

# Investigating a Nonconservative Invariant of Motion in Coordinated Rhythmic Movements

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The dimensions of an animal's limbs are fixed, but in locomotion and other rhythmic activities, they oscillate at a number of different frequencies. How might the physical conditions for this frequency variation be characterized? Kugler and Turvey (1987) hypothesized that the conditions might be adiabatic. A rhythmic system undergoes an adiabatic transformation of frequency when the stiffness is changed without a transfer of energy by heating. By standard definitions, *adiabatic transformability* is achievable only in conservative systems and only at infinitely slow rates of transformation. Kugler and Turvey's (1987) hypothesis extends adiabatic to systems that are dissipative and transformed rapidly by internal sources of energy, such as biological movement systems. Two predictions follow from the hypothesis. The first prediction is that a relation should be obtained in frequency-energy coordinates that has constant slope (Ehrenfest's adiabatic relation, a semipermanent invariant of motion) and an energy intercept less than zero (constant energy dissipation regardless of frequency). The second prediction is that the positive linear relation in frequency-energy coordinates can be satisfied by different relations in period-amplitude coordinates: amplitude increasing, amplitude increasing then decreasing, amplitude decreasing. The predictions were

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evaluated in four experiments with the same three participants. In each experiment, the rhythmic movement unit was defined by a pendulum of fixed dimensions held in the right hand that was made to oscillate at frequencies in the range 0.6 Hz to 1.8 Hz by the requirement of 1:1 frequency locking with a pendulum of different dimensions held in the other hand. Changes in the period of a pendular rhythmic movement were accompanied by statistically significant changes in the amplitude. Amplitude's systematic dependence on period differed, however, among the three participants in the experiments. Despite the period-amplitude differences, the relations in frequency-energy coordinates for all three participants in Experiments 1 and 2, and for two participants in Experiments 3 and 4, tended to be of constant positive slope and nonzero intercept. Discussion focuses on (a) the relevance of the data for the notion of a nonconservative invariant of motion in biological movement systems, and (b) the implications of the fact that the participants in the experiments resolved the problem of assembling sustained coordinated rhythmic movements in consistent but unidentical ways.

The cyclic movements of mammalian limbs can occur at a number of different frequencies. From walking to trotting to cantering, the limb frequencies of quadrupeds vary over a range of about 0.7 Hz in very large animals and about 1.5 Hz in much smaller animals. To give some examples from Pennycuick's (1975) observations of animals in the Serengeti (see Table 8.3 in Kugler & Turvey, 1987): Thompson's gazelle, weighing about 20 kg, walks on the average at a frequency of 1.25 Hz and canters on the average at a frequency of 2.60 Hz; the impala, weighing about 50 kg, walks on the average of 0.95 Hz and canters on the average at 2.15 Hz; the kongoni, weighing about 170 kg, walks on the average at 0.84 Hz and canters on the average at 1.85 Hz; the zebra, weighing about 350 kg, walks on the average at 0.90 Hz and canters on the average at 2.22 Hz; and the giraffe, weighing about 1,000 kg, walks on the average at 0.48 Hz and canters on the average at 1.20 Hz. The rhythmic movements of limbs in a given locomotory gait have been characterized as pendular clocking movements in recognition of the fact that they entail the raising and lowering of a mass against gravity and they are repeated with approximately the same duration from cycle to cycle (Kugler & Turvey, 1987). In this article, we address the mechanism by which frequency changes of the kind typical of locomotion might be brought about. We do so through experiments in which humans perform rhythmic, upper body movements of a pendular clocking nature over a range of frequencies comparable to the ranges found in locomotion. These experiments, in addressing the mechanism of frequency change, simultaneously addressed the mechanism underlying the relation between movement frequency and movement amplitude. Recent research with humans has found systematic variations in the amplitude of rhythmic movements accompanying variations in the period of rhythmic movements (Kay, Kelso, Saltzman, & Schöner, 1987; Kugler &

Turvey, 1987). With respect to quadruped locomotion, it has been observed that the amplitude of limb movements decreases as animal size and limb cycle time increase (MacMahon, 1984).

### FELDMAN'S LAMBDA HYPOTHESIS

Feldman (1966a, 1966b, 1980, 1986) developed an account of muscular activity that addresses how the stiffness of a rhythmic movement unit and, therefore, its frequency, is adjusted. In experiments examining the maintenance of a static posture, it was shown that when a joint angle is intentionally set, an externally produced deviation from this resting angle produced a resistant torque proportional to the deviation. If unimpeded, this torque would return the limb to its resting position. Feldman reasoned that the behavior of the limb is analogous to the behavior of a nonlinear spring:

$$N = S(\lambda_1 - \lambda_0) \quad (1)$$

where  $N$  is the torque produced and  $\lambda_1 - \lambda_0$  is the angular deviation of the limb from its rest position ( $\lambda_0$ ). The function  $S$  proved to be invariant for any given rest position but variable from one rest position to another.

Feldman's equilibrium point or  $\lambda$  hypothesis follows from these findings. According to this hypothesis, for the movement of a limb about a joint from one static position (A) to another (B) only one parameter is controlled, namely, the threshold length ( $\lambda_0$ ) of the stretch reflex. If the  $\lambda_0$  for position B is established while the limb still resides at position A, a necessary and sufficient torque ( $N$ ) will be produced to move the limb from A to B.

Let us now see how the  $\lambda$  hypothesis applied to rhythmic movements about a joint. For dynamic behavior, Equation 1 becomes:

$$N = S(\lambda_1 - \lambda_0 + \mu V). \quad (2)$$

In this refinement of the postural equilibrium-point model, the restorative torque ( $N$ ) is dependent not only on the deviation of the oscillation from the resting position of the muscle but also on the velocity of the movement ( $V$ ) and the centrally controllable damping parameter known as  $\mu$  (Feldman, 1986). This dependency of the restorative torque on the velocity of the movement is a direct consequence of the fact that the reflex threshold is a decreasing function of velocity. Furthermore, this dependency results in a decrease in the activation area of motoneuron recruitment and, hence, a decrease in peak amplitude at higher frequencies of oscillation (assuming that higher velocities are associated with higher frequencies of oscillation).

Also, Feldman identified two different modes of rhythmic movement. The

first mode comprises very low-frequency movements (under 1 Hz) that are accomplished by discretely changing the  $\lambda_0$  (and, hence, the invariant characteristic) of the flexors and extensors at a joint, producing a trajectory that is a smooth sum of discrete targeting movements. The second mode comprises high-frequency rhythmic movements, accomplished by the functional fusing of the invariant characteristics of the flexors and extensors into a single invariant characteristic. The natural frequency of such a system is given by:

$$f = 2\pi \sqrt{K/I} \quad (3)$$

where  $f$  is the natural frequency,  $K$  is the stiffness or elastic potential of the joint (the linearized slope of the "mutual" invariant characteristic), and  $I$  is the moment of inertia of the limb. Feldman (1966b) demonstrated that an increase in  $I$  (produced by adding weight) yielded expected decreases in the maximum  $f$ . For constant  $I$ ,  $f$  can be controlled by the manipulation of  $K$ . Feldman (1980) presented an elegant mechanism whereby the stiffness of the joint can be controlled: The more the flexors and the extensors have overlapping resting lengths ( $\lambda_0$ ), such that for a subset of angular positions both are active (there is tonic coactivation), the steeper is the resultant mutual invariant characteristic and, hence, the stiffer is the "spring" assembled at the joint. Hogan (1984) similarly suggested that the relation between agonist and antagonist activity at a joint controls the stiffness (and, hence, impedance) at a joint.

Feldman (1980) observed a decrease of the maximum amplitude of a rhythmic movement with an increase in frequency: As the cycle time for the movement becomes shorter, the space traversed by the movement shrinks. This relation between spacing and timing is a natural consequence of the mechanism controlling stiffness. As the amount of tonic coactivation increases, the amount of reciprocal contraction possible for producing an extension or a flexion decreases. Hence, as the frequency increases and stiffness increases, the maximum amplitude of the movement decreases.

### EXPLORING THE SPACING-TIMING RELATION THROUGH A HYBRID OSCILLATOR

Feldman's account, although elegant and parsimonious, does not model explicitly the dissipative and self-sustaining nature of human rhythmic movements. Whenever a movement is performed, energy is lost to dissipation—friction with the air and in the musculature provides a basis for the transformation of the mechanical energy of the movement into heat energy at the microstructural level. Because energy is lost from a movement, if a movement is to be rhythmically sustained, then energy must be somehow injected into the system to keep it going. Hence, self-sustaining oscillatory systems, as seen in human move-

ments, must have an energy source and must have a mechanism that provides the system with energy from this source.

In oscillation theory (Jordan & Smith, 1977; J. M. T. Thompson & Stewart, 1986), such a mechanism is called an *escapement*. Classically, escapements are of two kinds: *autonomous*, in which energy is injected as a function of the system's intrinsic variables (e.g., position, velocity, and phase); or *nonautonomous*, in which energy is injected as a function of an extrinsic variable (e.g., time). Sustained oscillatory systems with either kind of escapement exhibit what is called *limit cycle behavior*. If left for a sufficiently long time (i.e., its limit set), the stable trajectory onto which the system settles is cyclic or periodic. If the system is perturbed to a position outside of its limit set, it will return to a trajectory on the limit set. Given such behavior, these systems are said to be governed by a limit cycle attractor. The relative magnitude of the energy injected into the system (or, alternatively, the dissipation it must overcome) is important in determining just how attractive a given limit cycle will be. More precisely, the relative proportion of energy dissipated by the system to the energy conserved by the system from cycle to cycle determines how stable the system will be.

Feldman's model of rhythmic movements does not countenance explicitly the dissipation inherent in such movements (although he is aware of its importance; Feldman, 1966b). His model is based on conservative dynamics, not dissipative dynamics. The question remains: How is the dissipative self-sustaining nature to be modeled?

Kay, in a series of studies (Kay, 1986; Kay et al., 1987), investigated this aspect of rhythmic movements. Kay et al. (1987) modeled human wrist movements with a self-sustaining oscillator that employs a combination of two classical escapements, the van der Pol and the Rayleigh. This hybrid oscillator has an equation of motion of the following form:

$$\ddot{x} + a\dot{x} + b\dot{x}^3 + gx^2\dot{x} + \omega^2x = 0. \quad (4)$$

Simple scaling of the linear ( $\omega^2$ ) stiffness in Equation 4, holding the restorative ( $a\dot{x}$ , with  $a$  negative) and dissipative ( $b\dot{x}^3$ ,  $gx^2\dot{x}$ ) terms constant, produces frequency and amplitude changes that fit an experimentally observed pattern of amplitudes decreasing with frequency better than either the van der Pol ( $gx^2\dot{x}$ ) or the Rayleigh ( $b\dot{x}^3$ ) term alone. The suggested stiffness adjustment could be brought about in the manner suggested by the  $\lambda$  hypothesis.

Kay (1986) provided further evidence that the dynamics underlying rhythmic movements is a dissipative limit cycle dynamics: The kinematics of human index finger movements were stable over perturbations, and the dimensionality of the attractor governing the trajectories was consistent with a limit cycle attractor with stochastic noise. Also, Kay (1986) found that the strength of the attractor decreased with increasing frequency. The strength of the attractor is determined by the relative magnitudes of the conservative and nonconservative (dissipative)

flow processes (i.e.,  $\epsilon =$  nonconservative processes/conservative processes) where the conservative processes are indexed by the frequency of oscillation  $\omega$  (because  $\omega \propto \sqrt{K}$ ). If the dissipation exhibited by the system was constant across frequency changes, then attractor strength would decrease.

