

ON THE CONCEPT OF COORDINATIVE STRUCTURES AS DISSIPATIVE STRUCTURES:
II. EMPIRICAL LINES OF CONVERGENCE*

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In this paper we pursue the argument that where a group of muscles functions as a single unit the resulting coordinative structure, to a first approximation, exhibits behavior qualitatively like that of a force-driven mass-spring system. Data are presented illustrating the generative and context-independent characteristics of this system in tasks that require animals and humans to produce accurate limb movements in spite of unpredictable changes in initial conditions, perturbations during the movement and functional deafferentation. Analogous findings come from studies of articulatory compensation in speech production. Finally we provide evidence suggesting that one classically-defined source of information for movement, namely proprioception, may not be dimension-specific in its contribution to coordination and control.

I. Introduction

In the first paper we have given a detailed theoretical argument suggesting that a group of muscles organized as a single functional unit is necessarily a thermodynamic engine, a dissipative structure, with the behavioral properties of a non-linear oscillator. That a constrained collection of muscles might well exhibit a likeness to oscillatory mechanisms was intuited some years ago by Bernstein (1947; see also Greene, 1978) and was advanced, on empirical grounds, by Fel'dman via a (now classical) mechanographic analysis of arm movements (Asatryan & Fel'dman, 1965; Fel'dman, 1966a,b). Fel'dman's departure point was that the muscles at a joint behave, on a first approximation, as a linear mass-spring system. His analysis revealed, however, that the behavior was more closely approximated by a non-linear oscillatory system and we have shown, in the preceding essay, how data such as Fel'dman's can be given an interpretation in the qualitative dynamics of a non-linear system. It remains, however, a simpler convention to address some aspects of the behavior of a constrained muscle collective in terms of the "first approximation" and in large part the evidence to be reported below is an elaboration of the mass-spring perspective.

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Before proceeding with a presentation of this evidence however, it is worth noting an important, but easily missed aspect of a mass-spring system that serves to bridge the two papers and preserve their unitary theme. We refer to the realization that a mass-spring system is intrinsically rhythmic or cyclic even though it does not have to behave rhythmically or cyclically. This claim can be readily established by reconsidering (for exemplary purposes only) the second-order differential equation of motion for a simple mass-spring system, $m\ddot{x} + c\dot{x} + kx = 0$ where x is the displacement of the system from equilibrium and \dot{x} and \ddot{x} are its velocity and acceleration respectively. The type of motion produced is dependent upon the intrinsic relationship between mass (m), stiffness (k) and the linear damping constant (c). Thus where $c^2 = 4mk$ critical damping occurs; the mass moves quickly to the equilibrium point without ever passing through it. Where $c^2 < 4mk$ light damping occurs and the system oscillates with amplitude of oscillation decreasing with time. Finally, in heavy damping $c^2 > 4mk$ and the system does not oscillate nor does it reach the equilibrium position (Volterra & Zachmanoglou, 1965). Accepting that real systems do not persist in the absence of a periodic forcing function (cf. Yates & Iberall, 1973), the message nevertheless is clear: a mass-spring system is a concrete example of a system that can oscillate or not depending on its parameterization. Thus, there is no need to conceive discrete and cyclical behaviors as arising from separate mechanisms. They are, in fact, different manifestations of the same underlying organization.

In the first part of this paper, then, we extend the observation that an oscillatory system analysis provides an apt account of the well-known ability of the human motor system to precisely produce limb movements to designated targets using a variety of movement trajectories and without regard to initial conditions. Second, we argue that it provides a much more parsimonious explanation of the "immediate adjustment" phenomenon in speech production than explanations currently in vogue. Third we shall discuss evidence, based primarily on our joint replacement studies that suggests it is unlikely that afferent information, as traditionally defined in the motor systems literature, is dimension-specific.

2. The Production of Single Trajectory Movements

A major characteristic of a mass-spring system is that it is intrinsically self-equilibrating; once set in motion the spring will always come to rest at the same resting length or equilibrium position. 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 for open systems as equifinality (von Bertalanffy, 1973). 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 systematic change in load resulted in a systematic change in joint angle (steady-state position) which was predictable as the behavior of a non-linear spring (Asatryan & Fel'dman, 1965). The question arises as to how such a spring might be controlled to produce different steady state positions. According to Fel'dman (1966; see also Houk, 1978) 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, x , varies from the resting length, 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 which need be set for voluntary movement in Feldman's model is resting length: namely, the length of the muscles for which differences in tension in opposing muscles 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 properties of stiffness and damping.

Recent data fit this perspective quite well, at least on a posteriori grounds. For example, Bizzi and his colleagues (e.g. Bizzi, Dev, Morasso & Polit, 1978; Polit & Bizzi, 1978; see also Bizzi this volume) 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 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 (Kelso, 1977) as well as patients in whom positional detectors in the joint capsule have been surgically removed (Kelso, Holt & Flatt, Note 1; see below). These results are not easily accommodated by currently popular closed-loop, feedback (e.g., Adams, 1977) or open-loop, programming accounts (e.g., Keele, in press). For example, although a closed-loop model could handle the finding that achievement of final position is possible in spite of changes in limb position prior to movement or the introduction of abrupt changes in load during execution, it is at a loss when the same findings can be demonstrated under deafferented conditions. Similarly, central programs that do not require ongoing feedback monitoring may handle deafferentation findings, but go awry when confronted with unforeseen changes in movement context. It seems more appropriate therefore to view terminal location as a steady-state position specified by the tuned parameters of the spring: it is thus impervious to unpredictable changes in initial conditions. Amplitude production, on the other hand, involves a change in the equilibrium point as a function of task demands, and hence a reparameterization of the spring function.

