Linear and nonlinear stiffness and friction in biological rhythmic movements

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Abstract. Biological rhythmic movements can be viewed as instances of self-sustained oscillators. Auto-oscillatory phenomena must involve a nonlinear friction function, and usually involve a nonlinear elastic function. With respect to rhythmic movements, the question is: What kinds of nonlinear friction and elastic functions are involved? The nonlinear friction functions of the kind identified by Rayleigh (involving terms such as $\dot{\theta}^2$) and van der Pol (involving terms such as $\theta^2\ddot{\theta}$), and the nonlinear elastic functions identified by Duffing (involving terms such as $\theta^3$), constitute elementary nonlinear components for the assembling of self-sustained oscillators. Recently, additional elementary nonlinear friction and stiffness functions expressed, respectively, through terms such as $\theta^2\ddot{\theta}^2$ and $\dot{\theta}\ddot{\theta}^2$, and a methodology for evaluating the contribution of the elementary components to any given cyclic activity have been identified. The methodology uses a quantification of the continuous deviation of oscillatory motion from ideal (harmonic) motion. Multiple regression of this quantity on the elementary linear and nonlinear terms reveals the individual contribution of each term to the oscillator's non-harmonic behavior. In the present article, the methodology was applied to the data from three experiments in which human subjects produced pendular rhythmic movements under manipulations of rotational inertia (experiment 1), rotational inertia and frequency (experiment 2), and rotational inertia and amplitude (experiment 3). The analysis revealed that the pendular oscillations assembled in the three experiments were compositionally rich, braiding linear and nonlinear friction and elastic functions in a manner that depended on the nature of the task.

1 Introduction

There have been a number of attempts to model the rhythmic movements of human limbs and limb segments as self-sustained oscillators (e.g., Haken et al. 1985; Kugler and Turvey 1987; Kay et al. 1987, 1991; Beek and Beek 1988; Beek et al. in press). A major challenge to this modeling is identifying the nonlinear friction and elastic functions. Well-known nonlinear friction functions are those described and investigated by Rayleigh in the context of musical instruments, and van der Pol in the context of electric circuits; and well-known nonlinear elastic functions are those described and investigated by Duffing in the context of mechanical devices (Abraham and Shaw 1983; Thompson and Stewart 1987). Biological rhythmic movements may exploit these functions either singly or in combination. In addition, they may exploit other functions—functions that may turn out to be describable and investigated most effectively in the context of biological motion. In theory, the methods for the identification of the relevant friction and elastic functions are provided by nonlinear dynamics. Broadly speaking, these methods fall into three categories, viz. (i) stability analysis (bifurcation and perturbation methods), (ii) analysis of space–time behavior (relations between frequency, amplitude and peak velocity, topological analyses of trajectories in the phase plane), and (iii) time-series analysis (spectral analysis and dimensionality analysis). It is the case, however, that methods to construct dynamical equations of motion and/or to determine parameter coefficients directly from the behavioral flow itself are few and far between (but see, e.g., Cremers and Hübner 1987; Breeden and Hübler 1990; Eisenhammer et al. 1991). The present article demonstrates a way in which the nonlinear functions underwriting rhythmic movement can be identified, and investigates how their contributions change with inertial loading, and with the frequency and amplitude of oscillation. In preview, the method assumes that the central nervous system employs limit cycle dynamics to produce rhythmic movements and that a strictly mathematical analysis of the movement kinematics can reveal the oscillatory components of limit cycle regimes. These
components may or may not have neurophysiological meaning. As such the method should be viewed as complementary to the investigation of neural mechanisms underlying the control of rhythmic movements.

1.1 The W-approach: assumptions and model

The approach to be pursued assumes that rhythmical movements in a plane (i.e., movements with a single mechanical degree of freedom) result from a second-order dynamic with a stationary origin, fixed inertial properties, and a fixed basic frequency \( \omega_0 \) (which is not necessarily identical to the eigenfrequency of the system). Quite generally, we write for such systems

\[
\ddot{x} + \omega_0^2 x + W(x, \dot{x})\omega_0 = 0
\]

(1)

in which \( x \) is the spatial deviation from the origin and a dot indicates differentiation with respect to time. Equation (1) represents the canonical oscillator (ideal mass-spring system, consisting of an inertial force and a linear restoring force) plus an ensemble function, the \( W \)-function, that contains all conservative and nonconservative (dissipative) deviations from the canonical oscillator.