Four problems stand in the way of the hybrid oscillator as a physically viable interpretation of a biological rhythmic movement system. First, there are no independent grounds (beyond data fitting) for assuming that the friction function is assembled from linear friction and Rayleigh and van der Pol terms in the way suggested. P. J. Beek and W. J. Beek (1988) showed that other elastic and dissipative functions exist beyond those classically defined in the study of musical instruments, electronic circuits, and mechanical vibrations. These additional functions, alone or in combinations, may be present in biological rhythms. P. J. Beek and W. J. Beek (1988) argued for the development of analytic tools for determining precisely the stiffness and friction terms from the phase portraits of biological oscillators. A second problem is posed by the fact that, whereas the hybrid model predicts declining amplitude with frequency, other space-time relations have been observed empirically, such as amplitude increasing with frequency and amplitude increasing then decreasing with frequency (Kugler & Turvey, 1987). A third problem follows from the observation in phase resetting experiments that, whereas the briefly perturbed hybrid oscillator predicts greater stability at higher than lower frequencies, Kay (1986) obtained experimental evidence favoring the opposite outcome for rhythmic movement. The remaining problem arises from the fact that the hybrid oscillator accounts for amplitude-frequency relations by assuming that stiffness can be changed without incurring any change in the friction function. As noted, Kay (1986) provided experimental evidence for this idea that the relative dissipation is constant across frequencies. The problem is that no physical basis is identified for this crucial property. What physical conditions would permit a change in stiffness in the manner identified by the  $\lambda$  hypothesis, without a change in energy dissipation?

### AN ADIABATIC TRANSFORMABILITY HYPOTHESIS

Kugler and Turvey (1987, chapters 10–12) hypothesized that the reciprocal notions of adiabatic transformation and adiabatic invariant apply to pendular rhythmic movement units of the kind witnessed in locomotion. Their account of the frequency variations in a rhythmic unit of fixed dimensions attempted to address in general physical terms the observed orthogonality of elastic and friction changes and the inverse relation between stability and frequency.

The term *adiabatic* was introduced by Rankine (1854). Literally, it means “to not go through” and was so used by Rankine to refer to processes in which heat—conceptualized at Rankine’s time as a substance—did not flow across a

system's boundaries. Under a more contemporary understanding of heat, the interpretation of adiabatic takes a different form. All energy interactions comprise two distinguishable processes: heat and work. Contrary to colloquial usage, these are names of methods, not things; precisely, heat and work refer to methods of transferring energy (Atkins, 1984). Heat is a way of transferring energy incoherently, meaning that the stimulated motions of the particles of a composite system are uncorrelated. In contrast, work is a way of transferring energy coherently, meaning that the stimulated motions of the particles of a composite system are correlated. No real process, however, is strictly heat (a perfectly balanced distribution of velocities is unattainable) or strictly work (inducing the same velocity in the same direction in all particles is not possible). It is in the context of the foregoing understandings of heat and work that adiabatic receives its contemporary interpretation: A system undergoes an adiabatic transformation when there is no transfer of energy by heating (see Dudevior, 1988, for an informed discussion).

An adiabatic change is usually characterized as an infinitely slow change, for example, a piston that moves with negligible velocity and, thereby, negligible friction, as it compresses the volume of a chambered gas and changes the frequency with which the gas molecules collide. Kugler and Turvey (1987, chapter 10) argued, however, that the classical rate limitation on adiabatic transformability need not apply when the torques producing the change in the system of interest are derived from energy sources internal to the system. If the torque is generated internally, then rapid, adiabatic transformations on the coordinates of motion can be induced. Additionally and relatedly, they argued that the term adiabatic applies even when there is dissipation of energy—contrary to the accepted definition—as long as the dissipation is independent of time (where dissipation is understood as the transfer of mechanical energy at the macrolevel to heat at the microlevel). The two arguments amount to a radical generalization of the term adiabatic (see Dudevior, 1988).

The most noteworthy nonconservative systems that derive forces from internal energy reservoirs are biological systems; an animal generates mechanical torques from chemical reservoirs carried "on-board" in the tissues of its body. Figuratively speaking, the energy reserves are strapped to the animal's limbs. Consequently, according to Kugler and Turvey's (1987, chapters 10 and 11) hypothesis, biological systems and biological subsystems, such as rhythmic movement units, can be transformed adiabatically, without rate limitations, using internally generated torques. What is especially significant about an adiabatic transformation is that it leaves certain quantities invariant. These quantities are termed *adiabatic invariants*. The quantity action, which is the ratio of average cycle energy to frequency, is one such invariant. Ehrenfest (1916/1959a, 1917/1959b) referred to adiabatic invariants as "semi-permanent quantities" and underlined their hybrid nature; action, for example, is a conserved quantity (energy) in ratio with a variable of motion (frequency). As

with invariants of motion more generally, adiabatic invariants constrain the degrees of freedom of a system. Given two variables linked by an invariant of motion, it is only necessary to keep track of one of them. From the perspective of a general understanding of how coordinated movements are assembled and executed, the promise of these semipermanent invariants of motion, if available biologically, is an understanding of a potentially significant method by which biological systems achieve a reduction of the degrees of freedom without physical representation. Namely, they exploit invariants that arise within the circumstances of the activity.

It is important to underscore the point just made that the term adiabatic can be applied to real systems only as an approximation. Arnold (1983) showed that the action variables of nonlinear systems are not precisely invariant, but "only almost adiabatic invariants," varying slightly across initial conditions. Because the transformation (in the nontrivial case) involves the addition of energy to the motion of the system and energy can only be added (and deleted) as kinetic energy, the invariant must oscillate relative to the kinetic energy and potential energy storage phases. If adiabatic quantities exist for biological movement systems, then we should expect those quantities to be only approximately constant but nonetheless sufficiently close to constant for purposes of effectively constraining coordination.

#### DETAILING THE RELATION BETWEEN MECHANICAL TRANSFORMABILITY AND THE ADIABATIC INVARIANT OF ACTION

Ehrenfest's (1916/1959a, 1917/1959b) original adiabatic hypothesis is that an invariant ratio exists between the oscillatory energy and frequency of a conservative periodic system during transformations that are conducted infinitely slowly. The hypothesis is depicted by a straight line in frequency-energy coordinates with constant slope (the action) that intersects the origin, as seen in Figure 1. According to the theoretical analysis of Kugler and Turvey (1987), if the frequency of a nonconservative oscillatory system of a given moment of inertia, such as a rhythmically moving limb, changes via an adiabatic transformation, then the system's constraints define the kinetic and kinematic characteristics depicted in Figure 2. The kinetic characteristics (Figure 2a) comprise a linear relation between average cycle energy ( $E_m$ ) and frequency ( $f$ ), with a constant slope ( $H$ ) and, importantly, a positive frequency intercept ( $f_{inc}$ ). The latter feature means that there is a negative energy intercept ( $E_t$ ). (The subscripts  $m$  and  $t$  denote mechanical and thermal, respectively.) The nonconservative adiabatic transformation of frequency is indexed by the constant  $E_t$  interpreted as the amount of energy (not observable in the laboratory reference frame) that is put into the cycle to offset the energy lost per cycle: Changes in cycle



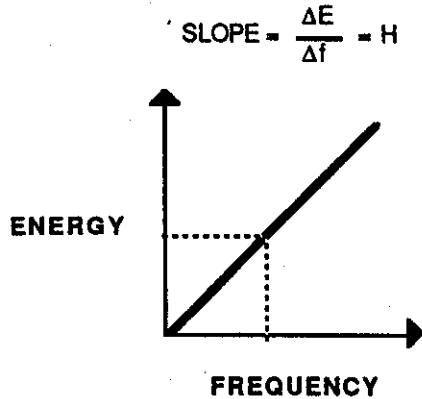


FIGURE 1 Ehrenfest's frequency ( $f$ )-energy ( $E$ ) relation for a conservative system with the constant of proportionality, the action ( $H$ ), given by the constant slope.

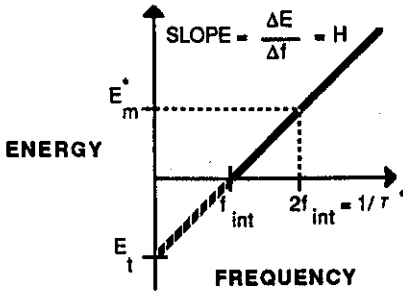
frequency (a coordinate of motion) incur no changes in the amount of energy dissipated per cycle (a thermodynamic quantity). The adiabatic invariant is the constant proportionality  $H$  found between  $E_m$ , observed in the laboratory frame of reference, and  $f - f_{inc}$ . The special advantage of constant action, Kugler and Turvey (1987) argued, is that the operation of the system is maximally independent of internal conditions in the sense of imposing the minimal possible demands on the regulation of the energy reservoir. For a rhythmic movement unit, strict compliance with the adiabatic invariant suggests that the contribution of muscular forces during oscillations may be limited to compensating frictional losses.

The kinematic characteristics of a nonconservative adiabatic system (see Figure 2b) comprise a nonmonotonic, nonlinear relation between amplitude ( $\Theta$ ) and period ( $\tau$ ), with an intercept at  $\tau_{inc}$  (the inverse of  $f_{inc}$ ) and a maximum value of  $\Theta$  occurring at  $\tau^*$ ,<sup>1</sup> which is twice  $\tau_{inc}$ . The  $\tau$ - $\Theta$  relation follows from expressing  $H$  as  $(E_i - 0) / (f_i - f_{inc})$  (see Figure 2b), approximating  $E_i$  by  $l/2(\Theta_i^2/\tau_i^2)$ , where  $l$  is moment of inertia, and rearranging terms. Thus,

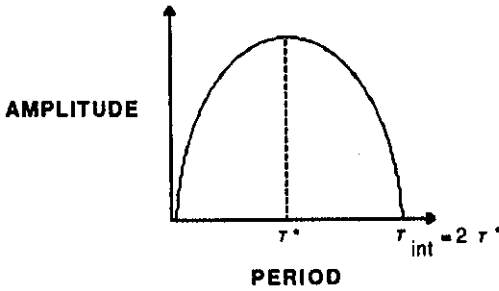
$$\Theta_i = \pm [2H_i\tau_i^2(f_i - f_{inc})/l]^{1/2}. \tag{5}$$

The frequency  $f^*$ , which is twice  $f_{inc}$ , has two important properties. One of them, which was already noted, is that it is the frequency at which amplitude is maximal. The other is that  $f^*$  is the frequency at which  $E_m = E_c$ . This identity at  $f^*$  follows most simply from a consideration of the geometry of the  $f$ - $E_m$  relation depicted in Figure 2a (see Figure 10.17 of Kugler & Turvey, 1987). The significance of  $E_m = E_c$  at  $f^*$  is that it identifies a special state in which a balance exists, over the cycle, between the energy put into the cycle and the energy lost

<sup>1</sup>In this article, the notation  $\tau^*$ ,  $f^*$  is used instead of the notation  $\tau_0$ ,  $f_0$ , which was used by Kugler and Turvey (1987). We changed the notation to avoid confusing the critical period/frequency with the natural period/frequency in isolation.



(a)



(b)

FIGURE 2 (a) Ehrenfest's  $f$ - $E$  relation for a nonconservative system.  $E_m^*$  is the mechanical energy at twice the intercept frequency;  $E_t$  is the negative energy intercept representing a constant energy dissipation for the different frequencies;  $f_{int}$  is the positive frequency intercept. (b) The relation of period and amplitude for a system governed by the non-conservative Ehrenfest  $f$ - $E$  relation. See text for details.

from the cycle. That is to say, the amount of mechanical energy appearing in the external coordinates of motion is exactly equal to the amount of thermal energy appearing in the internal coordinates of motion. For a rhythmic movement unit, it means that no energy in a cycle of limb motion is conserved in a macroscopic storage mode, specifically, a potential energy storage mode (e.g., the elastic recoil of muscles; Cavagna, 1977) or an inertial energy mode (e.g., the energy carryover from one cycle to the next). The latter state of affairs is true, of course, for the

range of values satisfying  $E_m \leq E_t$ . Under this condition of  $E_m \leq E_t$ , the operation of the system is independent of the macro (potential and kinetic) storage modes and, thereby, stable (within limits) to external perturbations of the coordinates of motion. Under this condition of  $E_m \leq E_t$ , the control of the coordinates of motion is achieved through muscular torques generated internally and, thereby, is minimally influenced by torques generated externally. Because the relation  $E_m \leq E_t$  is found at lower frequencies and the adiabatic trajectory corresponds to stability against internal perturbations, the overall stability of an adiabatically transformed system will increase as  $f$  decreases. Put another way, the system's resistance to perturbations from internal and external sources increases with the increasing dominance of nonconservative processes that characterizes slower oscillations.

