

Exploring a Vibratory Systems Analysis of Human Movement Production

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SUMMARY AND CONCLUSIONS

1. Two experiments were conducted to determine the efficacy of a vibratory systems analysis of finger localization on humans. In both experiments the subject's task was to move the finger rapidly to a previously learned target location. The second experiment also included a condition in which subjects were functionally deafferented by means of a child's sphygmomanometer cuff inflated around the wrist. In both experiments the finger was displaced on 50% of the test trials by brief torque loads (perturbations) injected at unpredictable points during the movement.

2. It was found that in both the normal and functionally deafferented subjects, perturbations did not affect accuracy in achieving final position, a finding that supports the equifinality characteristic of a mass-spring. That is, a mass spring will always reach an invariant final position or equilibrium point no matter how perturbed. In addition, it was found that none of the kinematic analyses computed (velocity, movement time, oscillation) violated the dynamic behavior of the mass-spring model.

3. A control system that takes advantage of the viscoelastic properties of the muscles and joints reduces the control problem for the brain in that once underway, movement to end points need no moment-to-moment intervention by central mechanisms. Furthermore initial conditions, such as starting position, are of little concern in this mode of control; that is, as long as an end point is specified, initial starting position and brief perturbations have no consequence on the end point reached.

4. Theoretically this finding is of some

significance since it reduces two problems for control of movement by the brain: degrees of freedom and context-conditioned variability.

INTRODUCTION

Perhaps the most desirable attributes of the human motor system are that it be capable of locating the limbs accurately in space using a variety of movement trajectories and that localization be accomplished relatively independent of changes in the initial conditions of the limbs. Although it is well documented that these features are characteristic of the behavioral repertoire of both animals and humans, less clear is the nature of the underlying control mechanism(s). Neither of the currently popular closed-loop, feedback (2), or open-loop programming accounts (37) seem completely adequate. For example, although a closed-loop model could accommodate the fact that achievement of final position is possible in spite of a) changes in limb position prior to movement (39) or b) the introduction of abrupt changes in load during movement execution (25, 35), it is at a loss when the same findings can be demonstrated under deafferentation conditions (8, 26, 35, 40). Similarly, central motor programs that do not require ongoing feedback monitoring may handle deafferentation findings, but go awry when confronted with unforeseen changes in the movement context. Indeed, even a hybrid model that incorporates internal, central feedback loops (14, 28) has great difficulty with the finding that normal accuracy may result when monkeys are deafferented and, consequently, subjected to unpredictable movement perturbations (35).

An alternative approach to problems of localization—stemming from Bernstein's (5) original work,¹ proposes that where muscles at a joint are constrained to act as a unit, the linkage is describable as a class of vibratory system with the physical and behavioral characteristics of a mass spring (4, 18, 35). There are several properties of a mass spring that are advantageous in explaining the style of control observed in localization experiments. Perhaps its major characteristic for our purposes is that it is intrinsically self-equilibrating; once set in motion the spring will always come to rest at the same resting length (equilibrium point). Neither an increase in 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 (45). Support for this account comes from experiments in which subjects were required to hold a steady angle at the elbow joint against a resistance and not to make adjustments when loads were added or removed. A change in load resulted in a change in joint angle (equilibrium point), which was predictable as the behavior of a nonlinear spring (4).

The question arises as to how such a spring might be controlled in order to produce different steady-state positions. According to Fel'dman (18) (see also Houk, Ref. 25), this can be accomplished by adjusting certain parameters—tuning the spring—prior to movement. In this account, the nervous system sets the values of resting length, λ , by adjusting the length-tension relationships of the muscles involved. If the length of the muscle, χ , varies from the resting length, "voluntary" movement takes place. If $\chi > \lambda$, an active tension develops in the muscle and if $\chi < \lambda$, the muscle is relaxed. The invariant character of the muscle is, therefore, the dependence of tension on length for any fixed value of λ . Thus, the only static parameter that need be set for voluntary movement in Fel'dman's model is resting length; namely, the length of the muscles for which differences in

tension sum to zero. On the other hand, kinematic changes in rate, acceleration, and periodicity in the joint-muscle collective are brought about by altering the dynamic parameters of stiffness and damping.

Recent data fit this perspective rather well, at least on a posteriori grounds. For example, Bizzi and his colleagues (7, 35) have shown for both head and arm movements that normal and rhizotomized monkeys can accurately achieve learned target positions even when constant and brief load perturbations were applied during the movement trajectory. They argue that the controlled variable must be an equilibrium point specified by the motor program in terms of the length-tension relationships in agonist and antagonist muscles. Similarly, a consistent outcome in human experiments has been the superior accuracy of attaining final position over amplitude from variable starting positions; a finding that extends to functionally deafferented subjects (26) as well as patients in whom positional detectors in the joint capsule have been surgically removed.² 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 and, hence, a reparameterization of spring parameters.

In the present experiments, we set out to determine—on an a priori basis—whether any of the observed kinematic characteristics that arise in localization, violate the mass-spring model. Specifically, our tack was to introduce sudden and unexpected torque loads—which acted to drive the limb (in this case the index finger) in the opposite direction—and observe consequent effects on localization. Unlike numerous other studies (see Ref. 12 for a review), we were not particularly concerned in evaluating the various reflex responses to changed loading

¹ Peter Greene (personal communication) alerted us to this fact for which we are grateful. The translated version of Bernstein's (5) work does not include a discussion of the mass-spring model.

² Data collected on patients with metacarpophalangeal joints removed and replaced with Silastic inserts (J. A. S. Kelso, K. G. Holt, and A. E. Flatt. Towards a theoretical reassessment of the role of proprioception in the perception and control of human movement. *Haskins Laboratories Status Report on Speech Research*, SR-59, 1979, p. 1-12. No deficits in finger-positioning capabilities were found.