Multiplication of (1) by \( dx/dt \) and subsequent integration leads to

\[
\frac{1}{2}(x^2 + \omega_0^2 x^2) + W(x, \dot{x})\omega_0 x dt = 0
\]

or, equivalently,

\[
-W(x, \dot{x}) = -\frac{d(\dot{x}^2 + \xi^2)}{2\omega_0} = \frac{d(\dot{x}^2 + \xi^2)}{2d\xi}
\]

(2)

where \( \xi = \omega_0 x \) and the fat dot (above \( \dot{\xi} \)) represents differentiation with respect to dimensionless time \( \tau = \omega_0 t \). It is evident from inspection of (2) that the value of \( W \) is computable from movement data. It is also evident, however, that (2) will not predict \( W \) accurately as \( d\xi/d(\xi^2/d\xi) \) approaches 0. The basic idea of what can be termed the \( W \)-method is to compute the value of \( W \) for each value of the state variables \( \xi \) and \( d\xi/d\tau \) and to regress these \( W \) values onto the lower order terms in the Taylor-series expansion \( \xi^2(d\xi/d\tau)^2 \) with the aim of determining (i) the stiffness and friction terms that contribute significantly to \( W \), and (ii) the magnitudes of their coefficients. The series expansion \( \xi^2(d\xi/d\tau)^2 \) can be developed as in Table 1 (following Beek and Beek 1988).

| Table 1. The conservative and nonconservative series expansions of the terms in \( W \) |
|---------------------------------|---------------------------------|
| Conservative terms            | Nonconservative terms           |
| Duffing series:               | Van der Pol series:            |
| \( \xi^1, \xi^3, \xi^5, \ldots \) | \( \xi^2 \xi_1, \xi^3 \xi_2, \xi^5 \xi_3, \ldots \) |
| \( x \)-mix odd series:      | Rayleigh series:               |
| \( \xi^1 \xi^2, \xi^3 \xi^4, \xi^5 \xi^6, \ldots \) | \( \xi^1, \xi^3, \xi^5, \ldots \) |
| \( x \)-mix even series:     | \( x \)-mix even series:        |
| \( \xi^1 \xi^2, \xi^3 \xi^4, \xi^5 \xi^6, \ldots \) | \( \xi^1, \xi^3, \xi^5, \ldots \) |

Well known and well studied, in both physics and biology, are the nonlinear functions identified by Rayleigh, van der Pol, and Duffing; largely unknown and largely unstudied are the nonlinear functions of the \( \pi \)-mix series. The terms in the odd \( \pi \)-mix series are quasi-conservative in that while their primary influence is on an oscillator’s frequency they simultaneously affect its energy balance (Pearson 1976; Beek and Beek 1988). Because the sign of these terms is determined by the sign of position, they can be thought of as a velocity-dependent control of stiffness. In contrast, the sign of the terms in the even \( \pi \)-mix series varies with the sign of velocity; these terms are nonconservative.

1.2 The \( W \)-approach applied to a pendular rhythmic activity

In the present article, the \( W \)-function is investigated within pendular rhythmic activity. Two important reasons dictate this choice of biological movement. First, the magnitude of the restoring torque for the canonical oscillator is known unequivocally (it is the restoring torque due to gravity), permitting, thereby, a means of circumventing the singularity in (2). Second, there is a well-established experimental paradigm, introduced by Kugler and Turvey (1987), for investigating pendular rhythmic movements in humans. Research using the paradigm has provided insights into the basic mechanisms of the pendular-like, clock-like behavior of individual limbs, and the 1:1 frequency locking between contralateral limbs, that are characteristic of terrestrial locomotion (e.g., Turvey et al. 1988; Schmidt et al. 1991, 1993; Sternad et al. 1992). In this paradigm, a seated person swings a single hand-held pendulum or two hand-held pendulums parallel to the sagittal plane with the pendular oscillations occurring about an axis in the wrist with other joint(s) essentially immobile. (Although, strictly speaking, the movements produced in this experimental task are spherical, the amplitude of the secondary angle is small relative to the primary angle (±10%) so that not much information is lost by restricting the analysis to the primary angle.) The pendulums can vary physically in shaft length and/or the mass of the attached bob. The eigenfrequency of an individual ‘wrist–pendulum system’ is the eigenfrequency of the equivalent simple gravitational pendulum, \( \omega = (g/L_{eq})^{1/2} \), where \( L_{eq} \) is the simple pendulum length and \( g \) is the constant acceleration due to gravity. The quantity \( L_{eq} \) is calculable from the magnitudes of shaft length, added mass, and hand mass, through the standard methods for representing any arbitrary rigid body oscillating about a fixed point as a simple pendulum (Kugler and Turvey 1987).