The ratio  $E_m/E_t$  functions as an index of the thermodynamic processes within a single oscillatory cycle. It is commonly referred to as the  $Q$ -factor of an oscillatory system. The  $Q$ -factor need not be unity. When  $Q \gg 1$ , the energy loss to be offset each cycle is comparatively small and the system is dominated by conservative, mechanical factors (i.e.,  $E_m$ ). When  $Q \ll 1$ , the energy loss to be offset each cycle is comparatively large and the system is dominated by nonconservative, thermodynamic factors (i.e.,  $E_t$ ). It is evident from Figure 2a that the adiabatic trajectory of  $(f, E_m)$  coordinates can only be achieved by varying the ratio of  $E_m$  to  $E_t$ , that is, by varying  $Q$ .

Figure 3 represents the relation between  $E_m$  and  $f$  in more detail. It shows that an adiabatic constant  $H$  and a  $Q$ -factor of unity define two distinct mappings that share a single common  $E_m$  value at  $f^*$ , namely,  $E_m^*$ . It also shows an

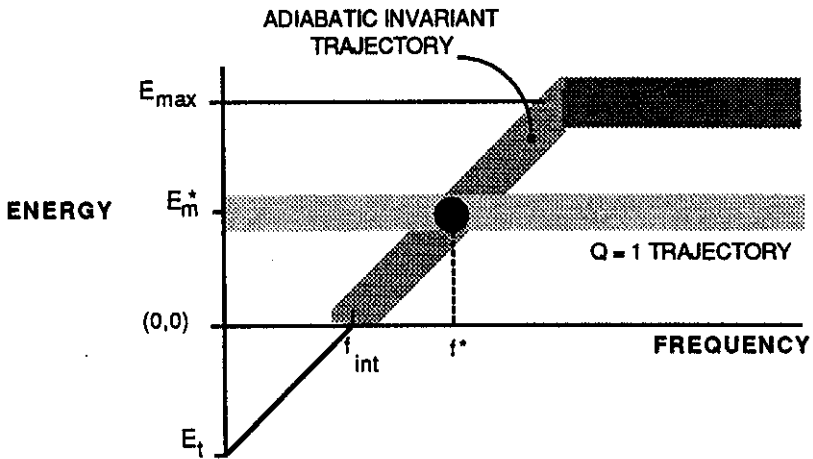


FIGURE 3 The biological work space depicting (a) the  $f$ - $E$  pairs satisfying the condition of an adiabatic invariant, (b) the  $f$ - $E$  pairs satisfying the condition of a constant  $Q = 1$ , (c) the coordinate pair  $(E_m^*, f^*)$  satisfying both conditions, and (d) the  $f$ - $E$  pairs satisfying  $E = E_{max}$ .

additional mapping that does not share  $E_m^*$ , defined by an upper limit on the cycle energy or, perhaps, the ability to vary  $Q$ . This latter mapping is introduced in recognition of the fact that biological rhythmic units are not infinitely resourceful. Collectively, these mappings define, within the  $f$ - $E_m$  space, sets of coordinate pairs that are preferred coordinate pairs, with a singularity ( $f^*$ ,  $E_m^*$ ) that could function as the most preferred coordinate pair.

## SEARCHING FOR NONCONSERVATIVE HOLONOMIC CONSTRAINTS

Before proceeding to a particular method for evaluating the generalized adiabatic hypothesis and the kinds of kinematic outcomes expected, we highlight the nature of the strategy motivating this evaluation. A core issue in the study of coordination concerns the constraining of the many (neural, muscular, and skeletal) degrees of freedom involved into task-specific organizations comprising dynamical systems of many fewer degrees of freedom (e.g., Kay, 1988). The pertinent questions are: How is this constraining achieved? What form do the constraints assume?

Ordinarily, physics distinguishes two classes of constraints, the *holonomic* and the *nonholonomic*. For our purposes, the main distinction between the two is that, whereas nonholonomic constraints require a specific material embodiment, holonomic constraints do not. For example, in biology the genetic code is materially embodied in DNA and is a much-discussed nonholonomic constraint (e.g., Pattee, 1973). A typical holonomic constraint at work in biology is the limitation on size and shape imposed by gravity (D. Thompson, 1917/1942). Obviously, as a constraint, gravity contrasts with DNA in the sense that there is no specific biological (or ordinary physical) material to which we could point and say that "that particular arrangement of matter embodies the gravitational constraint."

When we think of coordinations as being achieved by means of motor programs, we are usually thinking in terms of nonholonomic constraints in the sense that a program must occupy some material degrees of freedom. Intuitively, some cells at some level must be preoccupied with the task of representing the details of the program. In contrast, when we think of coordinations being achieved by means of dynamics, we are usually thinking in terms of holonomic constraints. The conservations are exemplary of such constraints. They prescribe, for example, a mandatory sharing of energy and momentum among interacting components and, in so doing, bring restrictions to bear on the variables of motion; they do not occupy any material degrees of freedom. If the conservations were playing a particular role in restricting behavioral degrees of freedom, then at no level of nervous function or biomechanical activity would we expect to find components preoccupied with the task of representing the

specifications of these invariants. In a word, the constraints on behavior provided holonomically come for *free*.

As noted, the conservations are primary examples of invariants of motion. Given the potential for saving on representations and computations that such constraints promise, a prudent strategy is to raise the question: What kinds of motion invariants, if any, figure significantly in coordinated movement? Because biological systems dissipate energy, this question must be extended in the direction of invariants of motion available under nonconservative conditions. Consequently, the questions this strategy poses are: (a) What kinds of nonconservative motion invariants are available?, and (b) Are they involved in the assembly of coordinated movements? The theoretical arguments in the preceding two subsections addressed the first question, and the remainder of this article addresses the second question.

### A "COMFORT MODE" METHODOLOGY

The rhythmic unit investigated in this article is a wrist-pendulum system—a hand-held rod with a weight attached at its lower end that is swung by oscillatory motions about an axis in the wrist. A wrist-pendulum exhibits a preferred frequency when the subject is instructed to oscillate at the most comfortable tempo. This comfort frequency depends on and is scaled to the mass and length of the wrist-pendulum system (Kugler & Turvey, 1987; Turvey, Schmidt, Rosenblum, & Kugler, 1988). If the magnitude is held constant, then changes in the rhythmic unit's frequency can be induced comfortably by the requirement that the subject swing another pendulum in the other hand such that the frequencies of the two pendulums are (a) the same (1:1 frequency locking or absolute coordination) and (b) the most comfortable for this coordination (Kugler & Turvey, 1987). The range of frequencies covered comfortably by the fixed wrist-pendulum system will depend, therefore, on the range of magnitudes of the other wrist-pendulum system with which it is absolutely coordinated. If the fixed wrist-pendulum system is that of the right hand, then the left wrist-pendulum system can be equal, larger, or smaller in magnitude.

The preceding paragraph identifies the fundamental experimental method—a rhythmic movement unit is made to oscillate (by the requirements of 1:1 frequency locking with another rhythmic unit) at many different frequencies, but each frequency is as comfortable as the circumstances allow. This method, introduced by Kugler and Turvey (1987), was designed to induce internally generated changes in the mechanism that regulates comfort frequency and energy flows. In applying this method, the goal was to evaluate (a) Ehrenfest's energy by frequency relation, and (b) the patterning of amplitude with respect to period when the Ehrenfest relation is defined for nonconservative systems.

## PREDICTIONS

If the relation between  $f$  and  $E_m$  in nonconservative rhythmic units is shaped primarily by adiabatic transformability, as argued, then the following observations should be made.

1. Mean amplitude and mean period will be related systematically. The systematic relation need not be fixed, however. It need not be the same from subject to subject or from one fixed wrist-pendulum system to another. As is evident from the  $\tau$ - $\Theta$  plot of Figure 2b, the nature of the relation (direct, inverse, direct and inverse) depends on where the observed periods lie with respect to  $\tau^*$ .

2. The relation between average cycle energy and frequency can assume one of two forms or a mix of both. These forms depend on where the observed frequencies lie with respect to  $f^*$ . The two forms are positive linear ( $E_m$  increases as  $f$  increases) and independent ( $E_m$  remains constant). When the form is positive linear, the  $f$  intercept ( $f_{int}$ ) should be nonzero and positive.

Returning to Prediction 1, if amplitude is observed to increase as period lengthens, then the prediction is that the subject is operating in the region of the work space in which frequencies exceed  $f^*$  and  $Q$  exceeds one. In the plot of  $E_m$  against  $f$ , this means that all data points lie to the right of the  $f$  value corresponding to twice the intercept  $f$  value. In contrast, if amplitude is observed to decrease as period lengthens, then the prediction is that the subject is operating in the region of the work space in which frequencies are less than  $f^*$  and  $Q$  is less than 1. In the plot of  $E_m$  against  $f$ , this means that all data points lie to the left of the frequency corresponding to twice the intercept frequency.

3. A proportional change in average cycle energy with respect to frequency is restricted to a frequency range with a lower bound at  $1/2f^*$  and an upper bound set by energy limitations (see Figure 3). Rhythmic movements can occur, however, outside this range. Two predictions can be made for data sets that lie close to or beyond the upper and lower bounds. For frequencies much higher than  $f^*$ , the prediction is that average cycle energy will be constant. The prediction for frequencies lower than  $1/2f^*$  is not so straightforward. A person can produce rhythmic movements at extremely low frequencies. Such movements will be associated with very low (externally observed) energy values. Consequently, it is to be expected that average cycle energy will decline asymptotically with decreasing frequency. The latter fact has implications for data sets that are in the region of frequencies approaching  $1/2f^*$ : In this region,  $E_m$  values must tend to deviate from a linear dependence on  $f$ . The point is that the trajectories in Figure 3 are ideal.  $E_m$ , in reality, will not go to 0 at  $1/2f^*$ ; the decline in energy will be graceful rather than catastrophic as the subject continues to satisfy the demands of the task in ways other than adiabatically.

4. As noted, Figure 3 identifies a biological work space. It defines how a person might meet the demands of producing comfortable rhythmic movements. At issue is the nature of the metabolic strategies by which a person

converts chemical energy resources into mechanical energy and the strategies by which a person recruits energy from external sources. These strategies may well be idiosyncratic and habitual. Consequently, individuals may differ systematically in how they assemble rhythmicities. Suggestions to this effect are to be found in the data of Kugler and Turvey (1987). In terms of Figure 3, this means that one person may habitually occupy a particular region of the work space that is different from that occupied habitually by another person. For example, it may be predicted that if a person was observed assembling rhythmic movements on a number of different occasions, then he or she might be seen to exhibit very much the same patterning among the relevant observables from one occasion to the next.

## EXPERIMENTS 1 AND 2

The experiments were designed with respect to two major considerations. First, inspection of Figure 3 suggests that not all regions of the proposed biological work space will provide evidence of adiabatic transformability. Some regions are more suited than others. They are those regions that lie well to the left of the frequency range over which energy is expected to remain constant. We cannot determine a priori what frequencies in the laboratory frame of reference will translate into these experimentally preferred regions of the work space simply because we do not know ahead of time what  $f^*$  is for a given person producing a given type of rhythmic movement. Nonetheless, a reasonable guess—looking at Figure 3—is that the lower the frequency of oscillation, the more likely it is that a system's behavior will be inside the regions in which Ehrenfest's relation is to be expected. An appropriate criterion of a "low frequency" might be a frequency that is less than the frequency exhibited by a rhythmic unit when it oscillates in isolation.