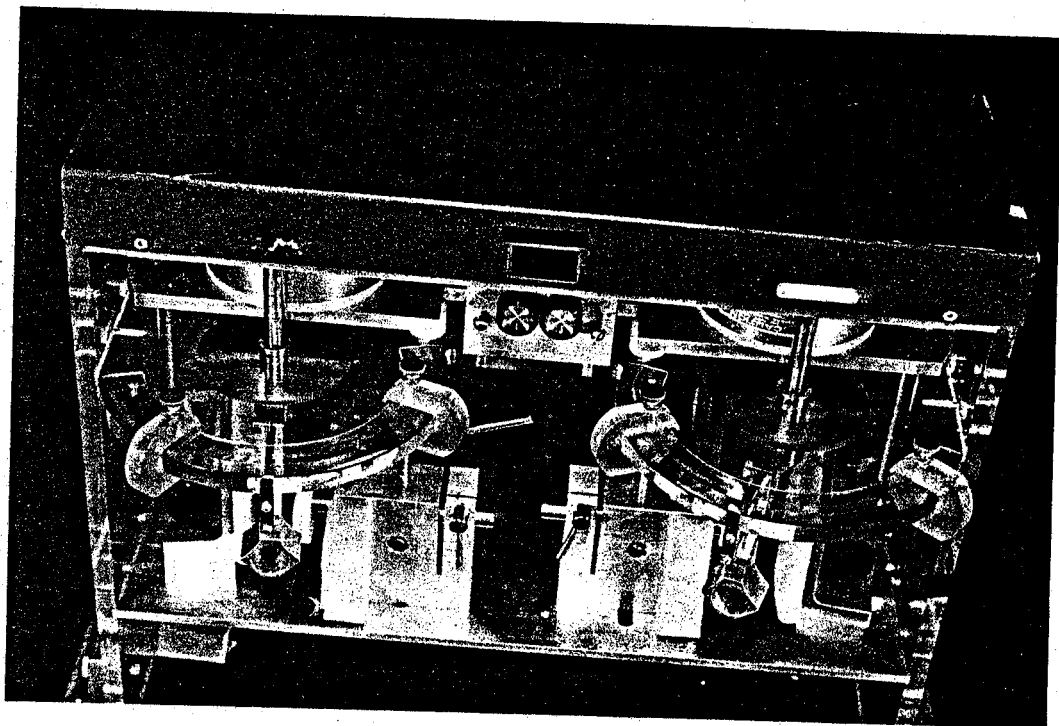


FIG. 1. Finger-positioning device showing programmable torque motors capable of producing a maximum torque of 81.6 ounce-inch about the metacarpophalangeal joint. Positioning errors were read directly from the pointer as it moved over the protractor, graduated in degrees. Amount of torque to produce a perturbation could be varied as a percentage of maximum, and the trigger point for the onset of perturbation was also controllable.

conditions. Rather, we wished to elucidate the effects of changing dynamic parameters and consequent kinematic variation on the attainment of a specified equilibrium position. In experiment 1 we show that the equilibrium position is accurately attained despite on-line perturbations. In experiment 2 we rule out possible alternative accounts by replicating this result in functionally deaf-ferented individuals.

Experiment 1

METHODS

The subjects were 12 (8 women, 4 men) right-handed graduate and undergraduate students who volunteered for the experiment and were not paid for their services. The apparatus consisted of a finger-positioning device (see Fig. 1) and the associated programming electronics. The movements allowed by the positioning device were 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 cylindri-

cal 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, which 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.

The electronics control package supported the programming of torque motor output with respect to the movement of the finger. Finger movements could be loaded by a system of gears that were driven by the motor producing a maximum of 81.6 ounce-inch of torque about the joint. A control was available, which varied the amount of resistance that could be applied before the perturbation (preperturbation) and after the perturbation (postperturbation). A second potentiometer enabled control of the amount of torque applied during the perturbation. The location (angle) at which the perturbation was triggered as well as its duration could be controlled directly from the electronic panel. A potentiometer mounted over the axis of motion provided information regarding the position and velocity of movement for recording purposes.

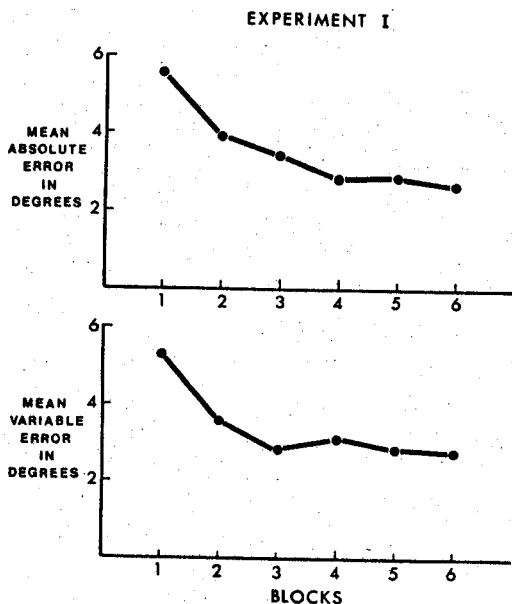


FIG. 2. Acquisition trends indicate a plateau effect after 15 to 20 trials with a mean absolute error of about 2.3° .

Electromyographic potentials were recorded with Beckman silver-silver chloride disk-type electrodes and amplified and recorded on a Beckman 5010 polygraph system.

Procedure

The skin above the right extensor digitorum and over the lateral aspect of the olecranon process (ground electrode) was prepared for electrode placement. In some cases the skin over the flexor digitorum superficialis was also prepared. The interelectrode resistances were $5\text{ k}\Omega$ or lower.

The subjects were blindfolded and seated in a dental chair such that the right arm and index finger could be comfortably but securely arranged in the positioning apparatus. The procedures for movement during acquisition and perturbation trials were then described for the subject and any questions answered. Through the experiment the subject's task—on the commands "ready" and "move"—was simply to move rapidly to the designated position. At that point the subject was to say, "there," following which the experimenter returned the finger to the starting position. The experiment proceeded in two parts. The first, 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). Verbal knowledge of results (KR) was given in qualitative (overshoot, undershoot, hit) and quantitative (number of degrees) terms. Movement errors

were recorded in degrees of angular displacement from the target position. 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 designated 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 among the 18 test trials. The subjects were informed that on some of the trials a perturbation would occur and that they should attempt to move through it and arrive at the learned location. The duration of the application of the perturbation was set at 100 ms throughout the experiment. Free movement was allowed in nonperturbed trials. During perturbed trials the movement was essentially free before and after the 100-ms torque duration. Extensor and flexor muscle activity, position, and velocity of movement were recorded simultaneously on the polygraph. Acquisition trials were recorded at $10\text{ mm}\cdot\text{s}^{-1}$ and test trials at $50\text{ mm}\cdot\text{s}^{-1}$.

RESULTS

For error scores, deviations from the target position were recorded. By convention an undershoot was signed negative ($-$) and an overshoot was signed positive ($+$). Absolute error (unsigned), constant error (signed), and variable error (standard deviation around mean constant error) were used for the purposes of analysis.

