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Constants underlying frequency changes in biological rhythmic movements

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Abstract. When an animal increases or decreases the frequency of its limb motions, how should the transformation in timing be characterized? It has been hypothesized that the transformation is adiabatic, even though the biological conditions are nonconservative and non-rate-limited (Kugler and Turvey 1987). An adiabatic transformation requires that the rhythmic system's action (energy/frequency) and entropy production remain time-invariant throughout the transformation. The non-conservative adiabatic hypothesis was evaluated through an experiment on human rhythmic hand movements. On each trial, a subject began at a prescribed frequency and then, over a 30 s interval, increased (or decreased) the frequency continuously at will. For each subject, on each increasing and decreasing trial, cycle kinetic energy was a linear function of cycle frequency with a negative energy intercept. By the adiabatic hypothesis, the slope of the function defines the constant action and the intercept defines the constant dissipation – changes in cycle frequency incur no changes in energy dissipated per cycle. Slopes and intercepts were correlated suggesting a common basis for the two constants, and the variety of cycle amplitude-cycle duration relations were in agreement with the nonmonotonic, nonlinear space-time function predicted by the hypothesis. The possibilities of addressing aspects of the data through *(a)* muscle modeled as a continuum of Kelvin bodies with a continuous relaxation spectrum, and *(b)* various classes of autonomous differential equations, were discussed. Most importantly, the discussion focused on the puzzling independence of energy cost and speed exhibited by locomoting animals differing in morphology, physiology, size, and taxa. It was suggested that the independence may reflect a very general principle – adiabatic transformability of biological movement systems.

1 Introduction

Humans and other animals can move their limbs rhythmically at a number of different frequencies. Indeed, rhythmic activities involving the limbs are rarely conducted at a single frequency and usually entail a variety of cycle times. Although increases and decreases in cycle time can be brought about by changes in limb configuration (e.g., a limb when flexed has a smaller moment of inertia and, therefore, will cycle faster under the same forcing conditions than when extended), they are most commonly brought about by changes that take place internally rather than externally. Our concern in the present article is with the basic nature of these internal transformations.

From a dynamic perspective on rhythmic limb movement, the major questions have to do with the functional constitution of the limb oscillator (Beek and Beek 1988; Kay et al. 1987; Kugler and Turvey 1987; Turvey 1990). A plausible departure point is that a rhythmic movement unit is a self-oscillating system (Andronov et al. 1987) meaning that *(a)* its oscillations are determined by its own properties rather than by the initial conditions, and *(b)* that it produces a periodic process at the expense of a non-periodic source of energy – the chemical fuel contained in the muscles. The necessity of the (non-periodic) energy source is dictated by the inevitable energy losses accompanying motion. These losses must be compensated if the oscillations are to continue. Following Andronov et al. (1987), a self-oscillatory system with one degree of freedom may be expressed by the equation

$$\ddot{x} + \omega_0^2 x = F(x, \dot{x}) - 2g\dot{x} = h(x, \dot{x}) . \tag{1}$$

In (1), the left hand side represents a linear oscillator with eigenfrequency ω_0 and the right hand side represents a force F dependent on displacement and velocity offsetting a frictional force (g is a damping coefficient) dependent on velocity. The function h collects the conservative and nonconservative (dissipative) forces involved in the sustained oscillation. Equation (1) is not proposed as a model of a rhythmic limb, it simply

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identifies the class of dynamics involved and provides a framework for discussion. Research by Kay and colleagues (Kay 1988; Kay et al. 1991) has confirmed that a rhythmically moving limb segment abides the limit cycle attractor dynamics of (1). Application of the spatial correlation procedure (Grassberger and Procaccio 1984) for computing the dimensionality of an attractor revealed a dimension closely approximating 1, the dimension of a limit cycle attractor.

In addition to being a self-oscillating system, a rhythmic movement unit is a self-assembling system (Kugler and Turvey 1987): The parameters of F in (1) are fabricated in accordance with the particular dynamic dictated by ω_0 and g and the particular intentionality (goal, purpose) defining the rhythmic task (see Shaw et al. 1992). The non-periodic energy source, the chemical energy carried on-board in the body's tissues, is used to assemble F's characteristic properties. This "assembling" role is in addition to the role the chemical energy plays in sustaining the oscillatory motion. With respect to the issue of concern in the present article, the ability of a biological rhythmic unit to oscillate at different frequencies is based on the cognate capabilities of *(a)* assembling different Fs for the same ω_0 and g, and *(b)* sustaining their operation. The theoretical angle to be taken on frequency change focuses on these dual features of self-assembling and self-oscillating, specifically, on the relation between the energy processes that underly them.

1.1 An adiabatic transformability hypothesis

On the basis of considerations of physical systems exhibiting frequency changes, Kugler and Turvey (1987, Chaps. 10–12) have argued that the ability of a rhythmic movement unit to operate at many different frequencies is anchored in the reciprocal notions of adiabatic transformation and adiabatic invariant. The term adiabatic means "to not go through". In its original use it referred to processes in which heat, conceptualized as a substance, did not flow across a system's boundaries (Rankine 1854). The contemporary understanding of adiabatic is different, derived from the modern interpretations of heat and work as ways of transferring energy: A system undergoes an adiabatic transformation when there is no transfer of energy by heating.

Usually an adiabatic change is defined as an infinitely slow change, for example, a piston that moves with negligible velocity and, thereby, negligible friction and energy transfer by heating, as it compresses the volume of a chambered gas and changes the frequency with which the gas molecules collide. Kugler and Turvey (1987) argued, however, that the classical rate limitation on adiabatic transformability need not apply when the forces producing the change in the system of interest are derived from an energy reservoir internal to the system. Under these latter conditions rapid transformations can be adiabatic. Kugler and Turvey (1987) also proposed 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.

Biological systems derive forces from an internal reservoir. Mechanical forces are generated from chemical energy carried "on-board" in the tissues of the body. Consequently, according to Kugler and Turvey's hypothesis, biological systems and biological subsystems, such as rhythmic movement units, can be transformed (in principle) adiabatically. The special significance of an adiabatic transformation is that it leaves certain quantities invariant. These quantities are referred to as adiabatic invariants. The quantity *action*, which is the ratio of average cycle energy to frequency, is an adiabatic invariant. Ehrenfest (1959) referred to adiabatic invariants as "semi-permanent quantities" to highlight their hybrid nature; action, for example, is a conserved quantity (energy) in ratio with a variable of motion (frequency). As with constants in general, adiabatic invariants reduce the number of active degrees of freedom – given two variables linked by a constant, only the value of one of the variables needs to be specified. These semi-permanent quantities, if available biologically, suggest a potentially significant method by which rhythmic movement systems might achieve a reduction in the degrees of freedom to be regulated (Turvey 1990): They can take advantage of constants that arise within the rhythmic activity.