Following (1), a wrist–pendulum system in motion can be modeled as

\[
mL_{eq} \ddot{\theta} + gmL_{eq} \sin \theta + W(\theta, \dot{\theta}) = 0
\]

(3)

where \( m \) is the total mass of hand, grip, rod, and bob, \( L_{eq} \) is the system’s simple pendulum equivalent length, and \( mL_{eq}^2 \) is the moment of inertia (I) relative to the center of rotation \( O \) located in the wrist; \( g \) is 9.81 m/s² while
\[ m, L_{eo}, \theta \] and its time-derivatives can be measured or calculated. The inertial torque \( mL_{eo}^2 \dot{\theta} \) can be calculated from a record of the position trajectory of the pendulum limb in an experimental situation. The gravitational torque \( g m L_{eo} \sin \theta \) that results from gravity acting on the center of mass of the pendulum limb can also be calculated from a record of the position trajectory. Knowing these two quantities, the generalized muscular torque \( W(\theta, \dot{\theta}) \) can be computed (see Schneider et al. 1989). The quantity \( W(\theta, \dot{\theta}) \) so derived indexes the biological contribution and is functionally equivalent to (2). The distinct advantage of (3) over (2) is the absence of numerical singularities. The \( W \)-values obtained can be regressed on the terms in the above-mentioned series (Table 1) that have a combined power \( p + q \) of 3 or less to determine which kind of oscillator terms (linear and nonlinear, conservative and nonconservative) are operating in the neuromuscular control of the rhythmic movement. Specifically, the coefficients – indexed by their respective \( p \) and \( q \) powers – of the following self-excitatory wrist–pendulum model are sought after

\[
ml_{eq}^2 \ddot{\theta} + gm_{eq} \sin \theta = -c_{10} \dot{\theta} - c_{30} \dot{\theta}^3 - c_{12} \dot{\theta}^2 \\
- c_{01} \dot{\theta} - c_{03} \dot{\theta}^3 - c_{21} \theta^2 \dot{\theta}
\]

(4)

2 Experiment 1

To move a hand-held pendulum rhythmically would seem to involve a harmonic dynamic (associated with the pendulum dimensions of the limb and the neuromuscular control of linear stiffness) and a relaxation dynamic (associated with nonlinear dissipative and metabolic control processes) (Beek and Beek 1988; Rosenblum and Turvey 1988). A harmonic dynamic is related primarily to conservative factors (affecting the frequency of the system); a relaxation dynamic is related primarily to nonconservative factors (affecting the energy balance of the system). The component dynamics interact such that the relaxation dynamic may be ‘tuned’ by the harmonic dynamic and, in turn, the harmonic dynamic may be ‘detuned’ by the relaxation dynamic. A reasonable hypothesis is that the relative contributions of the two dynamics depend on pendulum size, with the relaxation dynamic less prominent at larger rotational inertias (e.g., Rosenblum and Turvey 1988). This hypothesis can be addressed with the \( W \)-method. Specifically, the conservative coefficients should increase with moment of inertia more so than the nonconservative coefficients. The more basic question, however, is that of the particular elementary functions used in producing the rhythmic behavior, whatever the rotational inertia. Which conservative terms \( \theta, \theta^3 \), and \( \theta \dot{\theta}^2 \) – and which nonconservative terms \( \theta \dot{\theta}, \theta^3 \), and \( \theta \dot{\theta}^2 \) – tend to define the assembled biological oscillator?

(3)

2.1 Method

Subjects. Five subjects (one male, four females) participated in this experiment. Three subjects were undergraduate students of the University of Connecticut and participated in partial fulfillment of their introductory psychology course requirements. The other two subjects volunteered to participate. All subjects were right-handed. All subjects were naive to the purpose of the experiment.

Materials. Nine different pendulums were used that defined the conditions of the experiment. The pendulums were composed of an aluminum rod of 1 cm diameter which was attached to a cylindrical wooden grip of 2.5 cm diameter and 12 cm length. Rods of five different physical lengths were used (0.20, 0.28, 0.34, 0.40, and 0.48 m) with differently weighted steel cylinders (ranging from 0.04 kg to 0.58 kg) attached at their ends by means of a set screw. The resulting moments of inertia of the nine pendulum systems were 0.060, 0.068, 0.073, 0.094, 0.124, 0.177, 0.184, 0.198, and 0.250 kg m².