Acquisition trials

Acquisition trials were divided into six blocks of five trials and the plot is presented in Fig. 2. As can be seen in the figure, there were improvements in performance as reflected in significant differences between trial blocks 1 and 6, $t(11) = 3.62$, $P < 0.01$ and 3.99 , $P < 0.01$ for absolute and variable error, respectively. An analysis of constant error failed to reveal significance, $P > 0.05$.

Test trials

To test for the principle of equifinality in our subjects, the nine nonperturbed trials were compared to the nine perturbed trials. Means were calculated for each subject (see Table 1) and served for paired t tests. The contrast between perturbed and nonperturbed trials failed significance for absolute error, $t(11) = 2.01$, $P > 0.05$. Constant and variable error comparisons revealed

TABLE 1. *Summary of results of experiment 1*

	Acquisition*	Nonperturbed†	Perturbed Total†	Perturbed‡		
				Short	Medium	Long
Absolute error, deg	2.81 ± 1.21	4.12 ± 2.44	5.61 ± 2.27	6.08 ± 3.96	6.17 ± 3.74	4.58 ± 2.74
Constant error, deg	-0.15 ± 1.88	-0.18 ± 3.95	1.37 ± 5.33	0.58 ± 7.33	1.61 ± 6.20	1.97 ± 4.89
Variable error, deg	3.14 ± 1.30	4.11 ± 2.08	4.54 ± 1.50	3.01 ± 1.50	4.10 ± 3.19	3.16 ± 1.89
Movement time, ms		194 ± 43	346 ± 62	302 ± 20	325 ± 30	410 ± 35

Values are means ± SD.
of three trials.

* Means of last nine acquisition trials.

† Means of nine trials.

‡ Means

similar results; $t(11) = 1.51$, $P > 0.05$, and $t(11) = 0.74$, $P > 0.05$, respectively. Examination of the raw absolute error data revealed that 9 of the 12 subjects showed little or no decrement in performance as a result of the perturbations. 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, $F_s(2,33) = 0.77$, $P > 0.05$, 0.16, $P > 0.05$ and 0.79, $P > 0.05$ for absolute, constant, and variable error, respectively.

For a physical mass spring with constant stiffness and damping parameters, certain invariant kinematic details will emerge. Velocity and periodicity, for example, are constants as is the overall movement time. Mean movement time data calculated from the first overt sign of movement in the potentiometer output to the point of target attainment are also presented in Table 1.

To test whether velocity was constant from trial to trial in this learned movement, velocity was computed from the linear part of the slope of the displacement curves for nonperturbed trials and averaged for all subjects (mean = $350^\circ \cdot s^{-1}$, SD = $86^\circ \cdot s^{-1}$). These values represent a mean variability of about 25%, and none of the subjects showed less than 16% variability. Thus, in a learned positioning task without external perturbations, it is clearly seen that the emergent kinematic variability in movement time and velocity indicates that one or both of the underlying dynamic parameters of stiffness or damping undergo change. To

test this finding further we investigated the oscillations of the finger around the equilibrium point. A spring system with constant stiffness and damping parameters will always produce one of three kinds of oscillation, light, critical, or heavy damping (44). A lightly damped system is defined as one in which the mass of the spring passes through the equilibrium point at least once before reaching steady state or equilibrium point. A heavily damped system has the characteristic that the mass does not pass through the equilibrium point and only reaches equilibrium at infinity. The critically damped system is one where the damping has the least value that will produce aperiodic motion; that is, the value at which the spring moves quickly to the equilibrium point without ever passing through it. Actual displacement curves of each of these forms of damping are presented in Fig. 3.

The above criteria were used to determine qualitatively whether a subject displayed one or more of these movement patterns. On examination of the raw data it was observed that of the 12 subjects, 9 demonstrated both critical and light damping characteristics and none showed heavy damping. There was a tendency toward critical damping in nonperturbed trials (76% of all trials critically damped), while in perturbed trials there was a slight tendency for light damping (54% lightly damped). Locus of perturbation had no obvious effect on oscillatory activity (53, 64, and 44% critically damped for perturbed short, medium, and long trials, respectively).

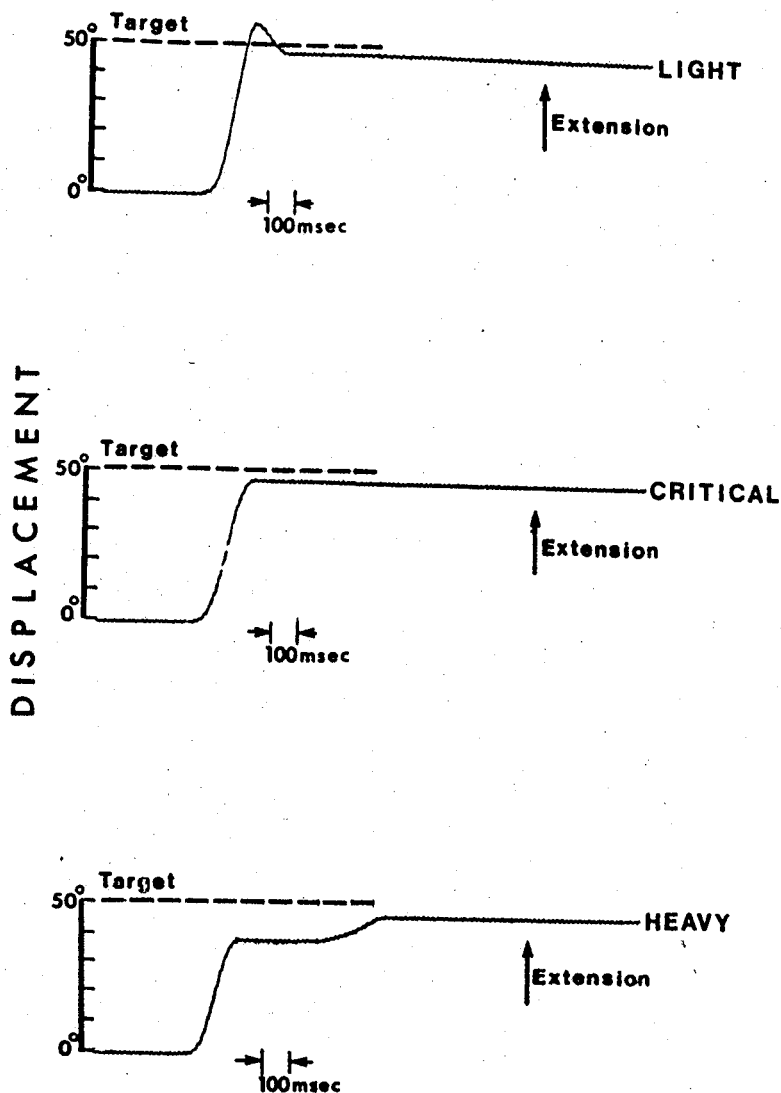


FIG. 3. Actual displacement curves from a single subject in nonperturbed trials indicate three kinds of oscillatory behavior about the equilibrium point. Similar variability in the movement patterns of most subjects provides evidence that the stiffness parameters of the agonist and antagonist muscles were variable, but that the ratio of activity between them was constant.