Ehrenfest's (1959) 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 a constant slope (the action) that intersects the origin. According to Kugler and Turvey (1987), if the frequency of a limb moved rhythmically by muscular contractions – a nonconservative oscillatory system – changes via an adiabatic transformation, then the system should behave as in Fig. 1a. That is, there should be a linear relation between average cycle energy (E_m) and frequency (f), with a constant slope (H) and a positive frequency intercept (f_{int}) and, therefore, a negative energy intercept (E_t), where 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 that is put into the cycle to offset the energy lost per cycle: changes in cycle frequency (a mechanical quantity) incur no changes in the amount of energy dissipated per cycle (a thermodynamic quantity). The adiabatic invariant is the constant proportionality H (the action) found betwen E_m and f–f_{int}. That is,

$$H = \text{constant} = (E_m - 0)/(f - f_{\text{int}})\,. \tag{2}$$

The kinematic character of a non-conservative adiabatic system is shown in Fig. 1b. It comprises a nonmonotonic, nonlinear relation between amplitude (θ) and period (τ) over the range $\tau = 0$ and $\tau = \tau_{\text{int}}$ (the inverse of f_{int}) with a maximum value of θ occuring at τ^* which is $1/2\tau_{\text{int}}$ (or $2f_{\text{int}}$). The τ–θ relation follows from (2) by writing E_m as $I/2(\theta^2/\tau^2)$, where I is moment

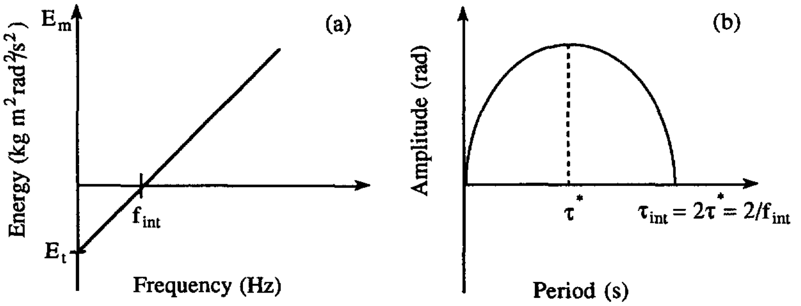

Fig. 1. **a** Theoretically derived relation between kinetic energy E_m and frequency f for a non-conservative, adiabatically transformed system; the slope represents the adiabatic invariant of action H, E_t is the constant energy dissipated per cycle, and f_{int} is the interception of the relation with the f axis. **b** Theoretically derived relation between amplitude θ and period τ for the system satisfying the $f-E_m$ relation in **a**

of inertia, and rearranging terms. Thus,

$$\theta = \pm[2H\tau^2(f-f_{\text{int}})/I]^{1/2}. \tag{3}$$

Equations (2) and (3) together provide the patterns of relations among the major observables that are predicted by the adiabatic hypothesis of frequency change in biological rhythmic movement systems.

From Fig. 1b, τ^* refers to that period of oscillation at which amplitude is maximal; τ^* is the rhythmic movement unit's resonant period. Referring to (1), although ω_0 and g might be fixed, the composition of F can be variable, meaning that τ^* can be variable. Variations in τ^* will rise by virtue of the important fact that F has to be assembled each time from a microstructure of many different components operating at many length and time scales (Schmidt et al. 1991). The assembling and, therefore, the determination of τ^*, is a "statistical mechanical" affair in which the particular ensemble of microcomponents used to produce the macroscopic system is inconstant from one instance to the next. Consequently, each different assembly of F for a given dynamic dictated by ω_0 and g means that the rhythmic movement unit will be characterized by a different τ^*. Inspection of Fig. 1b suggests that if θ is observed empirically to increase as τ increases, then the rhythmic movement unit must be operating in the region in which τ exceeds τ^*. In the plot of E_m against f (Fig. 1a) this means that all data points lie to the right of $2f_{int}$. In contrast, if θ is observed to decrease as τ increases, then the rhythmic movement unit must be operating in the region in which τ is less than τ^*. In the plot of E_m against f (Fig. 1a) this means that all data points lie to the left of $2f_{int}$.

1.2 Testing the adiabatic hypothesis

It is useful to introduce the phrase "dynamic run" (Jackson 1989) for an experimental situation in which an oscillator is observed behaving under fixed values of its parameters. The parameters are the aspects of the system that remain constant (e.g., mass, damping coefficient, stiffness coefficient, and so on) within a dynamic run and are variable only across dynamic runs. The evidence collected to date favoring an Ehrenfest relation has been obtained in a situation in which a biological oscillator is assembled at the outset of a trial and sustained for the duration of a trial (Kugler and Turvey 1987; Kugler et al. 1990). The changes in frequency and, therefore, the changes in the parameters responsible for frequency – occurred discretely across trials, that is, across dynamical runs, with the magnitudes of the changes dictated in largest part by the differences in the conditions imposed across trials. In comparison, locomotory activity (walking, running) is characterized by changes in frequency in which shifts to higher or lower frequency occur continuously, with the timings of the changes, and the sizes of the changes, determined by the locomoting animal. An ordinary bout of locomotory activity, therefore, is not truly a dynamical run. At best, it is a succession of connected dynamical runs. An experimental paradigm directed at evaluating the hypothesis of an Ehrenfest relation in rhythmic movement would do well to mimic the foregoing conditions of movement frequency modulation. In the present research we use a simple approximation to this ideal. A subject begins at a prescribed frequency and then over a given interval of time alters the frequency at will and continuously in either an increasing or decreasing direction. Of concern experimentally is the energetic and spatial changes in the rhythmic movement that accompany the frequency changes. Because of the fluidity of the rhythm and the spontaneity of the changes, analysis is at the level of the individual cycles (e.g., their amplitudes, their durations) and not at the level of mean states.

