Task Dynamics and Resource Dynamics in the Assembly of a Coordinated Rhythmic Activity

Geoffrey P. Bingham
Indiana University

R. C. Schmidt and M. T. Turvey
Center for the Ecological Study of Perception and Action
University of Connecticut
Haskins Laboratories, New Haven, Connecticut

Lawrence D. Rosenblum
University of California, Riverside

Task dynamics corresponding to rhythmic movements emerge from interactions among dynamical resources composed of the musculature, the link segments, and the nervous and circulatory systems. This article investigated whether perturbations of interlimb coordination might be effected over circulatory and nervous elements. Stiffness of wrist-pendulums oscillated at a common tempo and at 180° relative phase was perturbed through the use of tonic activity about an ankle. Left and right stiffnesses, the common period, and the phase relation all changed. Stiffnesses increased with ankle torque in proportion to the wrist's inertial load. Despite different changes in stiffness at the two wrists, isochrony was preserved. The stability was shown to be consistent with the proportionality of changes in stiffness to the inertial loads. The phase departed from antiphase in proportion to the asymmetry of inertial loads. The size of departures decreased with increasing ankle torque. An account was developed in terms of muscular, circulatory, and nervous functions.

To perform familiar tasks, like patting a cat, pumping up a tire, scratching an itch, or walking the dog, the human action system assembles coordinated rhythmic movements from a profusion of resources composed of the musculature, the jointed link segments of the skeleton, and the myriad elements of the nervous and circulatory systems. Each of the components used has a particular nonlinear dynamic. From complex interactions among these dynamical resources emerges the coherent, low-dimensional task dynamics corresponding to the rhythmic movements themselves (Kugler & Turvey, 1987; Saltzman & Kelso, 1986). Although the functionally prescribed task dynamic can be observed and measured directly, the resource dynamics used to assemble it can, with few exceptions, be evaluated only indirectly (Bingham, 1988). In this article, we investigate interactions that originate in resource-dynamic components that have not been considered traditionally as constraining movement organization. We consider whether and how the circulatory system (as well as the nervous system) might constrain interlimb coordination. Might perturbations be effected over distances mediated only by circulatory and nervous elements? By using tonic activity about an ankle, we perturbed the task dynamics corresponding to coordinated rhythmic movements about the wrists.

Intralimb Interactions

Studies of coordination focus predominantly on the timing or phasing of joint activity. Interactions among moving joints

place strong constraints on possible timing relations. Intralimb joint motions can interact because of properties of the link segments as well as of the muscles (Aleshinsky, 1986; Bingham, 1988; Whiting, 1984). Link-segment motions around a given joint give rise to reaction torques that affect motions at other joints in the chain (Brady, Hollerbach, Johnson, Lozano-Perez, & Mason, 1982; Hollerbach & Flash, 1982; Saltzman, 1979). Furthermore, angular positions at more distal joints determine effective inertial properties for segments joining at more proximal joints (Hogan, 1985; Saltzman, 1979). Finally, biarticular muscles can produce energy flows between joints and allow positions at one joint to affect torques generated at another (Bobbert, 1988; Van Ingen Schenau, 1989).

Producing a prescribed movement by controlling applied torques at the joints so as to counteract interactions is a difficult problem. The problem grows in complexity as the number of degrees of freedom associated with the joints used increases (Whiting, 1984). In addition, such organization would be very inefficient in the use of energy. Energy originally generated through applied torques is wasted in reaction torques, whereas additional energy is consumed in actively resisting reaction torques. Inspired by these observations, Nicholas Bernstein hypothesized that movement is so organized that it takes advantage of the interactions that arise (Whiting, 1984). In fact, many motor achievements are possible only because interactions are used to develop sufficient energy for the act (Aleshinsky, 1986; Bingham, 1988; Bobbert, 1988; Van Ingen Schenau, 1989). This is true, for instance, of overhand throwing, which entails a flow of mechanical energy over the link segments from the trunk to the hand (Bingham, Schmidt, & Rosenblum, 1989; Jöris, van Muyen, Van Ingen Schenau, & Kemper, 1985).

Bernstein's perspective has led to a program for the study of motor organization in terms of coordinative structures or

task dynamics (Bingham, 1988; Kelso, Tuller, Bateson, & Fowler, 1984; Kugler, Kelso, & Turvey, 1980; Saltzman & Kelso, 1986; Turvey, 1977; Turvey, Shaw, & Mace, 1978; Whiting, 1984). This approach construes actions as performed through controllable higher order functional units that are assembled from link-segment, muscular, nervous, and circulatory components. The functionally coherent structure to be controlled in performance is hypothesized to emerge from interactions of components that are known to be nonlinear. The approach partitions the original problem of control into two problems (Bingham, 1988). The first is the problem of assembly. How are nervous, circulatory, muscular, and link-segment components organized into a unitary, stable, and suitable task-specific structure? The second problem is the problem of control. How are the appropriate control parameters discovered and used? Because a controllable structure is a prerequisite for control, the problem of assembly takes precedence.

The emphasis in this approach to motor organization falls naturally on interactions among assembled components, because the functionally coherent and effective organization of interest is hypothesized to emerge from such interactions. Interactions undoubtedly play a role in intralimb movement because of flows of mechanical energy that occur along the contiguous connected elements of a link chain. What interactions might arise to constrain organization in interlimb coordination?

Interlimb Interactions

Link-segment interactions are sometimes relevant in the context of interlimb coordination. In tasks like overhand throwing or running, the energy flows used to develop sufficient energy for the task mean that joint motions in one limb affect those in another. In the absence of such energy flows, however, the only possible sources of interaction are the nervous and circulatory systems.

The existence of constraints on possible interlimb coordinations is obvious to anyone who has tried to tap in 3/4 time with one hand and in 4/4 time with the other. The possible coordinative modes are limited (Beek, 1989). Kelso and his colleagues have studied stable modes of coordination in bimanual activity (Kelso, 1984; Kelso, Scholz, & Schöner, 1986; Kelso, Schöner, Scholz, & Haken, 1987; Scholz, Kelso, & Schöner, 1987). They have found that stable phase relations for isochronous rhythmic movements change from either inphase or antiphase to only antiphase with increasing frequency. However, where the constraints on these phase relations originate is not yet clear.

Observed phase relations have often been ascribed to timing properties intrinsic to the nervous system (Grillner, 1981; Kopell, 1988; Rand, Cohen, & Holmes, 1988; Stein, 1976). The hypothetical origins of timing in the nervous system vary from single element generators to nonlinear networks. In all cases, neural timing is imposed on concurrent activity in different limbs. An alternative but not mutually exclusive account has focused on responses of the musculature in different limbs to homogeneous neural input (Rosenblum & Turvey, 1988). In this case, phase relations would originate

from the response time of the musculature in the face of different force requirements. The muscle property has been invoked as a determinant factor in coordination, combined with a lack of correction or differential modulation by the nervous system.

Both of these accounts only require a flow of activity from the nervous system to the muscles. No flow in the reverse direction is entailed. Thus, there is no suggestion in either instance that the specific activity at a joint might directly influence activity at a joint in another limb. Nevertheless, there are reasons to expect this possibility. With respect to the nervous system, activity at the periphery can determine, through afferents, tonic levels of activity in the spine and brain that, in turn, can influence activity in other peripheral areas (Arshavsky, Gelfand, & Orlovsky, 1986). With respect to the circulatory system, activity in a muscle can affect the level of heart activity, which, in turn, can influence activity in other muscles (Hollander & Bouman, 1975; Laughlin & Armstrong, 1985). These observations imply that the level of activity in one limb might be affected directly by the specific level of activity in another. Because the levels of activity of muscles vary continuously over the course of movements, interactions among respective levels of activity at coordinated joints strongly constrain the potential forms of coordination. In the present research, we studied how the level of voluntary activity in one limb might affect rhythmic activity in another. Specifically, we investigated whether a steady torque exerted about one joint would influence simultaneous rhythmic activity about joints in other limbs, and furthermore, whether the level of tonic activity would be reflected in the degree of change in rhythmic activity.

In choosing the particular combination of joints, we wished to capture a common circumstance in daily activity. People often perform manual activity while standing and maintaining balance. The frequency of the activity in the upper limbs is typically high relative to the frequency of modulations at the ankles. The essential properties of this situation can be captured in a task that requires coordinated rhythmic activity about the wrists in the context of tonic activity about an ankle.[1] The question is, what is the effect of the perturbation, controlled at the ankle, on the coordination between the wrists?

We used a bimanual task in which seated participants were asked to swing two weighted rods, held in either hand, at the most comfortable common tempo. The rods were oscillated in antiphase. The lengths of the two rods were varied. We selected this manual task for three reasons. First, the task has been studied extensively and much is known about it (Kugler & Turvey, 1987; Rosenblum & Turvey, 1988; Turvey, Rosenblum, Schmidt, & Kugler, 1986; Turvey, Schmidt, Rosen-

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[1] This approximation reflects a strategy in dynamical systems in which a dynamic is partitioned into fast and slow components (Percival & Richards, 1982; Thompson & Stewart, 1986). The slow components are then treated as control parameters used to perturb the fast dynamic. After perturbation or change in the control parameters, the fast dynamic is allowed to settle and is then examined to discover what properties of the original behavior remain the same after perturbation.

blum, & Kugler, 1988). Second, the task entails controlled variation of asymmetric loadings in the two hands. This is an aspect common to a wide assortment of bimanual activities. Third, the behavior is characteristically stable and reliably reproduced by participants. In a number of studies, the periods and relative phases of movement have been found to be highly stable within trials and reproducible over trials that were separated by months in some instances.

The specific questions that we investigated were formulated in the context of a task-dynamic model of extant results from investigations of this task.

The Wrist-Pendulum Dynamic

The fundamental question addressed in previous studies concerned observed periods. How did participants reliably select stable periods corresponding to the most comfortable tempos? Kugler and Turvey (1987) suggested that the answer lay in the character of the assembled task dynamic. A model of a task dynamic simulates trajectories observed in a given experimental task. The components of the model describe observable dynamical elements of the actor and the environment involved in the execution of the activity. Kugler and Turvey modeled a single hand-held pendulum as a "simple pendulum" in which movement is constrained by gravity and an elastic stiffness. The stiffness parameter was used to represent contributions to movement by the musculature. The inertial variables include both hand and pendulum masses. The model is shown in Figure 1. The equation for the period derived from the linear form of the model is as follows (Turvey et al., 1988):

$$\tau = \left[\frac{4\pi^2 ML^2}{K + gML}\right]^{1/2}, \qquad (1)$$

where M and L are the simple pendulum mass and length, g is gravitational acceleration, K is the stiffness, and where M, L, K, and τ should be subscripted R or L for the right or left
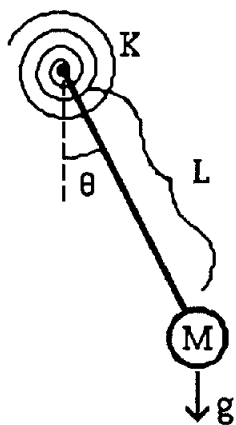

Figure 1. The wrist-pendulum model. (In using a torsional spring, we have removed a parameter [b] that appears in Turvey, Schmidt, Rosenblum, & Kugler [1988] and represents the distance from the point of attachment of a compression spring to the axis of rotation. See the text for a description of the parameters.)

hand respectively. A simple pendulum consists of a mass conceptualized as sitting at a point located at the end of a massless string. Kugler and Turvey (1987) computed the simple pendulum equivalent mass and length for the compound pendulum consisting of a hand and a wooden dowel with lead weights affixed to its end (see also Turvey et al., 1986).

The period of a simple pendulum is predicted by its length. If stiffness can be ignored (i.e., K = 0), then, according to the model, the period of a single hand-held pendulum swung in isolation would be expected to scale with simple pendulum length raised to the one-half power, that is, $\tau \propto L^{1/2}$. Observations conformed to this scaling relation confirming the intuition that the "most comfortable" stiffnesses should be close to zero, that is, letting gravity do the swinging (Kugler & Turvey, 1987).

The question is, what happens when two pendulums are swung together at the same tempo? If the pendulums are of the same simple pendulum length, one might guess that the resulting period should be the same as that of the individual pendulums swung in isolation. Furthermore, if the pendulums are of different simple pendulum lengths, one might suppose that the coordinated period should lie between the periods for the respective pendulums in isolation. However, both of these expectations have been violated by observations (Kugler & Turvey, 1987; Turvey et al., 1986). For instance, periods for pendulums of equal length swung in coordination were typically longer than the period for either pendulum swung in isolation. The conclusion these researchers reached was that varieties of period averaging can not be used to model the periods exhibited in coordinated movement.

As an alternative explanation, Kugler and Turvey (1987) suggested that periods for pendulums swung in coordination should be predicted by the same relation that was used to predict periods for pendulums swung in isolation. However, Equation (1) requires values for the mass and length of a single simple pendulum. Their suggestion was that the separate hand-held pendulums be treated as if they were coupled rigidly into a single virtual compound pendulum. Accordingly, they used the simple pendulum masses and lengths of the separate pendulums to compute in each instance an equivalent virtual simple pendulum length (L_v) and mass (M_v). These values were used in a virtual wrist-pendulum model described as follows:

$$\tau = \left[\frac{4\pi^2 M_v L_v^2}{K_v + gM_v L_v}\right]^{1/2}, \qquad (2)$$

where $M_v = M_R + M_L$ and

$$L_v = \frac{M_R L_R^2 + M_L L_L^2}{M_R L_R + M_L L_L}.$$

As before, if $K_v = 0$, then $\tau = [4\pi^2/g]^{1/2}L_v^{1/2}$ so that $\tau \propto L_v^{1/2}$, that is, period scales with virtual length to the one-half power. Observed departures from this scaling relation were attributed to nonzero values of K_v, (Turvey et al., 1988). As K_v grows large the effect of the ($gM_v L_v$) term diminishes in proportion and, at limit, $\tau = [4\pi^2/K_v]^{1/2}[M_v L_v^2]^{1/2}$ so that $\tau \propto (M_v^{1/2}L_v^1)$. Thus, the value of the scaling exponent on virtual

length increases with increasing values of K_v with an asymptote at 1. Observed departures from an exponent of $1/2$ corresponded as predicted to nonzero values of K. Also, with nonzero K_v values, M_v enters the scaling with an exponent increasing in proportion to increasing K_v to an asymptote at $1/2$. Nevertheless, because the "most comfortable" K_v values were close to zero, observed periods for pendulums swung in coordination scaled approximately with $L_v^{1/2}$.