DISCUSSION

The finding that equally accurate performance was obtained in both perturbed and nonperturbed trials strongly supports the equifinality property that is characteristic of vibratory systems. Although comparisons are tenuous, our results appear even more favorable for the concept than those obtained on arm movements in monkeys where the errors are quite large (35) (see Fig. 2). In

addition, this is the first time to our knowledge that equifinality in the face of unpredictable perturbations has been observed in human subjects. Perhaps surprisingly, the kinematic variability in velocity, movement time, and oscillations points also to variability in at least one of the dynamic parameters of stiffness and damping. We might have expected that in a learned motor activity, the central nervous system would maintain these parameters constant from

trial to trial. However, it may be argued that since the task demanded only target attainment, the movement patterns by which this goal was achieved were relatively unimportant. Thus the control system could feasibly afford several variations in the specification of parameters for achieving the equilibrium position. That there was a tendency toward greater amplitude of oscillation in perturbed trials may be viewed as a result of injecting more energy into a system with constant damping; an interpretation that is congruent with the dynamic response characteristics of a mass-spring system.

Clearly, the data obtained in experiment 1 can more than adequately be explained by a mass-spring model of localization. However, the findings fail to rule out an alternative hypothesis based on a closed-loop conceptualization of control. Thus, our results could be accounted for by supposing that central commands are modified during movement execution by the action of fast-acting peripheral feedback loops (11, 17, 25) or given sufficient time, through resetting the central commands following perturbation. Although the latter possibility is unlikely due to the ballistic nature of the movements employed (see Table 1), we do not rule out the role of afferent information in reparameterizing the system following movement termination. A major prediction with respect to the spring model, however, is that a continuous readout of proprioceptive information is not a necessary condition for the achievement of the equilibrium position. The second experiment was designed to examine this issue by injecting load perturbations during the localization movements of individuals who had joint and cutaneous information removed using the wrist-cuff technique (21, 26, 32). The advantage of this procedure is that muscle function is preserved in the long finger flexors and extensors that lie high in the forearm, while sensory inputs to the hand itself are effectively eliminated.

Experiment 2

METHODS

Six volunteers from the student and faculty population served as subjects. None of the sub-

jects had been involved in the first experiment. All were informed of the sensations involved in the wrist-cuff procedure, and only those who felt they could handle the situation participated.

The apparatus used in this experiment was identical to that employed in experiment 1.

Procedure

We felt it necessary to replicate entirely the results of the first experiment. Thus, the first part of experiment 2 followed the earlier procedure exactly. After the 30 acquisition trials with knowledge of results available, 9 perturbed and 9 nonperturbed trials (together designated pre-cuff trials) were given in randomized order with error-information withdrawn. On completion of this aspect of the study, subjects were removed from the apparatus and the wrist cuff applied and inflated as discussed in detail elsewhere (26). The subject's arm and hand were replaced in the apparatus in the same posture as before. Sensory testing was conducted at 1-min intervals 5-10 min after wrist-cuff application in order to let the subjective experience of "pins and needles" subside. Subjects were instructed to label the fingers one through five (from thumb to little finger) and to specify the sensation tested (e.g., "touch four," "movement two"). Tactile sensation was tested using a cotton wool-covered stick applied to the skin. Movement-position sense was similarly tested by the experimenter moving the digits in specific directions at variable rates. The order of stimulus presentation was random for both modalities to further insure discriminating responses on the part of the subject. Occasionally catch trials were included in which no stimulation was given in order to reduce guessing by the subject. When the subject was no longer capable of reporting touch or localizing position and movement in the digit being tested on two consecutive occasions, the experimenter defined this point as the respective cutoff point for that digit. When all digits succumbed to this criterion, the final end point was assumed and its time of occurrence recorded. Following the establishment of sensory cutoff,³ a further 18

³ Three independent sources of evidence speak to the viability of the wrist-cuff technique as a tool in reducing proprioceptive sensations. First, passive displacements of the metacarpophalangeal joint up to an estimated 90°/s were undetected. Second, subjects when instructed to produce a movement but prevented from doing so, consistently perceived that they had executed the movement. If muscle afferent information were capable of accessing consciousness, this would have been an unlikely finding. Third, it has been consistently verified that the loss of background facilitation from joint and cutaneous sources using this procedure reduces stretch-reflex function (e.g., Refs. 26, 30 for review.)

TABLE 2. *Summary of results of experiment 2*

	Acquisition*	Nonperturbed†	Perturbed Total†	Perturbed‡		
				Short	Medium	Long
Absolute error, deg	2.33 ± 0.80	5.61 ± 3.42	5.21 ± 2.48	6.22 ± 4.46	3.84 ± 1.62	5.56 ± 2.18
Constant error, deg	0.33 ± 1.89	-4.50 ± 4.19	-3.72 ± 3.80	-5.11 ± 5.90	-1.95 ± 3.23	-3.67 ± 3.74
Variable error, deg	2.52 ± 0.55	3.35 ± 1.06	4.36 ± 0.83	3.31 ± 1.22	2.87 ± 0.75	4.07 ± 2.39
Movement time, ms		192 ± 39	352 ± 53	317 ± 28	335 ± 40	396 ± 47

Values are means ± SD.
of three trials.

* Means of last nine acquisition trials.

† Means of nine trials.

‡ Means

trials were given to the subject, half of which were perturbed at three different loci. These trials (designated cuff trials) were yoked to the precuff trials so that the subject performed them in the same randomized order. Again, these were performed in the absence of knowledge of results. On completion of these movements, the wrist cuff was deflated and the subject remained seated for a mandatory recovery period of 10 min before leaving the laboratory.

RESULTS

Acquisition trials

Almost identical results to those obtained in experiment 1 were obtained for acquisition trials (see Fig. 2). The comparison of trial blocks 1 and 6 for both absolute and variable error were significant, $t(5) = 10.9$, $P < 0.01$ and 5.03 , $P < 0.01$, respectively.