The trajectories of the wrist–pendulum movement were measured using a Sonic 3-Space Digitizer (SAC Corporation, Westport, CT). In order to acquire the position time series of the wrist–pendulum, a sonic emitter was attached at the end of each pendulum. Using a sonic 'spark' that is issued from the emitter 90 times per second, the digitizer calculates the distance of the emitter from the three microphones positioned on the floor to form a Euclidean coordinate grid. In order to eliminate sound reflections off hard surfaces in the room, egg-shell shaped mattresses were used for sound insulation. The digitized information was stored on a 80286-based microcomputer using MASS digitizer software (Engineering Solutions, Columbus, OH). Using the MASS data reduction and analysis software, the period and angular position (\( \theta \)) of each wrist–pendulum system trajectory were calculated.

Procedure. The subjects sat in a chair and placed their arm on an arm rest. They were given a pendulum and told to swing it from the wrist joint in the sagittal plane. Further, the subjects were told to look straight ahead at the wall in front of them instead of looking at the pendulum and to use only the wrist joint in swinging the pendulum not their fingers. After receiving instructions from the experimenter, each subject was given some practice swinging each pendulum. Before each trial, the subject was told to hold the pendulum in a vertical position and a calibration ‘spark’ was emitted so that the digitizer could determine the length of the pendulum and the position of the axis of rotation of the movement. The subject was asked to begin swinging the pendulum at a tempo that he or she deemed comfortable (e.g., ‘that you could do all day’) and to say ‘ready’ when that goal had been achieved (usually in a matter of 5–10 s). The experimenter then started to record the trial for 30 s. Each trial ended by the verbal instruction ‘stop’ of the experimenter, and the experimenter replaced the pendulum with one for the next trial. The overall experiment took about 40 min. per subject. Subjects received no feedback about their performance. Each condition had four trials. The order of the conditions was randomized across the 40 trials. Subsequent to the experiment, the data were analyzed according to the \( W \)-approach.

2.2 Results and discussion

Figure 1 shows the three torques calculable from (3) for each point in a part of the time series of an arbitrarily chosen trial, with \( W(\theta, \dot{\theta}) = mL_{eo}^2 \ddot{\theta} - gmL_{eo} \sin \theta \). A stepwise linear regression (with an \( F \) value of 4 to enter) of the \( W(\theta, \dot{\theta}) \) of the entire trial was conducted on the two conservative terms \( \theta, \theta^3 \), the quasi-conservative term \( \theta \dot{\theta}^2 \), and three nonconservative terms \( \theta, \theta^3, \theta \dot{\theta}^2 \) as independent variables. The regression revealed that 98% of the variance in \( W \) was accounted for by \( c_{10} = 4.640, c_{30} = -0.635, c_{12} = -0.229, c_{01} = 0.087, \) and \( c_{21} = 0.405 \). That is, the particular oscillator assembled on this arbitrarily chosen trial was constituted primarily by three elastic elements – a linear spring, a cubic ('softening') spring, and a velocity-dependent nonlinear spring (expressed by \( \theta \dot{\theta}^2 \)) – and by a combination of friction terms.
suggestive of a van der Pol oscillator, viz. \( c_{01} \) and \( c_{21} \). The torques corresponding to the significant coefficients can be substituted for \( W \) in (3), to provide an expression of (3) in which all components are defined explicitly. Under the assumption that the signal contains no noise, the frequency of this model equation should be identical to the frequency of the system depicted in Fig. 1 if the \( W \)-method is a reliable tool for determining the conservative components of a biological oscillator. This frequency, estimated numerically through a fourth-order Runge-Kutta integration routine, approximated the observed frequency: 1.20 Hz vs 1.14 Hz, respectively. Unfortunately, however, the oscillation of the derived model equation is not self-sustaining, because the coefficients of the linear damping term and the van der Pol term are both positive, implying a gradual loss of energy until the oscillator has come to a standstill. Applying this procedure to all 180 trials of experiment 1 revealed that the method produced reliable estimates for the coefficients of the conservative components but failed to produce self-sustaining oscillator models in the vast majority of the trials.

There may be two reasons for this result. The first is that the limit cycle itself does not contain sufficient information for reliable estimates of the nonlinear coefficients because, quite literally, it is the trajectory in phase space along which energy loss and energy uptake are in balance (cf. Eisenhammer et al. 1991). The second is that a small inaccuracy in the estimate of the linear damping coefficient, which may easily arise because the origin of oscillation is not exactly known, is already sufficient to induce a sign reversal (and, hence, a qualitative change from a limit cycle to a point attractor). Focusing on the second reason, we decided to exclude \( c_{01} \) from the multiple linear regression and to estimate it separately on the basis of the observed amplitude \( \lambda \) and frequency \( \omega \) and the significant estimates of the nonlinear damping coefficients \( c_{03} \) and \( c_{21} \), using the post-hoc approximation (cf. Haken et al. 1985; Kay et al. 1987):

\[
- c_{01}(P) = (3c_{03} \omega^2 + c_{21})(\lambda/2)^2
\]