Revision and Simplification of the Model

What is a virtual stiffness, K_v? Kugler and Turvey (1987) described relations between the Ms and Ls for the individual and virtual wrist-pendulums respectively, but they did not describe the relation between K_v in Equation (2) and the stiffnesses of the separate left- and right-hand wrist-pendulums. Because these stiffnesses represent the contribution of the person and his or her musculature, nervous system, and so on to the assembly, maintenance, coordination, and control of this activity, understanding their relation to the model of coordinated activity is of focal importance.

A virtual stiffness would have to be assembled from the stiffnesses associated with the right- and left-hand wrist-pendulums represented by the correspondingly subscripted versions of Equation (1). The movement task required that the two pendulums be swung with a common period, $\tau_R = \tau_L = \tau$. This allows us to set the right- and left-hand versions of Equation (1) equal to one another. With rearrangement and canceling of terms, this yields the following:

$$\frac{M_R L_R^2}{M_L L_L^2} = \frac{K_R + gM_R L_R}{K_L + gM_L L_L}. \tag{3}$$

In words, if the two wrist-pendulums are to run at a common period, then the ratio of their summed harmonic terms, elastic and gravitational, must equal the ratio of their inertias. If both stiffnesses, K_R and K_L, equal zero, this equation tells us that the two pendulums must be of the same length, which is just the case if two simple pendulums are to run under gravity alone at a common tempo within the range of motion suitably approximated by the linear model. (See Appendix A for a discussion of the adequacy of the linear approximation.) For equal pendulums, the stiffnesses may take on equivalent nonzero values. As soon as the hand-held pendulums are of unequal simple pendulum lengths, K_R and K_L must take on nonzero values. Given a value for one of the two Ks, Equation (3) determines the value of the remaining K. There remains a degree of freedom in the selection of the initial K value. Participants vary in their range of preferred K values, but reliably select values within their own preferred range (Turvey et al., 1988, Figure 15, p. 303).

How do the combined stiffnesses of the right- and left-hand systems act together with the lengths and masses of the respective pendulums to determine the period of coordinated movement? Kugler and Turvey (1987) addressed this question by focusing on the lengths and masses of the pendulums and formulated the virtual system model in answer. With an alternative focus on K_R and K_L, we have sought a solution through the respective equations of motion of the two wrist-

pendulum systems:

$$M_R L_R^2 \ddot{\theta}_R(t) + [K_R + gM_R L_R]\theta_R(t) = 0,$$

$$M_L L_L^2 \ddot{\theta}_L(t) + [K_L + gM_L L_L]\theta_L(t) = 0. \tag{4}$$

From these equations, using the task requirement of a single common period, we derived a single equation of motion in variables common to the individual systems (see Appendix B):

$$[M_R L_R^2 + M_L L_L^2]\ddot{\theta}^*(t) + \{K_R + K_L$$
$$+ g[M_R L_R + M_L L_L]\}\theta^*(t) = 0. \tag{5}$$

Integrating this equation yielded the equation for the period as follows:

$$\tau = \left[\frac{4\pi^2(M_R L_R^2 + M_L L_L^2)}{K_R + K_L + g(M_R L_R + M_L L_L)}\right]^{1/2}. \tag{6}$$

This equation is an analytically equivalent but greatly simplified form of Equation (2), the model for the virtual wrist-pendulum (when written out in terms of right- and left-hand masses and lengths). Equation (6) describes how two separate wrist-pendulums run together at a common period. Reference to a single virtual system is no longer appropriate because the quantities that would describe the properties of a virtual system do not reside in this equation in a form that can be isolated analytically. However, L_v is contained in the equation in nonanalytic form. Thus, the equation accounts for the observed approximate scaling relation between τ and $L_v^{1/2}$. Given the analytical equivalence of Equations (2) and (6), they must be equivalent in accounting for the observed scaling relations.

Kugler and Turvey (1987) originally had developed an understanding of the observed scaling between period and pendulum lengths and masses based on a set of empirically derived biological scaling constants. Turvey et al. (1988) rejected this approach in favor of a derivation of the scaling relations directly from the wrist-pendulum dynamic. Nevertheless, Turvey et al. (1988) preserved an account in terms of a virtual pendulum invoking an assumed (simulated) rigid coupling. The current revision reveals that observed scaling can be attributed entirely to the wrist-pendulum dynamic at each of the two wrists given the task requirement of swinging the two pendulums at the most comfortable common tempo. Reference to a virtual length or to virtual mass or stiffness is no longer appropriate, and the notion of a rigid coupling between the pendulums is not required.[2] Equation (6) describes the dependence of observed periods on pendulum

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[2] Initially, we had inquired as to the relation between K_v and K_R or K_L. The relation conveys the superfluity of the virtual pendulum analysis: $K_v = [1/(M_R L_R + M_L L_L)][M_v L_v][K_R + K_L]$. To obtain Equation (2), Equation (6) must be multiplied by the ratio of $M_v L_v$ to itself and by the ratio of $(M_R L_R + M_L L_L)$ to itself, followed by rearrangement of terms. That is, Equation (6) must be multiplied by one twice. We consider the (nonanalytic) appearance of the equivalent simple pendulum length in Equation (6) to be coincidence. However, if the action system was discovered to be taking advantage of this approximate circumstance, this would provide a good instance of a smart device (Bingham, 1988; Runeson, 1977).

masses and lengths as well as on the stiffnesses assembled at the two joints. Equation (3) describes the relation between the left- and right-hand stiffnesses required for phase locking at a common period.

Interlimb Perturbation of Stiffness

How are the stiffnesses at the two wrist joints assembled so as to run the pendulums at a common period? Intrinsic interactions between the wrists would constrain any potential coordination. This leads us to consider the relation between the task dynamic and the component resources used to assemble it. Are the components used in the assembly of stiffness essentially local and restricted in their effect to the particular limb, or might some components having a global character contribute to interactive effects in the two stiffnesses?

The way to investigate this question is to try to perturb or change the stiffness corresponding to rhythmic activity about a wrist by manipulating activity about a joint in another limb. Using phasic perturbations would introduce the problem of distinguishing the perturbation of a given dynamic from the assembly of a new and distinct dynamic with a new oscillatory regime. Resulting effects might be attributed solely to the dynamics of the nervous system acting to generate a new type of oscillatory pattern. In contrast, tonic perturbations provide a continuum along which perturbations may be metered without adding rhythmic complexity, that is, more oscillators. Of course, interpretation of any resulting effect will depend on the parameters found to mediate the perturbation.

Using data from an experiment reported in Kugler and Turvey (1987), we were able to determine that the stiffness of the wrist-pendulum dynamic can be perturbed by tonic activity in another limb. In that experiment, four different participants swung a single pendulum in one hand while squeezing a dynamometer in the other hand. Participants swung four different pendulums that varied in length and mass. They squeezed the dynamometer at levels equal to either 0%, 25%, or 50% of their maximum grip force. Kugler and Turvey (1987) analyzed and presented results for periods. By using their reported means and Equation (1), we computed the corresponding stiffnesses and reanalyzed their data.

The results appear in Figure 2, where it can be seen that for some pendulums stiffness increased significantly with increasing force levels in the other hand, whereas for other pendulums, stiffness increased less or not at all. In a two-variable repeated-measures analysis of variance (ANOVA) performed on stiffness, with force level (0%, 25%, and 50%) and simple pendulum length (1–4) as variables, both force level, $F(2, 6) = 8.80$, $p < .02$, and simple pendulum length, $F(3, 9) = 66.57$, $p < .001$, were significant, as was their interaction, $F(6, 18) = 7.54$, $p < .001$.

These results show that tonic perturbation of the stiffness of a wrist-pendulum was produced by force-generating activity in a different limb. However, the significant interaction indicates that the perturbation was significant for some pendulums and not others. In simple effects tests, the force level factor was significant at the $p < .02$ level or better for Pendulums 3 and 4 but not significant for Pendulums 1 and 2. What determined the extent of the effect of force level on the
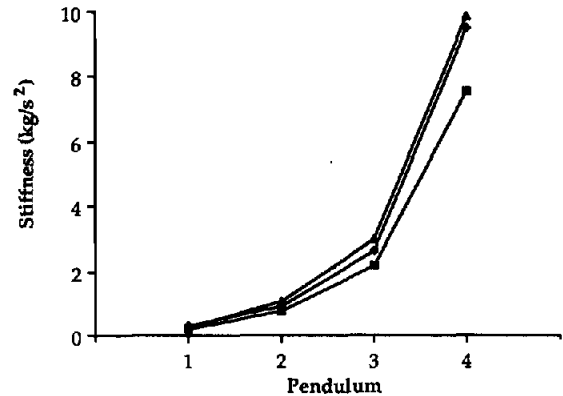

Figure 2. Mean stiffness values for each of four different pendulums at three different levels of torque exerted at the opposite hand. (Derived from data reported by Kugler & Turvey [1987]. Squares represent 0% torque; diamonds, 25% torque; triangles, 50% torque.)

stiffness? There were two potentially relevant properties that varied, both increasing, across Pendulums 1–4. The first was the inertial load. Simple pendulum length (and hence rotational inertia [ML^2]) increased from Pendulum 1 to 4. Second, the observed stiffness of the wrist-pendulums at the 0% force level increased from Pendulums 1 through 4.

As expected from these observations, the amount of increase in stiffness with increases in tonic force level correlated with both inertial load and 0% (or unperturbed) stiffness. We subtracted 0% stiffnesses from corresponding 50% stiffnesses and regressed inertia and 0% stiffness alternatively on the difference scores. For inertia, the relation was significant, $F(1, 30) = 31.18$, $p < .001$, $r^2 = .510$. For 0% stiffness, the relation was similarly significant, $F(1, 30) = 60.84$, $p < .001$, $r^2 = .670$. The slopes were positive and the intercepts near zero in both instances. Because inertial load and base stiffness covaried in the design, we could not distinguish their effects. The regression of inertia on 0% stiffness was significant, $F(1, 30) = 369.72$, $p < .001$, $r^2 = .925$, with a positive slope and near-zero intercept.

These results shed light on the relation between task and resource dynamics in assembly. Force-generating activity in one limb affected task-dynamic stiffness in another. The clear implication is that between-limb interactions were mediated by either the nervous system or the circulatory system, or both. The existence of such interactions becomes especially important when we consider the perturbation, through ankle torque, of coordinated bimanual activity at the wrists.

Would the coordination between the wrists be preserved despite perturbation of the respective stiffnesses by activity at a joint in a third limb? Examination of Equation (3) reveals that different stiffnesses are required for isochronous swinging of wrist pendulums with different inertias. If ankle torque perturbation to the stiffness was proportional to the unperturbed stiffness, then the isochrony of the wrist-pendulums would be destroyed. Once again, by using the common left- and right-hand period, we can set the respective equations for the left- and right-hand periods equal to one another. Change in stiffness, ΔK, in response to perturbation, if proportional

to the unperturbed stiffness, would be equivalent to aK, where a is the proportionality constant. However, because aK_L would not equal aK_R in general, the addition of these factors to the left- and right-hand sides of the equation would violate the equivalence:

$$\left[\frac{4\pi^2 M_L L_L^2}{K_L + (aK_L) + gM_L L_L}\right]^{1/2} = \tau_L \neq \tau_R$$

$$= \left[\frac{4\pi^2 M_R L_R^2}{K_R + (aK_R) + gM_R L_R}\right]^{1/2}.$$

With manipulation of terms, we derive a form comparable to Equation (3):

$$\frac{K_L + gM_L L_L}{M_L L_L^2} + \left(\frac{aK_L}{M_L L_L^2}\right) \neq \frac{K_R + gM_R L_R}{M_R L_R^2} + \left(\frac{aK_R}{M_R L_R^2}\right).$$

The structure of Equation (3) and hence the task-specific coordination would not be preserved over variations in ankle torque.

However, if change in stiffness in response to ankle torque perturbation was proportional to the respective inertia, then the relation between the stiffnesses would be preserved despite the perturbation. If proportional to inertia, the change in stiffness, ΔK, would be equivalent to aML^2, where again a is the proportionality constant:

$$\frac{K_L + gM_L L_L}{M_L L_L^2} + \left(\frac{aM_L L_L^2}{M_L L_L^2}\right) = \frac{K_R + gM_R L_R}{M_R L_R^2} + \left(\frac{aM_R L_R^2}{M_R L_R^2}\right).$$

Thus, the inertias divide out and the as cancel, leaving Equation (3) unaltered. This means that the relation between the stiffnesses, and thus the coordination, would be preserved.