1.3 Expectations from the adiabatic hypothesis

In the continuous-frequency-change task just decribed, the subject is required, at the outset of each trial, to assemble a rhythmic movement unit that oscillates at a frequency f specified by a metronome. Then the subject has to change f continuously in a specified direction (higher or lower, depending on the trial). What should be expected of this rhythmic activity? If the continuous changes in f conform to adiabatic transformations, as hypothesized, then the following outcomes should be observed.

(1) The amplitudes θ of the cycles and the periods τ of the cycles will be related systematically. The expected systematic $\tau-\theta$ relation need not be fixed, however. It need not be the same from subject to subject; and for a given subject, it need not be the same from trial to trial. As is evident from the $\tau-\theta$ plot of Fig. 1b, the nature of the relation (direct, inverse, direct and inverse) evident in any given trial depends on where the observed cycle durations lie with respect to the τ^* characterizing the oscillator assembled for that trial.

(2) The relation between cycle E_m and cycle f should be positive linear (E_m increases as f increases) with the f intercept (f_{int}) nonzero and positive or, synonymously, the E_m intercept (E_t) nonzero and negative. (The hypothesis of Kugler and Turvey (1987) predicts that E_m can also be independent of f. This alternative is restricted to conditions in which E_m is at or near the maximum possible. The present experiment was designed to keep the E_m magnitudes comfortably below this upper bound. In consequence, the constant E_m of f mapping was not expected.)

Predictions (1) and (2) were evaluated through an experiment using the procedure identified above.

2 Method

Subjects. Eight graduate students (two women and six men) between the ages of 21 and 33 participated in the experiment.

Materials. A T-shaped rod was fashioned from wood, with the stem part longer than the branch part (18 cm vs. 13.5 cm, respectively). To one end of the branch was attached a cylindrical mass of 197 gm to amplify the rod's rotational inertia. When held, the T-shaped rod was grasped at the branch so that during oscillation the stem would be parallel to the ground and the branch would be perpendicular to the ground, with the attached mass below the hand.

Apparatus. Data acquisition was through an Ultrasonic 3-Space Digitizer (SAC Corporation, Westport, CT). An ultrasound emitter was attached to the tip of the stem of the T-shaped rod. The sound emissions at 90 Hz during oscillation were recorded by four microphones arranged in a square 80 cm by 80 cm and attached to a board aligned perpendicularly to the stem of the T-shaped rod. The axis through the stem was approximately centered at the middle of the square formed by the four microphones. The x, y and z motions of the stem were recorded and the digitized data stored on a 80286 based microcomputer using MASS digitizer software (Engineering Solutions, Columbus, OH). This software and analogous routines on a Macintosh II calculated the basic characteristics of the trajectories of the trials: angular displacement, cycle periods, cycle amplitudes, cycle energy, etc. Further statistical analysis was performed on a Macintosh II computer.

Procedure. The subject sat with the right arm on an arm rest. The subject was instructed that all rhythmic motions were to take place about the right wrist and that during a rhythmic bout the right elbow was to retain a fixed position on the arm rest. That is, the subject was instructed to restrict the generation of the rhythm to the muscles controlling the movement of the hand and to resist using motions of the fingers and motions of the forearm. The basic procedure on each trial was for the subject to move the T-shaped rod rhythmically at a frequency of either 0.66 Hz or 2.0 Hz set by a metronome, and then, with the metronome off, to change frequency continuously within a fixed interval of 30 s. The values of the initial frequencies and the length of trials were selected on the basis of pilot experiments. The instructions given to the subject referred only to the frequency of the movement. No instructions were given about initializing and changing the amplitude of the motions. Trials for which the initial frequency was 0.66 Hz, were trials on which the subject was instructed to increase frequency continuously; trials for which the initial frequency was 2.0 Hz, were trials on which the subject was instructed to decrease frequency continuously. Specifically, the subject began each trial attempting to synchronize his or her motions with the metronome frequency. The trial proper began once synchronization was achieved. At that point, the recording of the rhythmic motions was initiated and the metronome was turned off, with the subject then performing under the instruction of either increasing or decreasing frequency for the 30 s trial duration. A signal was given at the 15 s mark to help the subject gauge his or her frequency changes; when to change frequency, and by how much, however, was left free to the subject. Six decreasing trials and six increasing trials were randomly interspersed, with 60 s between trials. The time taken for initial synchronization on a trial varied between 3 and 5 s.

2.1 Results

For each cycle of each 30 s trial, the cycle period τ (that is, $1/f$), E_m, and θ (cycle amplitude) were computed. To facilitate the data presentation, we first identify the pattern of results for one arbitrarily chosen subject (Subject 4) and establish, thereby, the overall structure and logic of the relevant analyses. A summary is then provided of these analyses for all 8 subjects.

Figure 2 (upper) shows, for the arbitrarily chosen subject, how f and θ varied across cycles in one of the six ascending trials and one of the six descending trials. The importance of the figure is that it demonstrates how the basic requirements of the task were satisfied. As can be seen, the change in f was essentially on a cycle to cycle basis; the change occurred relatively continuously. As can also be seen, θ changed systematically with cycle but, as inspection of Table 1 reveals, not necessarily in the same direction that f changed.

Figure 2 (middle) shows, for the arbitrarily chosen subject, how E_m varied with f in one of the six ascending trials and one of the six descending trials. (Because the T-rod was a constant throughout the experiment, moment of inertia is ignored and E_m is expressed simply in units of $\text{rad}^2\,\text{s}^{-2}$.) Two main features are to be noted: *(a)* E_m was a linear function of f in both the ascending and descending trial; *(b)* f intercepts were greater than zero, and E_m intercepts were negative, in both the ascending and descending trial. In short, these data of Subject 4 conform to the Ehrenfest relation for nonconservative systems identified by Kugler and Turvey (1987) and depicted in Fig. 1a: In both kinds of

