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EVIDENCE FOR A MASS-SPRING MODEL OF HUMAN NEUROMUSCULAR CONTROL

J.A. Scott Kelso and Kenneth G. Holt
Haskins Laboratories, New Haven, Connecticut
and

Departments of Biobehavioral Sciences and Psychology
The University of Connecticut, Storrs, Connecticut

Recent work is summarized on the production of finger movements in normal and functionally deafferented subjects as well as patients without joint receptors under various conditions of torque loading (perturbation). The results from those experiments reveal that achievement of final position of the finger is attained regardless of changes in initial conditions and the imposition of brief load perturbations designed to disrupt the movement trajectory. A dynamic rather than representational account of the findings is tentatively proposed, emphasizing the equifinality characteristic of neuromuscular systems. In addition, the functional role of kinesthetic receptors is re-evaluated. Mechanoreceptors may play a tuning or modulatory function on the interneuronal pool in the spinal cord, rather than providing dimension-specific information to the central nervous system.

Les auteurs résument leurs récents travaux sur la production du mouvement des doigts chez des sujets normaux aussi bien que chez des patients ne possédant pas de récepteurs articulaires (déafférence fonctionnelle) sous des conditions variées de surcharge (perturbation). Les résultats de ces expériences révèlent qu'un sujet peut produire une position finale sans subir l'effet des changements de positions initiales du mouvement et de la présence brève d'une surcharge modifiant la trajectoire du mouvement. Une interprétation dynamique plutôt que cognitive est proposée, mettant l'emphasis sur le principe de l'équifinalité du contrôle neuromusculaire. De plus, le rôle fonctionnel des récepteurs kinesthésiques a été ré-évalué. Les mécano-récepteurs auraient ainsi une fonction modulatrice (pré-adaptation) des ensembles d'interneurones médullaires plutôt que de fournir au système nerveux central une information spécifique.

That nature might take advantage of the viscous and elastic properties of muscle-joint systems in the control and coordination of movement is a view that has just recently gained recognition in this country (e.g. Polit & Bizzi, 1978). However, the notion had its birth as long ago as 1947 in Bernstein's proposal (reported in Bernstein, 1967) that when muscles acting at a joint are constrained to act as a unit, the linkage is describable as a class of vibra-

tory system whose physical and behavioral characteristics are qualitatively similar to a mass-spring (see also Turvey, 1977). The research of Fel'dman and his colleagues (Asatryan & Fel'dman, 1965; Fel'dman, 1966) extended Bernstein's intuitions by demonstrating that when subjects were required to hold a steady angle at the elbow joint against a resistance, a change in the load resulted in changes in joint angle that were predictable as the behavior of a non-linear spring. In this paper we briefly review evidence from our laboratory that is consonant with—and an elaboration of—the mass-spring perspective.¹

It proves to be the case that a mass-spring account of limb localization reduces many of the problems that have confronted theorists in movement control. Perhaps its major characteristic for our purposes is that it is intrinsically self-equilibrating; once set in motion the spring will always come to the same resting length for any particular load value. Neither an increase in the initial deflection of the spring from its resting length nor temporary perturbations will prevent the achievement of the equilibrium point, a property known as equifinality (von Bertalanffy, 1973).

One of the major concerns for many theorists has been the role of feedback for the ongoing control and termination of movements. We would argue from the present perspective that to reach a particular end point it is necessary only to adjust certain parameters—to "tune" the spring—prior to movement. To achieve this, according to Fel'dman (1966; see also Houk, 1978), the nervous system sets the values of resting length, λ , by adjusting the length-tension relationships of the muscles involved. Consider for simplicity's sake a single agonist-antagonist pair represented by parallel length-tension curves whose slopes correspond to muscle stiffness. A change in innervation rate to one muscle of the pair will shift the equilibrium point of the system (i.e. the point at which the length-tension curves intersect). Thus the only parameters to be set for voluntary movement in Fel'dman's model are stiffness and resting length; once these are specified there is no necessity for feedback control of the ongoing movement for its termination.

A second concern for theorists has been how the brain is able to accommodate variability in the context within which movements occur: the problem of functional non-univocality (Bernstein, 1967) or *context-conditioned variability* (Turvey, Shaw, & Mace, 1978). Simply stated this refers to the lack of an invariant relationship between centrally generated signals and movement outcomes. It is clear that a mass-spring account, with its disregard for

¹The research referred to here, along with extended discussions of the data (Kelso & Holt, in press; Kelso, Holt & Flatt, Note 1; Kelso, Holt, Kugler & Turvey, in press; Kugler, Kelso & Turvey, in press), appears in a number of diverse places. We have summarized it here at the Editors' request.

initial conditions and imperviousness to perturbations of the movement trajectory, alleviates this problem considerably.