However, the common period would change as a result of the change in stiffnesses. Changes in the period would be a function of a constant, a, added to the quotient term under the radical in Equation (6), which with some manipulation yields

$$\frac{1}{\tau} = \left[\frac{K_L + K_R + g(M_L L_L + M_R L_R)}{4\pi^2 (M_L L_L^2 + M_R L_R^2)} + \frac{a}{4\pi^2}\right]^{1/2}. \quad (7)$$

In our investigation, we asked two questions: (a) Is the wrist-pendulum coordination stable in the face of perturbation by ankle torque, and (b) is change in the stiffness of left- and right-hand wrist-pendulums proportional to the respective unperturbed stiffness or to the respective inertial load? We used phase-locked coordination and the relation described in Equation (3) to decouple variations in the inertial load of pendulums from the corresponding unperturbed stiffnesses of the wrist-pendulums. In principle, given the form of Equation (3), participants could select stiffnesses that mirror respective variations in inertial load. In practice, however, participants do not perform in this manner. We kept inertial load constant for the right hand and varied it in the left hand. Three left-hand loads were less than the corresponding right-hand loads, and three were greater. We required of participants that they oscillate the six resulting combinations of pendulums in antiphase coordination at the most comfortable common tempo.

Method

Participants

Three male graduate students at the University of Connecticut participated in the experiment. The participants' ages ranged from 23 to 29 years. All participants were right handed and none had motor disabilities. All were moderately trained in fitness activities.

Materials

The hand-held pendulums were 0.02 m diameter wooden (ash) rods with a rubber grip over the top end (providing a comfortable handle) and with weights and associated hardware attached close to the bottom end of the rod. This hardware consisted of a 0.006 m-diameter 0.05-kg metal bolt that was inserted through the rod. Aluminum weights of 0.05 m diameter were secured onto this bolt using a number of aluminum washers and nuts (0.05 kg). The bolt, weights, and hardware were placed on the rod at an angle perpendicular to the direction of movement at 0.04 m from its lower end. A small metal plate (0.03 m × 0.06 m × 0.001 m; 0.01 kg) was attached at approximately 0.15 m from the upper (handle) end of each rod. A photocell was attached to these plates for recording purposes.

A single wrist-pendulum, given the distribution of its mass in relation to the point of rotation, was a compound pendulum. Three masses, including the mass of the pendulum shaft or rod, the mass of the added weights, and the mass of the hand, rotated about a point in the wrist joint. The mass and length of the equivalent simple pendulum was calculated by idealizations of the mass shapes and by applications of the parallel axis theorem (Turvey et al., 1986). Seven pendulums were constructed. The pendulums consisted of six different left-hand pendulums and one right-hand pendulum. The simple pendulum masses and lengths are given in Table 1. Because the mass of the participant's hand enters into the computations, the pendulum magnitudes differ for the 3 participants.

The apparatus used to measure the pendulum trajectories was a TECA-PN4 Polgon goniometer. Polarized light from two sources placed 1 m to either side of the participant was picked up by four photocells, two for each wrist-pendulum (see Figure 3). One photocell was placed on a pendulum's metal plate and the other was fastened onto the participant's forearm with a velcro-secured metal plate. The photocells generated voltages proportional to the angle between them. The torque produced at the ankle was measured with a Cybex II isokinetic dynamometer with a plantar flexion–dorsiflexion footplate attachment.

We recorded the voltages from the dynamometer and the goniometer for future analysis on a Tandberg series 100 4-track FM tape drive. Voltage output was monitored on a Tektronix 468 oscilloscope.

Procedure

Participants sat on a Cybex II S-D-H Exertest table configured with a backrest. They were instructed to gaze straight ahead without looking at either wrist-pendulum. At the start of the experiment, a calibration trial was conducted for each hand so that an angular reference could be established for later use in the analyses. These trials consisted of a participant holding a pendulum first at 60° in relation to his horizontally aligned forearms (and, therefore, to the ground plane) and then at 90° in relation to his forearms (and therefore perpendicular to the ground plane). A chiropractor's goniometer was used in determining these angles. Also at the start of the experiment, the maximum torque that the participant could apply by

Table 1
Simple Pendulum Lengths and Masses of the Wrist-Pendulum Systems

Participant	Pendulum						
	Left 1	Left 2	Left 3	Left 4	Left 5	Left 6	Right
1							
Length (m)	0.304	0.336	0.387	0.479	0.497	0.547	0.424
Mass (kg)	0.979	0.987	1.001	1.028	1.033	1.047	1.013
2							
Length (m)	0.312	0.342	0.392	0.484	0.502	0.552	0.429
Mass (kg)	0.921	0.929	0.943	0.970	0.975	0.989	0.995
3							
Length (m)	0.307	0.339	0.390	0.482	0.500	0.550	0.427
Mass (kg)	0.921	0.929	0.943	0.970	0.975	0.989	0.955

using the plantar flexion of the ankle joint was measured with the dynamometer.

Each participant was asked to grasp the pendulum handle in such a way as to have complete control over the entire movement from the wrist; each participant was also instructed to oscillate the pendulums forward and back smoothly by using only the wrist joint (while keeping forearms parallel to the ground plane). The wrist-pendulums were oscillated in two modes: the single right-hand pendulum in isolation or the right-hand pendulum swung together with one of the six left-hand pendulums at a common tempo (1:1 frequency locking) at a phase relation of 180°. Both modes were performed while participants applied each of three levels of torque by using plantar flexion of the ankle. These levels were 0%, 25%, and 50% of the participant's maximum level of torque.

For each trial, the participant first attained and maintained the appropriate level of ankle torque. The participant was guided to the appropriate level by the experimenter, who was watching the torque level on the Cybex gauge as well as on the oscilloscope. Once the appropriate level of torque was achieved, the participant started to oscillate the wrist-pendulum(s). The participant was instructed to search, as he started swinging, through a range of possible frequencies until he felt that he had settled on the most comfortable, stable tempo. When the participant felt that a comfortable tempo had been achieved (typically within a few seconds), he gave a verbal signal to the experimenter, who then started the recording process. Each recorded trial lasted for 15 s. After each trial had been recorded, the experimenter told the participant to stop swinging; a new pendulum combination was placed into the participant's hands, and a new ankle torque level was set for the next trial according to a predetermined condition ordering. Participants rested for 1 min between trials and for 2 to 3 min every seven trials. In addition, participants were given a 15-min rest period halfway through the experiment, during which

they were allowed to take refreshment and walk around. The rest periods significantly reduced the amount of fatigue that participants inevitably began to experience in their legs toward the end of an experimental session. The participants' behavior was closely monitored throughout the experiment. An experimental session for each participant lasted about 3 hr.

There were 21 conditions (seven wrist-pendulum combinations and three ankle torque levels), with six trials in each condition. The number of total trials (126) was divided into a number of blocks, each of which involved one trial of every condition type. Trials within each block were given a random ordering that was different for each of the three participants. The six combinations of left and right wrist-pendulums are referred to as *wrist-pendulum systems*, ordered in terms of the simple pendulum length of the left wrist-pendulum.

Data Analysis

After the data for all participants had been collected on tape, we transduced the recorded voltage outputs to digital form with a DATEL ST-PDP 12-bit analogue-to-digital converter at a sampling rate of 200 Hz. Programs implemented on a Macintosh II computer calculated cycle periods, cycle amplitudes, cycle stiffness, cycle relative phase (of the coupled systems), and the means and standard deviations of these quantities for each trial. Preceding these calculations, the data were smoothed with a 35-ms triangular window. A peak picking algorithm was used to determine the time of peak flexion and extension of the wrist-pendulum trajectories. From the peak extension times (t_n), the period of oscillation for the nth cycle (τ_n) was calculated as $\tau_n = [t_n - t_{n-1}]$. From the cycle periods, the stiffness exhibited at the wrist was estimated as $K_n = (2\pi ML^2/\tau_n) - 9.81 ML$, where M is the simple pendulum mass, 9.81 is the gravitational acceleration, and L is the simple pendulum length of the wrist-pendulum. From the peak extension (α) and flexion (β) positions, the angular excursion of oscillation for the $n$tt cycle (θ_n) was calculated as $\theta_n = [\alpha_n - \beta_n]$. The amplitude was estimated to be one half of the angular excursion. The relative phase for the nth cycle (ϕ_n) was calculated as $\phi_n = 360[(t_{1n} - t_{2n})/(t_{1n} - t_{1(n+1)})]$, following Yamanishi, Kawato, and Suzuki (1979), where $1n$ refers to the nth cycle of Pendulum 1, $2n$ refers to the nth cycle of Pendulum 2, and $1(n + 1)$ is the $(n + 1)$th cycle of Pendulum 1. The means and standard deviations of these quantities were found over the n cycles of a trial and the mean of these means over all the trials in a condition.

Figure 3. The arrangement for a participant in the experiment.

Results

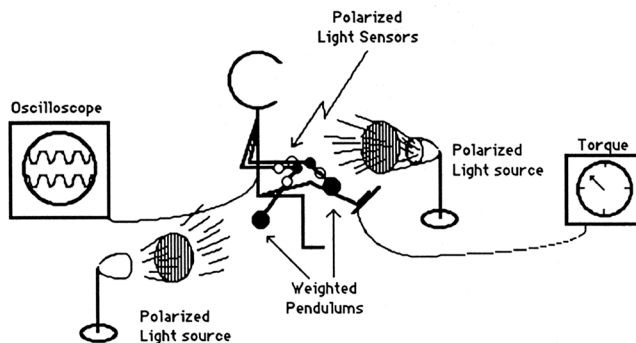The main focus of this investigation was on the effect of levels of ankle torque on stiffness at the wrists. However,

changes in stiffness were accompanied by changes in period as well as by changes in the relative phase relation between the two pendulums. Results for all three measures reflect the global character of components used in the assembly of the task-specific dynamics.

Stiffness

The effect on stiffness of variations both in simple pendulum length and in the amount of torque exerted about the ankle can be seen in Figure 4. The oppositely directed changes in stiffness for the two hands over increases in the left-hand simple pendulum length are quite apparent. In ANOVAs performed on the data for each participant with hand (left or right), ankle torque (0%, 25%, or 50%), and system (1–6) as variables, the Hand × System interaction was significant in all cases: $F(5, 25) = 443.4$, $MS_e = .107$, $p < .001$, for Participant 1; $F(5, 25) = 92.6$, $MS_e = .113$, $p < .001$, for Participant 2; and $F(5, 25) = 334.9$, $MS_e = .060$, $p < .001$, for Participant 3. The three-way interaction was significant as well for Participant 1, $F(10, 50) = 3.4$, $p < .002$, and marginal for Participant 2, $p < .06$. Because of these interactions, we performed separate analyses by participant for each hand with ankle torque and system as variables. First, we report the results for the left hand, then those for the right hand.

For the left hand, system was significant for all 3 participants: $F(5, 25) = 32.8$, $p < .001$, for Participant 1; $F(5, 25) = 14.6$, $p < .001$, for Participant 2; and $F(5, 25) = 49.4$, $p < .001$, for Participant 3. Left-hand stiffness increased with increasing left-hand simple pendulum length. Ankle torque was significant for Participants 1 and 2, but not for Participant 3: $F(2, 10) = 16.6$, $p < .001$, for Participant 1; $F(2, 10) = 9.7$, $p < .005$, for Participant 2. Furthermore, the Ankle Torque × System interaction was significant for Participant 1, $F(10, 50) = 3.1$, $p < .004$, and marginal for Participant 2, $p < .08$. Left-hand stiffness increased with increasing levels of ankle torque for 2 participants. Increases were minimal or nonexistent for shorter pendulums and increasingly strong for successively longer pendulums. These results replicated those

derived from Kugler and Turvey (1987). Of 4 participants in that study, one showed no effect of tonic force levels from squeezing a dynamometer in the opposite hand, whereas the remaining 3 exhibited effects similar to Participants 1 and 2 in the current study.

In an ANOVA performed on the combined left-hand data of all 3 participants with participant as a between-subject variable and ankle torque and system as within-subject variables, both the Ankle Torque × Participant interaction, $F(4, 30) = 7.2$, $p < .001$, and the main effect for torque, $F(2, 30) = 20.0$, $p < .001$, were significant. In addition, though the three-way interaction was not significant, the Ankle Torque × System interaction was significant, $F(10, 50) = 3.9$, $p < .001$. Thus, the overall pattern of results for the left hand was increasing stiffness with increasing left-hand simple pendulum length and an increase in stiffness with increasing ankle torque for longer pendulums but not for the shortest pendulums. Because these results replicate those derived from Kugler and Turvey (1987), we turned to the results for the right hand to see if we succeeded in decoupling variation in 0% stiffness levels from variations in inertial load. Because the same pendulum was always oscillated in the right hand, the inertial load was always the same; we hoped that the 0% stiffness level was not always the same.

For the right hand, separate ANOVAs performed on the data for each participant with ankle torque and system as variables showed that system was significant for all three participants: $F(5, 25) = 72.0$, $p < .001$, for Participant 1; $F(5, 25) = 42.5$, $p < .001$, for Participant 2; and $F(5, 25) = 19.6$, $p < .001$, for Participant 3. Although the inertial load did not vary in the right hand, the (unperturbed) 0% stiffness did vary. In contrast, with left-hand data, right-hand stiffness decreased with increasing length of the pendulum held in the left hand. Decreases in right-hand stiffness matched increases in left-hand stiffness, crossing at the point where left-hand simple pendulum length was equal to that for the right hand. Variations in the left-hand load perturbed the right-hand stiffness. We therefore succeeded in decoupling variations in 0% stiffness from variations in inertia in the right hand.
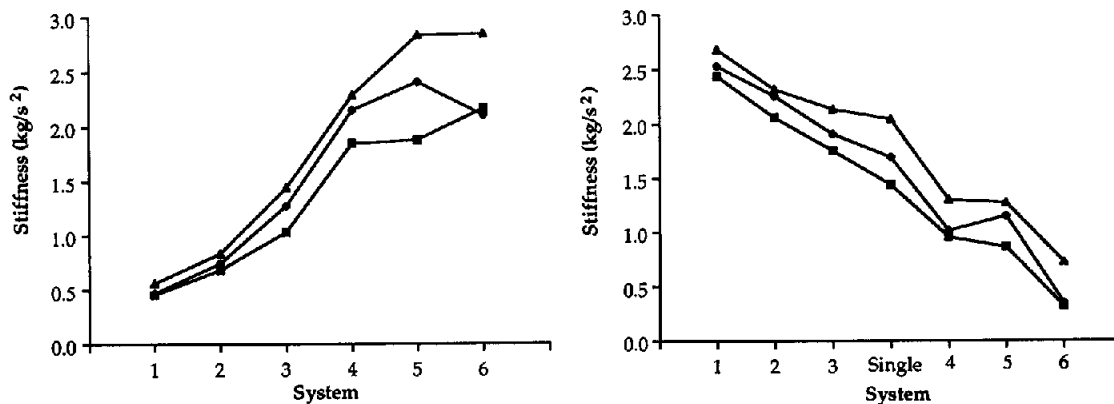

Figure 4. Mean stiffness for each of six different wrist-pendulum systems at three different levels of ankle torque: Means of the data from 3 participants. (The left- and right-hand panels contain data from the left and right hands, respectively. Squares represent 0% torque; diamonds, 25% torque; triangles, 50% torque.)