Precuff test trials

These trials were analyzed as in experiment 1. Absolute, constant, and variable error means are presented in Table 2. No significant differences were found in the pairwise comparisons of perturbed and non-perturbed trials for absolute and constant error, $t(5) = 0.86$, $P > 0.05$ and 1.52 , $P > 0.05$, respectively. Significantly larger variable error was found in the perturbed trials, $t(5) = 4.03$, $P < 0.01$. However, as can be seen in Table 2, this difference was small, in the order of 1° . Examination of the absolute error means revealed that all six subjects showed little or no decrement in performance on perturbed trials. Locus of perturbations was not found to be a significant factor, as indicated by analysis of

variance, $F_s(2,15) = 1.00$, $P > 0.05$, 0.76 , $P > 0.05$, and 0.84 , $P > 0.05$ for absolute, constant, and variable error, respectively. Mean movement time data are also presented in Table 2 and mirror those of the previous study. Results of velocity computations were similar to those of experiment 1 (mean = $346^\circ \cdot s^{-1}$, SD = $67^\circ \cdot s^{-1}$), with the exception that the mean variability in this case was slightly lower (20%).

Four of the six subjects showed oscillations in movement pattern indicative of both light and critical damping. The effects of perturbation were even more pronounced in this experiment. While 70% of non-perturbed trials revealed critical damping, only 30% of perturbed trials were critically damped. Again, locus of perturbation had no obvious effects on oscillatory behavior with critical damping in 28, 28, and 33% of perturbed short, medium, and long trials, respectively.

Cuff trials

Mean error scores for subjects performing under wrist-cuff conditions are presented in Table 3. A comparison of nonperturbed and perturbed trials revealed no significant differences for absolute error, $t(5) = 0.19$, $P > 0.05$. Analysis of constant, $t(5) = 3.33$, $P < 0.05$ and variable error, $t(5) = 3.88$, $P < 0.05$, however, indicated significant differences. 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 nonperturbed trials. It may be noted,

TABLE 3. Summary of results of experiment 2 under wrist-cuff conditions

	Nonperturbed*	Perturbed Total*	Perturbed†		
			Short	Medium	Long
Absolute error, deg	13.52 ± 7.87	11.66 ± 5.88	13.56 ± 9.66	10.28 ± 6.14	9.58 ± 3.56
Constant error, deg	4.89 ± 15.74	0.00 ± 12.78	-3.55 ± 16.03	4.61 ± 11.09	4.25 ± 8.67
Variable error, deg	6.25 ± 2.28	8.36 ± 2.57	8.46 ± 3.94	5.07 ± 1.99	6.53 ± 3.53
Movement time, ms	417 ± 90	454 ± 79	418 ± 52	451 ± 50	485 ± 39

Values are means ± SD.

* Means of nine trials.

† Means of three trials.

however, that the differences are very modest indeed compared to the boundary conditions set by Polit and Bizzi (35) for accurate arm movements in monkeys (in the order of 12–15°).

Locus of perturbation was found not to be a significant factor, as indicated by analysis of variance, $F_{s(2,15)} = 0.46$, $P > 0.05$, 0.74, $P > 0.05$ and 1.21, $P > 0.05$ for absolute, constant, and variable error, respectively.

Movement time data are also presented in Table 3. Interestingly, there was an overall increase in movement time in cuff trials, and this was accompanied by changes in both velocity and oscillation patterns. The mean velocity for wrist-cuff trials was less than that of precuff trials (mean = $260^\circ \cdot s^{-1}$, SD = $80^\circ \cdot s^{-1}$, representing a mean variability of 31%). Without exception, the displacement curves for all subjects under both perturbed and nonperturbed conditions showed a critical damping pattern only.

It is not legitimate to compare accuracy scores from precuff to cuff trials due to the substantial time lapse that was necessary for the nerve block to take effect (between 1 and 1.5 h in all subjects). Thus the modest increase in error is likely accounted for by the time delay combined with the absence of knowledge of results regarding performance. Of course, to discount completely the possibility of proprioceptive influences on target accuracy in perturbed and nonperturbed cuff trials is not possible within the present experimental paradigm (see GENERAL DISCUSSION).

Electromyographic data

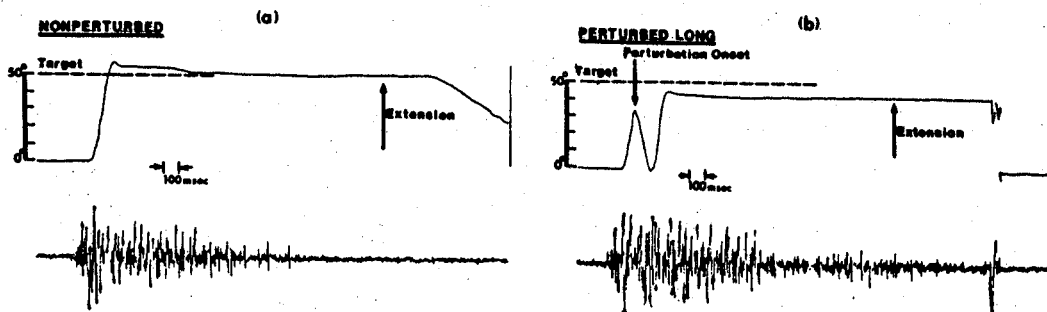
Qualitative differences in EMG activity were examined in precuff and cuff trials. Examples are given in Fig. 4 along with accompanying displacement records illustrating perturbed and nonperturbed movements. As shown in Fig. 4b, there is an increase in agonist EMG activity following perturbation onset due presumably to proprioceptive stimulation and consequent initiation of fast-acting reflex loops (e.g., Refs. 15, 30). In cuff performance, however, electrical activity was constant throughout the movement and signs of stretch reflex activity were largely absent (Fig. 4c and d). A notable observation was that the activity of the antagonist muscle (flexor digitorum superficialis) was close to base line during precuff trials but highly active during and after target localization in cuff conditions.

DISCUSSION

There were two principal outcomes of this experiment. First, it replicated in full the major results of our first experiment. Equifinality was observed under normal localization conditions and when movements were unexpectedly perturbed by suddenly applying a torque load that drove the finger in the opposite direction (see Fig. 4). Second, the equifinality characteristic was present even when the subject was functionally deafferented, a finding that lends converging support to the mass-spring model.