A final concern to which a mass-spring account speaks is that of how end-points might be achieved through a variety of movement trajectories and diverse kinematic details (such as velocity, amplitude, etc.). It seems clear when one considers the visco-elastic properties of muscles and joints that it is not kinematic features, but the underlying dynamic parameters of mass, stiffness, and viscosity that are important for the regulation of movement. It is the specification of dynamic parameters that determines kinematic details. Variability in these parameters will affect the equilibration process only in terms of the observed kinematics but not in terms of achievement of equilibrium position.

In the present experiments we sought to determine on an a priori basis whether any of the observed kinematic characteristics that arise in localization violate the mass-spring model. One clear-cut prediction from the mass-spring model is that terminal location will be superior to amplitude production. Terminal location may be viewed as an equilibrium point specified by the tuned parameters of the spring; it is thus impervious to unforeseen changes in initial starting position. Amplitude production, on the other hand, involves a change in the equilibrium point as a function of variable initial conditions, hence reparameterization of the spring parameters. Evidence presented previously in humans (Kelso, 1977) and animals (e.g. Bizzi, Polit, & Morasso, 1976; Polit & Bizzi, 1978) supports this prediction. If, indeed, it is the case that ongoing feedback control is unnecessary, the same predictions should hold for patients whose positional detectors in the joint capsule have been surgically removed. To test this hypothesis we examined the accuracy of movement reproduction of the index finger following complete surgical removal of the metacarpophalangeal joint in the hands of patients suffering from rheumatoid arthritis (Kelso, Holt, & Flatt, Note 1).

The subjects were 13 patients who were examined and tested during a period from two days to four weeks following total joint arthroplasty of the index finger of either hand. The apparatus (which was the same for all the experiments summarized here) consisted of a finger positioning device that allowed flexion and extension of the index finger about the metacarpophalangeal joint. The distal end of the moving finger was fitted with a plastic collar which slipped into an open-ended cylindrical support. The support revolved about the metacarpophalangeal joint and prevented movement of the distal joints of the finger. Attached to the end of the support was a pointer that moved over a protractor graduated in degrees. The device was also equipped with padded adjustable clamps with which to secure the subject's wrist, hand, and remaining fingers and thumb during the movements. Only

the preferred hand was placed in the device while the other rested in the patient's lap. Vision of the hand was obscured by an aluminum screen.

We examined performance under conditions where the starting position changed for the reproduction movement, thereby disrupting either the amplitude moved or the final end position reached. Under one condition the patient was asked to produce the final position while another condition required the patient to reproduce the same amplitude or distance. Examination of errors revealed a significant interaction between movement conditions and starting position ($p < .01$). It is clear from Table 1(a) that location is superior overall to amplitude and that the effect is magnified at the extreme starting position. Interestingly, amplitude performance is biased in the direction of the final position presented. Thus, while location performance is hardly affected by changes in starting position, amplitude performance appears to reflect a bias to reproduce *location*. These findings are not particularly compatible with a closed-loop view of localization in which an internal referent mechanism (itself a stored record of receptor firing functions) is compared in an ongoing manner to feedback from angular-specific joint receptors (cf. Adams, 1977). But the data are consonant with the equifinality characteristic of a mass-spring system. That is, despite changes in initial conditions (displacement of a limb to a new starting position) a mass-spring system will always reach an invariant final position or equilibrium point as determined by its parameters.

Another prediction from a mass-spring account is that the introduction of unexpected torque loads, which act to slow the limb down or drive it in the opposite direction from which it is moving, should not cause a decrement in the accuracy with which a target location is achieved. We examined this prediction in two experiments. In one experiment (see Kelso, Holt, Kugler, & Turvey, in press) we applied a constant torque load (via a D.C. torque motor situated above the MP joint of the index finger) at the beginning of the movement and released the load at unpredictable points during the movement trajectory. Thus subjects ($N=10$) initially learned the target movement (50° finger extension) with knowledge of results available and then performed a set of nine test trials (six of which were perturbed by sudden load releases). According to the mass-spring model, an unexpected addition of an external load should cause an initial undershooting of the target. Once the external force is removed, however, and given that the parameters of the system have not changed, the limb will equilibrate at the desired position. The movement trajectories bore this analysis out completely; neither were any accuracy differences observed between perturbed and non-perturbed trials ($p > .10$).