Did ankle torque produce increases in right-hand stiffness? If so, did the size of the increases vary with the 0% stiffness level? The torque factor was significant for Participants 1 and 2 but not for Participant 3: $F(2, 10) = 12.2$, $p < .002$, for Participant 1; and $F(2, 10) = 14.4$, $p < .001$, for Participant 2. Stiffness did increase with ankle torque. The Ankle Torque × System interaction was not significant in any instance ($p > .3$ or greater). The size of the increases did not vary with 0% stiffness level. These results are different from those for the left hand as well as from those of Kugler and Turvey (1987). The contrast is apparent in mean slopes from linear regressions that regress left-hand simple pendulum lengths on either left- or right-hand stiffnesses. Slopes increased for the left hand across torque conditions but not for the right hand. Mean slopes (and standard deviations) for the left-hand 0%, 25%, and 50% torque conditions, respectively, were 7.4 (2.7), 7.9 (3.1), and 10.2 (3.9), with mean r^2s of .542 (.209), .545 (.176), and .621 (.252). Corresponding mean slopes for the right hand were −8.4 (4.4), −8.7 (3.8), −7.8 (4.3), with mean r^2s of .624 (.182), .642 (.209), and .514 (.221). All regressions were significant, $p < .001$. These results represent the pattern for each participant except Participant 3, for whom left-hand slopes did not increase over torque conditions.

In an ANOVA on combined right-hand stiffnesses with participant, ankle torque, and system as variables, once again both the Ankle Torque × Participant interaction, $F(4, 30) = 7.6$, $p < .001$, and the main effect for torque, $F(2, 30) = 15.6$, $p < .001$, were significant. However, neither the Ankle Torque × System interaction nor the three-way interaction were significant, $p > .5$. The change in right-hand stiffness as a result of perturbation by ankle torque was not modulated by the unperturbed 0% stiffness levels.

The right-hand pendulum was swung in isolation subject to the ankle torque manipulation. How did the extent of changes in stiffness compare when a pendulum was swung alone versus in coordination with another pendulum? An ANOVA was performed on right-hand stiffnesses for the single pendulum mode with participant (between-subject) and torque (within-subject) as variables. Participant was significant, $F(2, 15) = 18.7$, $p < .001$; torque was significant, $F(2, 30) = 10.6$, $p < .001$; the interaction was not significant. The means across participants for the single pendulum were incorporated into the graph for right-hand data in Figure 4. The effect of ankle torque on the stiffness of the right-hand pendulum was larger when it was swung in isolation than when it was swung in coordination with a left-hand pendulum. A difference score was computed by subtracting 0% stiffnesses from corresponding 50% stiffnesses. For each participant, mean right-hand 50%–0% stiffnesses for each of the six trials was computed across the six double pendulum conditions. The difference between 50%–0% stiffnesses for the single right-hand trials and for the mean double right-hand trials was tested through an ANOVA with participant and mode (single vs. double) as variables. Only the mode variable was significant, $F(1, 15) = 5.5$, $p < .03$.

Overall, increasing ankle torque resulted in increases in right-hand stiffness. Changes in right-hand stiffness did not vary with left-hand pendulum lengths as did changes in left-

hand stiffness. Finally, greater changes in right-hand stiffness occurred for the isolated as opposed to coordinated swinging.

The results for perturbation of stiffness derived from Kugler and Turvey (1987) did not allow us to distinguish whether changes in stiffness were proportional to the unperturbed 0% stiffness or alternatively to the inertial load on the musculature. An intent in our study was to decouple the unperturbed stiffness from the inertial loads on the musculature of the left and right wrists. The inertial loads are represented by the right and left simple pendulum lengths respectively because simple pendulum lengths and moments of inertia covary. Because the right-hand stiffness varied with no variation in the inertial load of the pendulum swung in the right hand, we succeeded in disassociating the two quantities. The amount of change in stiffness with variations in ankle torque was derived by subtracting 0% stiffnesses from 50% stiffnesses for corresponding trials within conditions and participants. The result of regressing unperturbed 0% stiffnesses on the difference scores for the three participants is shown in Figure 5. The regression was not significant, $p > .5$, and the slope was flat. The group result is representative of those for individual participants. Thus, increases in stiffness that occurred with increasing levels of ankle torque were not proportional to the unperturbed stiffness values.

It was apparent in Figure 4 that changes in stiffness with increasing ankle torque were proportional to the inertial load. The inertial load of the right-hand pendulum fell between that for Systems 3 and 4 of the left hand. The relatively constant amount of change in stiffness across the right-hand systems appeared about equal to the amount of change in stiffness occurring between Systems 3 and 4 for the left hand. Thus, as can be seen in Figure 6, placing stiffness differences for the right hand between Systems 3 and 4 for the left hand produced an increasing change in stiffness in proportion to inertial loads as indexed by simple pendulum length. We next performed a sequence of analyses to establish that changes in stiffness in response to perturbation by ankle torque were proportional to the inertial load at the wrist.
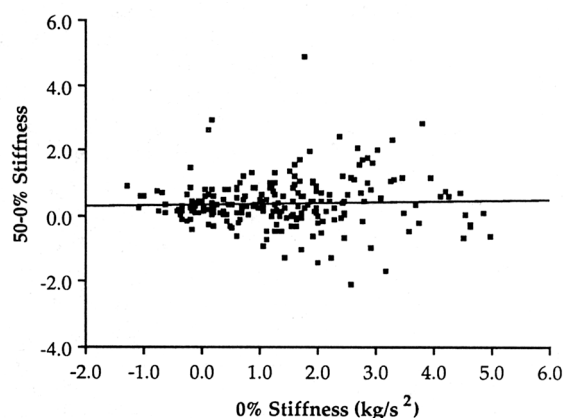

Figure 5. Changes in stiffness from the 0% to 50% ankle torque conditions plotted against 0% stiffness levels: Data for both hands for all 3 participants and all pendulum systems. (The line is the least squares linear regression, for which the slope can be seen to be quite flat.)
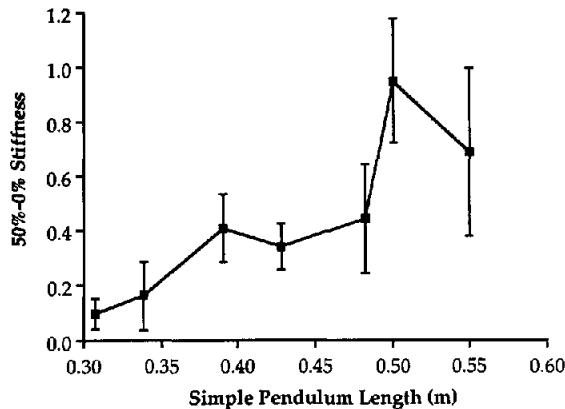
Figure 6. Mean changes in stiffness from the 0% to 50% ankle torque conditions computed for each pendulum and plotted by pendulum length. (The middle point corresponds to the pendulum held in the right hand. Error bars represent the standard error.)
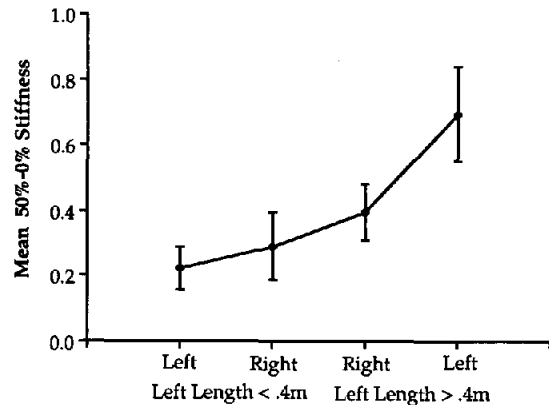
Figure 7. Mean changes in stiffness from the 0% to 50% ankle torque conditions computed for each hand for conditions in which the left pendulum was shorter than the right and for conditions in which the left pendulum was longer. (Error bars represent the standard error.)

We performed on ANOVA on 50%–0% stiffness differences with order of simple pendulum lengths (1–7) as a repeated-measures variable and participants as a between-subject variable. Length was significant, $F(6, 12) = 3.9, p < .002$; participant was significant, $F(2, 15) = 11.1, p < .001$; but the Length × Participant interaction was not significant. Separate ANOVAs performed on the data for each participant with length order as the variable were significant for Participants 1 and 2: $F(6, 30) = 2.9, p < .02$, for Participant 1; $F(6, 30) = 2.8, p < .03$, for Participant 2.

When left pendulum lengths were regressed only on right 50%–0% stiffness differences, the result was not significant, $r^2 = .007$, with a flat slope, $y = .7x + .05$. Right-hand difference scores did not vary across Systems 1–6. When left pendulum lengths were regressed on left 50%–0% stiffness differences, the result was significant, $r^2 = .085, p < .002, y = 2.8x - .74$. When left and right pendulum lengths were combined and regressed on left and right 50%–0% stiffness differences, the result was significant, $r^2 = .050, p < .001, y = 2.8x - .78$. Adding right-hand difference scores to the regression of length on left-hand difference scores did not appreciably alter the original regression results, because right-hand 50%–0% stiffness differences accord with the proportion between length and amount of difference exhibited by left-hand data.

Finally, the mean stiffness differences for the short (Systems 1–3) and long (Systems 4–6) pendulums were computed separately for the left and right hand to allow a more coarse-grained analysis of the effect of inertial load on changes in stiffness in response to perturbation by ankle torque. Each mean plotted in Figure 7 represents 44 difference scores. One-tailed unpaired t tests were performed on all combinations of these means. The two right means were not significantly different from one another. However, the long left and right means were significantly different, $t(106) = 1.8, p < .04$; the left long and the right short were significantly different, $t(106) = 2.3, p < .01$; and the left short and right long difference was marginally significant, $t(106) = 1.6, p < .06$. Left short and

right short were not significantly different. Taken together, these results reveal that the right-hand mean difference scores are equivalent to one another but generally different from left-hand mean difference scores for longer and shorter pendulums. The right-hand means fall together between those for the left short and long.

Our overall conclusion from this sequence of analyses is that changes in stiffness at the left and right wrists in response to torque exerted about the ankle were proportional to the inertial load on the respective musculature.

Period

Increases in stiffness should correspond generally to decreases in period; this was predominately the result we obtained. The pattern of results for periods was not, however, identical to that for stiffness. The task required that participants swing the left- and right-hand pendulums at the same period. One of the questions we investigated was whether isochrony would be preserved over changes induced in wrist stiffness by ankle torque. We found that changes in stiffness were proportional to the inertial load at the respective wrist. Accordingly, our model predicted that isochrony should have been preserved over the perturbations.

How well did participants maintain isochrony? Mean values (and standard deviations) across participants for regressions of left on right periods reveal a mean slope of .98 (.05), a mean intercept of .03 (.06), and a mean r^2 of .963 (.035) for the 0% ankle torque condition; a mean slope of .95 (.06), a mean intercept of .06 (.06), and a mean r^2 of .964 (.044) for the 25% ankle torque condition; and a mean slope of .95 (.10), a mean intercept of .06 (.12), and a mean r^2 of .946 (.061) for the 50% ankle torque condition. All regressions were significant, $p < .001$. These results show that participants succeeded in maintaining isochronous cycles in the two hands, as we expected.

We performed an ANOVA on periods for all three participants, with participant as a between-subject variable and

hand, ankle torque, and system as within-subject variables. The participant variable was significant, $F(2, 15) = 30.8, p < .001$. Participants swung at different characteristic periods. Neither the main effect of hand nor any of the interactions with hand were significant; thus, once again the pattern of results for the two hands was the same. System was significant, $F(5, 75) = 107.9, p < .001$. Periods increased over Systems 1–6, more so for some participants than others, as shown by the fact that the System × Participant interaction was significant, $F(10, 75) = 2.2, p < .03$. Both the Ankle Torque × Participant interaction, $F(4, 30) = 7.8, p < .001$, and the main effect of torque, $F(2, 30) = 21.8, p < .001$, were significant. The Torque × System interaction was significant, $F(10, 150) = 2.6, p < .006$, but the three-way interaction was not significant. Periods tended to decrease with increasing ankle torque, more so for Systems 4–6 and less so for Systems 1–3.

A separate ANOVA was performed on periods for each participant with hand, ankle torque, and system as variables. For Participant 1, system was significant, $F(2, 25) = 65.0, p < .001$, torque was significant, $F(2, 10) = 17.2, p < .001$, and the Torque × System interaction was significant, $F(10, 50) = 2.0, p < .05$. For Participant 2, system was significant, $F(5, 25) = 38.8, p < .001$, and torque was significant, $F(2, 10) = 19.5, p < .001$. For Participant 3, only system was significant, $F(5, 25) = 18.2, p < .001$. Periods increased over Systems 1–6 for all participants, getting larger for larger inertial loads. For Participants 1 and 2, periods decreased with increasing ankle torque, decreasing more for Systems 4–6. For example, for Participant 2 simple effects tests on torque were significant ($p < .05$ or better) for Systems 3–6 but not for Systems 1 and 2. A similar pattern was obtained for Participant 1. In no instance was the hand variable or any of its interactions significant. The pattern of results, therefore, was the same for the left- and right-hand periods, as required for isochrony.