In our recent work we have 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 (cf. Kelso & Holt, in press). Specifically our task 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. In these experiments, we were not particularly concerned in providing a detailed analysis of the various reflex responses to changed loading conditions (see Desmedt, 1978 for numerous studies). Rather we wished to elucidate the effects of changing dynamic parameters and consequent kinematic variation on the attainment of a specified steady-state position. Subjects performed extension movements of the index finger on a device that allowed precise measurement of movement around the metacarpophalangeal joint. An electronic control system supported the programming of D. C. torque motor output with respect to movement of the finger (max. = 81.6 oz. in.). The location (joint angle) at which the perturbation was triggered as well as its duration (100 msec throughout) could be con-

trolled directly by the experimenter from the electronic panel. A potentiometer mounted over the axis of motion provided information regarding the position and velocity of movement. Electromyographic activity was recorded from the right extensor digitorum and flexor digitorum superficialis via Beckman silver-silver disk type surface electrodes.

Experiment 1 proceeded in two phases. 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 throughout at 20° flexion). Quantitative knowledge of results (KR) was provided by the experimenter. Following the acquisition phase there were 18 test trials (without KR) of which half were perturbed via the programmable torque motor. The locations of the perturbation were designated as short (applied after 10° of movement), medium (after 25°) or long (after 40°). There were three trials at each of the three perturbation locations, and these were randomly ordered amongst the 18 test trials. The subjects ($n = 12$) were informed that on some of the trials a perturbation would occur and that they should move through it in attempting to reach the learned location. Deviations from the target position were recorded. By convention an undershoot was signed negative (-) and an overshoot was signed positive (+). Absolute (unsigned), constant (signed) and variable error (standard deviation around mean constant error) were used for analysis purposes. During acquisition there were obvious improvements in performance and these were borne out statistically ($p < .05$).

The test trial data for constant and variable error are shown in Figure 1 indicating no significant differences between perturbed and non-perturbed responses. Examination of the raw data revealed that nine of the 12 sub-

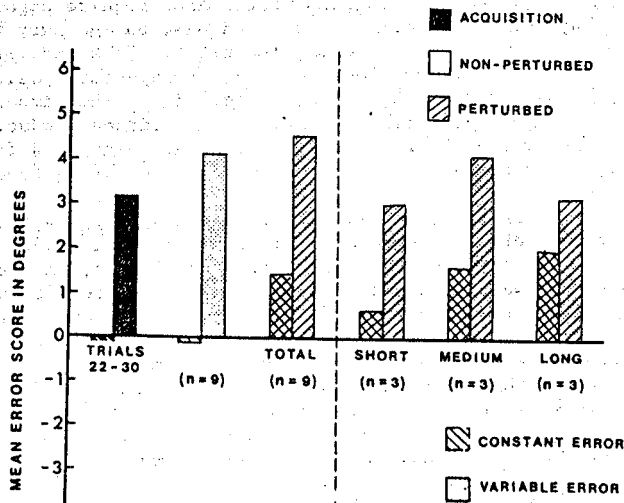


Figure 1 - Mean constant and variable errors (in degrees) for the last nine acquisition trials as well as perturbed and non-perturbed conditions. Perturbations were brief torque loads applied at three different loci during the movement.

jects showed little or no decrement in performance as a result of perturbations. No significant effects were observed for any of the dependent variables between the three perturbation loci. Somewhat surprisingly there was kinematic variability in velocity, movement time and oscillations, a result which either points to variability in at least one of the dynamic parameters of stiffness and damping or to the fact that we are looking at a system which is reliable but "dirty" (cf. Greene, in press). In fact, of the 12 subjects nine demonstrated both critical and light damping characteristics and none showed heavy damping (for actual examples see Figure 2).

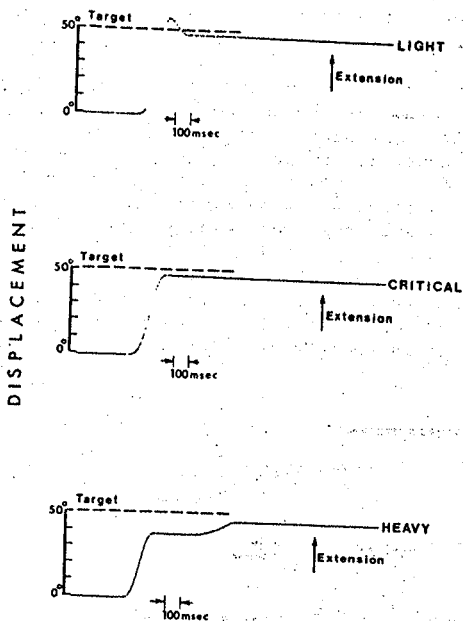


Figure 2. Actual records of one subject performing finger extension movements to a learned target. Figure illustrates light, critical and heavy damping.

There was a tendency towards critical damping in non-perturbed trials (76%) while in perturbed trials there was a slight tendency for light damping. We might have expected that in a learned motor activity these parameters would be maintained constant from trial to trial. Since the task demanded only target attainment, however, the movement patterns by which this goal was achieved probably played a less significant role. Clearly, the system can afford several variations in parameter specification for achieving the steady-state.¹

We confirmed the equifinality result in a second experiment in a variation of the theme employed in Experiment 1. In this case, instead of injecting a brief torque load during the movement, we applied a constant load at the beginning of the movement and released it at unpredictable points during the trajectory. Thus the subjects ($n=10$), after learning the target position as before, performed a set of nine test trials (without knowledge of results), six of which were perturbed and three of which were not. The load was held constant throughout the 50 deg. extension movement (70% max. torque output), until its sudden release at one of three points during the movement (after 10, 25 or 40 deg.). Perturbed and non-perturbed test trials were randomly interspersed for each subject and deviations from the target position noted as before.