The second consideration is that lower and upper bounds on comfortable limb cycle frequency in locomotion are separated, as noted in the introduction, by about 0.7 Hz for larger animals. Moreover, the lower bound is in the vicinity of 0.5 Hz to 0.9 Hz and the upper bounds is in the vicinity of 1.2 Hz to 2.2 Hz. Our major interests are: How do pendular clocking rhythms in locomotion change in frequency, and what determines the corresponding change in amplitude? Given the characteristic parameters of these rhythms, we assume that the relevant mechanism may be trapped in a narrow range of small frequencies. The general idea, as expressed by Greene (1982), is that solutions of coordination problems may be much more simple than we think, because of the domains of reduced generality in which animals function. Abiding these two different considerations, the data in Experiments 1 and 2 were collected for rhythmic units operating (a) at tempos slower than their characteristic tempos and (b) at tempos between 0.6 Hz and 1.2 Hz.

## Method

**Subjects.** The same three people, all men, were used in both experiments. Two of them were graduate students at the University of Connecticut; the third person was a member of the university's faculty.

**Materials.** The rhythmic units in the experiments were hand-held pendulums. The hand-held pendulums were 0.02 m diameter wooden (ash) rods with a rubber grip over the top end (providing a comfortable handle) 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 which was inserted through the rod. Weights of 0.05 m diameter were secured onto this bolt using a number of 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 (see Figure 1). A small metal plate (0.3 m  $\times$  0.06 m  $\times$  0.001 m; 0.01 kg) was attached at approximately 0.15 m from the upper (handle) end of each rod. These magnetically attractive plates each held one magnetic photocell used for recording purposes.

A single wrist-pendulum system, when looked at just in terms of the material distribution relative to the point of rotation, is a *compound pendulum* (a term that applies to any rigid body that is free to oscillate in a vertical plane about a fixed horizontal axis under the influence of gravity). There are three masses rotating about a point in the wrist joint: the mass of the pendulum shaft or rod, the mass of the added weights, and the mass of the hand. The moment of inertia of each system was calculated by idealizations of the mass shapes and by applications of the parallel axis theorem.

The moments of inertia for the (constant) right systems and the range of moments of inertia for the (variable) left systems for each subject in each of the two experiments were as follows. In Experiment 1, the moment of inertia ( $\text{kg}\cdot\text{m}^2$ ) of the fixed right wrist-pendulum system was .0132, .0131, and .0125 for Subjects 1, 2, and 3, respectively. The moment of inertia ( $\text{kg}\cdot\text{m}^2$ ) of the left systems ranged between .0630 and .6136, .0634 and .6251, and .0626 and .6381 for Subjects 1, 2, and 3, respectively. In Experiment 2, the moment of inertia ( $\text{kg}\cdot\text{m}^2$ ) of the fixed right wrist-pendulum system was .0076, .0075, and .0071 for Subjects 1, 2, and 3, respectively. The moment of inertia ( $\text{kg}\cdot\text{m}^2$ ) of the left systems ranged between .0635 and .6381, .0639 and .6508, and .0631 and .6644. Because the mass of the subject's hand enters into the computation of these moments, the pendulums' moments of inertia differ for the three subjects.

**Apparatus.** The recording system used a TECA-PN4 Polgon goniometer. Polarized light from two sources situated roughly 1.2 m on either side of the subject was picked up by four TECA photocells, two for each wrist-pendulum system. One photocell (from each system) was placed on a pendulum's metal



plate while the other was fastened onto a subject's wrists via a velcro-secured metal plate. Each photocell was oriented in such a way (90° relative to each other) so as to pick up the angular motion occurring about the wrist joint of the subject as he or she swung the pendulum. Once bathed in polarized light, these photocells generated voltages proportional to this angular rotation. These voltages were passed to an SE 7000 12-track FM tape drive where they were held for future analysis. Voltage output was exhibited on a Tektronix 468 oscilloscope, which allowed for the monitoring of both subject and apparatus performance.

At some time after each experiment, the recorded voltage outputs were transduced to digital form via 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 energy, and the means and standard deviations of these quantities for each trial. A peak picking algorithm was employed to determine the time of peak flexion and extension of the wrist-pendulum trajectories. From the peak extension times, the period of oscillation for the nth cycle was calculated as:

$$\tau_n = (\text{Time of Peak Extension}_n - \text{Time of Peak Extension}_{n-1}).$$

From the peak extension and flexion positions, the angular excursion of oscillation for the nth cycle was calculated as:

$$\theta_n = (\text{Position of Peak Extension}_n - \text{Position of Peak Flexion}_n).$$

The amplitude was estimated to be one half of the angular excursion. The energy of the nth cycle was calculated as the mean squared instantaneous velocity:

$$0.5 I \left( \sum_n^{n+200\tau_n} (dx/dt)^2 \right) / 200\tau_n$$

where dx/dt is the instantaneous velocity at a sample (200/s), I is the inertia of the pendulum and n is the sample corresponding to the peak extension beginning of the nth cycle. The means and standard deviations of these quantities were found for the n cycles of a trial and the mean of these means over all the trials in a condition.

*Procedure.* Subjects (run one at a time) sat on a .65 m stool with their feet planted firmly on a .12 m stand. They were instructed to gaze straight-ahead without looking at either wrist-pendulum system. At the start of each experiment, a calibration was conducted for each hand so that an angular reference could be established for later use in the analyses.

Each subject was given the same verbal instructions in both experiments. He was asked to grasp the pendulum handle in such a way as to have complete control over the entire movement. The subject was also instructed to oscillate smoothly the pendulums forward and back using only the wrist joint (while continually keeping his forearms parallel to the ground plane). The subject was further directed to swing both pendulums with a single, common tempo (1:1 frequency locking) at  $180^\circ$  out of phase. Importantly, the subject was told that as he first started swinging, he was to search through a range of possible frequencies until the subject felt that he had settled on the most comfortable, stable tempo. The subject was given as long as he needed before each recorded trial to attain this preferred state (usually 5–10 s). When the subject felt that a comfortable tempo had been achieved, 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 subject to stop swinging, and the next set of pendulums (according to a predetermined condition ordering) was placed into the subject's hands. Subject behavior was closely monitored throughout both experiments.

In Experiment 1, there were eight coupled wrist-pendulum conditions and one single right wrist-pendulum condition. In Experiment 2, there were 11 coupled wrist-pendulum conditions and one single right wrist-pendulum condition. In Experiment 1, there were eight trials per condition; in Experiment 2 there were six trials per condition. In both experiments, the total trials were divided into a number of blocks, each of which involved one trial of every condition type. Trials within each block were randomly ordered, and this ordering was different for each of the three subjects.

## RESULTS AND DISCUSSION

### Period ( $\tau$ ) by Amplitude ( $\Theta$ )

The different conditions of 1:1 frequency locking meant that the fixed right system oscillated at a number of different frequencies. To reiterate, there were eight different conditions repeated eight times in Experiment 1, and 11 different conditions repeated six times in Experiment 2. As planned, these conditions produced frequencies lower than the frequencies of the right units in isolation. (The isolation frequencies in Experiments 1 and 2 were 1.140 and 1.367 Hz for Subject 1, 1.320 and 1.730 Hz for Subject 2, and 1.493 and 1.916 Hz for Subject 3, respectively.) The mean right-system  $\tau$  value and the mean right-system  $\Theta$  value were computed across trials for each condition. The resultant pairs of mean values in an experiment were used to construct the  $\tau$ - $\Theta$  relation for the right wrist-pendulum system of each subject. These  $\tau$ - $\Theta$  relations for the two experiments are presented in the two panels of Figure 4. Table 1 gives the

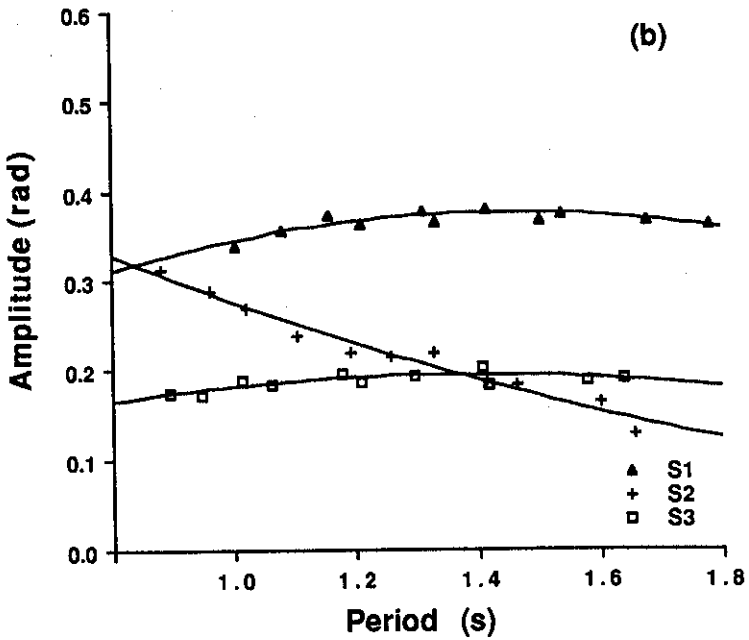
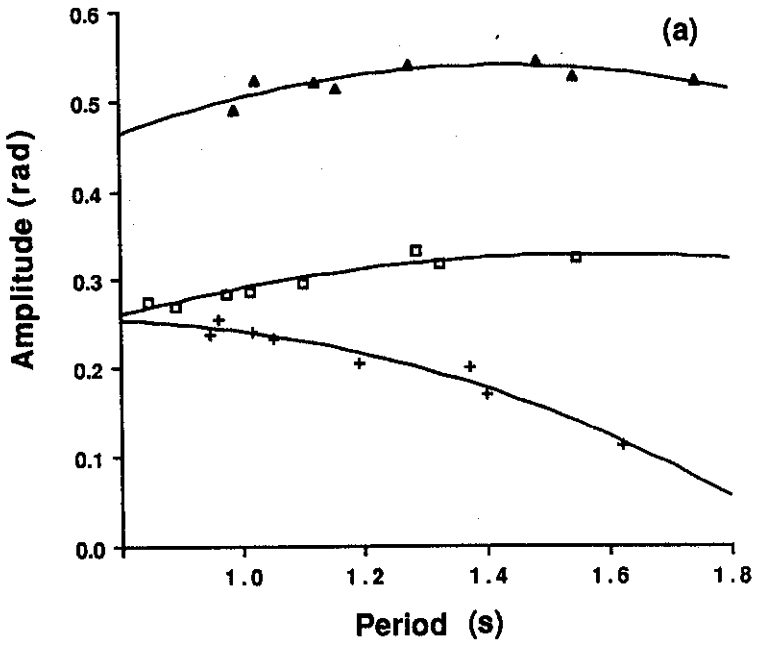


FIGURE 4 Period-amplitude functions for each of the three subjects in Experiment 1 (a) and Experiment 2 (b).

TABLE 1  
Results of the Polynomial Regression of Amplitude (rad) on Period(s) in Experiments 1 and 2

Subject	$x^2$	$x$	Intercept	$r^2$
Experiment 1				
1	-.188	.540*	.152	.663
2	-.174	.255	.161	.958**
3	-.107	.344	.054	.916**
Experiment 2				
1	-.149**	.433**	.060	.711**
2	.064	-.371*	.583	.965**
3	-.083*	.233*	.031	.636*

\* $p < .05$ . \*\* $p < .01$ .

second-order polynomial regression of  $\Theta$  on  $\tau$  for each curve in Figure 4. The linear and quadratic coefficients are reported, together with their levels of significance.