We found that increases in stiffness were proportional to the inertia at the wrist. As described before, change in left- and right-hand stiffness can therefore be represented by $aM_LL_L^2$ and $aM_RL_R^2$, terms added to Equations (3) and (6), where a is the proportionality constant for a given level of ankle torque perturbation. Equation (7) was derived by adding the aforementioned terms to Equation (6) with the result that changes in the period in response to perturbation by ankle torque should be a simple function of the proportionality constant, a.

To verify that changes in stiffness were proportional to inertia, we used Equation (7) to predict observed changes in period. To do this, we needed an estimate of the proportionality constant, a, for each participant at a given level of ankle torque. We obtained a values for the 50% ankle torque level by regressing, for each participant, inertia on mean 50% − 0% stiffness differences computed for each wrist-pendulum. The results were as follows: Participant 1, $y = 6.78x - .47, r^2 = .788, p < .001$; Participant 2, $y = 4.21x - .30, r^2 = .479, p < .02$; Participant 3, $y = .97x - .19, r^2 = .066, p > .4$. These equations describe the relation between inertia and change in stiffness from the 0% to the 50% ankle torque levels. Ignoring the intercepts, we used these slopes as values for a. We used the value for Participant 3, despite the regression's not reach-

ing the $p < .05$ level. Putting these values into Equation (7) along with respective pendulum mass and length values and derived K values for the 0% ankle torque condition, we computed predicted values for τ in the 50% ankle torque condition.

After computing predicted periods for the 50% ankle torque condition, we computed predicted and actual changes in period by subtracting actual 0% periods from predicted and actual 50% periods. Finally, we regressed 0% periods on both the predicted and actual changes in period. The results for each participant appear in Figure 8 and in Table 2, along with results for means computed across participants for each wrist-pendulum. The 0% periods for all three participants were regressed on both predicted and actual changes in period in a multiple regression, along with a vector coding for predicted versus actual changes and an interaction vector created by multiplying the first two vectors (Pedhazur, 1982). The result was significant, $r^2 = .180, F(3, 208) = 15.19, p < .001$. Only 0% period was significant (partial $F = 10.05, p < .002$). When the regression was redone without the interaction vector ($r^2 = .179, p < .001$), both 0% period (partial $F = 24.69, p < .001$) and the coded category vector (partial $F = 20.80, p < .001$) were significant.

Equation (7) accurately predicted the changes in period. Predicted changes were parallel to actual changes, with a consistent overestimation by about 50 ms. The overestimation might be attributed to our having ignored the intercepts in the linear relations between inertia and mean 50%–0% stiffness differences. This result strongly supports our conclusion that changes in wrist-pendulum stiffness, resulting from ankle torque perturbations, were in proportion to the inertial loadings at the wrists.

Relative Phase

In addition to isochrony, relative phase is another measure of the coordination between the two wrists. Although isochrony was preserved, the phase relation might have been perturbed by significant levels of ankle torque.

Rosenblum and Turvey (1988) found that the mean relative phase between two pendulums swung at a common tempo was a function of both the relative loads on the musculature spanning the two wrists and the period of movement. Rosenblum and Turvey assumed that neural activations at the two wrists were phased 180° apart in accordance with the task instructions. Following Partridge (1966, 1967, 1979), they suggested that observed deviations from a strict antiphase relation between the two pendulums were introduced by latencies associated with the muscular response, where the latencies were proportional to the load on the musculature.

Because relative phase and the change in stiffness in response to perturbation by ankle torque are both mediated by loading on the musculature, we examined relative phases for an effect of the ankle torque manipulation. Because both the relative inertial load and the period of movement ultimately determine relative phase according to Rosenblum and Turvey's analysis, we investigated whether the relative stiffness (i.e., the difference in stiffness between the two hands) would
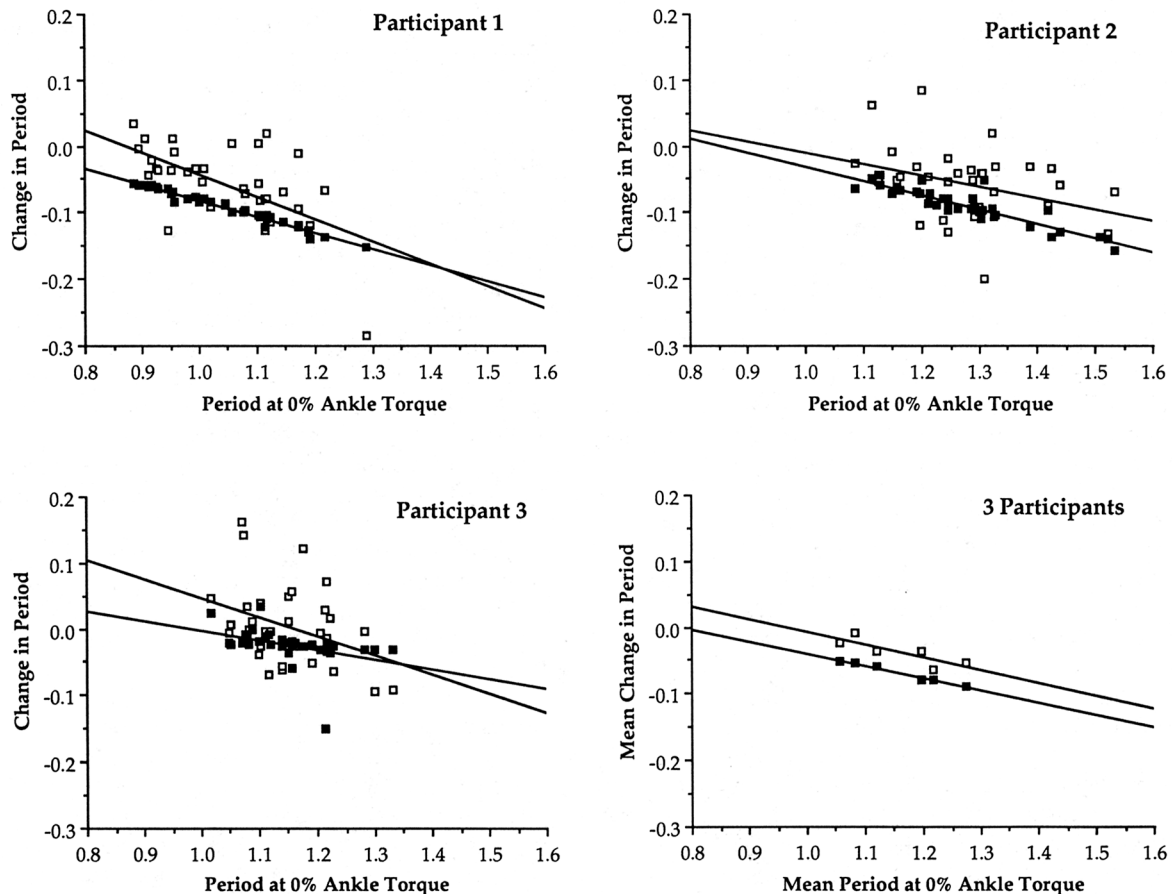
Figure 8. Changes in period from the 0% to 50% ankle torque conditions plotted against the period at 0% ankle torque. (The lower right panel contains means computed for each double pendulum system across the 3 participants. Open squares indicate change computed by subtracting measured 0% periods from 50% periods; filled squares indicate change computed by subtracting measured 0% periods from predicted 50% periods.)

index variations in relative phase.[3] Relative stiffness was derived by subtracting left- from right-hand stiffness. Variations in relative phase with changes in ankle torque are shown in Figure 9 plotted against relative stiffness. Relative stiffness was regressed linearly on relative phase for each of the three torque conditions, 0%, 25%, and 50%. The results for each

of the three participants and for the combined data appear in Table 3.

The y-axis marks zero relative stiffness, which is where left and right stiffnesses were equal. All regression lines crossed the y-axis at or very close to a relative phase of 180°. Intercepts for the combined data fell within 2 degrees of 180°. For all ankle torque conditions, as shown by significant slopes in all regressions, relative phase deviated from 180° as relative stiffness became increasingly nonzero. The right-hand pendulum led by more than 180° when right stiffness exceeded left

Table 2
Regressions of 0% Periods on Predicted and Actual Changes in Period

Participant	Predicted change	Actual change
1	$y = -.24x - .16$ $r^2 = .966, \quad p < .001$	$y = -.34x - .29$ $r^2 = .361, \quad p < .001$
2	$y = -.21x - .18$ $r^2 = .802, \quad p < .001$	$y = -.17x - .16$ $r^2 = .132, \quad p < .03$
3	$y = -.15x + .14$ $r^2 = .172, \quad p < .02$	$y = -.29x + .33$ $r^2 = .136, \quad p < .03$
M	$y = -.18x + .14$ $r^2 = .987, \quad p < .001$	$y = -.19x + .19$ $r^2 = .668, \quad p < .05$

[3] Stiffness is the task-dynamic measure of force generation by musculature marshaled to handle the inertial load of a pendulum at a given period of movement. When two pendulums representing different loads are to be swung at a common period, greater stiffness is exhibited at the wrist corresponding to the larger load. When the pendulums are of the same length, the loads are equivalent, as are the stiffnesses at the two wrists. Finally, when a given load is to be moved with a smaller or larger period, the stiffness is increased or decreased accordingly. Thus, relative stiffness contains information about both the relative loadings and the periods of movement and accordingly should be the best index of variations in relative phase.
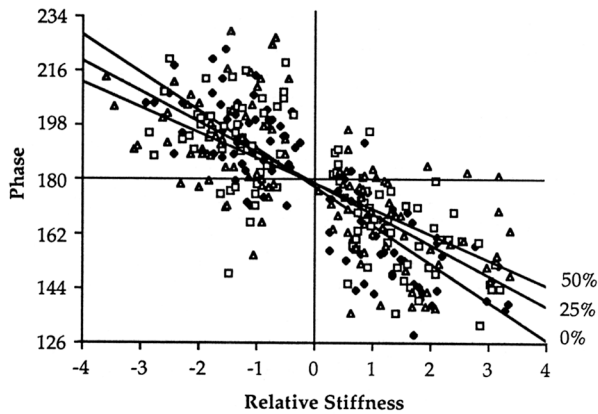
Figure 9. Relative phase plotted against relative stiffness for the three ankle torque conditions: Data for all 3 participants. (Filled circles represent 0% torque condition; open squares, 25% torque condition; open triangles, 50% torque condition.)

stiffness and by less than 180° when right stiffness was less than left stiffness. These results replicated those of Rosenblum and Turvey (1988).

Slopes decreased with increasing ankle torque, whereas intercepts remained essentially invariant, meaning that the regression lines rotated around the (0, 180°) coordinate point. The 0% and 25% lines crossed one another at (−0.28, 181.4°), whereas the 25% and 50% lines crossed at (0, 178.6°) and the 0% and 50% lines crossed at (−0.17, 180°). The tendency of relative phases to deviate from 180° with nonzero relative stiffness diminished with increasing ankle torque. Overall, the relative phases approached 180° as ankle torque increased from 0% to 50%. To test the significance of this trend, multiple regressions were performed on relative phases of all three participants with a vector for relative stiffness, a vector coding for ankle torque level, and a vector representing the interaction. The regression for the total model was significant, $r^2 = .602$, $F(3, 208) = 104.88$, $p < .001$. The partial F for relative stiffness was significant, $F = 311.8$, $p < .001$, whereas that for ankle torque was not significant. However, the interaction vector was significant, partial $F = 12.64$, $p < .001$.

Similar analyses were significant for all three participants, $r^2 = .795$, $F(3, 68) = 87.89$, $p < .001$, for Participant 1; $r^2 = .647$, $F(2, 66) = 40.34$, $p < .001$, for Participant 2; $r^2 = .760$, $F(3, 66) = 69.55$, $p < .001$, for Participant 3. Relative stiffness was significant for all three, $p < .001$. Ankle torque was not significant for Participants 1 and 2 but was significant for Participant 3, partial $F = 5.03$, $p < .03$. The interaction was significant for Participants 1 and 2—partial $F = 15.35$, $p < .001$, for Participant 1, and partial $F = 5.7$, $p < .02$, for Participant 2—but not for Participant 3.

Overall deviations in relative phase from strict antiphase with nonzero relative stiffness decreased with increasing ankle torque. The slopes of the regression lines decreased as the lines rotated around 180° relative phase at zero relative stiffness. According to the analysis in Rosenblum and Turvey (1988), these results could be explained either by an increase in periods or by a decrease in the relative latencies associated with the musculature. Because increasing ankle torque was accompanied by decreases in periods, the results must be attributed to a decrease in relative latencies.

Summary

Left and right stiffnesses, the common period, and the phase relation between the wrist-pendulums all exhibited changes in response to torques exerted about the ankle.

Stiffnesses increased with increasing ankle torque. Increases were proportional to the inertial load at the respective wrist. Stiffness of the right wrist-pendulum increased more in response to ankle torques when the right wrist-pendulum was oscillated alone than when it was oscillated together with the left wrist-pendulum.

Isochrony was preserved over perturbations by ankle torque. The common period decreased with increasing ankle torque. The stability of coordination was consistent with the proportionality of changes in stiffness to the local inertial load.

As found in previous studies, the phase relation between the wrist-pendulums departed from strict antiphase in proportion to the asymmetry of the inertial loads, and thus, of the stiffnesses at the wrists. The size of these departures was found to decrease with increasing ankle torque.