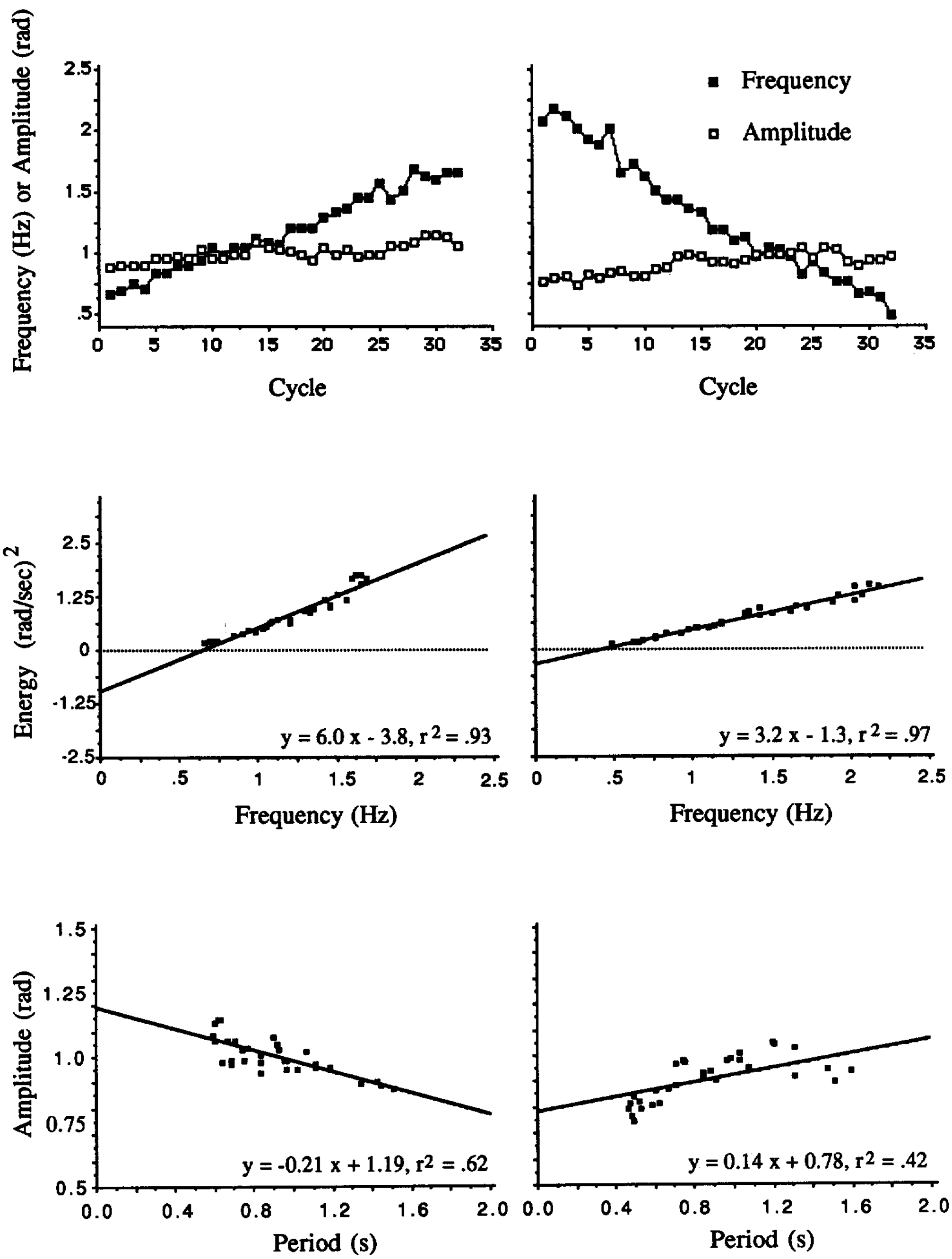

Fig. 2. Upper panel shows the changes in cycle amplitude θ and cycle period τ over the cycles of an ascending trial (*left*) and a descending trial (*right*) of Subject 4. Middle panel shows the linear dependency of kinetic energy E_m on frequency f (that is, $1/\tau$) in the two trials depicted in the upper panel, with the ascending trial on the left and the descending trial on the right. Lower panel shows how θ varied with τ in the ascending (*left*) and descending (*right*) trials depicted in the upper panel

trials, the subject brought about a change in frequency f in such a manner that the cycle energy E_m changed proportionately; in both kinds of trials, the linear dependency of E_m on f was characterized by a positive f intercept (negative E_m intercept). There is a third feature of Fig. 2 (middle) that should be noted. By hypothesis, the slope and E_m-intercept of the functional dependency of E_m on f identify, respectively, the action constant H and the constant energy dissipation per cycle E_t. As inspection of Fig. 2 (middle) reveals, across the two trials the magnitudes of H and E_t varied. Were these variations in H and E_t and those across the other 10 trials independent of each other? Importantly, the answer is "no". Linear regression of the E_t values of the twelve functions of the twelve trials (see Table 1) onto their respective H values revealed the linear dependency: $E_t = -1.08(H) + 0.54$, $r^2 = 0.99$ ($p < 0.0001$). The implication is that for Subject 4, E_t and H were not free to vary independently of each other across the ascending and descending trials of the experiment. Given that

$\tau^* = 2f_{\mathrm{int}}$, and that E_t and f_{int} covary of necessity, it follows from the preceding that the different τ^* magnitudes evident from trial to trial were related systematically.

An important quality of a system abiding the nonconservative Ehrenfest relation depicted in Fig. 1a is the nonmonotonic dependency of θ on τ as shown in Fig. 1b. An implication of this dependency is that either increasing, or decreasing, or increasing-decreasing, or stationary, relations between θ and τ can be expected in any given data set in which frequency is freely modulated. Which particular relation holds within a given data set depends on where the cycle durations produced by the subject lie in relation to the τ^* value for which $d\theta/d\tau = 0$ (see Fig. 1b). To simplify the quantification of the $\tau - \theta$ relation a linear regression can be conducted on the full array of (θ, τ) pairs provided by a given trial of the present experiment. Such a regression would capture, for the data set from each trial, the mean direction and mean rate of change in θ as a function of τ. In Fig. 2 (lower) the $\tau - \theta$ relations for an ascending and descending trial of Subject 4 are presented with the corresponding simple linear regressions. Inspection of Fig. 2 (lower) reveals variants of the $\tau - \theta$ relation noted in the preceding. As is evident from inspection, the associated regression parameters – the slopes and intercepts – differ between the two trials with the descending trial of positive slope and the ascending trial of negative slope. When faced with the task of reducing frequency from an initial 2.0 Hz, Subject 4 expanded the spatial extent of the rhythmic movement as the cycle duration of the movement expanded. Conversely, when faced with the task of increasing frequency from an initial 0.66 Hz, Subject 4 expanded the spatial extent of the rhythmic movement as the cycle duration of the movement compressed. Were these different strategies and the different variants of these strategies unrelated? Regressing the intercepts of the 12 $\tau - \theta$ regressions reported in Table 1 onto their respective slopes reveals that, to the contrary, the seemingly different space-time dependencies were closely related: $\tau - \theta$ intercept $= -0.91$ ($\tau - \theta$ slope) $+ 0.94$, $r^2 = 0.96$ ($p < 0.0001$).