For Subjects 2 and 3 in both experiments, and for Subject 1 in Experiment 2, the magnitude of  $\Theta$  varied systematically with the magnitude of  $\tau$ . The  $\tau$ - $\Theta$  relation was not, however, the same for each subject. A simple characterization is that Subject 3 tended to increase the amplitude of oscillation with increasing cycle duration, Subject 2 tended to decrease the amplitude of oscillation with increasing cycle duration, and Subject 1 tended to hold amplitude either nearly constant (Experiment 1) or to increase and then decrease its value (Experiment 2) with increasing cycle duration. On the basis of the relation depicted in Figure 2b, it would have to be claimed that Subject 3 was operating at periods that were shorter than  $\tau^*$ , Subject 2 was operating at periods that were longer than  $\tau^*$ , and Subject 1 was operating at periods close to  $\tau^*$ . All in all, the results concur with the first prediction advanced in the introduction.

### Frequency ( $f$ ) by Energy ( $E_m$ )

A mean cycle energy was computed for each trial of a condition. The means of the trial means yielded the average cycle energy for the condition. In Experiment 1, there were eight average cycle energies and a corresponding eight average cycle frequencies; in Experiment 2, there were 11 average cycle energies and a corresponding 11 average cycle frequencies. The two panels of Figure 5 give the  $f$ - $E_m$  relation for each subject in each of the two experiments. All six plots suggest a highly linear dependency of energy on frequency, with constant slope and a positive frequency intercept. Regression analyses confirm these suggestions with the possible exceptions of (a) the intercept values of Subject 3 (in neither experiment did the intercept differ significantly from 0), and (b) the  $f$ - $E_m$  relation for Subject 2 in Experiment 2 (this relation has a significant quadratic

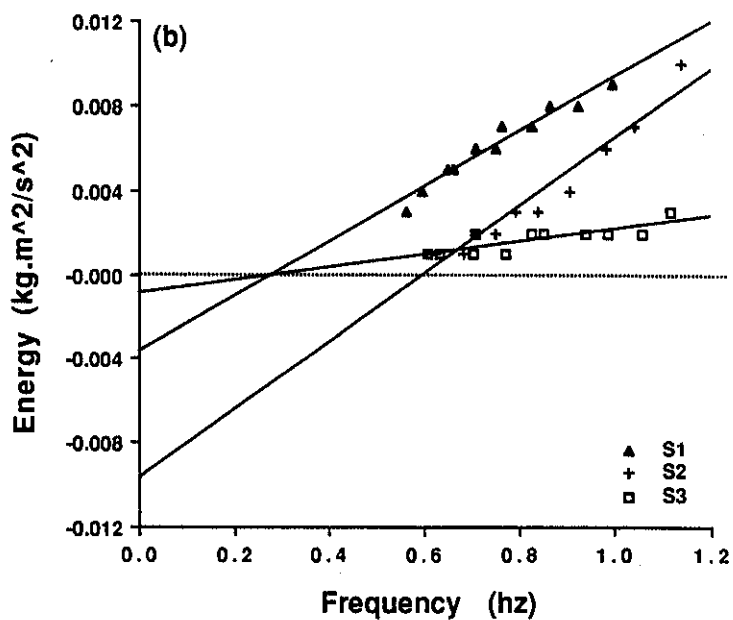
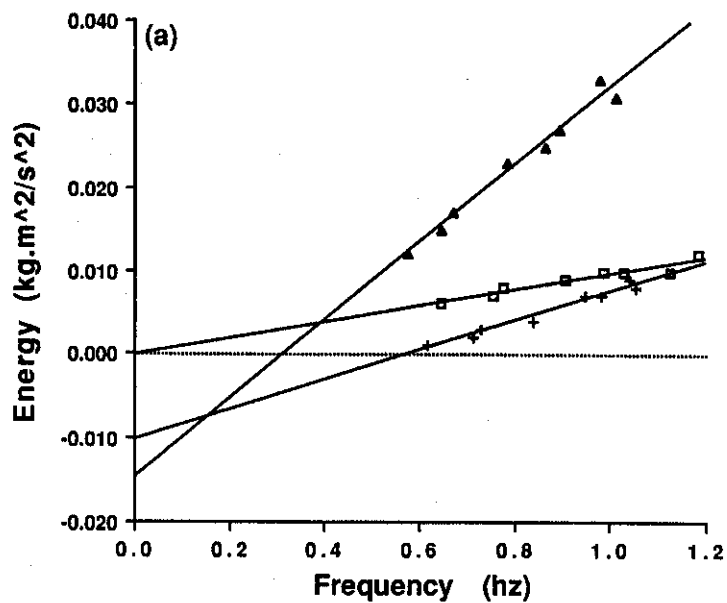


FIGURE 5 Frequency–energy functions for each of the three subjects in Experiment 1 (a) and Experiment 2 (b).

component,  $p < .001$ ). The implication from Prediction 3 is that Subject 2 in Experiment 2 must have been approximating the lower bound on the Ehrenfest adiabatic relation.

The linear regression statistics are summarized in Table 2. Although the three subjects differed in the direction of the  $\tau$ - $\Theta$  relation (see Figure 4), each expressed a tendency for energy to increase proportionately with frequency. The rate of increase is not the same for the three subjects, however, and neither is the magnitude of the frequency (or energy) intercept. Overall, the results conform to Prediction 2: An Ehrenfest type relation was found for (nonconservative) biological rhythmic movements in the ranges of frequencies induced in the two experiments.

### Identifying the Nature of Strategic Differences Among Subjects

Figures 4 and 5, and the regression analyses reported in Tables 1 and 2, indicate systematic differences among the three subjects in assembling sustained, comfortable, pendular clocking movements. They also suggest that the differences were of the same kind in the two experiments; apparently, the individual subject assembled the rhythmic movements the same way in each experiment. To gain further insight into these individual characteristics, we conducted two additional analyses. First, we generated for each subject in each experiment the functional dependence of amplitude on period as determined from the slope and intercept values of the energy by frequency relations. As was noted, Kugler and Turvey (1987) derived a nonmonotonic, nonlinear function linking amplitude to period from the equation for constant action in a nonconservative system (see Figure 2b). Figures 6 and 7 present the derived (Equation) period-amplitude relation and the actual period-amplitude data for each subject in Experiments 1 and 2. The significance of these graphs is that they reveal clearly the differences

TABLE 2  
Results of the Linear Regression of Energy ( $\text{kg}\cdot\text{m}^2\text{s}^{-2}$ ) on Frequency ( $\text{s}^{-1}$ ) in Experiments 1 and 2

Subject	Slope	Intercept	$r^2$
Experiment 1			
1	.0480	-.0156*	.981**
2	.0184	-.0107*	.986**
3	.0104	-.0005	.935**
Experiment 2			
1	.0132	-.0038*	.971**
2	.0171	-.0104*	.938**
3	.0027	-.0005	.884**

\* $p < .01$ . \*\* $p < .001$ .

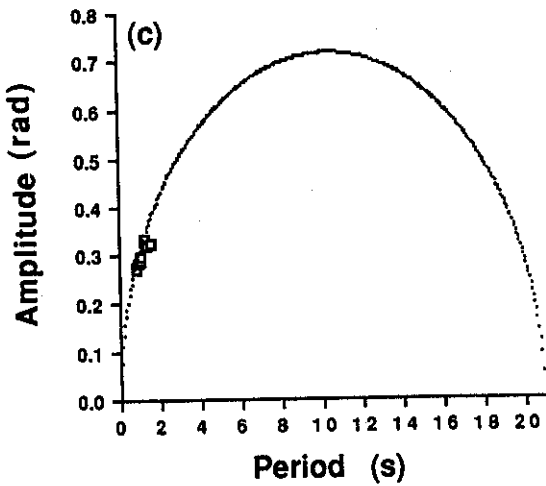
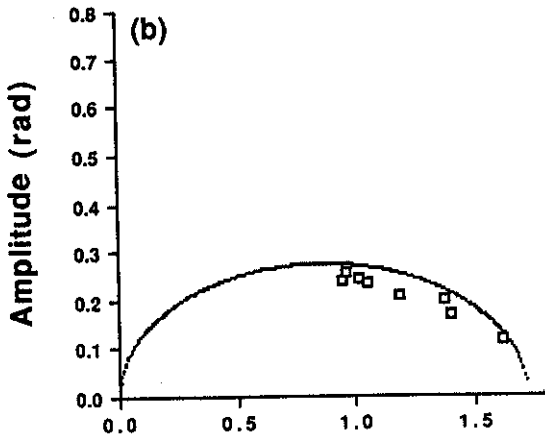
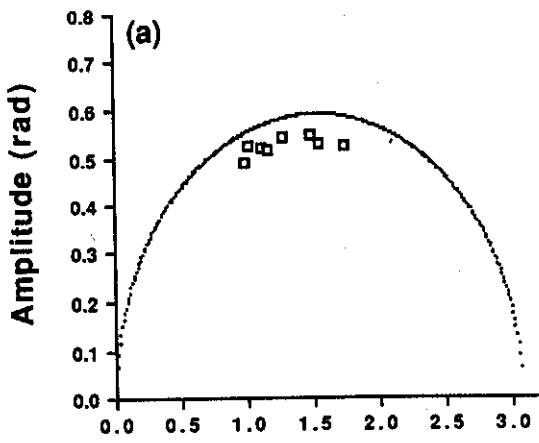


FIGURE 6 Comparison of period-amplitude relations derived from the parameters of the f-E relations and actual period-amplitude relations in Experiment 1: (a) Subject 1, (b) Subject 2, (c) Subject 3.

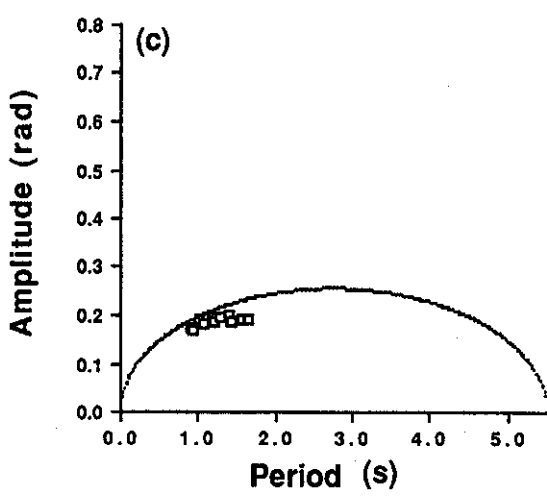
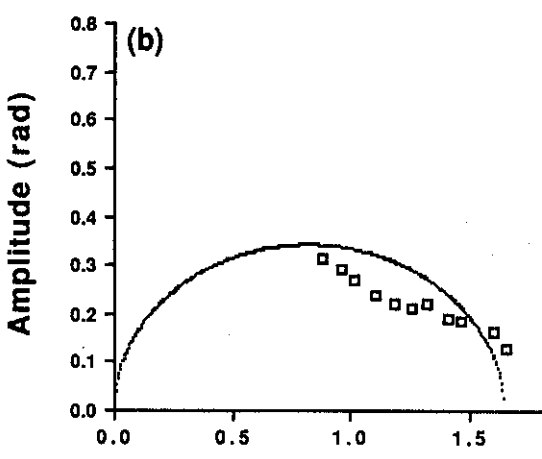
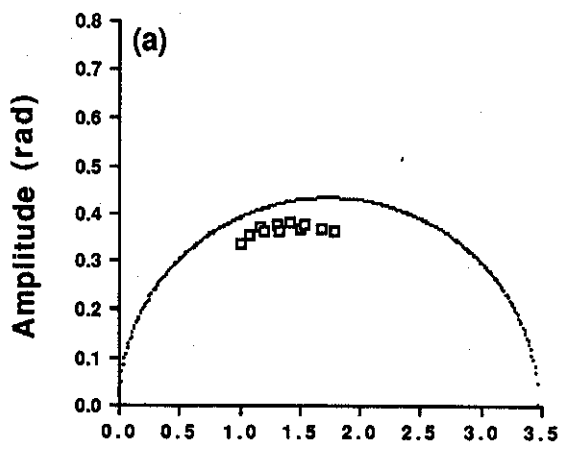