A mass-spring model, consonant with the theoretical analysis provided in the previous paper, predicts that the unexpected addition of an external load should lead to an initial undershooting of the target. Once the external force is removed however, and provided the parameters of the system have not been changed, the limb will move to the desired resting length. This is exactly what happened in Experiment 2. Examples of actual recordings from two subjects are shown in Figure 3 and the error data for the ten subjects are presented in Table 1. None of the differences between perturbed and non-perturbed conditions proved significant for either absolute or constant error ($p > .10$). There was an overall tendency to undershoot the target position in both perturbed and non-perturbed trials but no differences were significant as a function of locus of release.

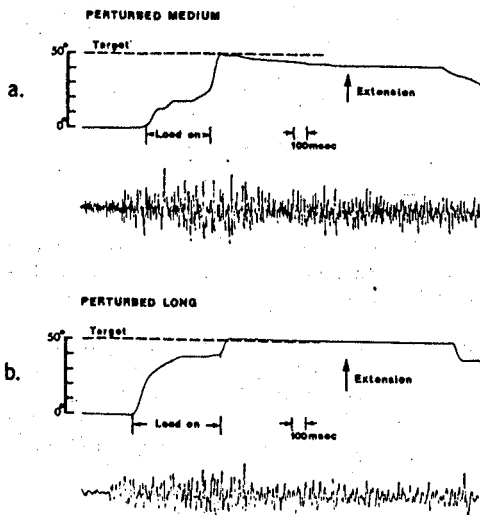


Figure 3. Actual recordings of two different subjects performing a learned movement when a load is suddenly applied at the beginning of the movement and released unpredictably during the trajectory. EMG is from extensor digitorum.

Table I

Means and standard deviations (in deg.) of absolute and constant error for non-perturbed and perturbed (load release) movements (N = 10).

Means		Non- Perturbed ^a	Perturbed ^b Total	Short	Perturbed ^c Medium	Long
Absolute	<u>M</u>	5.97	6.73	5.75	6.70	7.75
Error	<u>SD</u>	4.76	4.23	5.21	4.56	4.83
Constant	<u>M</u>	-4.75	-4.32	-3.79	-4.49	-4.70
Error	<u>SD</u>	-5.86	-6.38	6.61	6.44	7.85

a Means of 3 trials per subject

b Means of 6 trials per subject

c Means of 2 trials per subject

The finding that equally accurate performance was obtained in perturbed and non-perturbed trials in both Experiments 1 and 2 strongly supports the stability property that is characteristic of non-linear oscillatory systems. Although comparisons are somewhat tenuous, our results appear even more favorable for the concept than those obtained for arm movements in monkeys where the errors are quite large (see Figure 2, Polit & Bizzi, 1978). In addition, this is the first time to our knowledge that equifinality in the face of unpredictable perturbations has been observed in human subjects (see also Kelso, 1977).

The foregoing results do not, of course, rule out the possibility of fast-acting peripheral feedback loops (e.g., Cooke & Eastman, 1977; Evars & Granit, 1976) that may have served to modify the movement during its execution. A major prediction of our model-construct however, is that a read-out of conventionally defined proprioceptive information (see Section 4 below) is not a necessary condition for the achievement of the equilibrium position. We therefore examined this issue by injecting load perturbations during the localization movements of individuals who had joint and cutaneous information removed using the wrist cuff technique (see Merton, 1964; Goodwin, McCloskey & Matthews, 1972; Kelso, 1977 for details). 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.²

In this experiment (see Kelso & Holt, in press, for detailed account) we built-in a replication of the first experiment and thus followed its procedure exactly. After the acquisition phase (30 trials with knowledge of results) subjects performed nine perturbed and non-perturbed trials (together designated pre-cuff trials) which were given in random order and with knowledge of results withdrawn. On completion of this phase, subjects 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) subjects performed a further

18 trials in the absence of knowledge of results half of which were perturbed at three different loci.

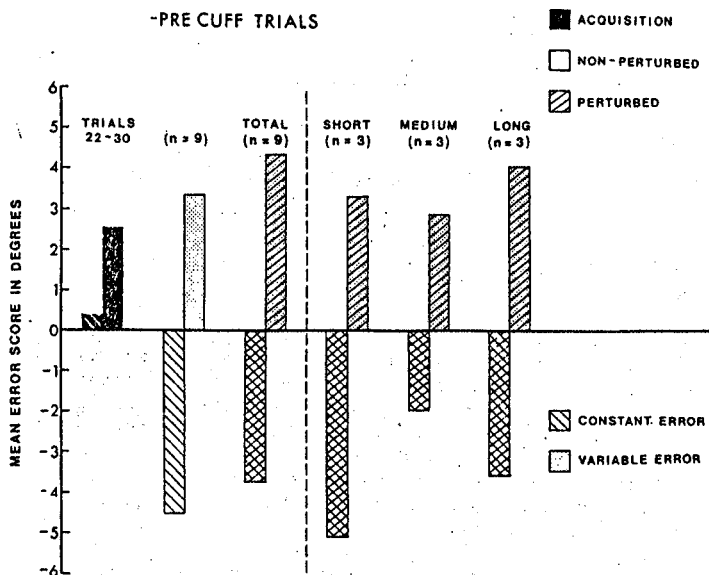


Figure 4. Mean constant and variable errors (in degrees) for acquisition, perturbed and non-perturbed trials prior to application of the wrist cuff.