An additional and interesting result was that movements in the wrist-cuff condition

PRE-CUFF TRIALS



CUFF TRIALS

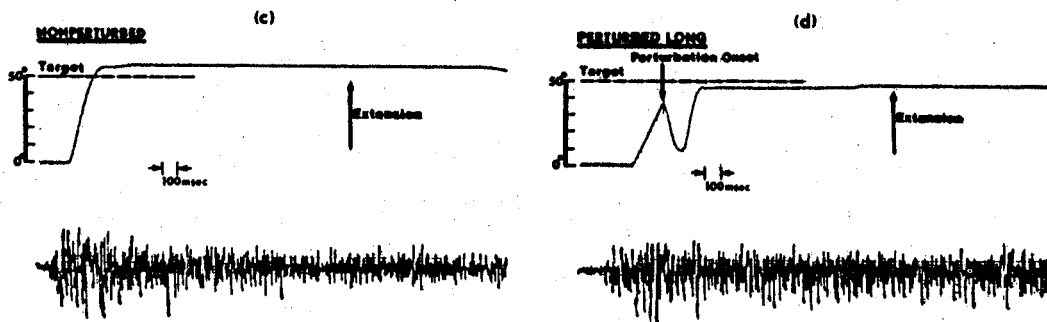


FIG. 4. EMG recorded via surface electrodes placed over the extensor digitorum indicate an increase in the duration of extensor activity under wrist-cuff conditions. An associated increase in activity of the flexor digitorum superficialis (not shown) indicates greater isometric influence. Movements were consequently slower (compare *a* and *c*, *b* and *d*), and without exception critically damped (*c*, *d*). The effect of perturbation in the wrist-cuff condition (*d*) was less pronounced—a finding consistent with an increased overall stiffness in a mass-spring system perturbed by a constant load.

were slower and movement patterns more consistent than in precuff trials. Bizzi et al. (7) also observed this differential effect in head movements between animals with and without intact proprioception, a finding they attribute to the fact that only the mechanical properties of the neck musculature (active and passive) remain for control purposes. In our study, an observed increase in EMG activity in flexor and extensor muscle groups under cuff conditions was combined with a perceived increase in effort in all subjects. We might expect that an increase in the conjoint activity of flexor and extensor muscles will have consequent stiffening effects on the metacarpophalangeal joint. Given parallel increases in frictional forces and muscle stiffness, the system will convert from lightly damped to critically damped (44), thus suggesting a reason why all our subjects showed

critical damping in cuff trials.⁴ It is also possible that the modest loss in accuracy observed under cuff conditions occurs as a result of the disruption of stiffness ratios in antagonist muscles that normally hold for particular equilibrium positions.

In sum, the results of experiment 2 suggest that proprioceptive information (as far as can be determined in a human preparation) is not a requirement for the accurate attainment of equilibrium position. This

⁴ This outcome is evident on consideration of the equation of motion for a freely damped mass-spring system: $m\ddot{x} + c\dot{x} + kx = 0$, where m is the mass, c is the linear damping constant, and k is stiffness. It can be shown that where $c^2 = 4mk$, critical damping occurs and where $c^2 < 4mk$, light damping occurs. Thus the relationship between spring constant (k), damping constant (c), and mass (m) determines the system's oscillation.

conclusion generally parallels very recent work showing that the neural reflex component has a relatively small contribution (10–30%) in counteracting applied disturbances during movement localization. In contrast, a significantly larger portion (60%) of this process is provided by mechanical properties (inertial, viscous, and elastic) of the neck musculature (7). Moreover, none of our findings refute the claim that the kinematic characteristics of movement observed in this experiment (or in experiment 1) violate any of the dynamic laws pertaining to a mass-spring system.

GENERAL DISCUSSION

The present experiments were designed to test the efficacy of a mode of control that takes advantage of the properties of a particular type of vibratory system, namely the mass spring. A most important characteristic of a mass-spring system is its equifinality (45), which emerges as the predominant feature in our data. Thus equifinality endured despite unexpected and abrupt load disturbances (experiment 1), functional deafferentation, and both in conjunction (experiment 2). These results fully complement our earlier work (26) and, corroborated by recent neurophysiological data (7, 25), provide a broad empirical basis for the mass-spring model.

There are some grounds for caution however. Although the pressure-cuff technique drastically reduces joint and cutaneous information, it is possible that muscle proprioception plays a role at some level in the achievement of final position. Although we envisage spring parameters to be set prior to movement, we cannot exclude muscle and tendon reception as playing a regulatory function. Regardless of whether this is the case or not, our basic tenet—borne out by the data and consonant with the mass-spring model—is that it is dynamic variables that are regulated.

It might further be argued that the significant increase in target acquisition time following perturbations observed in both experiments is a consequence of "reaction-time" movements that are proprioceptively based (e.g., see Ref. 25 for review). While we cannot completely rule out such a view, we should reemphasize that the duration of

the perturbation was 100 ms. Inspection of Table 1 shows that unless such reaction-time components are embedded in the perturbation duration, the response at the short-perturbation locus, for example, would be around 8 ms, which is well outside the boundaries of proprioceptive reaction time. Perhaps a more parsimonious explanation exists in terms of the amount of force produced by the limb muscles at different stages during the trajectory. For instance, early in the movement larger forces are necessary to overcome inertia and to accelerate the limb. Consequently, the effect of a perturbation (a force vector operating in the opposite direction) will be less than in the case where the limb is at constant velocity or decelerating. Thus the locus of the perturbation (whose characteristics are constant for all trials) in the movement trajectory will determine the amount of deflection of the limb and the time to return the limb to the point at which it was perturbed. The systematic effects of locus of perturbation on target acquisition time (see Tables 1 and 3), render this explanation as a viable—and testable—alternative to a reaction-time account.

Given the foregoing caveats, let us now turn to the broader implications of our findings. The mass-spring model of localization promoted here represents a significant departure point from other conceptualizations of control. It is fairly common, for example, for researchers to speak of central motor programs for movement amplitude and duration (10, 40), or to view the achievement of final position (location) as the continually sensed position of the limb in reference to a perceptual referent or spatial coordinate system (36). Although these modes of control are conceptually distinct and may refer to different types of movement (e.g., ballistic versus slow (13)), they nevertheless envisage the controlled variable as a kinematic prescription. In contrast, the behavior of a mass-spring system, while describable in kinematic terms such as displacement, rate, and frequency, is totally determined by dynamic properties such as mass, viscosity, and stiffness. Although it is difficult to account conclusively for the kinematic variability in our data in terms of a singular dynamic parameter, there is good reason to believe that stiffness is the regu-

lated entity, while damping is a constant of the viscous properties of the joint and muscle groups involved (18, 25, 34).