FIGURE 7 Comparison of period-amplitude relations derived from the parameters of the f-E relations and actual period-amplitude relations in Experiment 2: (a) Subject 1, (b) Subject 2, (c) Subject 3.



among the subjects, and the consistencies in a subject's behavior over the two experiments.<sup>2</sup> The suggestion is that the subjects operated at different regions within the biological work space: Subject 1 close to  $f^*$ , Subject 2 greater than  $f^*$  (less than  $\tau^*$ ), and Subject 3 less than  $f^*$  (greater than  $\tau^*$ ). The second additional analysis makes the same point. Using the parameters from the  $f$ - $E_m$  plots (Table 2), new variables were created for the data of the two experiments, viz,  $f/f^*$  and  $E_m/E_c$ . The data of each subject in both experiments are collected in Figure 8. Given the interpretation of  $E_m/E_c$  as defining a  $Q$  value (see the introduction to this article), it appears that Subject 1 produced rhythms in the two experiments with  $Q$  values close to but greater than 1, that is, with conservative terms just dominating nonconservative terms; Subject 2 produced them with  $Q$  values uniformly less than 1 (see the inset of Figure 8), that is, with nonconservative terms dominating conservative terms; and Subject 3 produced them with  $Q$  values greatly in excess of 1, that is, with conservative terms very much dominating nonconservative terms. With respect to Subject 2, Figure 8 (inset) identifies that this subject was assembling rhythms for some frequencies very close to the lower limit of the Ehrenfest adiabatic relation. As was anticipated, and following from Prediction 3, this latter fact may be advanced as the reason for the curvature in Subject 2's  $f$ - $E_m$  function in the second experiment.

In sum, the two additional analyses concur with the fourth prediction identified in the introduction. The three subjects were distinguished by the systematic ways in which they assembled periodic movements. Rhythmic behaviors are built from energy reservoirs, available both internally and externally. We might conclude, on the basis of Figures 6, 7, and 8, that the three subjects in our experiments tapped these reservoirs differently, and that they have habitual strategies for the assembling of sustained rhythmic movements.

### EXPERIMENTS 3 AND 4

The hypothesized biological work space identified in Figure 3 has an *organizing center* or *attractor* at  $(f^*, E_m^*)$ . The data from Experiments 1 and 2 and from the experiment of Kugler and Turvey (1987), suggest that the values comprising this coordinate pair will differ from one rhythmic unit to another and, for rhythmic units of identical dimensions, from one person to another. These data also suggest that, generally speaking, the conditions under which a rhythmic movement is to be produced will rarely permit a rhythmic unit to operate as its  $(f^*, E_m^*)$ . More usually it will operate at some remove (large, moderate, or small) from the *organizing center*. Such departures are expected of an open system under

<sup>2</sup>The discrepancy between the model and the data in these figures stems partly from the facts that the model equation (a) assumes that the cycle is symmetric, that is, that flexion and extension have identical displacements; and (b) is built in terms of amplitude. In contrast, the calculation of the observed kinetic energy (and, hence, the parameters  $h$  and  $f_{in}$ ) uses (a) the real time series with asymmetric flexion and extension displacements and (b) is computed from squared velocity.

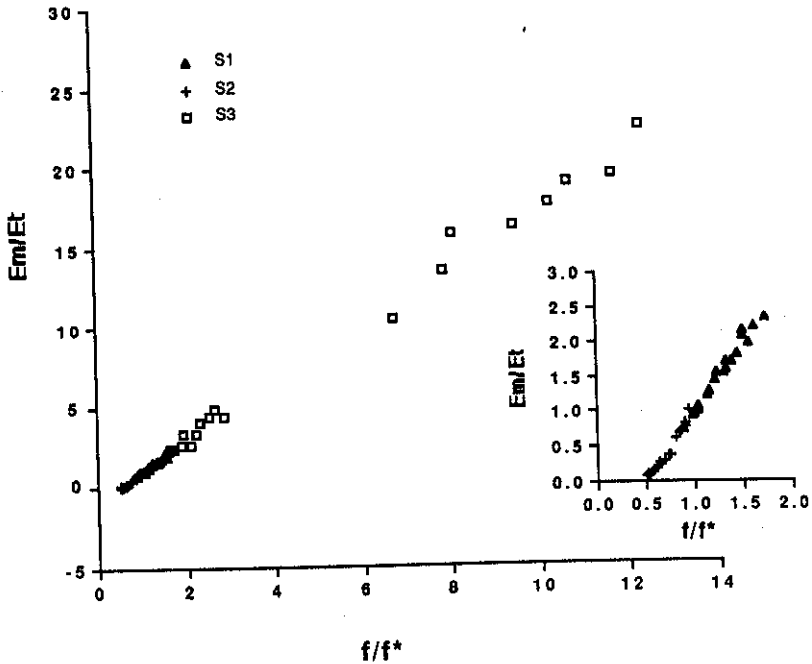


FIGURE 8 The data of the three subjects in Experiments 1 and 2 expressed as the relation of  $Q = E_m/E_t$  to  $f/f^*$ . Inset presents data of Subjects 1 and 2 that lie within  $Q$  values close to 1. Coordinates are dimensionless.

imposed boundary conditions. The equilibrium state will be approximated as closely as possible but not necessarily attained. Pursuing this fact, we can ask, with respect to pendular clocking movements, if there is some way to determine how much displacement (disequilibrium) we can expect for some given experimental circumstances (boundary conditions). Although a quantitative answer is not forthcoming, some qualitative predictions are possible.

Consider Figure 9. The figure is very similar to Figure 8 except for the replacement of  $f/f^*$  by  $f/f_g$ . The new x-axis identifies a right rhythmic unit's frequency relative to the frequency of its gravity pendulum equivalent. The advantage of this metric is that  $f_g$  can be determined without experimentation. It is, of course, calculable from the dimensions of the wrist-pendulum system. Inspection of Figure 9 shows that the hypothesized  $Q$ -factor increases as a certain rate of the increase in a wrist-pendulum system's deviation from its gravitational frequency. The rate of increase differs among the three subjects, being most for Subject 3<sup>3</sup>

<sup>3</sup>For Subject 3, the  $E_m/E_t$  values of Experiment 2 were calculated using an  $E_t$  from a regression of  $E_m$  on frequency that included the single right-hand system. This procedure was followed for this subject and not the others because Subject 3's data had such a small  $E_t$  value (see Table 2). Small

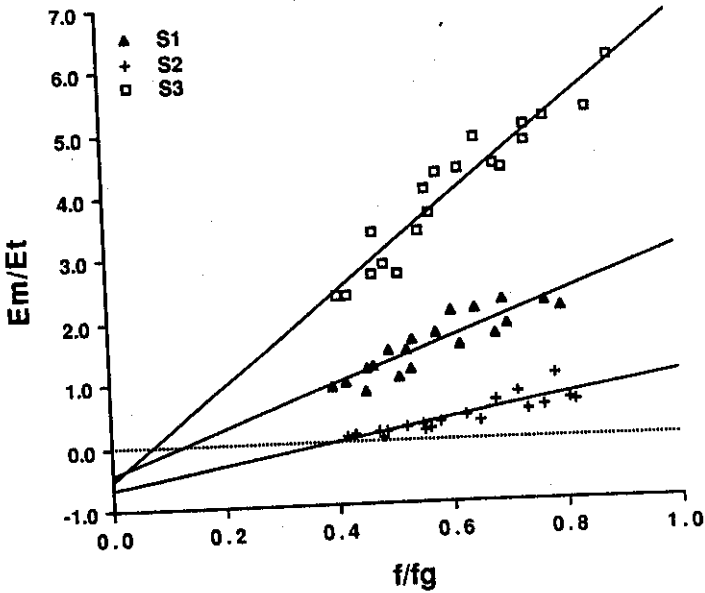


FIGURE 9 The data of the three subjects in Experiments 1 and 2 expressed as the relation of  $Q = E_m/E_t$  to  $f/f_g$ . Coordinates are dimensionless.

and least for Subject 2. When viewed in the context of the biological work space depicted in Figure 3, the relations evident in Figure 9 suggest that at some range of higher  $f/f_g$  ratios we might expect to see Subject 3 tending toward a constancy of energy with variation in frequency, rather than a constant energy-frequency ratio, and Subject 2 continuing to differ from both of the other subjects but exhibiting, in all likelihood,  $f-E_m$  patterns more like Subject 2 than Subject 3.

Two further experiments were conducted to test these predictions. The constraints of these experiments were: (a) to keep within the range of normal locomotory frequencies, as in Experiments 1 and 2; and (b) to have individual subjects operate at frequencies that were higher multiples of  $f_g$  than the frequencies in Experiments 1 and 2. These constraints were satisfied by using larger right wrist-pendulum systems than those used in the first two experiments, coupled with left wrist-pendulum systems both smaller than and larger than the right system. The dimensions of these left systems were such that under the demand of 1:1 frequency locking a fixed right system should oscillate at frequencies higher and lower than its frequency when considered as a strictly gravitational pendulum.

errors in the evaluation of  $E_t$  that occur in a regression analysis with a small sample size ( $n = 8$ ) produce extremely large errors in the evaluation of  $E_m/E_t$ .

## Method

*Subjects.* The same subjects who were used in Experiments 1 and 2 were used in the third and fourth experiments.

*Materials and apparatus.* In Experiment 3, the moment of inertia ( $\text{kg}\cdot\text{m}^2$ ) of the fixed right wrist-pendulum system was .093, .093, and .094 for Subjects 1, 2, and 3, respectively. The moment of inertia ( $\text{kg}\cdot\text{m}^2$ ) of the left systems ranged between .0068 and .6551, .0069 and .6614, and .0064 and .6643. In Experiment 4, the moment of inertia ( $\text{kg}\cdot\text{m}^2$ ) of the fixed right wrist-pendulum system was .0409, .0409, and .0396 for Subjects 1, 2, and 3, respectively. The moment of inertia ( $\text{kg}\cdot\text{m}^2$ ) of the left systems ranged between .0068 and .6551, .0069 and .6614, and .0064 and .6643. The design of the pendulums, the apparatus performing the motion analysis, and the computational methods for measuring the parameters of oscillation were as in the previous experiments.

*Procedure.* The experiments were conducted in exactly the same way as Experiments 1 and 2. In both experiments, there were eight conditions of 1:1 frequency locking. There were eight repetitions of each condition in Experiment 3 and four repetitions of each condition in Experiment 4.

## RESULTS AND DISCUSSION

### Frequency ( $f$ )

The different conditions of 1:1 frequency locking in the two experiments were intended to produce oscillations of the fixed right system at a number of different frequencies. The 1:1 frequency locking conditions produced different ranges of frequencies across the three subjects. In Experiment 3, the ranges were .616 Hz to 1.087 Hz, .708 Hz to 1.351 Hz, and .783 Hz to 1.668 Hz, for Subjects 1, 2, and 3, respectively. Expressed in terms of  $f/f_g$ , these ranges were: .693-1.221, .796-1.518, and .896-1.853. Clearly the coupling conditions (variable left systems) of Experiment 3 did not have exactly the same effects on each subject. In Experiment 4, the frequency ranges were .653 Hz to 1.247 Hz, .711 Hz to 1.229 Hz, and .749 Hz to 1.368 Hz, and the  $f/f_g$  ranges were .605-1.155, .641-1.108, and .674-1.234.