The results of the acquisition and pre-cuff phases replicated the previous studies in virtually all respects. Collectively these results are shown in Figure 4 for variable and constant error. The only departure from the previous findings was a very modest, but significant increase in variability between perturbed and non-perturbed trials (in the order of 1°). For cuff trials, a comparison of non-perturbed and perturbed trials revealed significant differences for constant and variable error. The mean constant error for non-perturbed trials was larger and more positive than that for perturbed trials and the latter also showed greater variability. As Figure 5 reveals, however, these differences are very modest indeed, and in fact are orders of magnitude less than the boundary conditions set by Polit and Bizzi (1978) for accurate arm movements in monkeys (12 to 15°). Neither pre-cuff nor cuff trials revealed differential error effects as a function of perturbation locus. It should be emphasized that it is not legitimate to compare the accuracy data shown in Figures 4 and 5 due to the substantial time lapse that was necessary for the pressure cuff to exert its effect (between 1 and 1.5 hr.). Although it is not possible to completely discount the possibility of proprioceptive influences on target accuracy, the modest increase in error is likely accounted for by the time delay combined with the absence of knowledge of results regarding performance.

Qualitative differences in EMG activity (extensor digitorum) were examined in pre-cuff and cuff trials. Examples are given in Figure 6 along

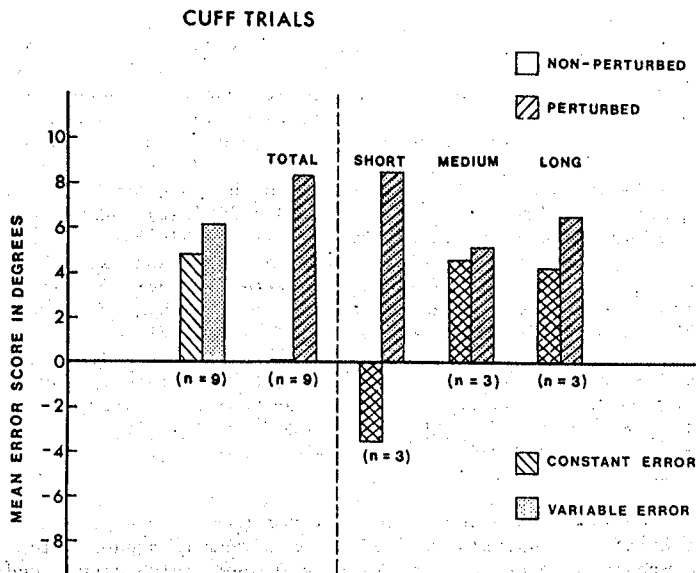


Figure 5. Mean constant and variable errors (in degrees) of perturbed and non-perturbed trials under wrist cuff conditions.

PRE-CUFF TRIALS

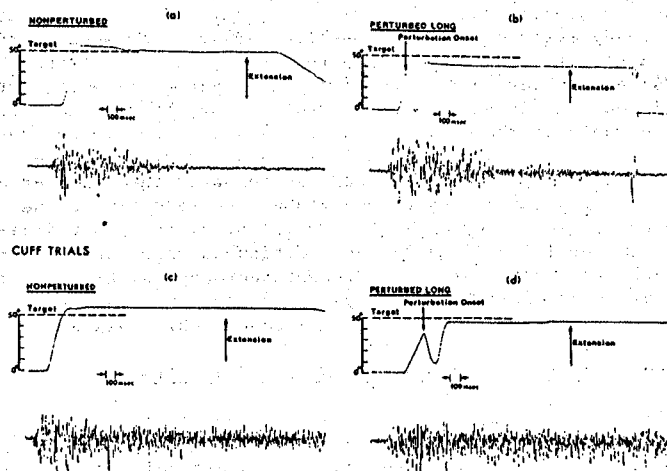


Figure 6. EMG activity of extensor digitorum and movement traces of perturbed and non-perturbed conditions with (c and d) and without wrist cuff (a and b).

with accompanying displacement records illustrating perturbed and non-perturbed movements. As shown in Figure 6(b) 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. Evarts, 1973). In cuff performance, however, electrical activity was constant throughout the movement and signs of stretch reflex function were largely absent (Figure 6(c) and 6(d)). A notable observation was that the activity of the antagonist muscle (not shown here) was close to baseline during pre-cuff trials but highly active during and after achievement of the equilibrium point in cuff conditions.

One final and interesting aspect of the results was that movements in the wrist cuff condition were slower ($\bar{M} = 260^\circ/\text{sec}$, $SD = 80^\circ/\text{sec}$) and movement patterns more consistent than in pre-cuff trials. This may well be related to the observed increase in EMG activity in flexor and extensor muscle groups during cuff movements which was combined (in not necessarily a causal way) with a perceived increase in effort in all subjects. One might suppose that an increase in the conjoint activity of flexors and extensors will have consequences qualitatively similar to increases in the stiffness parameter of a mass-spring system (Fel'dman, 1966). Given a constant damping parameter and increased stiffness, a mass spring system will convert from lightly damped to critically damped (Volterra & Zachmanoglou, 1965), thus suggesting a reason why all our subjects showed critical damping in cuff trials.

In summary, these data which are only briefly summarized here bear out aspects of the theoretical analysis of the system's dynamic organization discussed in the previous paper (Kugler, Kelso & Turvey, this volume) and strongly suggest a mode of coordination and control that has behavioral consequences qualitatively similar to those of a non-linear oscillatory system. Perhaps the most important characteristic of a non-linear system is its stability in the face of perturbations (see Part I) which emerges as the predominant feature in our data. Thus the limb terminates at the steady state originally specified despite unexpected and abrupt load disturbances, functional deafferentation and both of these in conjunction. Harkening back to the geometrodynamical perspective of Part I, we note that this outcome is exactly that predicted by the traveler journeying on a curve whose geometry defines a valley positioned at the resting length of the system and with ascending walls whose slope indexes stiffness. While our manipulations may be seen to force the traveler up the sloping walls of the curve they do not change the tendency of the traveler to return to the valley or stable region of systemic organization. Moreover, our empirical findings are continuous with earlier work (Kelso, 1975; 1977) and, corroborated by recent neurophysiological data, provide a broad basis of experimental support for the model construct proposed here (see also Bizzi, this volume and Cooke, this volume).