What theoretical advantages might a mass-spring account of localization provide? An adequate answer to this question requires us to address briefly two fundamental problems of motor organization that are often overlooked in both behavioral and neurophysiological investigations of motor mechanisms. The first of these is the issue of functional nonunivocality (6), or context-conditioned variability (43); simply stated, there is no invariant relationship between centrally generated signals and movement outcomes. Movements cannot be direct reflections of neural events because muscular and nonmuscular (reactive) forces must be taken into account. Similarly, at a cellular level, direct monosynaptic control of α -motoneurons is the exception rather than the rule in neural regulation of movement. Whether a motoneuron fires or not is contingent on the influences of supra-, inter-, and intrasegmental neurons whose status varies from one instant to the next (16). The point is that descending information is continually modulated by virtue of the active state of the segmental machinery. Thus we cannot ignore the contextual background against which supraspinal signals are realized.

Although it is possible, in theory, to solve the problem of context-conditioned variability by making available detailed information about the current states of muscles and joints, such an account fails to address the second problem; namely, how the degrees of freedom of the motor apparatus are regulated.⁵ One solution toward resolving this dilemma (6, 20, 23, 42) is to claim that skeletomuscular variables are partitioned into collectives where the variables within a collective change relatedly and autonomously. This results in a reduction of the degrees of freedom since higher brain centers now have only to activate or tune lower-level, functional groups of muscles.

That such functional units or synergies

(9) constitute the significant units of control is revealed in a broad range of activities—from the regulation of animal gait (24, 38) and the maintenance of vertical posture (33) to aiming the arm at a target (3) and coordinating the upper limbs to perform different tasks (27). Similarly, tuning is demonstrated by experiments that sample the state of the neuromuscular system just prior to movement. Thus it can be shown that augmentation of the H-reflex in the gastrocnemius muscle occurs when it is compatible with the intended movement (plantar flexion) and depressed when it is not (22, 29). Functional groupings of muscles arise then, presumably as a result of such tuning or biasing in the interneuronal pools of the spinal cord (20, 23).

The mass-spring model is fully compatible with the style of control that we have briefly elaborated here. The spring system in this case represents a functional collective of muscles (23, 42), and its dynamic parameterization is reflective of tuning. It thus provides at least a partial solution to some of the problems that confront investigations of movement production possessing the following advantages. First, the desired position of the limb may be specified independent of initial conditions (equifinality). Thus, what constitutes a context-conditioned variability problem in traditional views of motor control is not a concern for the mass-spring proposition. Second, the desired behavior of the limb is closely approximated by the laws of mechanics. Given the existence of constant damping, the limb pursues its own trajectory in a stable manner. Both these advantages eliminate the requirement for continuous regulation via feedback. Third, speed can be controlled by specifying stiffness which, as revealed in elementary mechanics as well as in the present experiments, may be regulated independently of resting length (equilibrium point). Thus, an invariant end point may be the outcome of varying combinations of kinematic properties. Fourth, repetitive movements can be produced by the natural oscillations of a spring system; all that needs to be specified—and then only once—is the equilibrium point. Instead of controlling time of arrival at each terminal position of the swing (a kinematic computation), timing could be regulated by altering

⁵ If we consider the degrees of freedom problem at the level of muscles alone, Tomovic and Bellman (41) have estimated the total number in the human body to be 792. For the brain to individually regulate these is surely an insurmountable task.

stiffness (the spring constant). A fifth advantage (P. H. Greene, personal communication) may be seen in the following example: consider the task of directing a finger to a desired position in space. Spring parameters of the trunk, shoulder, elbow, and wrist could be temporarily coupled so that when the equilibrium point of the entire linkage is reached, the finger is in the correct position.⁶ If for some reason the location is not reached, then the position error of the finger alone—not the n -tuple errors of all the degrees of freedom—can be used to regulate the equilibrium point of the coupled system. This is an important point for it reconciles to some degree the problem that some theorists have had (19) with formulations that have knowledge of results regulate motor learning (1). If the skeletomuscular variables are constrained to act as a unit, error information will be relevant to that unit alone, and not the singular degrees of freedom that constitute it.

Finally, a neuromuscular system with the dynamic properties of a spring complements

the dynamic nature of the environment. For example, in a recent paper, McMahon and Greene (31) have demonstrated that running performance shows impressive improvement when the compliance of the track surface is closely matched to the spring parameters of the runner. Also, as Houk (25) points out, when we encounter an immovable obstacle during movement, it is more beneficial for the musculature to yield, rather than to regulate joint position needlessly since this would require a complete readjustment of other body parts. In summary, we feel there is much to commend a mass-spring account, especially in terms of economy of neural control. A number of challenging questions remain, however, particularly those that address the physiological nature of the tuning process.

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REFERENCES

- ADAMS, J. A. A closed loop theory of motor learning. *J. Mot. Behav.* 3: 111–150, 1971.
- ADAMS, J. A. Feedback theory of how joint receptors regulate the timing and positioning of a limb. *Psychol. Rev.* 84: 504–523, 1977.
- ARUTYUNYAN, G. A., GURFINKEL, V. S., AND MIRSKII, M. L. Investigation of aiming at a target. *Biophysics* 13: 642–645, 1968.
- ASATRYAN, D. G. AND FEL'DMAN, A. G. Functional tuning of the nervous system with control of movement or maintenance of a steady posture. I. Mechanographic analysis on the work of the joint on execution of a postural task. *Biophysics* 10: 925–935, 1965.
- BERNSTEIN, N. A. *On the Construction of Movements*. Monograph (in Russian). Moscow: Medgiz, 1947.
- BERNSTEIN, N. A. *The Coordination and Regulation of Movements*. London: Pergamon, 1967.
- BIZZI, E., DEV, P., MORASSO, P., AND POLIT, A. Effects of load disturbances during centrally initiated movements. *J. Neurophysiol.* 41: 542–556, 1978.
- BIZZI, E. AND POLIT, A. Processes controlling visually evoked movements. *Neuropsychologia* 17: 203–213, 1979.
- BOYLLS, C. C. A theory of cerebellar function with applications to locomotion. II. The relation of anterior lobe climbing fiber function to locomotor behavior in the cat. *COINS Tech. Rept.* 76-1. Dept. of Computer and Information Science, University of Massachusetts, Amherst, 1975.
- BROOKS, V. B. Some examples of programmed limb movements. *Brain Res.* 71: 299–308, 1974.
- COOKE, J. D. AND EASTMAN, M. J. Long-loop reflexes in the tranquilized monkey. *Exp. Brain Res.* 27: 491–500, 1977.
- DESMEDT, J. E. (editor). *Cerebral Motor Control in Man: Long Loop Mechanisms*. Basel: Karger, 1978.
- DESMEDT, J. E. AND GODEAUX, E. Ballistic skilled movements: load compensation and patterning of the motor commands. In: *Cerebral Motor Control in Man: Long Loop Mechanisms*, edited by J. E. Desmedt. Basel: Karger, 1978, p. 21–55.
- EVARTS, E. V. Feedback and corollary discharge: a merging of the concepts. *Neurosci. Res. Prog. Bull.* 9: 86–112, 1971.
- EVARTS, E. V. Motor cortex reflexes associated with learned movement. *Science* 179: 501–503, 1973.
- EVARTS, E. V., BIZZI, E., BURKE, R. E., DELONG, M., AND THACH, M. T. Central control of movement. *Neurosci. Res. Prog. Bull.* 9: 1–171, 1971.