### Period ( $\tau$ )-Amplitude ( $\Theta$ ) Relation

In Figure 10, the period-amplitude relations for the fixed right wrist-pendulum systems of the three subjects in the two experiments are presented. The  $\tau$  and  $\Theta$  values are means for conditions computed across the trial data as described in

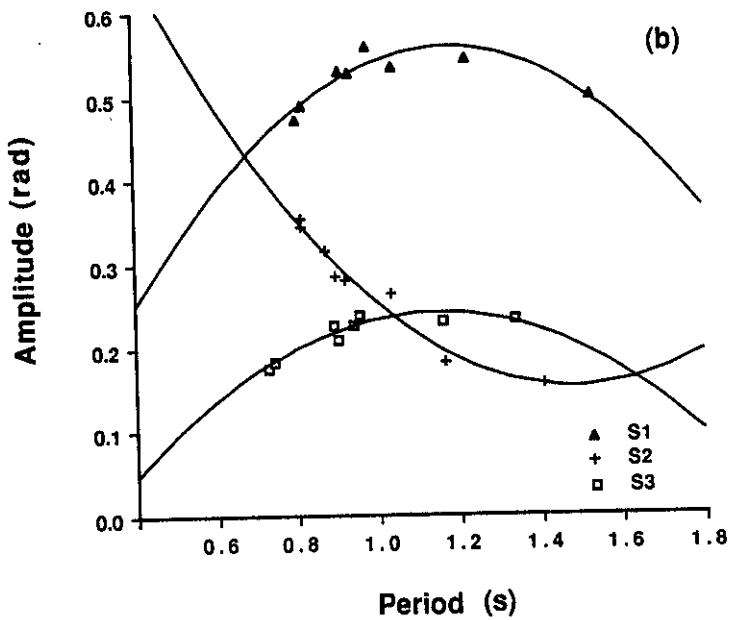
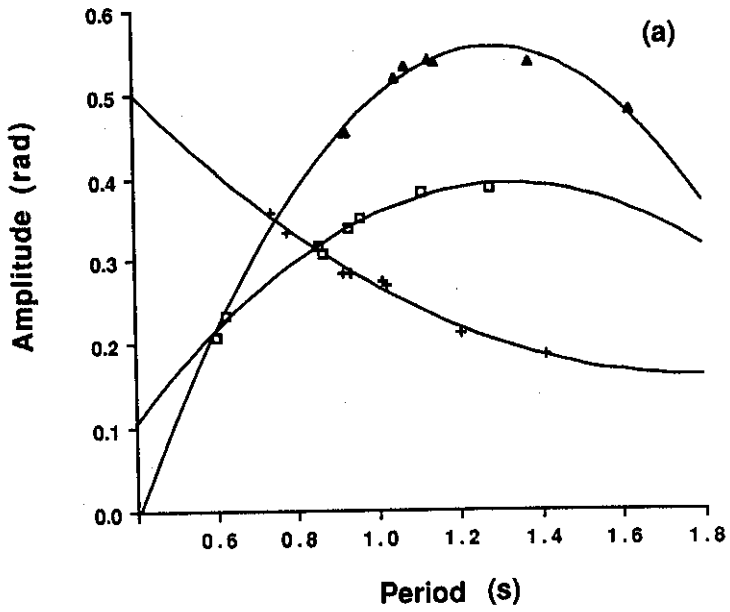


FIGURE 10 Period-amplitude functions for each of the three subjects in Experiment 3 (a) and Experiment 4 (b).

the analysis of the first two experiments. In all six instances, the space-time relations were systematic; amplitude changed significantly with period. The polynomial regressions are given in Table 3. As in Experiments 1 and 2, the nature of the change was not the same for each subject, although each individual subject exhibited similar  $\tau$ - $\Theta$  relations in both experiments. On the basis of the relation depicted in Figure 2b, Subject 3 was operating at periods that were shorter than  $\tau^*$ , Subject 2 was operating at periods that were longer than  $\tau^*$ , and Subject 1 was operating at periods on either side of  $\tau^*$ .

### Frequency ( $f$ )-Energy ( $E_m$ ) Relation

Figure 11 gives the  $f$ - $E_m$  relations for each subject in the two experiments. Again, the presented values are for the fixed right systems. Looking at the data from Experiment 3 (Figure 11a), it is evident that an Ehrenfest-type relation does not characterize the behavior of Subject 3. For Subject 3, energy was constant over the frequency variation. An Ehrenfest-type relation with positive frequency intercept is suggested in the data of both Subject 1 and Subject 2. The relation, however, appears to break down at the higher frequencies for Subject 1 and is marred by a significant quadratic component in the data of Subject 2. In reference to the hypothesized biological work space depicted in Figure 3, Subject 1's data might reflect proximity to the region in which an invariant energy-frequency ratio gives way to invariant energy, and Subject 3's data might reflect proximity to the lower bound on the Ehrenfest relation, as discussed in Prediction 3. The regression analyses are summarized in Table 4. As can be seen, although Subject 1's data conform to a linear relation, the intercept did not differ significantly from 0, an outcome probably attributable to the flattening of the function at the higher frequencies. A regression computed for the data of the experiment minus the two higher frequencies yielded a significant nonzero intercept,  $E_c = -.1672$ ,  $p < .01$ .

TABLE 3  
Results of the Polynomial Regression of Amplitude (rad) on Period(s) in  
Experiments 3 and 4

Subject	$x^2$	$x$	Intercept	$r^2$
Experiment 3				
1	-.715**	1.846	-.636	.958**
2	.179*	-.636**	.726	.984**
3	-.335**	.890**	-.199	.988**
Experiment 4				
1	-.507**	1.202	-.153	.819**
2	.435*	-1.289*	1.107	.966**
3	-.343**	.791	-.216	.893**

\* $p < .05$ . \*\* $p < .01$ .

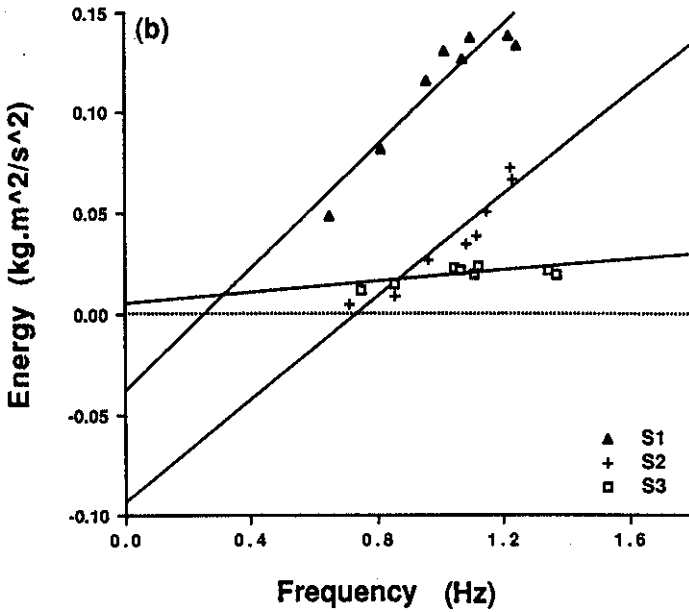
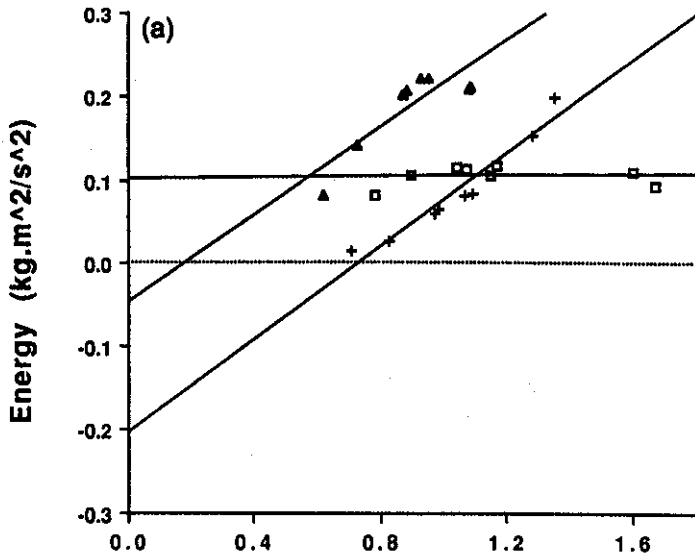


FIGURE 11 Frequency-energy functions for each of the three subjects in Experiment 3 (a) and Experiment 4 (b).

Turning to the data of Experiment 4 depicted in Figure 11b, a similar pattern can be observed. For Subject 3, energy changed with frequency in a marginally significant manner, and with a negative frequency intercept. For both Subjects 1 and 2, an Ehrenfest-type relation is suggested with positive frequency intercept. Again, however, there are signs that the relation is weaker at the higher frequencies for Subject 1, and that Subject 2's data has a curvilinear component. The suggestions made in the preceding paragraph with respect to these deviations from an invariant  $f-E_m$  relation in Experiment 3 are applicable to the data of Experiment 4. Table 4 provides the regression analyses. For Subject 1, it is again the case that the intercept is insignificantly different from 0 when all data points are considered, but differs significantly when the two higher frequencies are excluded from the regression,  $E_c = -0.0802, p < .01$ .

### Identifying the Nature of Strategic Differences Among Subjects

It was argued, in the introduction to Experiments 3 and 4, that if the data of the first two experiments reflected habitual strategies for assembling rhythmic movements, then Subject 3 might tend toward constant  $E_m$  rather than a constant slope in  $f-E_m$  coordinates when pressed to assemble pendular clocking movements at higher multiples of  $f_g$ . On similar grounds, it was argued that, under the same conditions, Subjects 1 and 2 might continue to exhibit the  $\tau-\Theta$  relation evident in Experiments 1 and 2, and preserve the systematic variation of  $E_m$  with  $f$  evident in those experiments. These expectations tended to be born out by the data.

For Subjects 1 and 2, the significant linear variation of  $E_m$  with  $f$  permits a more precise evaluation of the question: How similar were the strategies of these subjects over the four experiments? Figures 12 and 13 present the complete data

TABLE 4  
Results of the Linear Regression of Energy ( $\text{kg}\cdot\text{m}^2\text{s}^{-2}$ ) on Frequency ( $\text{s}^{-1}$ ) in Experiments 3 and 4

Subject	Slope	Intercept	$r^2$
Experiment 3			
1	.2625	-.0479	.745**
2	.2799	-.2041**	.937**
3	.0034	.1021	.008
Experiment 4			
1	.1510	-.0384	.879**
2	.1271	-.0941**	.902**
3	.0137	.0048	.499*

\* $p < .05$ . \*\* $p < .001$ .



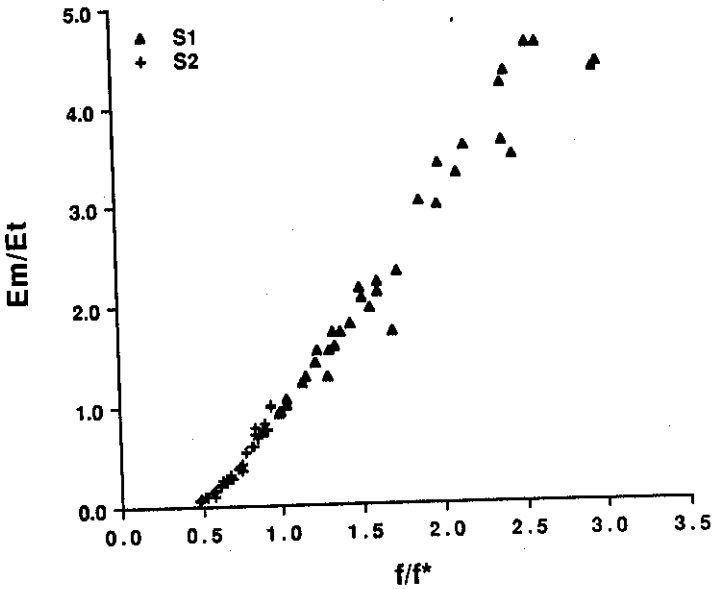


FIGURE 12 The data of Subjects 1 and 2 in all four experiments expressed as the relation of  $Q = E_m/E_t$  to  $f/f^*$ . Coordinates are dimensionless.

of Subjects 1 and 2 in  $f/f^*-Q$  coordinates and  $f/f_g-Q$  coordinates. Inspection of these figures reveals a remarkable consistency across experiments. The two subjects are characterized by idiosyncratic methods for assembling pendular clocking rhythmic movements. Importantly, there are intimations that these idiosyncracies are understandable in terms of common principles.