Discussion

Ignoring the gravitational or pendulum aspect momentarily, the wrist-pendulum situation corresponds to a rotational mass-spring as follows: $I\ddot{\theta} = -K\theta$ and $\ddot{\theta}/\theta = -K/I$. The an-

Table 3
Right–Left Stiffness Regressed on Relative Phase

| | Ankle torque | | |
Participant	0%	25%	50%
1	$y = -.033x + .500$ $r^2 = .806$	$y = -.027x + .504$ $r^2 = .830$	$y = -.020x + .506$ $r^2 = .769$
2	$y = -.051x + .510$ $r^2 = .846$	$y = -.036x + .524$ $r^2 = .674$	$y = -.032x + .524$ $r^2 = .431$
3	$y = -.033x + .470$ $r^2 = .779$	$y = -.027x + .461$ $r^2 = .672$	$y = -.029x + .457$ $r^2 = .728$
Combined	$y = -.035x + .494$ $r^2 = .724$	$y = -.028x + .496$ $r^2 = .584$	$y = -.023x + .496$ $r^2 = .464$

Note. All regressions were significant at $p < .001$.

gular acceleration at each position is determined by the ratio of the stiffness to the inertia. Both the task-dynamic stiffness and the inertial load determine the torque levels generated by the musculature spanning the joint that actually moves the joint through its trajectory. Despite this, we found that only the inertial load, not the 0% stiffness, determined the amount of change in stiffness produced by ankle torques. Ultimately, the perturbations must be mediated by the musculature spanning the wrists and reflected in the torques generated by that musculature. How can two quantities that both determine the torques generated by the musculature be dissociated in mediating the extent of changes in response to ankle torque perturbation? The answer lies in the fact that the muscle torques are not necessarily equivalent to the applied torques actually generating movement. It is possible that only a fraction of the muscle torques might contribute to the observed movements and thus to the task-dynamic stiffness. The total muscle torque, therefore, may vary with the inertial load in a manner independent of variations in task-dynamic stiffness.

Relation of Task-Dynamic Stiffness to Muscle Activity

Task-dynamic stiffness corresponds to variations in torques actually producing movement. Task-dynamic stiffness is not necessarily equivalent to muscle stiffness and thus is not generally an index of muscle torques. The nonunique relation between the two is immediately apparent in the following demonstration. While grasping a pencil and keeping your forearm, hand, and wrist otherwise relaxed, oscillate your wrist at a given tempo back and forth from abduction to adduction. Next, move the wrist at the same tempo while forcefully gripping the pencil as hard as possible. In both cases, the torques exerted in moving the hand and pencil back and forth were the same because the trajectories were, in principle, the same. Despite this, in the latter instance the muscles were generating substantial amounts of torque, whereas in the former instance they generated considerably less. Torques that directly produce movement are not necessarily equivalent to muscle torques. The relation between task-dynamic stiffness and joint stiffness is nonunique. The task-dynamic stiffness was ideally the same in both instances, whereas joint stiffness varied from low in the first case to high in the second case.

Stiffness has been used in the movement literature at different levels of analysis that should be distinguished from task-dynamic analysis. Stiffness has been used to refer to the length–tension relation for isolated muscle (Bizzi, Accornero, Chapple, & Hogan, 1981). This is appropriate as long as the conditions in which the relation was derived are respected, namely, isometric contractions against an external load (McMahon, 1984; Partridge, 1979). The usefulness of stiffness, however, is severely limited in such static situations.

Stiffness has also been used to refer to the forces muscles generate while actively shortening or being lengthened. In such circumstances, the force–velocity relation for muscle must be taken into account, as well as complex potentiation effects associated with the stretch–shortening cycle (Komi, 1986; McMahon, 1984). The energetic state of the muscle also affects the stiffness (Åstrand & Rodahl, 1977). The resulting variation in force is a highly nonlinear function of

muscle states and history (Partridge, 1979). No extant modeling equation has captured all of the interrelated mechanical properties of muscle. Hasan, Enoka, and Stuart (1985) pointed out that stiffness is defined as the time invariant ratio of change in force to change in length and that, therefore, no stiffness can be assigned to isolated muscle because the ratio varies over time. Only when muscle is modeled in the context of spinal reflexes does it exhibit behavior that can be described in terms of a stiffness. Thus, stiffness can only be used in the context of movement to describe behavior that emerges from the collective organization of neural, circulatory, and muscular components.

Probably the best known use of stiffness in the movement literature concerns joint stiffness. In this case, stiffness is produced by the activity of at least two opposing muscles spanning a joint and acting to preserve the position of the joint in the face of sudden perturbations. Experimental determination of joint stiffness requires the sudden application of an external perturbing torque to a limb segment so that the ratio of change in torque to change in angular position can be measured. Stiffnesses of reflexively innervated agonist and antagonist muscles combine additively to determine the respective joint stiffness.[4] However, opposing muscles need not be actively generating torque in a sustained fashion to produce observed joint stiffnesses. Using afferents to detect perturbation, the muscles can be mobilized reflexively to counter resulting changes in position. Furthermore and most important, either strategy can be used. Both underlying organizations of joint stiffness have been observed (Berkinblit, Feldman, & Fukson, 1986; Hasan et al., 1985).

There is no necessary or obvious relation between joint stiffness and muscular activity in the context of voluntary movement. However, Bizzi and Feldman (among others) suggested that limb movements are generated by moving the equilibrium point for joint stiffness (Berkinblit et al., 1986; Bizzi, 1980; Feldman, 1980, 1986). Bizzi (1980) implied that muscle stiffnesses should be actively maintained throughout the process, whereas in Feldman's conception this need not necessarily be the case (Berkinblit et al., 1986). Bizzi and colleagues have produced rather striking evidence in favor of equilibrium point control of movement (Bizzi, Accornero, Chapple, & Hogan, 1981, 1984). The de-afferented limb of a monkey was moved surreptitiously to a required target position in advance of voluntary movement. When the limb was released after movement initiation, it was observed to travel back to a position along the intended movement trajectory before reversing and completing the intended movement to the target. By varying the time at which the limb was released, the investigators sampled the hypothesized trajectory of the equilibrium point.

Despite the vividness of this demonstration, there are reasons to be cautious about the hypothesis. First, as is elaborated in the following, the necessarily predominant role of afference in the functional organization of behaviors has only recently been recognized, but is now well established. In view of the essential role of afferents in determining forms of behavior,

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[4] Although opposing torques subtract, the stiffnesses of opposing muscles sum (Hogan, Bizzi, Mussa-Ivaldi, & Flash, 1987).

de-afferent preparations are rather suspect and must be evaluated with extreme care, ultimately in the light of an understanding of behavior performed with the normal benefit of afference. For example, Terzuolo, Soechting, and Ranish (1974) found that the normally effective antagonist activity in loaded arm movements became random and incoherent with de-afferentation. Second, as pointed out by Hasan et al. (1985), equilibrium point control seems rather inappropriate when the goal of movement is not a position of equilibrium, as for instance in throwing a javelin, hitting a ball with a racquet, or jumping to a maximum height (Bingham et al., 1989; Bobbert, 1988; Jöris et al., 1985; Van Ingen Schenau, 1989). Although we might expect equilibrium point control in selected behaviors, there is no reason to believe it universal. Third, and more to the point, patterns of muscle activation, as observed through electromyograph (EMG) recordings, vary considerably depending on the speed of movement and the inertial load, among other factors (Berkinblit et al., 1986; Hasan, 1986; Lestienne, 1979; Wallace, 1981). Distinct one-burst (agonist), two-burst (agonist–antagonist), three-burst (agonist–antagonist–agonist), and multiburst patterns have been recorded, in addition to patterns in which activations overlap either at points througout movement or—perhaps most characteristically for movements to an endpoint—at the endpoint of movement. Those who wish to argue for equilibrium point control certainly cannot argue that the conjoined stiffnesses of muscles actively and continuously generating torques are being modulated universally throughout all movements. Rather, the most general conclusion is that functional flexibility is predominant in motor organization. The organization of the musculature is different in different tasks and also varies among individuals within a task.

From this, we can conclude that there was probably flexibility or variability in the way that the underlying musculature was orchestrated in the assembling of observed task-dynamic stiffnesses in wrist-pendulum oscillation. Given that our participants were operating in "comfort mode," extensive use of cocontractions was not likely. However, a finding in the EMG literature is that cocontraction tends to increase with inertial load, particularly during the decelerative phases of movement (Hasan, 1986; Lestienne, 1979). The natural inference is that cocontractions are used to ensure the stability of movement and of the joint. Thus, although we might not expect cocontraction or significant joint stiffness throughout the pendulum swinging movements, we might expect increasing joint stiffness at the endpoints of movement with increasing inertia. In this case, there would be increases in muscle torques associated with increasing inertial loads, which would not be apparent from an external frame of reference without the external perturbations required to reveal changes in joint stiffness.

How could the task-dynamic stiffness increase in proportion to the inertial load and not the 0% stiffness? We have suggested that muscle torque levels might vary with inertial loads in a manner independent of the observed task-dynamic stiffnesses. The next question is, how might muscle torque levels determine the extent of changes in stiffness produced by ankle torques? Other questions also remain. Why should the stiffness be increased more by ankle torque when only one pendulum is being swung? How might changes in stiffness

be related to correlated changes in the phase relation between the two wrists? Answers to these questions require that we examine the relation between task-dynamic stiffness and underlying resource dynamics in addition to the musculature. How might either the nervous system or the circulatory system mediate interactions between lower and upper limb activity?

Before addressing these questions, it is helpful to consider one possible reason for the third participant's failure to exhibit a response to the ankle torque perturbation. A possibility is that this participant did not use cocontractions as much as did the others for stability of movement. If so, then we should expect to see a difference in fluctuations. We computed the von Holst amplitude and period fluctuations as described by Rosenblum and Turvey (1988). The advantage of these measures is that they take into account potential asymmetries between the flexion and extension phases of a movement cycle. Computed for each trial, fluctuations are described as a percentage of mean trial amplitude or period, respectively.

We performed an ANOVA on amplitude fluctuations with participant as a between-subject variable and ankle torque, hand, and system as within-subject variables. The only significant main effect was for hand, $F(1, 15) = 6.09, p < .03$. The Participant × Hand interaction also was significant, $F(2, 15) = 9.21, p < .003$. The result can be seen in Figure 10. Where Participants 1 and 2 exhibited equivalent amplitude fluctuations in the left and right hands, Participant 3 did not. Furthermore, left-hand fluctuations for Participant 3 were greater than those for Participants 1 and 2. In simple effects tests, the hand variable was significant only for Participant 3, $F(1, 15) = 24.29, p < .0001$, whereas the participant variable was significant only for the left hand, $F(2, 15) = 12.37, p < .001$. The results for period fluctuations reflected those for amplitude fluctuations in that left- and right-hand fluctuations were equivalent for Participants 1 and 2 and unequal for Participant 3. For Participant 3, the left-hand fluctuation was significantly greater, as shown in a simple effects test, $F(1, 15) = 4.84, p < .05$.

Participant 3 seems to have used a strategy in assembling task-dynamic stiffness that allowed greater variability in re-
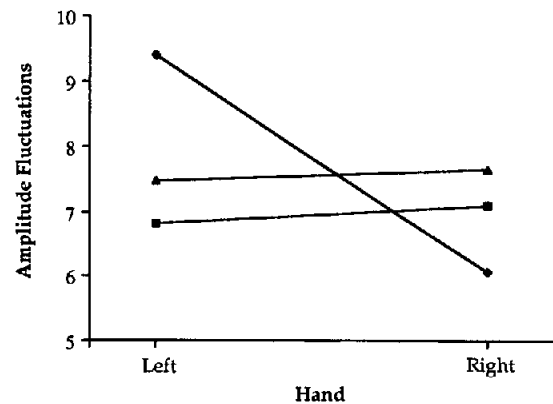

Figure 10. Mean left- and right-hand amplitude fluctuations for each participant. (Fluctuations are expressed as percentages of mean amplitude for a trial. Squares represent Participant 1; triangles, Participant 2; circles, Participant 3.)

sulting left-hand trajectories. This participant may have tolerated greater variability while avoiding cocontractions and maximizing relaxation into comfort mode. As a result, muscle torques would not have varied or would have varied less with inertial loads for Participant 3.

We now turn to a consideration of how the circulatory system might have mediated interactions between lower and upper limb activity.

Interactions Mediated by the Circulatory System

Torques generated about the ankle produced increases in stiffness at the wrists. How might blood circulation be relevant to increases in stiffness? Blood flow brings oxygen and fuel to a muscle and carries away metabolites that if allowed to accumulate would impair functioning (Åstrand & Rodahl, 1977; McMahon, 1984). Determinants of blood flow act as a throttle on muscle construed as a motor (Bloch & Iberall, 1982). Power output based on anaerobic metabolism can continue for a brief period following cessation of blood flow, after which the muscle effectively shuts down (Åstrand & Rodahl, 1977; Laughlin & Armstrong, 1985). More relevant to our concern, however, is the fact that the power output of a muscle increases with increased oxygen made available by increased blood flow, all else being equal. Active motor units absorb the additional oxygen made available and use it to generate additional power (Åstrand, Cuddy, Saltin, & Stenberg, 1964; Åstrand & Rodahl, 1977; Bloch & Iberall, 1982; Ekblom, Huot, Stein, & Thorstensson, 1975; Fagreus, Karlsson, Linnarsson, & Saltin, 1973; Hill, Long, & Lupton, 1924; Hughes, Clode, Edwards, Goodwin, & Jones, 1968). Power is the time rate of mechanical energy production. Increases in power show up as increases in stiffness. Might the activity of muscles spanning the ankle joint produce increased blood flow through the muscles spanning the wrists? Circulatory organization has rarely been considered by human-movement scientists as a source of constraint on forms of movement. What are the determinants of blood flow?