3. The Immediate Adjustment Phenomenon in Speech Production

Let us now consider the foregoing analysis of limb movements in relation to an intriguing phenomenon in speech production, namely, how talkers can spontaneously adjust the movement patterns of their articulators in response to various types of disruption yet still produce intelligible acoustic output. Speech researchers have examined this phenomenon quite closely with the intent of discovering the nature of underlying adaptive mechanisms. The broader question of interest concerns, of course, the

issue of context-independency in speech control--the fact that any single phoneme-phoneme transition places unique mechanical demands on the articulators involved--a problem discussed in some detail by MacNeillage (1970) and others (cf. Abbs, 1979; Perkell, 1979).

Consider the intuitive example of the pipe-smoker talking with his/her teeth clenched firmly on the pipe (cf. MacNeillage, 1970). To produce the open vowel /a/ requires some type of compensation for the fact that normal downward mandibular movement does not take place. For example, when speaking with a raised jaw, the normal trajectory of tongue movement is impeded by the fixed mandible. How does the talker accommodate such induced changes? At least two possible explanations seem to be immediately excluded. Lindblom, Lubker and Gay (in press) confirming the earlier work of Lindblom and Sundberg (1971) found that subjects were able to produce natural, steady state vowels with the jaw fixed in an unnatural physiological state by a bite-block without the need for acoustic feedback. "Normal-range" formant patterns were produced in the first glottal pitch-pulse of speech before any auditory information could have assisted the discovery of the appropriate articulator organization. While these studies suggest that adjustment was immediate and that acoustic feedback was insignificant they are not conclusive because they allow the subject to search for the appropriate positioning of the tongue before the production of the sound. Hence compensatory search behavior could feasibly occur before the onset of a measurable acoustic output. A recent study by Fowler and Turvey (Note 2) seems to preclude the articulatory search interpretation. The logic behind the experiment was simply this: In response to a visually presented vowel, a subject will typically require some time to organize the appropriate response. An extensive period of training should ensure a reasonably reliable measure of vocal reaction time under normal conditions. If a bite block is now inserted, and subjects employ an articulatory search strategy before producing an acoustic signal, then vocal reaction time should increase over non bite-block conditions. Preliminary analysis of the data reveals that this is not the case. Moreover, it matters not whether subjects performing under bite block conditions are instructed to maintain reaction time within normal bounds or whether the time stress is removed altogether. Vocal reaction times are the same in each as are the acoustic frequencies of the first and second formant patterns. There is then no speed-accuracy trade-off in the two groups. Thus, articulatory organization does indeed appear to be spontaneous and immediate under bite-block conditions.

How then can such a totally novel and unfamiliar task be produced so rapidly and without any apparent trial and error? What type of system could take into account such dramatic changes in context? An open-loop interpretation can be readily dispensed with for reasons we have outlined earlier (see also, MacNeillage, 1970; Schmidt, 1975). Similarly, a classical closed-loop, servomechanism using peripheral feedback to continually update motor commands to produce a desired state--would be much too slow to account for bite-block phenomena (but see arguments below for dynamic speech case). An alternative espoused by Lindblom and his colleagues (Lindblom et al. in press; Lindblom, McAllister & Lubker, 1977), proposes that the peripheral feedback loop is replaced by a simulation component that derives the sensory consequences of the motor command before it is executed. An internal comparison between the sensory goal and the simulated sensory consequences yields an error which can provide the basis for subsequent motor commands. This type of predictive simulation is

variously referred to as dynamic loop (Eccles, 1973) or model-referenced control (e.g., Arbib, 1972 and this volume; Ito, 1970). To account for their bite block findings, Lindblom et al. (in press) argue that since the predictive component precedes peripheral phonetic output it can provide the system with a simulated set of sensory error signals before the actual motor pattern is sent to the musculature. Thus the system in their words 'learns' from its simulated mistakes before they can exert their effects on the periphery.

Aside from the fact that this model ignores the conjoint problems of degrees of freedom and context-conditioned variability (Bernstein, 1967; Turvey, Shaw & Mace, 1978) as well as the logical problems associated with any servomechanism whether peripherally or internally based (cf. Fowler & Turvey, 1978), it is not consistent with recent data. For example, one interpretation of predictive simulation is that the simulation requires additional computation time to achieve a match between the simulated sensory consequences and the desired state. Given this interpretation it is difficult to imagine why longer than normal reaction times were not realized under bite block conditions in the Fowler and Turvey (Note 2) study. Perhaps more damaging to the simulation model, however, is the finding that vowels whether isolated or inserted in dynamic speech material (e.g. "it's a /pip/ again"), can be produced without any serious acoustic consequences under bite block conditions combined with anesthesia (bilateral sensory blockage of the temporomandibular joint and extensive application of topical anesthetic to structures in and around the oral cavity) and the presence of auditory masking noise (Kelso & Tuller, Note 3). This result is obviously incompatible with a model that proposes the generation of "appropriately revised motor commands on the basis of the feedback positional information available before onset of phonation" (Lindblom et al., in press). If such were the case, much more dramatic effects of sensory interference on acoustic output should have been evident, but this was not so.