Using this amended procedure, the \( W \)-values calculated from (3) for each of the 180 trials (five subjects by 36 trials each) were subjected to a stepwise linear regression with the two conservative terms \( \theta, \theta^2 \), the quasi-conservative term \( \theta \theta^2 \), and the two nonlinear damping terms \( \theta \theta^2, \theta^2 \theta \) as independent variables. Subsequently, the significant coefficients were collected according to condition and subject and the linear damping coefficients \( c_{01}(P) \) were estimated on the basis of (5). The 180 regression \( r^2 \) values were all significant and ranged between 0.41 and 0.97 with a mean of 0.86. Each of the candidate components occurred as significant contributors, but not on every trial and not to the same degree for every moment of inertia. The linear, cubic, and velocity-dependent stiffness terms were significant in 99%, 95%, and 95% of the trials, respectively; the Rayleigh and van der Pol friction terms were significant in 99% and 100% of the trials, respectively. For each trial, numerical simulations were performed on the basis of (4), in which the significant coefficients found in the regression analysis were inserted. All models were self-sustaining. Figure 2 is an example of an observed and a simulated phase portrait. The numerically estimated \( \omega \) and \( \lambda \) were regressed on the observed \( \omega \) and \( \lambda \), respectively. It was found that
simulated \( \omega \) accounted for 85% of the variance in actual \( \omega \) with a slope of 0.92 (SE = 0.031) and an intercept of 0.08, while simulated \( \dot{\omega} \) accounted for 97% of the variance in actual \( \dot{\lambda} \) with a slope of 1.10 (SE = 0.015), indicating a slight overestimate of the actual \( \dot{\lambda} \) and an intercept of -0.04.

We can now ask how the neuromuscular oscillator adjusted to the different-sized pendulums. Table 2 shows how the coefficients averaged over trials and subjects (insignificant coefficients were assigned a value of zero) varied with moment of inertia. As moment of inertia increased, \( c_{10} \) became increasingly more positive (significant linear regression of \( r^2 = 0.70, p < 0.01 \), \( c_{30} \) decreased \( r^2 = 0.57, p < 0.05 \)) and \( c_{12} \) became increasingly more negative \( r^2 = 0.95, p < 0.0001 \). These findings suggest the presence of a neuromuscular spring of increasing stiffness and increasing nonlinearity as well as the presence of a velocity-dependent spring property with a negative detuning effect. Additionally, as moment of inertia increased, \( c_{03} \) and \( c_{21} \) became increasingly more positive \( r^2 = 0.97, p < 0.0001 \) and \( r^2 = 0.60, p < 0.05 \), respectively, which is suggestive of a neuromuscular damping function that adjusted to inertial load by changing both its nonlinear coefficients.

To enhance the understanding of the inertial dependency of the contributions of the respective linear and nonlinear friction terms, a nondimensional quantity was computed that indexes the degree to which a system is governed by a relaxation dynamic. The values of the nonconservative coefficients obtained in the stepwise regressions were normalized by transforming them into their dimensionless counterparts. The moments of inertia \( (I) \) and the eigenperiods \( (T) \) of the nine wrist-pendulum systems as well as the amplitudes \( (A) \) produced in each trial were used in this transformation: the \( c_{0i}(P) \) coefficients were multiplied by \( T/I \), the \( c_{21} \) coefficients by \( T^2/I \), and the \( c_{03} \) coefficients by \( T^3/I \). The sum of the absolute normalized coefficients of the nonconservative terms was then calculated for each trial. Simple regression on the mean values of this quantity for each of the wrist-pendulum systems revealed a linear inverse dependency \( r^2 = 0.83, p < 0.001 \) consistent with the hypothesis motivating experiment 1: increasing moment of inertia was associated with a decreasing relaxation dynamic.

In summary, the results of experiment 1 suggest that the biological pendular motions under investigation were vibratory systems that (a) were essentially hybrids of the well-known van der Pol and Rayleigh oscillators (Haken et al. 1985; Kay et al. 1987, 1991) with the addition of conventional position-dependent and nonconventional velocity-dependent nonlinear stiffnesses, and (b) became increasingly dominated by nonconservative components with decreasing rotational inertia.