Let us examine in greater detail the data of Subject 3, because they bring to light certain problems in the current formulation of the extended adiabatic hypothesis. The depictions in Figures 2 and 3 are for a rhythmic unit limited to motion in two dimensions. With respect to the experimental investigation of such units instantiated by wrist-pendulum systems, the observed rhythmic motions are treated as the motions of a planar pendulum. In actuality, the motions of a wrist-pendulum system are those of a spherical pendulum. The motions occur in three dimensions, and there are two amplitudes—the major amplitude  $\Theta$  defined in the vertical plane through the point of rotation and the minor amplitude  $\psi$  defined in a plane parallel to the horizontal plane through the point of rotation. The modeling expressed in Figures 2 and 3 is with respect to only the amplitude defined in the vertical plane. The energy limitation of Figure 3 is, therefore, a limitation on the energy carried in  $\Theta$ ; further energy increases could be absorbed, in principle, in the secondary amplitude  $\psi$  beyond the upper bound on the capacity of the primary amplitude  $\Theta$ . Our point in

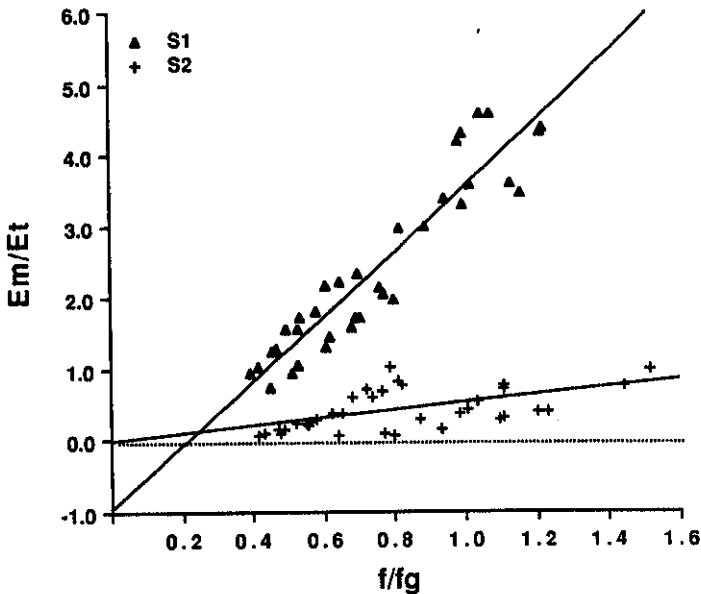


FIGURE 13 The data of Subjects 1 and 2 in all four experiments expressed as the relation of  $Q = E_m/E_t$  to  $f/f_g$ . Coordinates are dimensionless.

underscoring the fact that the observed motions were those of a spherical pendulum is that if we had monitored  $\psi$ , then we might have seen that Subject 3's data in these two experiments continued to conform to an Ehrenfest relation. Keeping this possibility open is important for maintaining the idea that a single mechanism is underlying frequency change in Subject 3's data in all four experiments.

## GENERAL DISCUSSION

Kugler and Turvey (1987, chapter 10) claimed that nonconservative processes that occur at a finite rate can exhibit Ehrenfest's adiabatic energy-frequency relation. Ordinarily, adiabatic transformability is reserved for conservative and infinitely slow processes. Kugler and Turvey's (1987) claim was made with special reference to the variations in frequency of rhythmic limb movements of the kind typifying walking and running, namely, pendular, clocking movements. From the perspective of control and coordination, the value of Ehrenfest's relation is that it reduces the free variation in a rhythmic unit's behavior. Ehrenfest's relation identifies an invariant of motion—the quantity called action—that fixes the energy for a given frequency or, relatedly, fixes the cycle amplitude for a

given cycle duration. The relation addresses the question that is the focus of this article, namely, given a rhythmic movement unit of fixed dimensions (constant inertial properties), how does it change frequency? Any observed frequency change must result, obviously, from a change in the unit's internal parameters. Internal parameters are mechanical and thermodynamical, and either or both can, in principle, be changed. Feldman's  $\lambda$  model shows how the internal mechanical parameter of stiffness can be changed by varying the overlap in resting lengths ( $\lambda_0$ ) of the flexors and extensors at a joint. The claim that frequency change is adiabatic—that a rhythmic movement unit abides the Ehrenfest relation—is a claim for the orthogonality of the internal mechanical and thermodynamic parameters. By hypothesis, stiffness can change in the manner suggested by Feldman without an accompanying change in the energy dissipated per cycle.

Two related predictions follow from Kugler and Turvey's (1987) claim and the theoretical analysis that accompanies it. The first prediction is that a relation should be obtained in frequency–energy coordinates that has constant slope and an energy intercept less than 0. The constant slope identifies the hypothesized Ehrenfest adiabatic relation (constant action); the negative energy intercept identifies the hypothesized constant energy dissipation regardless of frequency. The second prediction is that the expected relation in frequency–energy coordinates can be satisfied by any one of three relations in period–amplitude coordinates: amplitude increasing, amplitude increasing then decreasing, amplitude decreasing.

The four experiments provided varying degrees of evidence in favor of the two predictions. With the exception of the data of one subject in one experiment, changes in the period of a pendular rhythmic movement were accompanied by statistically significant changes in the amplitude. Importantly, the direction of amplitude's systematic dependence on period was not fixed, but differed among the three participants in the experiments. Despite the qualitatively different trajectories observed in period–amplitude coordinates, the relations in frequency–energy coordinates for Subjects 1 and 2 in all experiments, and for Subject 3 in Experiments 1 and 2, tended to be of constant positive slope and nonzero negative energy intercept (although the latter did not always achieve significance).

The evidence provided by our experiments for an Ehrenfest-type relation—and, therefore, for a nonconservative invariant of motion—in human rhythmic movement, adds to the original evidence provided by Kugler and Turvey (1987). The summed evidence, however, must be judged conservatively. Because of the radical nature and theoretical significance of the proposed extension of Ehrenfest's adiabatic relation to systems that are (a) transformed rapidly by internal sources of energy and (b) dissipative, much more than the data currently available is needed to evaluate the claim. The available evidence is suggested but far from conclusive. Important additional evidence would be

provided by converging independent measures of dissipation and stability, of the kind explored by Kay (1986). The stability prediction (more stable at lower frequencies) of the generalized Ehrenfest adiabatic relation has not been evaluated.

Simulations of differential equation models of oscillators should also prove helpful. Dudevoir (1988) examined the frequency–energy relations of various conservative mechanical systems (pendulums, rotators, a mass-spring system) and a nonconservative auto-oscillatory system (van der Pol oscillator). He found that the conservative oscillators conformed to the Ehrenfest energy–frequency relation even under conditions of rapid transformations, in agreement with one part of Kugler and Turvey's extension of the adiabatic hypothesis. Dudevoir, however, was unable to provide evidence for the other part of the extended adiabatic hypothesis. The simulated van der Pol oscillator did not yield the Ehrenfest energy–frequency relation. Little can be concluded from this negative outcome, however. The van der Pol oscillator maintains a constancy of amplitude with variation in period and, therefore, can be ruled out as the nonconservative oscillatory mechanism underlying the space–time relations observed in human rhythmic movements. Relatedly, neither the Rayleigh oscillator nor Kay et al.'s (1987) hybrid oscillator (see introduction), involving both van der Pol and Rayleigh terms, yield the Ehrenfest relation (Kay, personal communication, October, 1989). Other differential equation models—perhaps less conventional—may provide a better fit to the human rhythmic movement data. P. J. Beek and W. J. Beek (1987) simulated oscillators whose friction functions are of neither the van der Pol nor Rayleigh type but of a new type in which van der Pol and Rayleigh terms form a product (P. J. Beek & W. J. Beek, 1988). The period–amplitude patterns of these oscillators are nonlinear and share, therefore, a feature in common with the period–amplitude patterns observed experimentally. Results such as these keep open the possibility that a class of oscillators can be identified that satisfy the generalization of Ehrenfest's adiabatic hypothesis to nonconservative systems.

It should be recognized that if an Ehrenfest-type relation does apply to animal movements, it is unlikely to apply without significant restrictions. Limitations in scope will arise from muscular and metabolic constraints and from the fact that biological movement systems can operate with reasonable success outside of optimal regimes. The conservative spring-like states that move a given load repetitively and quickly are assembled through dissipative processes. Any rhythmic movement within the adiabatic regime will be indexed by a proportionality of conservative to nonconservative processes. The conservative/nonconservative ratio cannot, however, magnify without limit. It is this understanding that is captured in the upper bound of  $E_m$  values in Figure 3. At the other extreme, minification of the ratio can proceed gracefully to a limit, especially in human behavior. Satisfying task demands often requires operating outside of highly preferred states. Thus, rhythmic movements at extremely slow,

uncomfortable rates and very low conservative/nonconservative ratios can be produced if required. They need not conform to adiabatic criteria. As just noted, from the perspective of this latter point, Figure 3 represents an idealized work space.

Our data raise important questions about the role of individual differences in the analysis of biological rhythmic movements. It appears that the three people in the experiments were resolving the problem of assembling sustained coordinated rhythmic movements in consistent but unidentical ways. From purely statistical considerations, it would be imprudent to average their data; the resultant numbers would not refer to any real process, and important effects would be obscured (see Kugler & Turvey, 1987, chapter 12). A similar caution can be distilled from other work on biological movement. Pronounced individual differences in the phasing of the limb activity of cockroaches has been observed by Delcomyn and Cocatre-Zilgien (1988). Although the alternating limb pattern is ostensibly that of  $180^\circ$  out-of-phase, individual cockroaches walking over identical terrain exhibit phase relations close to but significantly different from  $180^\circ$ , with the size and direction of the deviation different from individual to individual. The reasons for these individual differences are not known, but Delcomyn and Cocatre-Zilgien (1988) speculated that factors such as different within-insect inequalities in limb size and muscle physiology and variations among insects in neural connectivity could contribute. Further, and to the point, they warned against the possibility of swamping subtle statistical differences by the larger variance due to grouping dissimilar animals.

In addition to statistical issues, the systematic individual differences raise questions about the investigation of lawful processes in biological systems. Actual patterns among observable quantities follow from laws and circumstances. The same law in different circumstances (boundary conditions, constraints, auxiliary conditions) produces different patterns. If it can be assumed that a common set of physical laws is at work in fashioning space-time relations in biological movements, then the different data patterns for the three participants can be assumed to reflect differences among them in their capacities as "circumstances" for these common laws. By this way of thinking, individual biological systems constitute different circumstances or coordinate spaces for the expression of general laws and principles (Kugler & Turvey, 1987). Revealing the lawfulness at work in fashioning biological movement patterns will depend on the ability to eliminate differences among these circumstances or coordinate spaces. In practical terms, this means finding intrinsic variables. To the extent that the measured variables are defined independently of the behaving systems, that is, extrinsically, the possibility is magnified of seeing variability rather than uniformity. The distance, time, and energy metrics with respect to which the participants in our experiments were assembling rhythmic movements are all defined intrinsically, scaled by their individual metabolic, cardiovascular, and neuromuscular processes. If the relations of interest in this study could have

been cast in terms of these intrinsic coordinates, then they may have been identical from person to person. In our opinion, identifying intrinsic measures poses a major problem to describing coordinated states (cf. Soechting, 1989) and understanding them in general terms.

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