The model construct proposed here promises a more elegant account of the immediate adjustment phenomenon. Given a set of variables (such as the components of the vocal tract) constrained to act as unit, the resultant system has properties qualitatively like those of a non-linear oscillatory system. By virtue of its dynamic configuration such a system is capable of attaining its goal -- which is intrinsic to the device -- from any starting point. Furthermore, if certain variables are fixed as a result, for example, of a bite block, the non-frozen variables will assume values appropriate to the constrained relation (see Fowler, Rubin, Remez & Turvey, in press, for the details of this account). Consonant with the theoretical analysis of the preceding paper and the experimental analysis presented in Section 2 of this paper, computationally defined sensory inputs are not a necessary condition for the operation of a group of muscles constrained to act as a functional unit. In theory, at least, our proposed model construct is equally applicable regardless of whether disruptions are static and anticipated (e.g., bite block) or time-varying and unanticipated. Thus Abbs and his colleagues have performed a number of recent studies (cf. Abbs, 1979 for review) in which anticipated disturbances to the lips and jaw were introduced during ongoing speech. "Compensatory responses" of short latency (25-50 msec) were observed in the articulator muscles to which loads were applied as well as in others contributing to the same vocal tract goal. For example, loads applied to

the jaw yielded compensatory adjustments in both inferior and superior orbicularis oris muscles in order to preserve ongoing articulation (e.g., Folkins & Abbs, 1975). In proposing a model to account for such immediate adjustment phenomena, Abbs (1979) suggests that "...while it is plausible to consider parallel pre-adjustment of multiple motor commands (through some sort of efferent copy), in response to steady-state, anticipated disturbances (Lindblom et al., in press) rapid adjustment to dynamic, unanticipated loads appears to require an afferent feedback control capability" (p. 323).

Notice that Abbs' proposal is suggestive of two possibly distinct mechanisms for responses to perturbations--one for anticipated disruptions (a predictive simulation mechanism) and one for unanticipated disruptions (a closed-loop, peripheral feedback mechanism). The present analysis views such a distinction as redundant: rather, immediate adjustment to perturbations of either kind is the necessary outcome of a dynamic system in which a collective of muscles is constrained to act as a unit. One final point is worthy of emphasis. The attainment of a goal for our model construct--producing a vowel, for example--is conceptually distinct from equating the production of a vowel with a spatial target. Vowel attainment is not determined by a set-point or reference value as in a closed-loop servo-mechanism. Granted, the production of a particular vowel may be seen as one member of a class of gestures that aims toward some specific vocal tract shape. But to equate this view of "vowels as gestures" with a "targets" model is to miss the obvious difference between a curve and its asymptotes (Fowler, et al., 1979). Moreover, the achievement of a particular vocal tract shape is a consequence of the vowel production system's parameterization: parameters are intrinsic to the system and do not constitute an externally defined set point which causally determines the system's behavior.

4. Information as intrinsic to the model construct

An oscillatory system does not require the availability of ongoing feedback to be used for comparison purposes with some desired state like a typical servomechanism. In a mass-spring system for example, there is no feedback monitoring or comparison procedure and hence no need to introduce special mechanisms for these purposes. What, then is the role of information in the ongoing control of movement? Clearly an adequate treatment of this issue requires a longer story than we can tell here (but see Kugler, Kelso & Turvey, in press). To be brief, we present some data that is relevant to the question of what information does: we take as an example, that information which is typically thought to be germane to movement, namely, kinesthetic stimulation.

One, not uncommon, view among psychologists is that kinesthetic information, primarily from joint receptors, serves to establish an internal referent of movement somewhere in the brain that can be used to elaborate motor commands and even as a basis for motor learning. Physiological models (usually of cerebellar function) incorporate this notion and extend it as an explanation of highly learned behavior. Thus, when the "internal model" or "perceptual referent" has been firmly established by the feedback and feedforward consequences of movement, the need for kinesthetic stimulation diminishes and "automatization" occurs (cf. Eccles, 1973; Ito, 1970).

Early physiological work on slowly adapting joint receptors in the cat's knee joint (e.g., Boyd & Roberts, 1953; Skoglund, 1956) seemed to pave the way for the view that kinesthetic stimulation is angular specific and served to establish spatial coordinate systems and the like (cf. Russell, 1976). Single neurons from joint receptors were shown to fire maximally at particular joint angles and with a sensitive range of 15 to 30 deg. Such findings have led to the assumption that "receptor firing functions for joint receptors are stored in the perceptual trace"³...Theoretically, learned timing is now seen as a consequence of an image of the firing functions for joint receptors stored in the perceptual trace, and learned position is the storage of which joint receptors have fired" (Adams, 1977, p. 514-515). Aside from the fact that recent and more expansive physiological data discount the earlier findings (for review see Kelso, 1978; Lee & Kelso, in press), from our perspective the "image" is no more a list of receptor firing functions than is the plan for an act a list of commands to muscles.

In the previous paper it was argued that the distinction between variables of control and coordination is not a fixed one, but rather is topologically defined by the system's dynamics. The argument, in brief; was that the informational predicates are qualitative rather than quantitative in nature. Moreover, information is conceived as information about the current state of the system's dynamics in the sense of information specific to the system's dynamics. For example, information regarding the properties of a surface (e.g. its sponginess or compliance) not only informs the individual of the surface attributes (e.g. soft or hard) but specifies in a complementary way, what the stiffness of the muscular system for postural support must be.

Experimentally, it can be shown that dimension-specific information--at least about joint angle--does not appear to be crucial to the perception and control of human movement. Briefly, we examined the movement production of 13 patients during a period from two days to four weeks following total joint replacement of the metacarpophalangeal joints (see Kelso, Holt & Flatt, 1979, Note 1). The operation involves complete surgical removal of the joint capsule--the supposed seat of position and movement detectors--and replacement of the articular surfaces. One experiment examined finger positioning accuracy under conditions where the starting position changed from trial to trial. Patients moved actively to various angles of finger flexion that defined criterion movements and then were passively returned to different starting positions. Under one condition the patient was asked to reproduce the final position of the criterion movement; in another condition the patient was required to reproduce the original distance or amplitude (see Kelso, 1977 for a detailed account of this paradigm). The findings which are shown in Table 2 were very clear: final position was much more accurate than amplitude and, as revealed by both constant and absolute error was hardly affected by changes in initial conditions. Moreover, amplitude performance reflected a bias to reproduce location. Even though task demands required the production of amplitude, the motor system appears to be predisposed to achieve final position. More important, the level of error in joint replacement patients was readily comparable with normal levels in 12 subjects (mean absolute error = 4.40 deg.).