The results of the analyses of Subject 4's data depicted in Fig. 2 and summarized in Table 1 conform to expectations from the adiabatic hypothesis and are in agreement with previous observations (Kugler and Turvey, 1987; Kugler et al. 1990). The additional insight they provide is with respect to the covariation in H and E_t. Apparently, on any given trial Subject 4 was free to set only one of these two quantities. An obvious question is whether or not this pattern in Subject 4's data was shared by the other subjects.

Tables 2 and 3 summarize the results for all 8 subjects. The most noteworthy features are *(a)* the uniformly strong linear dependencies of E_m on f as indicated by the r^2 values of the simple linear regressions ($r^2 > 0.38$, $p < 0.001$, $23 < df < 58$), *(b)* the uniformly negative E_m intercepts, and *(c)* the nonuniformity of the dependencies of θ on τ. With respect to *(c)*, subjects varied in the manner in which they changed θ as a function of the task requirements of decreasing f (increasing τ) or increasing f (decreasing τ). As is evident from inspection of Tables 2 and 3, all variants of the relation between θ and τ – increasing, decreasing, increasing-decreasing, stationary – occurred across trials (both descending and ascending) and subjects.

Regressing the E_t values of each subject onto their corresponding H values reveals in each case a system-

Table 2. Lower (L) and upper (U) values for each subject of the slopes, intercepts, and predicted variances (r^2) of the 12 regression analyses (6 descending and 6 ascending trials) of Θ vs. τ

Subject	Slope		Intercept		r^2	
	L	U	L	U	L	U
1	−0.27	0.37	0.73	1.28	0.06	0.76
2	0.38	0.35	0.60	1.48	0.00	0.78
3	−0.72	−0.06	0.88	1.52	0.13	0.79
4	−0.65	0.31	0.64	1.55	0.14	0.68
5	−0.34	0.48	0.89	1.95	0.26	0.85
6	−0.56	0.64	0.68	1.51	0.00	0.77
7	−1.20	0.38	0.47	1.95	0.01	0.68
8	−0.20	0.37	0.60	1.31	0.07	0.83

Table 1. Regression analysis of Θ vs τ and E_m vs. f together with the calculated τ^* for the 6 descending and 6 ascending trials of the arbitrarily chosen subject, Subject 4

Trial	θ vs. t			E_m vs. f			τ^*
	Slope	Intercept	r^2	Slope	Intercept	r^2	
Descending							
1	0.14	0.78	0.42	0.80	−0.32	0.97	1.25
2	0.31	0.64	0.41	0.89	−0.48	0.82	0.92
3	−0.20	1.17	0.18	1.50	−1.02	0.93	0.74
4	0.20	0.79	0.51	1.06	−0.57	0.96	0.94
5	0.13	0.90	0.19	1.14	−0.59	0.95	0.97
6	0.16	0.76	0.14	0.67	−0.19	0.83	1.72
Ascending							
1	0.21	1.19	0.62	1.48	−0.96	0.93	0.77
2	0.47	1.35	0.60	2.05	−1.72	0.82	0.59
3	−0.65	1.55	0.68	2.58	−2.26	0.91	0.57
4	−0.08	0.98	0.22	1.10	−0.67	0.93	0.83
5	−0.16	1.05	0.26	1.26	−0.87	0.90	0.73
6	−0.21	1.02	0.48	1.08	−0.72	0.91	0.75

Table 3. Lower (L) and upper (U) values for each subject of the slopes, intercepts, and predicted variances (r^2) of the 12 regression analyses (6 descending and 6 ascending trials) of E_m vs. f, together with the upper and lower values of the calculated τ^*

Subject	Slope		Intercept		r^2		τ^*	
	L	U	L	U	L	U	L	U
1	0.86	2.16	−1.50	−0.33	0.86	0.96	0.71	1.41
2	0.61	2.55	−2.65	−0.12	0.90	0.98	0.64	2.60
3	0.78	3.08	−3.29	−0.44	0.79	0.98	0.47	0.89
4	0.08	2.58	−2.26	−0.19	0.82	0.97	0.57	1.72
5	1.13	4.36	−2.77	−0.22	0.91	0.99	0.78	2.58
6	1.02	2.78	−2.28	−0.47	0.70	0.99	0.56	1.36
7	0.60	7.04	−11.08	−0.30	0.39	0.93	0.42	1.00
8	0.61	1.98	−1.32	−0.03	0.69	0.99	0.75	1.17

Table 4. Regression analyses of E_t vs. H

Subject	Slope	Intercept	r^2
1	−0.79	−0.37	0.76
2	−0.90	−0.44	0.99
3	−0.42	−0.42	0.47
4	−1.08	0.54	0.99
5	−0.80	0.83	0.95
6	−1.14	0.75	0.94
7	−1.55	1.26	0.96
8	−0.92	0.47	0.94

atic dependency between the two quantities. As identified for the arbitrarily chosen subject, Subject 4, the data of each of the other seven subjects reveal that the two quantities E_t and H are not free to vary independently of each other. The linear regressions are summarized in Table 4. Indeed, when all 96 (12 trials × 8 subjects) E_t values are regressed onto the corresponding 96H magnitudes, a single dependency emerges $-E_t = -1.14(H) + 0.78$, $r^2 = 0.81$ $(p < 0.0001)$ – suggesting that the 8 subjects linked E_m variations to f variations according to a single, common principle. The latter is reinforced by the regressions of the $\tau-\theta$ intercepts onto the $\tau-\theta$ slopes. For all 96 pairs, $\tau-\theta$ intercept $= -0.68$ ($\tau-\theta$ slope) $+ 1.07$, $r^2 = 0.49$ $(p < 0.0001)$.