Blood flow through a muscle is determined by three factors (Åstrand & Rodahl, 1977; Laughlin & Armstrong, 1985). The first is the local capacity for flow determined by the relative dilation of the blood vessels in a muscle. The extent of dilation is determined by smooth muscles surrounding the vessel walls. These respond both to signals from the sympathetic nervous system and to levels of local metabolites produced by muscle activity. The second factor is global blood pressure, which is a function in turn of the heart rate together with the sum of the local resistances in all the muscles.[5] The third factor is the pumping action of muscular contraction itself (Laughlin, 1987). When the muscle contracts, venous blood is forced out of the muscle vessels. When the muscle relaxes, a vacuum is created in the vessels that draws arterial blood into the muscle. The strength of the pump is relative to the strength of muscular contractions.[6]

Assuming constant relaxation and maximum dilation, intramuscular blood flow is a linear function of the global perfusion pressure. Assuming relaxation and constant perfusion pressure, blood flow is a linear function of the capacity of the vasculature. Addition of contraction–relaxation cycles

reduces the time during which the muscle is receptive to flow and adds locally to the perfusion pressure during relaxation in proportion to the strength of preceding contraction.

Blood flow through a muscle increases immediately with muscle activity. Moderate activity induces about a three-fold increase in flow. The increase is produced by both increased cardiac rate and a decrease in the resistance of the muscle vasculature. The flow is targeted to the active muscle by sympathetic nervous activity that increases the resistance in inactive muscles in proportion to the changes in heart rate (Laughlin & Armstrong, 1985). In fact, these two changes together increase the global blood pressure. The vasculature in the active muscle is made insensitive to the sympathetic nervous signals by its response to local muscle metabolites and a local linkage to motoneurons. The extent of the resulting dilation is proportional to the level of contractile activity in the muscle.

An increased heart rate is elicited with the initiation of activity in a muscle through redundant central and peripheral control. A muscle-to-heart reflex path produces an increased heart rate within 500 ms of muscle activation, as shown by inducing contraction through extrinsic electrical stimulation (Hollander & Bouman, 1975). A central pathway provides redundant control, as shown by the production of increased heart rate with voluntary contraction and a blockade of the reflex (Leonard et al., 1985). The cardiovascular response is proportional both to the amount of muscle mass and to the strength of contraction (Hollander & Bouman, 1975; Lind, Dahms, Williams, & Petrofsky, 1981). However, increases in heart rate and blood pressure are disproportionally greater for static exercise (Asmussen, 1981; Lind et al., 1981).

From this information about the circulatory system, we deduced the circulatory effect of ankle torques on the rhythmic activity about the wrists. The receptive state of the vasculature of the wrist muscles is determined by the level of their contractile activity. We have suggested that this should vary primarily with the inertial load at the wrist. With contraction of the muscles spanning the ankle, the heart rate accelerates in proportion to the level of that contraction. The acceleration is also in proportion to the relevant muscle mass about the ankle. The muscles used in plantar flexion include the gastrocnemius, the soleus, peroneus longus, peroneus brevis, flexor hallucis longus, and tibialis posterior. Together, these muscles compose a large muscle mass. The gastrocne-

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[5] Resistance to flow and capacity for flow are the inverse of one another.

[6] The typical time required for blood to refill the vessels is about 700 ms. This figure is striking because it is close to preferred periods of cyclic motions observed in many studies, including ours. The timing of activity in the musculature is crucial given this relaxation time and the need for arterial blood to maintain aerobic metabolism. In particular, "the amount of time spent in contraction and relaxation is important because blood flow is impeded during muscle contraction and, as a result, most (if not all) blood flow occurs during relaxation" (Laughlin, 1987, p. H995). Clearly, circulatory dynamics contribute strongly to the determination of timing in coordinated rhythmic movements.

mius alone composes the majority of the mass in the calf of the lower leg.

With the increase in heart rate, the global blood pressure increases, increasing the blood flow through the active muscles at the wrist. The total flow through each wrist muscle is a function of both the global pressure and the local capacity. Those with greater capacity exhibit a greater net increase in flow. With increased flow, the power generated by the muscle increases. A small additional increase in flow accrues from the increased action of the muscle pump. Altogether, for a given torque exerted about the ankle, the power output at the wrists increases in proportion to the local capacity, which is determined in turn by the inertial load.

Does heart rate actually increase with the level of ankle torque, and if so, how much? We investigated this question at Indiana University (Bloomington, Indiana) with 4 male participants, different from the 3 participants in the original study. The participants ranged from 23 to 35 years of age. Three were moderately physically fit, and the fourth participant was a well-trained runner. First, resting pulse levels were measured at the wrist during 15-s intervals. Then maximum ankle torque levels were determined on the Cybex machine. Finally, participants alternated by trial in exerting either 25% or 50% ankle torque on the Cybex. Each participant performed four trials at 25% and four trials at 50%. The 25% and 50% trials were alternated. All four participants performed the first 50% trial, then the first 25% trial, then the second 50% trial, and so forth. For each trial, the resting pulse was measured for 15 s. The participant next established the requisite ankle torque level. This took 2.25 s ($SD = 1.15$) on average. A record of torque levels was produced on paper tape with a Dual Channel Recorder. Each participant then maintained the torque level for 15 s while his pulse was measured.

The results in terms of proportion of increase above resting level for each participant can be seen in Figure 11. A repeated-measures ANOVA was performed on heart rates with ankle torque (0%, 25%, and 50%) and trial (1–4) as variables. Only the ankle torque factor was significant, $F(2, 6) = 5.69$, $p < .04$. The mean heart rates in beats per minute for the 0%,

25%, and 50% ankle torque conditions were 67.75, 72.00, and 77.25, respectively. However, as shown in Figure 11, results varied between participants. The runner showed almost no increase in heart rate, even at 50% ankle torque, whereas 2 other participants exhibited 20% increases, and the fourth showed a 12% increase. The lack of increase in heart rate for the exceptionally fit participant provides another possible account for the results of Participant 3 in the original study. This participant was a particularly fit practitioner of aikido and may have experienced no significant changes in heart rate, with a consequent lack of change in stiffnesses at the wrists.

How significant is a 20% increase in heart rate for its impact on global perfusion pressure? First, this figure may somewhat underestimate increases that occurred in the original study, because heart rate continues to increase under conditions of isometric contraction, reaching steady state only after at least a minute (Leonard et al., 1985). The need to coordinate pendulum swinging with activity at the ankle meant that somewhat longer intervals of ankle torque intervened before the 15-s measurement period was initiated in the original study. Nevertheless, a 20% increase above resting level is significant in terms of its impact on perfusion pressure. One reason is that the effect of the heart on perfusion pressure is a function not only of heart rate, but also of stroke volume, or the volume of blood pumped at each stroke. Stroke volume varies with heart rate. In seated subjects, stroke volume increases from about 60% of maximum stroke volume at resting heart rates to about 80% of maximum stroke volume at heart rates 20% above resting level (Åstrand & Rodahl, 1977). Thus, stroke volume increases by about 33% of its level at resting heart rates. This means that the amount of blood pumped by the heart increases by about 50% as heart rate increases from resting to 20% above resting level.

A second reason for this being a significant increase is that global profusion pressure is a function of the sum of the local resistances as well as of heart rate (and stroke volume). For a given increase in heart rate, the increase in pressure is less if more muscles are active and receptive. This effect is important generally because the capacity of the peripheral vascular beds exceeds the ability of the heart to fill them with flow (Saltin, Gollnick, Rowell, & Sejersted, 1986). There is a need for the sympathetic nervous activity, which increases the resistance of inactive muscles to prevent increases in flow through them with changes in heart rate. With ankle muscles active but contracted and thus unreceptive, and only wrist muscles active, and thus receptive, the increase in perfusion pressure for the wrist muscles should be significant, with a 50% increase in the amount of blood pumped by the heart.

The increase in flow through the muscles about a given wrist for a given increase in heart rate also should be greater when the muscles about the other wrist are inactive. We found that the increase in stiffness for the right wrist-pendulum in response to ankle torque was greater when it was oscillated alone than when it was oscillated in coordination with the left wrist-pendulum. If this was an effect of differential blood flows for single versus double wrist-pendulums, then the stiffness for any given wrist-pendulum oscillated in isolation should be greater than its stiffness when oscillated in coordi-
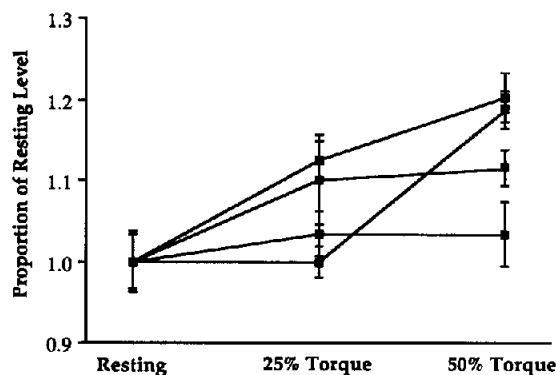

Figure 11. Changes in heart rate for 4 participants as a proportion of mean resting heart rate. (Rates were normalized by using the mean resting heart rate for each participant, respectively. Error bars represent the standard error.)

nation with another wrist-pendulum, all else being equal. This is indeed the general finding.

As we mentioned in the introduction, the period for a pendulum swung together with another pendulum of the same length is typically longer than that for a pendulum swung in isolation. Kugler and Turvey (1987) reported periods, masses, and lengths for four different pendulums, all swung in isolation and in combination by each of 4 participants. Returning to those data, we computed the stiffnesses for the four wrist-pendulums oscillating in isolation and oscillating in coordination with pendulums of equal length and mass. The mean stiffnesses for the four pendulums swung either in coordination or in isolation are shown in Figure 12. In a repeated-measures ANOVA with context (isolation or coordination), hand, and pendulum (1-4) as variables, only the context variable was significant, $F(1, 3) = 101.9$, $p < .002$. The overall mean stiffness values were .568 kg/s^2 in isolation and .220 kg/s^2 in coordination. Thus, there was a drop in stiffness when a wrist-pendulum was oscillated in coordination with another wrist-pendulum of equal length. This drop has been observed in other experiments that used the pendulum-swinging task (Schmidt & Turvey, 1989). The implication is that the additional musculature receptive to blood flow slightly reduces the blood flow to the given muscles, with a resultant drop in stiffness.

In sum, circulatory organization provides a reasonable preliminary account for observed increases in stiffness with increasing ankle torque and for the proportionality of increases in stiffness to inertial load. Circulatory organization also accounts for the relatively larger increase in stiffness that occurs for a wrist-pendulum oscillated alone, and this result becomes consistent with the finding that stiffnesses were generally higher for wrist-pendulums oscillated alone than for those oscillated in combination with a wrist-pendulum of equal length.

Interactions Mediated by the Nervous System

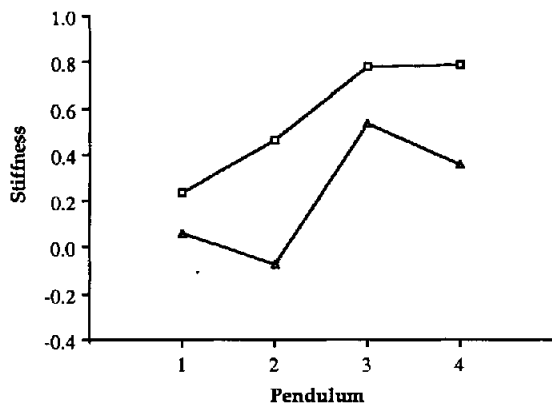How might we account for the observed interactions between ankle and wrist activity as mediated by the nervous

Figure 12. Mean stiffness for each pendulum swung either in isolation or together with another pendulum of equal length and mass: Data derived from Kugler and Turvey (1987). (Open squares represent single pendulums; open triangles, double pendulums.)

system? Until fairly recently, the overriding focus of research on the neural generation of rhythmic movements has been on central pattern generators (CPGs). The CPGs had been considered the predominant factor responsible for the patterns of observed behavior (Grillner, 1975, 1976, 1981, 1985). De-afferented preparations exhibited many properties common to normal rhythmic movement. Also, in so-called "fictive locomotion," patterns comparable to normal locomotion have been measured by recording the activity of neurons in the spinal cords of paralyzed animals. The need for afferent input has always been recognized, however, because the frequencies exhibited by de-afferented and paralyzed preparations were substantially below those observed in normal activity. Afferent input was considered to have a role in determining tonic influences used merely to tune the frequencies of rhythmic patterns predetermined by a CPG (Grillner, 1976, 1985; Rossignol, Lund, & Drew, 1988). It has also been recognized that afferents are required for precise coupling between limbs, for sufficient and exact force levels, and for precision in positioning. But none of these challenged the surmised role of afferents as mere tonic influences on preestablished phasic processes.

More recently, however, the essential role of afferent elements in establishing phasic patterns of behavior has become recognized (Gelfand, Orlovsky, & Shik, 1988; Pearson, 1989). Rhythmic units in locomotion exhibit autonomous organization by allowing proprioceptors to determine switching between flexion-extension phases of movement on the basis of the limb's reaching a prescribed endpoint position. If the limb is delayed in transit, switching does not occur until the limb reaches the requisite position. The advantage of autonomous organization is independence and stability in the face of external perturbations or changes in the properties of the musculature, such as fatigue (Pearson, 1989). Of course, this does not exclude tonic afferent influences on rhythmic units.