One way of interpreting the differences between location and amplitude

TABLE 2

Mean errors (in degrees) for amplitude and location conditions as a function of changes in starting position in patients (N=13) following total metacarpophalangeal joint replacement.

		Amplitude		Location	
		Absolute Error	Constant Error	Absolute Error	Constant Error
^a Starting Position ₁	<u>M</u>	5.71	3.67	3.67	1.36
	<u>SD</u>	3.17	5.23	2.05	3.66
Starting Position ₂	<u>M</u>	9.19	8.34	4.29	-0.19
	<u>SD</u>	5.47	6.26	2.54	4.41

^a The starting position was either 5 deg (SP₁) or 15 deg (SP₂) beyond the original starting position of 20 deg flexion, i.e., in 15 deg and 5 deg flexion respectively.

conditions is that there is a location code based on information provided by some type of peripheral receptor or set of receptors. Reproduction of location may then be viewed as a matching of receptor inputs to the stored referent or spatial code. Reproduction of amplitude however is more difficult in that the change in starting position requires an additional subtractive process relative to the spatial code. Thus to reproduce accurately, a new spatial code must somehow be derived to take into account the change in starting position (e.g. Stelmach & McCracken, 1978).

But an alternative, more parsimonious account and one that is entirely consonant with an oscillatory system analysis, equates the achievement of location with the steady state of the system determined only by its dynamic organization. Note how the two interpretations discussed here differ in perspective. In the former, kinematic details, such as the position coordinates of the limb are represented in some internal reference system. In contrast, a system that is like a mass-spring system cannot be said to represent a kinematic detail such as final position; to the contrary, the dynamic parameters determine the kinematic consequences.

With reference to the present data, the argument that a muscle system behaves qualitatively like a mass-spring system clearly negates reliable reproduction of amplitude (a kinematic detail) from variable initial conditions. Furthermore, the finding that accurate positioning is possible in the absence of slowly adapting joint afferents dampens enthusiasm for the view that angular specific receptors contribute to the development of a spatial code. While such receptors have typically been regarded as contributing--or not contributing--specific types of kinematic information (e.g. position, rate) to a central interpreting device, our predisposition is to suppose that peripheral receptor information is not dimension-specific. Instead, their function may be to tune or modulate lower-level spinal centers (interneuronal pools) so that simple, undifferentiated supra-spinal signals may exert optimum facilitatory effects on the muscles served by such pools.

The research of Aizerman and his colleagues (e.g. Aizerman & Andreeva, 1968; Chernov, 1968; Litvintsev, 1972), has provided evidence for this tuning viewpoint with reference to kinesthetic stimulation in such activities as postural adjustment, pain avoidance and precision aiming. In the latter task, for example, the subject is instructed to maintain the position of the radio-carpal joint consonant with a point on an oscilloscope screen whose gain factor is increased such that a 1 to 2 min. angle takes the point beyond screen limits (Chernov, 1968). During 'precision aiming' the electromyographic envelopes of the two muscle antagonists display alternating peaks at around 10 Hz. These peaks oscillate such that when the joint is moved in one direction a large peak arises approximately once a period (around 100 msec). It should be emphasized that both muscles pull at 10 Hz, but one is apparently biased to have a slightly higher amplitude than the other and so the limb moves. An identical result holds for rapid shaking of the wrist joint: only the amplitude of oscillation changes. To account for these and other findings Aizerman and Andreeva (1968) coin the term simple search mechanism whose central elements are a set of randomly interconnected neurons in the spinal cord, the random interneuron pool (RIP) and a mathematical function which, in the case of precision aiming, depends on the magnitude and velocity of joint angle (or, more precisely the muscle states that define these values).

The RIP output is determined by the number of interneurons, N_e , excited at any moment. In response to an impulse volley the value of N_e increases to a maximum defining the magnitude of the RIP 'peak' and then drops to a mean value about which it oscillates. The resting state of the autonomous RIP therefore corresponds to this value and the oscillation itself constitutes tremor. Clearly the background state of the RIP can affect the magnitude of the 'peak'; the actual duration of the descending signal or its intensity characteristics have little effect. Thus, during the task of 'precision aiming' non-differentiated impulses are sent simultaneously to both muscle antagonists involved in controlling joint angle. Peaks of muscular activity therefore arise in both muscles, but the larger peak arises in the muscle that is at that moment extended; that is muscle spindle inputs from the temporarily extended muscle lower the background state of the interneuronal pool and thereby insure that the extensor obtains the stronger peak. If one such peak serves to change joint angle in the direction of extension, the flexor muscle is lengthened: thus, on the next downward signal, the stronger peak occurs in the flexor and so the cycle is repeated.

Perhaps a more intuitive example comes from the maintenance of posture (Litvintsev, 1972). If a person in a relaxed position is pushed in the back, the muscle spindles in the gastrocnemius and hamstring muscle groups will be stretched. An undifferentiated supraspinal command pulse results in the activation of only those muscles whose spindle inputs define the background state of the interneuronal pool. Consequently, selective activation of the stretched muscles automatically gives rise to forces that preserve vertical posture. It seems imminently possible that kinesthetic stimulation in general (and not just muscle spindle inputs alone) serves a similar "tuning" function.⁴ One obvious advantage of the simple search mechanism is that it obviates the need to select which muscles to contract; rather selective contraction occurs by virtue of the state of the interneuronal pools. Notice also that oscillation in the interneuronal pools is not some aberrant characteristic to be regulated. It is, instead an

intrinsically periodic process that appears to be exploited for movement control purposes. But even more important for the present discussion is the proposal--borne out in part by the data presented here and the Aizerman type of analysis--that kinesthetic "information" does not provide quantitative values on certain kinematic variables to some interpreting device. Rational considerations and a commitment to the primacy of dynamics persuade us that "information," however conceived is not likely to be something that contributes to a reference mechanism whose goal resides outside the system itself.