3 Experiment 2

Experiment 2 added a manipulation of frequency of oscillation to the manipulation of pendulum moment of inertia made in experiment 1. Patently, for a hand-held pendulum to oscillate at frequencies other than its preferred frequency, the oscillator's composition must change. With respect to (3) and the associated W-methodology, a distinct pattern of detunings should become evident when pendular rhythmic movements are conducted above and below eigenfrequency. Because linear stiffness is the major neuromuscular determinant of frequency, \( c_{10} \) should be positive for frequencies higher than the eigenfrequency (the neuromuscular stiffness must be in the same direction as the gravitational restoring torque), negative for frequencies lower than the eigenfrequency (the neuromuscular stiffness must oppose the gravitational restoring torque), and close to zero at the eigenfrequency. This expected detuning pattern should depend on moment of inertia. For example, the linear stiffness required to bring about a frequency higher than the eigenfrequency should be greater for a larger than for a smaller pendulum.

3.1 Method

Subjects. Four graduate students at the University of Connecticut (three men, one woman) volunteered to participate. All were naive to the purpose of the experiment.

Materials and procedure. The same movement data acquisition system as used in experiment 1 was used in the present experiment. Using three lengths of rod (0.33, 0.49, and 0.64 m) and two added weights (0.20 and 0.50 kg), six different pendulum systems were defined with moments of inertia of 0.061, 0.080, 0.140, 0.206, 0.250, and 0.354 kg m² and eigenfrequencies of 0.954, 0.941, 0.777, 0.763, 0.682, and 0.673 Hz. The task in this experiment was similar to that of experiment 1 except that an auditory metronome pulse was used to pace the oscillations of a pendulum about the wrist joint at 0.80\( N_0 \), 1.05\( N_0 \), and 1.60\( N_0 \), where \( N_0 \) is the wrist-pendulum's eigenfrequency. The subjects were instructed to match the back-stroke of the pendulum cycle to the auditory signal. In combination, these manipulations resulted in a 3 (frequency) × 6 (moments of inertia) design. The experiment was performed in three sessions distributed over 5 days. Each session contained one 23 s trial per condition. The order of the conditions was randomized across the 18 trials of a session.

3.2 Results and discussion

As in experiment 1, \( W(\dot{\theta}, \dot{\theta}) \) was calculated for each point in the time series of a trial. These \( W \)-values were then subjected to a stepwise linear regression (with an \( F \) value of 4 to enter) on the two conservative terms \( \dot{\theta}, \theta^3 \), the quasi-conservative term \( \theta^2 \dot{\theta} \), and the two nonlinear damping terms \( \dot{\theta}^2 \) and \( \theta^2 \dot{\theta} \) for all 216 (4 × 54) trials. The
significant coefficients were collected according to condition and subject, and used to estimate $c_{01}(P)$ on the basis of (5). Across the trials, the $r^2$ values ranged between 0.10 and 0.99 with a mean of 0.79 and a standard deviation of 0.16. Numerical simulations revealed that 98% of the model equations were self-sustaining.

Figure 3 shows the muscular torques as a function of angular position calculated from (3) for three trials with 1.05$\omega_0$ (top panel), 0.80$\omega_0$ (middle panel), and 1.60$\omega_0$ (bottom panel). The slopes indicating the neuromuscularly assembled linear stiffness are, respectively, zero, negative, and positive, in accordance with the expected detuning pattern. Note that the positive detuning condition is distinguished from the negative detuning condition by a steeper absolute slope, reflecting the difference in absolute detuning between 0.80$\omega_0$ and 1.60$\omega_0$, and by the presence of a cubic component. The mean values of $c_{10}$, $c_{20}$, $c_{12}$ for 0.80$\omega_0$, 1.05$\omega_0$, and 1.60$\omega_0$ are presented in Fig. 4A. An ANOVA on $c_{10}$ revealed significant effects of frequency, $[F(2, 6) = 83.88, p < 0.0001]$, moment of inertia $[F(5, 15) = 9.13, p < 0.001]$, and the frequency $\times$ moment of inertia interaction $[F(10, 30) = 12.91, p < 0.0001]$ – the increase of $c_{10}$ with moment of inertia was more pronounced at 1.60$\omega_0$ than at 0.80$\omega_0$ and 1.05$\omega_0$. With respect to both $c_{30}$ and $c_{12}$, the effect of moment of inertia was significant $[F(5, 15) = 4.43, p < 0.05$ and $F(5, 15) = 5.93, p < 0.05$, respectively], as were the interactions with frequency $[F(10, 30) = 3.69, p < 0.05$ and $F(5, 15) = 3.40, p < 0.05]$ – both terms decreased with moment of inertia, especially in the 1.60$\omega_0$ condition.