3 Discussion

The results of the experiment are consistent with the expectations from the adiabatic hypothesis. The relation between cycle E_m and cycle f tended to be positive linear (E_m increased as f increased) with the E_m intercept (E_t) nonzero and negative, in agreement with Fig. 1a. According to the hypothesis, the constant proportionality between E_m and f–f_{int} observed on a given trial identifies an adiabatic invariant of action, H (kg m^2 s^{-1}). Likewise, according to the hypothesis, the constant E_t observed on a trial identifies an amount of energy put into a cycle to offset the energy lost per cycle that is invariant over variations in cycle duration. Additionally, the experiment showed that cycle θ and cycle τ tended to be related systematically in varied ways – sometimes θ increased with τ (that is, $1/f$), sometimes θ decreased with τ, and sometimes both directions of change seemed to be in evidence. Such diversity is expected from oscillatory regimes conforming to the $\tau-\theta$ plot of Fig. 1b, with the nature of the $\tau-\theta$ relation manifest in any given trial dependent on the τ^* characterizing the oscillator assembled for that trial. As underscored in the introduction, variations in τ^* will arise by virtue of the important fact that F in (1) has to be assembled each time from a microstructure. The particular ensemble of microcomponents used to produce the macroscopic rhythmic system (the one whose behavior is observed and measured in the laboratory) will not be fixed from one trial to the next. An especially important feature of the present results, with bearing on the mechanism of assembling, is the observation that the parameters characterizing a rhythmic movement unit during a trial – the constancies H and E_t – were not independent of each other. One reading of this interdependency is that, given a particular microscopic ensemble, H and E_t are coordinately determined. How might such co-determination arise? Considerations of the viscoelasticity of muscle suggests some directions that can be taken in search of an answer.

3.1 Modeling living tissue as a continuum of Kelvin bodies

The features of viscoelasticity are hysteresis, relaxation, and creep. When examined in vitro, tissues of the body (especially muscle) exhibit a hysteresis loop in cyclic loading and unloading that is largely indifferent to the frequency of the cycle (Fung 1981). The implication is that the internal friction of the tissue is frequency independent. How this independence is understood – that is, how it is modeled – has implications for the invariants observed in the present experiment and the question concerning co-determination of H and E_t. It is commonplace to model viscoelastic materials through combinations of linear springs (that give a deformation proportional to load) and dashpots (that give a velocity proportional to load). The primary combination is the Kelvin model or body; it consists of a spring and a dashpot, in parallel with another spring. A Kelvin body is characterized by a number of properties most notable among which, for present purposes, is its relaxation time, that is, a time scale for the decrease in stress following a sudden, and then maintained, straining of the body. If just one Kelvin body, or a certain finite number of them, is used to model the properties of living tissue, then the hysteresis loop of the model proves to be dependent on the loading-unloading frequency. The key to simulating the independence actually seen in living tissue is to superimpose very many Kelvin bodies with a continuous (rather than discrete) spectrum of relaxation times (Fung 1981). Let the continuous relaxation spectrum be defined as

$$S(\tau) = c/\tau \quad \text{for} \quad \tau_1 \leqslant \tau \leqslant \tau_2 \tag{4}$$

$$S(\tau) = 0 \quad \text{for} \quad \tau < \tau_1, \tau_2 < \tau \tag{5}$$

where c is a constant, and τ designates relaxation time. The consequence of any fairly flat and broad continuous spectrum is an orthogonality of dissipation and stiffness over a relatively wide range of values of the loading-unloading frequency ω. Specifically, log-linear stiffness and constant dissipation hold for $\tau_1 \leqslant 1/\omega \leqslant \tau^2$ with the dissipation proportional to

$$\tan^{-1}[1/2(\tau_1/\tau_2 - \tau_2/\tau_1)^{1/2}] \tag{6}$$

Mathematically, with a shortening of the range $\tau_1 \leqslant 1/\omega \leqslant \tau_2$, the dissipation magnitude and stiffness will both increase for a given loading-unloading frequency (see the full equation set in Fung 1981). That is, if the continuous spectrum of relaxation times expressed by (4) and (5) (roughly, the composition of the ensemble of Kelvin bodies) could be manipulated, then the tissue's constant friction and the tissue's stiffness, for a given range of ω, would change coordinately.

For present purposes, the preceding is illustrative of how a single set of conditions might be defined on muscle microstructure so as to simultaneously endow it with the abilities to *(a)* function as different macroscopic springs without incurring different energetic costs, and *(b)* exhibit linkages between its stiffness and friction parameters. Of course, the ideas expressed in the preceding were intended to address tissue properties in vitro than in vivo. They are, nontheless, worthy of consideration because they expand the ways in which we can think about the relation between macroscopic and microscopic movement dynamics and the basis for the mutual dependencies among the kinetic and kinematic quantities of the present experiment. Additionally, it is reasonable to suppose that this inherent dynamical character of muscular tissue is complemented, rather than opposed or ignored, by neural processes. That is, in the assembling and execution of rhythmic movements, one can imagine that neural processes provide boundary conditions (e.g., τ_1 and τ_2) that harness the tissue dynamics in task-specific ways. A pertinent question, therefore, is whether ideas analogous to those of a continuum of Kelvin bodies associated with a continuous spectrum of relaxation times could be developed in the direction of an understanding of the present pattern of results. Efforts below to address the present data through the current repertoire of well-defined dynamical systems puts the latter question into perspective.

3.2 Seeking an appropriate autonomous differential equation

If biological rhythmic movements units are characterized by the kinetic and kinematic patterns depicted in Fig. 1a and 1b, then it is important to ask whether or not there is a differential equation that can model nonconservative systems with adiabatic invariance. An overview of candidate equations follows. As will become apparent, none of them are fully satisfactory.

