consider worth orchestrating.

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The motor system controls what it senses

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Is Stein’s last paragraph (a) common sense, (b) a pleasantly veiled threat, (c) the capitulation of a frustrated reductionist, (d) divine wisdom revealed to the persevering, or (e) all of the above? The typical student would complain that such a question was ambiguous. Any answer could be correct, depending on the mood and past history of the author. This appears to be Stein’s answer to his title: any parameter may be controlled given the goal of the motor system at the time. I enthusiastically agree with this conclusion, but because it was arrived at rather abruptly by a process of elimination, I will attempt to outline how it may be developed in a different manner.

In any control system, what is ultimately regulated is that which is sensed. This is implicit throughout Stein’s article. In technological situations single variables are generally transduced, often with their time derivative, so that it is obvious what parameter is being controlled. The moving limbs of vertebrates differ on two counts. First, they incorporate a wide variety of sensory receptors, and second, none of the receptors reliably transduces a single variable such as joint angle or torque. Measures of limb position, for example, are made at a high level in the CNS, possibly not below the perceptual sphere, on the basis of analysis across a population of sensory influx (Goodwin 1977).

Although the perceptual signal at any one time may be predominantly one of limb position or tension, etc., it is more generally a mixture of fundamental parameters, and at the neuronal level it invariably comprises many information channels. Anyone who has ever tried teaching someone else a motor skill is aware of the complexity of the perceptual signal. The learner must acquire the “feel” of the correct performance through practice; it is impossible to give an adequate verbal description.

The importance of the perceptual signal or sensory profile is paramount. For control to be exercised, the sensory profile must be kept matching a reference signal (D. M. MacKay 1964; Powers 1979). The reference signal is a template of the sensory profile expected when the movement proceeds as intended or programmed. The reference template, therefore, is as complex as the sensory profile itself, with a specification for every sensory channel involved.

The motor-output signals are not precisely computed vectors of the requisite force or muscle length, for instance, but heuristically shaped assemblies of unit activity that result in a satisfactory match of the sensory profile of the movement to the desired template. Muscle control is largely a feedforward mechanism (D. M. MacKay 1964) whereby muscle variables are manipulated in order to produce a specific sensory-input profile. The output repertoire of the motor system may be conceived as sets of muscle patterns known by experience effectively to eliminate specific mismatches between sensory profiles and templates.

On the basis of this approach, which is consistent, I believe, with Stein’s conclusion, one can lodge two complaints against the target article. First, if the total perceptual signal is of primary importance in motor control, many arguments in the paper fall by the wayside. We can control virtually any parameter that we perceive, regardless of whether the stretch reflex or a certain Betz cell is responsible. It is probably not permissible to extrapolate to the entire motor-system control properties of a single reflex or of a set of neurons (even if we did know them). They give too fragmentary a picture. Second, the question in Stein’s title is indeed poorly posed, as Stein indicates that it may be.

Perception, specifically of the body in relation to the environment, extends far beyond the limits of muscle. Cutaneous and joint sensation, plus visual features of the limb nearing targets, all contribute as well. The nervous system controls muscles in relation to all of these inputs, which in effect means that it adjusts the state of muscle contractility until the sensory profile achieves the desired configuration. The implication is that the nervous system is not directly concerned with controlling any “muscle variable” per se, but with matching inputs to a reference. This is basically the strategy of Robinson’s (1975) “bang-bang” controller of eye saccades: the eye is maximally driven as long as there is a mismatch between where the eye is and where it is supposed to be.

Ironically, as soon as muscles are viewed as a means to the end and not the end in themselves, it is possible to formulate a “single underlying variable” that is controlled by the motor system: the perception of body movement. This may appear as a sneaky way out, because the perceptual signal is determined by muscle activity. But as far as the CNS is concerned, it is the perceptual signal that it is controlling; this is all of which it is aware.

How modest is the gain of the stretch reflex?

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In the literature there has been a wide range of estimates of the degree of load compensation provided by stretch reflexes, from claims of little compensation to claims that stretch reflexes provide strong and effective compensatory forces. Stein implies that stretch-reflex gains are modest and might be used to minimally assist movements or to help prevent instabilities from developing. In this commentary, we discuss some reasons for our belief that the gain of stretch reflexes may be reasonably large, and we consider possible reasons why some investigators