Tonic influences originate in muscle receptors, such as primary spindle endings and golgi tendon organs, which respond in proportion to the contractile state of individual muscles, as indexed by the number of active fibers (Loeb, 1985). This influence is projected through Ia and Ib fibers, respectively, to the spinal cord, where it is conveyed to the cerebellum through the dorsal and ventral spino-cerebellar tracts (Arshavsky, Gelfand, & Orlovsky, 1986; Gelfand et al., 1988). The dorsal tract (DSCT) in particular transmits information proportional to the level of activity of individual muscles. The reticulo-spinal (RS) tract receives input from the DSCT both in the cerebellum and preceding the cerebellum. The RS neurons exert a descending tonic influence on limb behaviors at the spinal cord. The timing of behaviors is not directly affected; only the level of activity in the respective muscles is affected. However, given the autonomous organization of rhythmic movements, the effect of tonically induced increases in muscle activations is to increase accelerations and peak velocities to fixed endpoints, which in turn increases the frequency of oscillation. The extent of the increase is proportional to the level of tonic activity in the original limb (Arshavsky et al., 1986).

This organization accounts for our observed increases in stiffness at the wrists in proportion to levels of torque at the ankle. Greater activity in ankle muscles results in proportional

tonically induced increases in wrist muscle activations. The proportionality of increases to the local inertial load is related to the recruitment of motor units within a muscle. Greater torque levels required by larger inertial loads are provided by activating a larger number of motor units. If tonic increases were distributed equally across all active motor units, then a greater number of active units means a greater total increase in torque levels. In addition, if tonic influences provoked additional recruitment following the size principle, the larger fast-twitch units are recruited with larger inertial loads (Henneman, Somjen, & Carpenter, 1965). That is, according to the size principle, the increment in torque is proportional to the level of torque at the time (McMahon, 1984). This also results in greater increases in torque with larger inertial loads.

However, nervous-system interactions seem to provide no account for the increased effect of ankle torque perturbations on wrist-pendulums oscillated in isolation. (None, in any case, that we could discover in the current literature.) The same is true with respect to an account for observed variations in relative phase. We have no intention of ruling out the possibility of such an account and state only that we are not currently aware of one.

Interactions and Changes in Relative Phase

The relative phase between the wrist-pendulums departed from strict antiphase in proportion to the difference in the inertial loads at the two wrists. The maximum lag times associated with these deviations from a 180° relative phase were on the order of 100 ms. These lag times may be attributed to the difference in electromechanical response because of the difference in force requirements, given different inertial loads and assuming strict antiphase of respective neural input (Rosenblum & Turvey, 1988). The variation in electromechanical response time with the level of force to be developed is a well-established result (Bell & Jacobs, 1986; Cavanagh & Komi, 1979; Norman & Komi, 1979) that has been attributed to the time required to stretch the series elastic component of muscle.[7] This attribution was inspired by the asymmetry of delay for eccentric and concentric muscle contractions, eccentric delays being smaller (Cavanagh & Komi, 1979). The series elastic component becomes stretched more rapidly if the muscle is being lengthened by external means during the contraction.

We found that the deviations of wrist movements from strict antiphase decreased with increasing ankle torque. The decreases were the opposite of what was expected from the fact that the periods of movement decreased. By itself, a decrease in period should produce an increase in the relative differences from antiphase because the difference in delay times make up a larger portion of the cycle time (Rosenblum & Turvey, 1988). In addition, the implied increases in muscle force should exacerbate the differences in delay because the electromechanical delay is an accelerating function of the force level to be attained (Bell & Jacobs, 1986). However, an account derived on the basis of an assumed increase in blood flow entails that not just the force but also the power generated by the muscle was increased by the increase in available oxygen. Power is the rate of energy production or, alternatively, force multiplied by velocity of shortening. The impli-

cation is that the contractile elements in the muscle shorten more rapidly. The result is a reduction of the electromechanical delay because the targeted force level is reached more quickly.

An account in terms of neural interactions requires that a shift in the relative phase of the respective neural innervations results from the tonic descending influence on the wrists. There is no evidence to support this possibility. Rather, the distinguishing characteristic of tonic as opposed to phasic influences is that tonic influences have no direct effect on the timing of muscle activations. A neurally based account, therefore, remains to be discovered.

Need for Analysis in Terms of Task-Specific Dynamics

Where are the interactions between ankle and wrists mediated—in the circulatory system or in the nervous system? We suggest that both systems must be involved. Interactions of the kind examined in this article are to be expected from the extant understanding of the physiology of these systems. The nervous, circulatory, and muscular systems are thoroughly interdependent (Åstrand & Rodahl, 1977; Bloch & Iberall, 1982; Iberall, 1974, 1990, and citations contained therein). The evidence that we have presented for circulatory involvement, reasoning in part from the literature as we have, is somewhat circumstantial. The next stage of research certainly requires direct measurements, during the pendulum-swinging task, of circulation in the musculature spanning the wrists. Nevertheless, the way that the pieces have consistently fallen into place in this complex puzzle provides fairly strong support for the role of circulatory interactions in determining observed forms of behavior. Of course, circulatory involvement presumes nervous activity, because among other reasons the smooth muscles that help control circulation receive neural input. The bottom line is that rhythmic movements about different joints are bound to interact though the global and continuous subsystems of the human action system.

Movement organization has often been conceived as a matter of imposing prescribed trajectories on the motor apparatus through appropriate control structures. Such an approach essentially reduces coordination to an implicit consequence of a solution to the problem of control. The challenge for such an approach is the need to anticipate and control for perturbations arising from interactions. The problem has been discussed most often in the context of interactions that arise among the link segments. Recent advances in computational schemes for inverse dynamics have given apparent promise to the so-called "trajectory formation" approach (Hinton, 1984). However, the progress is limited to link-segment interactions. Interactions produced by biarticular muscles have not been addressed. Interactions associated with the circulatory system create extreme difficulty for an explicit control-oriented approach.

The alternative is to consider ways that the action system might perceive qualitative properties of its own emerging dynamics arising from interacting nonlinear resources and to

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[7] The effect of variations in the inertial load has also been recognized in the reaction time literature (Anson, 1989).

explore how those resources, when manipulated, contribute to the resulting dynamic (Beek, 1989; Beek & Bingham, in press; Bingham, 1988; Bingham et al., 1989; Kelso & Kay, 1986; Kugler, 1986; Kugler & Turvey, 1987, 1988; Schöner & Kelso, 1989; Thelen, Kelso, & Fogel, 1987). Certainly, we should not be able to control anything that we cannot perceive.[8] The universal nonlinearity of components (e.g., link segments, muscles, nerves, and circulation) and the thoroughness with which interactions pervade the system also ensure that perception is required to keep track of the organization that emerges. Of course, no functionally effective behavior is possible without control, but it seems best to first discover what organizations arise to be controlled (Beek, 1989; Bingham, 1988). The difficulty we encounter when exploring emergent organization is functional flexibility. There are different ways of performing a given task: Our only alternative is to focus on the constraints that limit possible organization or performance. Many constraints originate in interactions, so we turn our attention to these.

We discovered that tonic activity about the ankle affected rhythmic activity about the wrists and that the extent of the perturbation was proportional both to the level of tonic activity and to the inertial load oscillating about the wrist. The result implies that the rhythmic activity in one wrist might interact with and thus constrain concurrent rhythmic activity at the other wrist. However, we are not yet in a position to model the coupling. The reason is that we lack information concerning the specific variation in perturbation with variation in the level of perturbing activity. For instance, the coefficient a in Equation (7) varies most likely as a nonlinear function of the level of ankle torque. The introduction of phasic variations in activity at the ankle has different consequences in terms of circulation or nervous activity. Oscillations will not communicate through the circulatory system, but they can follow neural routes similar to those described earlier to exert phasic descending influences on rhythmic activity at the wrists (Arshavsky et al., 1986). Thus, specifically rhythmic perturbations need to be investigated before the resulting coupling can be described.

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[8] Note in this regard that participants were not aware of either the increases in stiffness or deviations in relative phase from strict antiphase. These properties of their movements, therefore, cannot have been controlled by them in these respects.

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Appendix A

Testing the Adequacy of a Linear Model

To determine the adequacy of the linear model for predicting periods, predictions from the linear approximation should be compared to those from the original nonlinear model. For given values of stiffness, pendulum length, and mass, the linear model produces a period value that is invariant over variations in amplitude. In contrast, the nonlinear model produces periods that vary with amplitude increasing at an accelerating rate with increasing amplitudes. For the simple pendulum alone, the linear model is a good approximation for amplitudes up to about 20° (Seto, 1964). This means that periods produced by the nonlinear simple pendulum model do not vary appreciably with amplitude within this range.

The equation for the nonlinear model corresponding to Figure 1 is as follows:

$$ML^2\ddot{\theta}(t) + K\theta(t) + gML \sin[\theta(t)] = 0. \qquad (A1)$$

The total force varies with position according to the contributions of the gravitational term and the stiffness term. The curvature of the graph of the total force versus position reflects the nonlinearity of the system as seen in the right panel of Figure A1. However, as seen in the left panel, the extent of the nonlinearity decreases with increasing values of the stiffness, K.

The adequacy of the linear approximation is determined by the

degree of variation in periods over the relevant range of amplitudes for the nonlinear system. The mean amplitudes exhibited by participants in the pendulum-swinging experiments vary across participants from about 5° to about 40°. Equation (A1) cannot be solved analytically. The periods must be derived by numerical methods. Using a fourth-order Runge-Kutta computation ($\Delta t = .025$), periods corresponding to amplitudes ranging between 5.7° (.1 rads) and 43.0° (.75 rads) were computed. We used a simple pendulum length of 0.5 m and a mass of 1 kg. These values represent the largest pendulum used in the experiment. Because the graphs corresponding to values for the shortest pendulum used look the same as in Figure A1, we computed periods only for the largest pendulum values. Stiffness values representing the maximum of the range of observed stiffness (K = 5) and a value somewhat greater than the minimum of the range of observed stiffness close to zero (K = −0.4) were used to capture the best and worst case instances, respectively, corresponding to the left and right panel of Figure A1, respectively.

For K small, periods at an amplitude of 43° increased by 4% of the value at 5.7°. For K large, periods increased by 2% over the same range. (Periods for an amplitude of 57.3° [1.0 rads] increased by 7% and 3%, respectively.) Thus, in the worst case, periods varied by only 4%, indicating that the linear form of the model is entirely adequate for the range of values employed in the experiment.
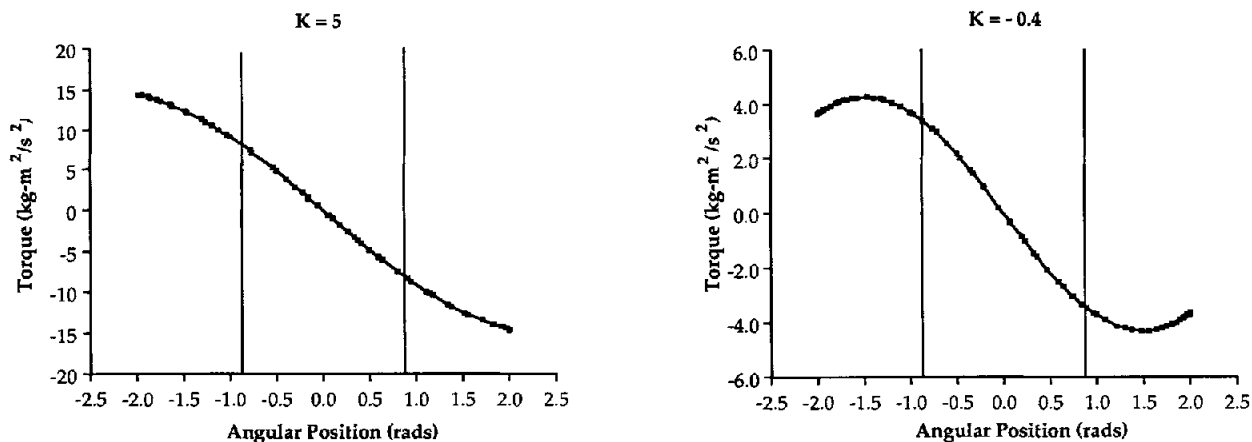
Figure A1. The top panel represents simulated variations in torque for the wrist pendulum system with a large amount of stiffness; the bottom panel represents those with a small amount of stiffness near 0. (Vertical lines mark the largest amplitude observed in participants' movements.)

Appendix B

Derivation of the Model

By integrating twice, solutions to Equation (4) may be written as follows:

$$\theta_R(t) = A_R \sin(\omega_R t + \phi^*),$$

$$\theta_L(t) = A_L \sin(\omega_L t + \phi^*), \tag{B1}$$

where A_R and A_L are the amplitudes, ω_R and ω_L are the frequencies, and $\phi^* = \phi_R - \phi_L$ is the relative phase. Because the task requires the two systems to run at the same frequency, $\omega_R = \omega_L = \omega$. Dividing each equation by the respective amplitude, we obtain

$$\theta^*(t) = \frac{\theta_R(t)}{A_R} = \frac{\theta_L(t)}{A_L} = \sin(\omega t + \phi^*). \tag{B2}$$

After dividing by the respective amplitudes and ML^2, Equation (4) may be written as follows:

$$\frac{\ddot{\theta}_R(t)}{A_R} + \omega \frac{\theta_R(t)}{A_R} = 0,$$

$$\frac{\ddot{\theta}_L(t)}{A_L} + \omega \frac{\theta_L(t)}{A_L} = 0. \tag{B3}$$

Given (B2) and the equivalence of the frequencies, we obtain

$$\ddot{\theta}^*(t) = \frac{\ddot{\theta}_R(t)}{A_R} = \frac{\ddot{\theta}_L(t)}{A_L}. \tag{B4}$$

Scaling Equation (4) by the respective amplitudes and using (B2) and (B4), we write the equations in common variables, as follows:

$$M_R L_R^2 \ddot{\theta}^*(t) + [K_R + gM_R L_R]\theta^*(t) = 0,$$

$$M_L L_L^2 \ddot{\theta}^*(t) + [K_L + gM_L L_L]\theta^*(t) = 0. \tag{B5}$$

Since the asterisked variables are simultaneously parameterized as in the two equations, we summed these two equations to obtain Equation (5).