In a similar type of experiment (Kelso & Holt, in press) we perturbed subjects ($N=12$) during the movement trajectory to a learned target by injecting

Table 1

(a) Reproduction errors for joint replacement patients for distance and location conditions as a function of starting position^a (from Kelso, Holt, & Flatt, 1979.).

		Distance		Location	
		AE	CE	AE	CE
SP ₁ (-5 deg)	<i>M</i>	5.72	3.67	3.67	1.37
	<i>SD</i>	3.17	5.23	2.05	3.66
SP ₂ (-15 deg)	<i>M</i>	9.19	8.35	4.29	-0.19
	<i>SD</i>	5.47	6.26	2.54	4.41

(b) Reproduction errors as a function of acquisition, perturbed, and nonperturbed trials (from Kelso & Holt, in press).

Acquisition ^b			Non-perturbed			Perturbed		Total
AE	CE	VE	AE	CE	VE	AE	CE	VE
<i>M</i> 2.81	-0.15	3.14	4.12	-0.18	4.11	5.61	1.37	4.54
<i>SD</i> 1.21	1.88	1.30	2.44	3.95	2.08	2.27	5.33	1.50

(c) Reproduction errors as a function of acquisition, perturbed, and non-perturbed trials, under normal and wrist cuff conditions (from Kelso & Holt, in press).

Acquisition ^b			Non-perturbed			Perturbed		Total
AE	CE	VE	AE	CE	VE	AE	CE	VE
Pre-cuff								
<i>M</i> 2.33	0.33	2.52	5.61	-4.50	3.35	5.21	-3.72	4.36
<i>SD</i> 0.80	1.89	0.55	3.42	4.19	1.06	2.48	3.80	0.83
Cuff								
<i>M</i>			13.52	4.89	6.25	11.66	0.00	8.36
<i>SD</i>			7.78	15.74	2.28	5.88	12.78	2.57

^aSince there were only 2 trials per combination, no estimate of variable error was computed.

^bMeans of the last nine acquisition trials.

a brief (100 msec) torque load at unpredictable points. This procedure served to drive the limb in the opposite direction from which it was moving.

The first part of the experiment, acquisition trials, consisted of 30 extension movements to a to-be-learned target position (50° movement from the starting position which remained constant at 20° flexion). Quantitative knowledge of results (KR) was provided throughout the acquisition phase. Following the acquisition trials there were 18 test trials (without KR) of which half were perturbed by the programmable torque motor. The locations of the perturbation were designed as short (applied after 10° of movement from the starting position), medium (after 25° of movement), or long (after 40° of movement). There were three trials at each of the three perturbation locations, and these were randomly ordered amongst the 18 test trials.

To test for the equifinality principle, the nine non-perturbed trials were compared to the nine perturbed trials by paired t-tests as shown in Table 1(b). The contrast failed significance for absolute, constant, and variable error ($ps > .05$). Perturbed trials were further subdivided according to the locus of perturbation (short, medium, or long) and analyzed in a one-way analysis of variance. No main effects were found for locus of perturbation ($ps > .05$).

Again, these findings—equally accurate performance obtained in both perturbed and non-perturbed trials—strongly support the equifinality property characteristic of vibratory systems.

The results of the foregoing studies do not, of course, rule out the possibility of fast-acting feedback loops acting in a closed-loop manner (e.g. Cooke & Eastman, 1977; Evarts & Granit, 1976; Houk, 1978). A final experiment in this series was designed to undermine this possibility by injecting load perturbations during the localization movements of subjects who had joint and cutaneous information removed using the wrist-cuff technique (for details see Merton, 1964; Kelso, 1977). The advantage of this procedure is that muscle function is preserved in the long finger flexors and extensors while sensory inputs to the hand itself are effectively removed. Moreover, the cuff technique has been shown to drastically reduce stretch reflex function (cf. Marsden, Merton, & Morton, 1972).