Rhythmic limb movements have been interpreted as self-sustained oscillators described by autonomous ordinary differential equations (ODEs) of the kind expressed by (1). Van der Pol, Rayleigh, and Duffing equations (see Jackson 1989; Thompson and Steward 1986) have figured prominently in such modeling, and a form of (1) involving both Van der Pol and Rayleigh terms has been advanced by Kay et al. (1987):

$$\ddot{x} + a\dot{x} + b\dot{x}^3 + cx^2\dot{x} + \omega^2 x = 0. \tag{7}$$

Arguments and analyses by Beek and Beek (1988) have opened the door to even more generic types of ODEs involving Van der Pol, Rayleigh, and Duffing terms to higher powers, and hybrid terms composed from them. For current purposes, the autonomous ODEs thus far applied to rhythmic movements (e.g., (7)) are inappropriate because they fail to exhibit the variety of dependencies of θ on τ expressed in the data of the present experiment and predicted by the adiabatic hypothesis (Fig. 1b). Usually, with increase in $1/\tau$, θ decreases (e.g., (7)) or is constant (e.g., the Duffing ODE). There are, however, autonomous ODEs that exhibit θ increase with increase in $1/x$, for example,

$$(1 + \varepsilon\dot{x})\ddot{x} + x = 0\,. \tag{8}$$

where ε is a small coefficient, and 1 is arbitrary. From (8) the $\tau - \theta$ relation can be estimated with a perturbation method. For this specific equation Linstedt's method (Jordan and Smith, 1977, p. 140) provides

$$\omega = 2\pi/\tau = 1 + \varepsilon^2\theta^2/12\,. \tag{9}$$

Equation (8) is different from the family of ODEs represented by (1) which can be expressed even more generally by:

$$\ddot{x} + \varepsilon h(x, \dot{x}) + g(x) = 0\,. \tag{10}$$

Typical of equations like (10) is that frequency is the fundamental control parameter of the system. In the adiabatic case, however, frequency assumes a different role, and one that is possibly more profound.

Returning to (8), autonomous ODEs of this kind may be good candidates to describe aspects of the results of the present experiment and other similar experiments because they exhibit an unusual dependence of $1/\tau$ and θ. At the same time, we cannot expect this class of ODEs to be fully satisfactory; they are not capable of accommodating all of the forms of the $1/\tau - \theta$ relation predicted and measured in the present experiment (see Tables 1–3). What is needed is an ODE that can produce a rising, a falling, and a constant $1/\tau - \theta$ relation, depending on the coefficients, that is, on the configuration of the physical parameters of the system. In a phrase, (8) is too strongly constrained for our purpose.

The phase trajectories of the rhythmic movements under study do not show any extreme deviation from more or less elliptically shaped orbits. In consequence, we can use the harmonic balance method – a kind of averaging – to simplify our search (Jordan and Smith 1977). Let us suppose that the general form of the ODE is

$$\ddot{x} + \varepsilon h(x, \dot{x})x = 0\,. \tag{11}$$

It can be assumed that there is a periodic solution that can be well approximated by the simple periodic function $x(t) = \theta \cos \omega t$. Then the h function can be written

$$h(x, \dot{x}) = A_1(\theta)\cos \omega t + B_1(\theta)\cos \omega t + \text{residual harmonics}\,. \tag{12}$$

From (11) and (12) the τ–θ relation can be derived:

$$[1 + \varepsilon A_1(\theta)/\theta]^{1/2} = \omega = 2\pi/\tau\,. \tag{13}$$

This latter relation promises more freedom within which to construct the required ODE. In principle, from this formula an appropriate $A_1(\theta)$ function can be identified to produce the intended dependency of θ on $1/\tau$ (increasing, decreasing, constant). Unfortunately, the successful identification of an $A_1(\theta)$ function would still leave the challenge of determining the corresponding h function of (11). Several attempts on our part to resolve this problem highlighted that the challenge is to overcome the singularity of the h function. Space does not permit a discussion of the technical details.

To conclude our search, we consider the family of homogeneous ODEs with time dependent coefficients. The available ODEs of physical systems exhibiting adiabatic invariants are not in autonomous form. They are usually Hamiltonians with slowly varying parameters. The thermally driven piston described in the introduction is a classic example; the pendulum with varying length is another. For the latter, it is well known that if the change of length is slow enough, then energy preserves a constant porportional relation to frequency. Classically, adiabatic invariants are quantities which are asymptotically preserved during the slow change of parameters. For instance, for the pendulum with varying length, the ratio of the total energy (area of the limit cycle) and the frequency is the known adiabatic invariant (see Kugler and Turvey, 1987, Chap. 10). The form of the equation is

$$\ddot{x} + \omega^2(\varepsilon t)x = 0\,. \tag{14}$$

In (14), frequency is the time dependent parameter. Generalizing from this pendulum example, we might expect the ODE for an adiabatic nonconservative system (of the kind under inquiry in the present article) to contain time-dependent coefficients. Given this possibility of inconstant parameters, and the obvious complexity of the biological movement system, it is apparent that the present effort to isolate the appropriate family of ODEs is insufficiently constrained. An additional source of difficulty is that, for many problems of biological movement, frequency cannot be limited to the role of a control parameter. Specificially, the present data interpreted through the adiabatic hypothesis, and very general features of the locomotry system (see below), suggest that important rhythmic movement phenomena do not reduce to frequency-controlled mechanisms. The upshot of these latter remarks, and of the above considerations of candidate ODES, is that if there is an ODE that satisfies the present data (and, by hypothesis, adiabatic transformability), then it must be different in kind from those thus far applied to rhythmic movement. As just highlighted, the prospects look best for an ODE from the family characterized by time dependent coefficients (see analyses in Beck et al. 1992). Elaborating the approaches expressed in (8) and (11), and incorporating further biomechanical assumptions of the type represented in (5) and (6), might prune the size of the candidate family.

3.3 The net cost of locomotion: a reflection of adiabatic transformability?

The present data, although motivated by the adiabatic hypothesis, can be regarded as significant to the general understanding of human rhythmic movements in their own right. Indeed, the efforts expanded above to seek a suitable ODE for the kinematic relations in the data point to weaknesses in our current understanding of the kinds of dynamical systems needed to model the space-time aspects of rhythmically moving limbs. With respect to Kugler and Turvey's (1987) adiabatic hypothesis, we can only claim that we have obtained results consistent in their overall pattern with that hypothesis. Confirmation would require considerably more evidence than that presented, and quite possibly experiments of a technically different nature (Iberall 1990). Despite the difficulties to be faced in shoring up the support for the adiabatic hypothesis, there are substantial reasons, both empirical and theoretical, for believing that it is correct in its essentials and that it should be pursued rigorously.