17. EVARTS, E. V. AND GRANIT, R. Relations of reflexes and intended movements. *Prog. Brain Res.* 44: 1-14, 1976.
18. FEL'DMAN, A. G. Functional tuning of the nervous system with control of movement or maintenance of a steady posture. III. Mechanographic analysis of execution by man of the simplest motor tasks. *Biophysics* 11: 766-775, 1966.
19. FOWLER, C. A. AND TURVEY, M. T. Skill acquisition: an event approach with special reference to searching for the optimum of a function of several variables. In: *Information Processing in Motor Control and Learning*, edited by G. E. Stelmach. New York: Academic, 1978, p. 1-40.
20. GELFAND, I. M., GURFINKEL, V. S., TOMIN, S. V., AND TSETLIN, M. L. *Models of the Structural-Functional Organization of Certain Biological Systems*. Cambridge, MA: MIT Press, 1971.
21. GOODWIN, G. M., MCCLOSKEY, D. I., AND MATTHEWS, P. B. C. The contribution of muscle afferents to kinesthesia shown by vibration induced illusions of movement and by the effects of paralyzing joint afferents. *Brain* 95: 705-748, 1972.
22. GOTTLIEB, G. L., AGARWAL, G. C., AND STARK, L. Interaction between voluntary and postural mechanisms of the human motor system. *J. Neurophysiol.* 33: 365-381, 1970.
23. GREENE, P. H. Problems of organization of motor systems. In: *Progress in Theoretical Biology*, edited by R. Rosen and F. Snell. New York: Academic, 1972, vol. 2, p. 303-338.
24. GRILLNER, S. Locomotion in vertebrates: central mechanisms and reflex interaction. *Physiol. Rev.* 55: 247-304, 1975.
25. HOUK, J. D. Participation of reflex mechanisms and reaction time processes in compensatory adjustments to mechanical disturbances. In: *Cerebral Motor Control in Man: Long Loop Mechanisms*, edited by J. E. Desmedt. Basel: Karger, 1978, p. 193-215.
26. KELSO, J. A. S. Motor control mechanisms underlying human movement reproduction. *J. Exp. Psychol.* 3: 529-543, 1977.
27. KELSO, J. A. S., SOUTHARD, D., AND GOODMAN, D. On the nature of human interlimb coordination. *Science* 203: 1029-1031, 1979.
28. KELSO, J. A. S. AND STELMACH, G. E. Central and peripheral mechanisms in movement. In: *Motor Control: Issues and Trends*, edited by G. E. Stelmach. New York: Academic, 1976, p. 1-40.
29. KOTS, Y. M. *The Organization of Voluntary Movements*. New York: Plenum, 1977.
30. MARSDEN, C. D., MERTON, P. A., AND MORTON, H. B. Stretch reflexes and servoactions in a variety of human muscles. *J. Physiol. London* 259: 531-560, 1976.
31. MCMAHON, T. A. AND GREENE, P. R. Fast running tracks. *Sci. Am.* 238: 148-163, 1978.
32. MERTON, P. A. Human position sense and sense of effort. *Symp. Soc. Exp. Biol.* 18: 387-400, 1964.
33. NASHNER, L. M. AND GRIMM, R. J. Analysis of multiloop dyscontrols in standing cerebellar patients. In: *Cerebral Motor Control in Man: Long Loop Mechanism*, edited by J. E. Desmedt. Basel: Karger, 1978, p. 300-319.
34. NICHOLS, T. R., AND HOUK, J. C. The improvement of linearity and the regulation of stiffness that results from the actions of the stretch reflex. *J. Neurophysiol.* 39: 119-142.
35. POLIT, A. AND BIZZI, E. Processes controlling arm movements in monkeys. *Science* 201: 1235-1237, 1978.
36. RUSSELL, D. G. Spatial location cues and movement production. In: *Motor Control: Issues and Trends*, edited by G. E. Stelmach. New York: Academic, 1976, p. 67-85.
37. SCHMIDT, R. The schema as a solution to some persistent problems in motor learning theory. In: *Motor Control: Issues and Trends*, edited by G. E. Stelmach. New York: Academic, 1976, p. 41-65.
38. SHIK, H. L. AND ORLOVSKII, G. N. Coordination of the limbs during running of the dog. *Biophysics* 10: 1148-1159, 1965.
39. STELMACH, G. E., KELSO, J. A. S., AND WALLACE, S. Preselection in short-term motor memory. *J. Exp. Psychol. Human Learning Memory*. 1: 745-755, 1975.
40. TAUB, E., GOLDBERG, I. A., AND TAUB, P. Deafferentation in monkeys: pointing at a target without visual feedback. *Exp. Neurol.* 46: 178-186, 1975.
41. TOMOVIC, R. AND BELLMAN, R. A systems approach to muscle control. *Math. Biosci.* 8: 265-277, 1970.
42. TURVEY, M. T. Preliminaries to a theory of action with reference to vision. In: *Perceiving, Acting and Knowing: Toward an Ecological Psychology*, edited by R. Shaw and J. Bransford. Hillsdale, NJ: Erlbaum, 1977, p. 211-265.
43. TURVEY, M. T., SHAW, R., AND MACE, W. Issues in the theory of action: degrees of freedom, coordinative structures and coalitions. In: *Attention and Performance VII*, edited by J. Requin. Hillsdale, NJ: Lawrence Erlbaum Assoc., 1978, p. 557-595.
44. VOLTERRA, E. AND ZACHMANOGLU, E. C. *Dynamics of Vibrations*. Columbus, OH: Merrill, 1965.
45. VON BERTALANFFY, L. *General System Theory*. London: Penguin, 1973.