The first part of this study followed the foregoing procedure exactly. After the 30 acquisition trials with knowledge of results available, nine perturbed and nine non-perturbed trials (together designated pre-cuff trials) were given in randomized order with error information withdrawn. On completion of this aspect of the study, subjects ($N=6$) were removed from the apparatus and the wrist cuff applied and inflated as discussed in detail elsewhere (Kelso, 1977). The subject's arm and hand were then replaced in the apparatus in the same posture as before. Following the establishment of sensory cut-off using the same criteria as our earlier work (Kelso, 1977), a further 18 trials were given to subjects, half of which were perturbed at three different loci. These trials

(designated cuff trials) were yoked to the pre-cuff trials so that the subject performed them in the same randomized order. Again, these were performed in the absence of knowledge of results.

For normal (pre-cuff) trials we found no significant differences between perturbed and non-perturbed movements for absolute and constant error ($p > .05$). Significantly larger variable error was found in the perturbed trials but the difference was small, in the order of 1° .

A comparison of non-perturbed and perturbed cuff trials revealed no significant differences for absolute error ($p > .05$). The mean constant error for non-perturbed trials was larger and more positive than that for perturbed trials, while the variability in the perturbed trials was greater than in non-perturbed trials as shown in Table 1(c). It may be noted, however, that the differences are very modest indeed compared to the boundary conditions set by Polit and Bizzi (1978) for accurate arm movements in monkeys (in the order of 12° to 15°). Note also in Table 1(c) that it is not legitimate to compare accuracy scores from pre-cuff to cuff trials due to the substantial time lapse that was necessary for the wrist cuff to have its effect (between 1 and 1.5 hr.). This, combined with the absence of knowledge of results, is likely responsible for the increase in error, although it is impossible to completely discount some effects of proprioceptive withdrawal.

In summary, the data from this series of experiments strongly support a mode of control that is qualitatively similar to a mass-spring system. A most important characteristic of such a system is its stability in the face of perturbations, which is the predominant feature of these studies. Thus the limb terminates at its steady, equilibrium state despite changes in initial conditions, unexpected and abrupt load disturbances, and all of these combined with functional deafferentation. These results are continuous with earlier work (Kelso, 1977), and, corroborated by recent neurophysiological data (Bizzi, et al., 1976; Polit & Bizzi, 1978), provide a broad basis of empirical support for the non-linear mass spring model.

One important implication of the mass-spring account of localization is that it demands a reconceptualization of the vocabulary of control (see Kelso & Holt, in press, for discussion of further advantages). We have talked in the past of control in terms of kinematics—distance, velocity, or spatial coordinates (e.g., Brooks, 1974; Russell, 1976; Taub, Goldberg, & Taub, 1975). In contrast, the behavior of a mass-spring system (and, we would argue, the muscle-joint system) is controlled by more fundamental dynamic parameters: mass, stiffness, and viscosity. One task facing the researcher, we would argue, is to elucidate the means by which these parameters are tuned by higher control centers and by environmental inputs (e.g., in the reflexes). It is on this latter point that the function of joint and cutaneous inputs may be clarified. Such

receptors have typically been regarded as contributing—or not contributing—specific types of kinematic information (e.g., position, rate, acceleration) to higher brain centers for use in control and termination of movements. Suppose, however, that peripheral receptor information is not dimension-specific; rather it merely serves to bias certain “nodal” points (Evarts, Bizzi, Burke, DeLong, & Thach, 1971)—interneuronal pools in the spinal cord—so as to lower the threshold at which signals may be generated to the musculature. Thus the function of mechanoreceptors is simply to ‘tune’ the interneuronal pool so that central signals may have an optimal facilitatory effect on the muscles served by that pool. Aizerman and his colleagues (Aizerman & Andreeva, 1968; Chernov, 1968; Litvintsev, 1972) have provided evidence to this effect for muscle spindle function in maintenance of upright posture, pain avoidance, and precision aiming. There is also evidence that visual (Thoden, Dichgans & Savidis, 1977) and auditory (Rossignol & Melvill-Jones, 1976) inputs may also facilitate voluntary and involuntary movements without central mediation. Thus, inputs from many sources may serve to facilitate or inhibit a particular pool and thus change the threshold at which activation of motoneurons occurs. The beauty of such a system is that it obviates the need to select particular muscles; rather, selective contraction occurs by virtue of the state of the interneuronal pools. In summary, the combined notions that we have introduced here, namely (a) that a collective of muscles behaves qualitatively like a (non-linear) mass-spring system, and (b) information as playing a tuning role, are rather different in their origins from current theories of motor behavior. They represent our initial attempts at providing a principled (dynamical) basis for the coordination and control of movement (see also Kugler, Kelso, & Turvey, in press). Much remains to be done.

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