The dependency of the nonconservative terms on the frequency manipulation is shown in Fig. 4B, which suggests that the van der Pol coefficient increased with the frequency of oscillation in relation to its eigenfrequency, while the Rayleigh coefficients remained roughly constant and the linear friction coefficients decreased. Whereas the first relationship was not statistically significant, $c_{01}(P)$ decreased significantly with frequency $[F(2, 6) = 7.20, p < 0.05]$. The ANOVAs also revealed that the frequency $\times$ moment of inertia interaction was significant for all three nonconservative terms. The relevant statistics were $F(10, 30) = 5.00, p < 0.001$ [for $c_{01}(P)$], $F(10, 30) = 2.64, p < 0.05$ (for $c_{20}$), and $F(10, 30) = 2.49, p < 0.05$ (for $c_{12}$); $c_{01}(P)$ decreased more strongly with moment of inertia at higher frequencies; $c_{20}$ increased more strongly with moment of inertia in the detuning conditions than in the 1.05$\omega_0$ condition; and $c_{21}$ increased strongly in the 1.60$\omega_0$ condition, but not in the other frequency conditions. In addition, there was a significant increase with moment of inertia as such for $c_{03} [F(5, 15) = 14.44, p < 0.0001]$ and a significant decrease for $c_{01}(P) [F(5, 15) = 7.54, p < 0.001]$. 

Fig. 3. Generalized muscle torque as a function of angular displacement and pendulum moment of inertia is shown for three different frequency conditions – at the eigenfrequency (top), less than eigenfrequency (middle), and greater than eigenfrequency (bottom) (see text). The circles represent the computation of the generalized muscle torque at each sampling of the 23 s bout of cyclic behavior with a sampling rate of 90/ s 

Fig. 4. A Average dependence in experiment 2 of the coefficients of linear stiffness ($c_{30}$), cubic stiffness ($c_{10}$), and velocity-dependent stiffness ($c_{12}$) on frequency expressed in units of the wrist–pendulum system’s eigenfrequency. B Average dependence in experiment 2 of the coefficients of linear friction ($c_{01}(P)$), Rayleigh friction ($c_{20}$), and Van der Pol friction ($c_{21}$) on frequency expressed in units of the wrist–pendulum system’s eigenfrequency.
The results of experiment 2 are important in two major respects. First, they reinforce the impression that the W-method expressed through (3) captures qualitatively the composition of biological pendular oscillators. To produce pendular oscillations deviant from the eigenfrequency requires a linear spring that must subtract from (for slower than eigenfrequency oscillations) or add to (for faster than eigenfrequency oscillations) the restoring torque due to gravity. Figure 4A and the accompanying ANOVA confirm that $c_{10}$ was negative, approximately zero, and positive, for $0.80 \omega_0$, $1.05 \omega_0$, and $1.60 \omega_0$, respectively. Second, the results of the present experiment reinforce the impression that the escapement sustaining a biological rhythmic movement is a hybrid of Rayleigh and van der Pol escapements, with the latter assuming greater importance, and suggest further that the form of this hybrid depends on the interaction between the pendulum's moment of inertia and the pendular frequency of oscillation in relation to its eigenfrequency.

4 Experiment 3

Where experiment 2 manipulated rotational inertia and frequency, experiment 3 manipulated rotational inertia and amplitude. The amplitude of oscillation was manipulated by defining end points of the pendular motion through markers at two spatial locations, one in the front and one in the rear of the sagittal plane in which the pendulum moved. Accordingly, to satisfy the spatial constraint, a subject had to control precisely the points at which pendulum velocity went to zero. This requirement suggests that for motions of different controlled amplitudes, different frictional (nonconservative) magnitudes will be required. Both van der Pol and Rayleigh terms are expected to appear in the analyses and to vary with the conditions of experiment 3: the van der Pol term indexes a position-dependent escapement, one that causes peak velocity to increase as frequency increases, while the Rayleigh term indexes a velocity-dependent escapement, one that causes amplitude to decrease as frequency increases (i.e., for $c_{12}$ and $c_{33}$ > 0 and $c_{03}$ < 0).

An accompanying change in the conservative terms can be expected for at least two reasons. First, oscillatory movements of a given pendulum system that differ in amplitude may also be oscillatory movements that differ in frequency. The observations of a systematic dependency of rhythmic movement amplitudes on rhythmic movement frequencies (e.g., Kay et al. 1987; Kugler and Turvey 1987; Kugler et al. 1990; Kadar et al. 1993) suggest that a similar dependency may hold in the converse direction. If so, variations in the conservative terms can be expected to accompany the explicit, subject-controlled variations in amplitude. Second, the nonlinearity in the muscle length–muscle stiffness relation becomes prominent at larger extensions, suggesting amplitude-related variations in cubic stiffness. One further expectation can be noted. For an oscillation of prescribed amplitude, stiffness control must be coordinate with rate control. Consequently, the $\pi$-mix term $\theta \theta^2$ of Table 1 should prove to be of significance given that it expresses a velocity-dependent stiffness.