5. Concluding remarks

In this paper as in its predecessor we have attempted to provide a principled basis for coordination and control, one that recognizes and emphasizes constraints on the free variables of a system as the necessary requirement for coordinated movement. True to Bernstein's problem, we have promoted a model construct that for us takes out the least loan on intelligence by minimizing the number of so-called "executive" decisions and the requirements for on-line control. Control and coordination arise we believe from the synergic relations among muscles: to a first approximation this synergy or coordinative structure is a force-driven oscillatory system with the qualitative characteristics of a mass-spring. More properly it is, as Yates, Marsh and Iberall (1972) remark, the minimal assembly of components that sustains periodic energy transformations (power fluxes) and information fluxes (see also Part 1).

Let us acknowledge in these final comments that of the data we have presented in favor of the model construct, none are individually persuasive. Collectively, however, they provide a compelling basis of support for an oscillatory system proposal while at the same time supplying empirical reasons for questioning machine-type theories of the conventional cybernetic and artificial intelligence kind. An oscillatory system conception brings with it, however, its own unique set of questions. For instance, it is not easy to distinguish the roles of efferent and afferent information, at least as they are classically defined. Servomechanisms, in contrast have an appeal to some in this regard: afference is input to a referent value and the consequent comparison (error) determines what the efferent output or correction will be. Efference and afference are conceptually distinct. But as we have taken pains to establish, a system such as a mass-spring is not a servo-mechanism and it would be erroneous to describe it as one. There is no afference to be monitored and compared nor errors to be computed and corrected. The system behaves as it does by virtue of its dynamic organization which is intrinsic to the system.

Elsewhere we have argued that where a collective of muscles functions as a unit the efferent-afferent distinction becomes superfluous. Thus if muscles are linked synergistically, information about the current state of a given muscle (afference) is also, by virtue of the linkage, a specification of the states of other muscles (efference) to which it is functionally linked (cf. Kugler & Turvey, in press). Different theories of motor control place undue importance on either efference (e.g. motor programs) or afference (closed-loop systems); in contrast, the constraint (geometrico-dynamic) perspective assigns primacy to neither but equal priority to both. Such a perspective is much more in line with the functional organization of the nervous system revealing interactions at all levels of the neuraxis

and the fact that the Bell-Magendie law is now extinct (cf. Smith, 1978). In addition, it is consonant with the view expressed many years ago by Sperry (1952) and more recently emphasized by Diamond (1979) that the classical post-central (sensory)-precentral (motor) cortex distinction does not fit the actual patterning of information flux in the cortex. Both "afferent" and "efferent" paths can be linked, for example, to post central cortex thus enabling this structure to perform both a "sensory" and a "motor" function. Our suspicion therefore, is that inquiry into the control and coordination of movement may be ill-served by the traditional distinction between sensory and motor (see Evarts, Bizzi, Burke, DeLong & Thach, 1971). In fairness, however, we should admit that the details of the informational support for an organization of muscles that is qualitatively like an oscillatory system such as a mass-spring system presents a major challenge.

A dominant theme throughout this paper--in acknowledgement of Bernstein's problem--has been to minimize the number of executive instructions and to keep those instructions simple in content. Multivariable systems may be optimally controlled via a small set of autonomously regulated variables constrained in such a way that just a few parameters are required. In this claim we mirror for movement, Runeson's (1977) requirement for "smart" perceptual devices that register directly a complex variable--a complex particular (Pittenger, Shaw & Mark, 1979; Turvey & Shaw, 1979)--yet consist of only a few specialized components which are capable of solving problems that repeatedly occur. There are a number of valid comparisons between our model construct as a "smart" motor device and the type of perceptual mechanism envisaged by Runeson (1977).

The guiding philosophy behind our approach to understanding motor systems should by now be blatantly apparent: Reject the introduction of new mechanisms and principles until, at least, the laws of dynamics have been fully explored. As Yates and Iberall (1973) emphasize, as did others in the past (e.g. von Bertalanffy, 1953; Weiss, 1941), it has been much easier to explain living (and we would say movement) systems in terms of a deus ex machina outside the system than to discover causality and start-up processes within the dynamic organization of the system itself. If nothing else in this paper and its companion we have given notice as to where our bets are placed.

Reference Notes

- ¹Kelso, J. A. S., Holt, K. G., & Flatt, A. E. Towards a theoretical reassessment of the role of proprioception in the perception and control of human movement. Manuscript in review.
- ²Fowler, C. A. & Turvey, M. T. Manuscript in preparation.
- ³Kelso, J. A. S. & Tuller, B. Manuscript in preparation.

Footnotes

- ¹This is readily apparent from the intrinsic relationship between c^2 and $4mk$ in the equation of motion for a simple mass-spring system (see earlier discussion).
- ²Three independent sources of evidence speak to the viability of the wrist cuff technique as a tool in reducing mechanoreceptive information. First,

passive displacements of the metacarpophalangeal joint up to an estimated 90°/sec went 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 be an unlikely finding. Third, it has been consistently verified that the loss of background facilitation from joint and cutaneous sources using this procedure depresses stretch reflex function (e.g., Marsden, Merton & Morton, 1972; Merton, 1974).

³ In Adams' (1977) words, "the perceptual trace is a learned reference of correctness for the movement based on feedback from response-produced stimuli" (p. 514).

⁴ It may be the case that visual and auditory information serve a similar tuning function via a form of reflex input into the interneuronal pools. There is evidence, admittedly preliminary in nature, that may be viewed as supportive of such a notion for vision (e.g. Thoden, Dichgans & Savidis, 1977) and for audition (e.g. Melville-Jones, Watt & Rossignol, 1973).

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