One of the most remarkable facts of locomotion, discovered in the course of the last three decades, is a puzzling independence of energy cost and speed summed up in the statement that "The amount of energy used to run a mile is nearly the same whether it is run at top speed or at a leisurely pace" (Kram and Taylor 1990). When mass (M)-specific rates of energy consumption, usually expressed as $\dot{V}_{O_2}/M$ (ml $O_2 \cdot s^{-1} \cdot kg^{-1}$), are plotted for a given animal as a function of locomotory speed, a straight line is obtained from an intersect with the vertical axis at zero (e.g., Kram and Taylor 1990; Full 1989; Taylor et al. 1970; Walton et al. 1990). This linear dependency of mass-specific rate of energy consumption on speed holds for bipeds, quadrupeds, and polypeds, for arthropods and vertebrates, for limbed and limbless animals. It is a dependency of great generality, suggesting a fundamental principle governing locomotion that is independent of morphology, physiology size, and taxa. Spelling out the types of quantities involved in the linear dependency we see that

Net Cost of Locomotion (NCL)

= (Energy per Unit Mass/Time)/(Distance/Time)

= (Energy per Unit Mass)/Distance. (15)

That is, NCL indicates the amount of energy required to move a unit mass of animal a given distance. The slope of mass-specific rate of energy consumption vs. speed varies inversely with mass. On the basis of the empirically determined slopes, it can be concluded that to move a unit of mass 1 m, a cockroach of 3 g dissipates twice as much energy as a crab or mouse of 30 g and nine times as much energy as a dog of 3 kg; small animals on a per gram basis require more energy per time and per distance (Full 1989). Conversely, if an arthropod, a snake, a bird, and a mammal, have similar mass, then the energy to be dissipated by each to move 1 m will be nearly identical (Full 1989; Taylor et al. 1982; Walton et al. 1990).

The key to linking the facts of NCL to the adiabatic hypothesis, and to the data of the present experiment, is the relation between frequency (of limb cycles in limbed locomotion and of lateral undulations in limbless locomotion) and speed of forward progression. This relation is linear up to the limit of frequency modulation. Animals increase speed by increasing frequency (beyond the limit, quadrupeds and polypeds achieve higher speeds by longer strides). A different energetic cost quantity can be defined, therefore, by an alternative linear function namely, mass-specific rate of energy consumption vs. frequency. The slope of this function, expressed in component quantities, yields

Energetic Cost per Cycle

= (Energy per Unit Mass/Time)/(Cycle/Time)

= (Energy per Unit Mass)/Cycle

That is to say, the slope of the mass-specific rate of energy consumption vs. frequency represents the fact that *the energy dissipated per locomotory cycle is a constant (for an animal of a given mass) over the range of aerobically sustainable frequencies*. From our perspective, this is the truly remarkable fact of locomotion: The invariance over frequency change of the energy dissipated per cycle is the property expressed by the E_t value of the Ehrenfest relation for non-conservative systems (Fig. 1a). According to the adiabatic hypothesis, changes in cycle frequency (a mechanical quantity) incur no changes in the amount of energy dissipated per cycle (a thermodynamic quantity). We conjecture, therefore, by way of conclusion, that the independence in locomotion of energy cost and speed holds over wide differences in animal morphology, physiology, size, and taxa, because it reflects a very general principle – adiabatic transformability of biological movement systems.

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References

Andronov AA, Vitt AA, Khaikin SE (1987) Theory of oscillators. Dover, New York

Beek PJ, Beek WJ (1988) Tools for constructing dynamical models of rhythmic movement. Hum Mov Sci 7:301–342

Beek PJ, Turvey MT, Schmidt RC (1992) Autonomous and nonautonomous dynamics of coordinated rhythmic movements. Eco Psychol 4:65–96

Ehrenfest P (1959) Collected scientific papers. North-Holland, Amsterdam

Fung YC (1981) Biomechanics: Mechanical properties of living tissue. Springer, Berlin Heidelberg. New York

Full RJ (1989) Mechanics and energetics of terrestrial locomotion: Bipeds to polypeds. In: Weiser W, Gnaiger E (eds) Energy transformations in cells and organisms. Thieme Verlag, New York, pp 175–182

Grassberger P, Procaccia I (1983) Measuring the strangeness of strange attractors. Physica 9D:189–208

Iberall A (1990) A commentary on Kugler, Turvey, Schmidt and Rosenblum's ecological approach to motor systems. Eco Psychol 2:275–293

Jackson EA (1989) Perspectives of nonlinear dynamics. Cambridge University Press, Cambridge

Jordan DW, Smith P (1977) Nonlinear ordinary differential equations. Clarendon Press, Oxford

Kay BA (1988) The dimensionality of movement trajectories and the degrees of freedom problem: A tutorial. Hum Mov Sci 7: 343–364

Kay BA, Kelso JAS, Saltzman ES, Schöner G (1987) Space-time behavior of single and bimanual rhythmical movements. J Exp Psychol: Hum Perc Perf 13:178–192

Kay BA, Saltzman ES, Kelso JAS (1991) Steady state and perturbed rhythmical movements: A dynamical analysis. J Exp Psychol: Hum Perc Perf 17:183–197

Kram E, Taylor CR (1990) Energetics of running: A new perspective. Nature 346:265–266

Kugler PN, Turvey MT (1987) Information, natural law and the self-assembly of rhythmic movement. Erlbaum, Hillsdale

Kugler PN, Turvey MT, Schmidt RC, Rosenblum LD (1990) Investigating a nonconservative invariant of motion in coordinated rhythmic movements. Eco Psychol 2:151–189

Rankine WJM (1854) On the geometrical representation of the expansive action of heat and the theory of thermo-dynamic engines. Phil Trans R Acad London 144:155–175

Shaw RE, Kadar EE, Sim M, Repperger D (1992) The intentional spring: A strategy for modelling systems that learn to perform intentional acts. J Mot Beha 24:3–28

Schmidt RC, Beek PJ, Treffner PJ, Turvey MT (1991) Dynamical substructure of coordinated rhythmic movements. J Exp Psychol: Hum Perc Perf 17:635–651

Taylor CR, Schmidt-Nielsen K, Raab JL (1970) Scaling of the energetic cost of running to body size in mammals. Am J Physiol 219:1104–1107

Taylor CR, Heglund NC, Maloiy GMO (1982) Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. J Exp Biol 97:1–21

Thompson JMT, Stewart HB (1986) Nonlinear dynamics and chaos. Wiley, Chichester

Turvey MT (1990) Coordination. Am Psychol 45:938–953

Walton M, Jayne NC, Bennett AF (1990) The energetic cost of limbless locomotion. Science 249:524–527