4.1 Method

Subjects. Four students from the University of Connecticut (three men, one woman) volunteered to participate. All were naive to the purpose of the experiment.

Materials and procedure. The same movement data acquisition system as used in experiments 1 and 2 was used in the present experiment. The pendulums used were identical to those in experiment 2. The subject's task in this experiment was to oscillate the pendulums so that the extent of the movements was determined by spatial markers placed in the front and rear of the sagittal plane in which the pendulums traveled. Three different spatial extents (amplitudes) were used for each pendulum. These distances were defined relative to the average amplitude at $\omega_0$ calculated over the four subjects in experiment 2. The smallest amplitude in each pendulum condition was two-thirds less than the $\omega_0$ amplitude, the median amplitude was the $\omega_0$ amplitude, and the largest amplitude was two-thirds greater than the $\omega_0$ amplitude. In sum, the experiment was a 3 (amplitude) x 6 (moment of inertia) design. It consisted of three sessions distributed over 5 days. Each session contained one 23 s trial per condition. The order of the conditions was randomized across the 18 trials of a session.

4.2 Results and discussion

The mean amplitudes produced for the smallest, intermediate, and largest amplitude conditions, averaged across the six moments of inertia, were 0.253, 0.508, and 0.708 rad, respectively. Larger amplitudes were associated with smaller frequencies: 1.167, 0.961, and 0.879 Hz, respectively.

As in experiments 1 and 2, $W(\theta, \dot{\theta})$ was calculated for each point in the time series of a trial. These $W$-values were then subjected to a stepwise linear regression (with an F-value of 4 to enter) on the two conservative terms, $\theta$, $\theta^2$, the quasi-conservative term $\theta \theta^2$, and the two nonlinear nonconservative terms $\theta^3$ and $\dot{\theta}^2 \theta$ for all 216 trials. The significant coefficients were collected according to condition and subject and estimates for $c_{00}(P)$ were derived on the basis of (5). Across the trials, the $r^2$ values ranged between 0.52 and 0.97 with a mean of 0.86 and a standard deviation of 0.10. Numerical simulations revealed that all model equations were self-sustaining.

Dependencies of the conservative terms. Each of the coefficients $c_{10}$, $c_{30}$, and $c_{12}$ was submitted to a repeated-measures ANOVA with moment of inertia and amplitude condition as independent variables. The $c_{10}$ and $c_{30}$ ANOVAs revealed a significant main effect of amplitude [$c_{10}$: $F(2, 6) = 51.54, p < 0.001$; $c_{30}$: $F(2, 6) = 16.38, p < 0.05$]: as amplitude decreased (that is, as frequency increased), the linear stiffness increased (from values near 2.5 to near 7.5) while the Duffing stiffness became increasingly negative (from values near −1 to near −35). In addition, the effect of the interaction between amplitude and inertia was significant for $c_{10}$ [$F(10, 30) = 2.96, p < 0.05$], but difficult to interpret. The ANOVA on the quasi-conservative coefficient $c_{12}$ yielded significant effects of amplitude [$F(2, 6) = 27.85, p < 0.001$] and rotational inertia.
[\( F(5,15) = 8.26, p < 0.001 \)], accompanied by a significant interaction between the two \( F(10,30) = 4.97, p < 0.001 \); the coefficient became increasingly more negative as amplitude decreased and as rotational inertia increased, while the former effect was stronger for the larger pendulums. As remarked in the introduction to the present experiment, the significance of this velocity-dependent stiffness is expected where stiffness and movement velocity must be controlled coordinately, as in the present task in which the precise points at which the movement must come to rest are prescribed. In experiment 2, where the task was to attain a particular frequency with amplitude free to vary, there was no main effect of frequency on \( c_{12} \).

Dependencies of the nonconservative terms. Each of the nonconservative coefficients was similarly submitted to a repeated-measures ANOVA with moment of inertia and amplitude as independent variables. As expected, the spatial precision requirements of the task were satisfied by changes in nonlinear damping. The interindividual means of \( c_{03} \) (the Rayleigh coefficient) for the three amplitude conditions were 0.10 (small), 0.02 (comfort), 0.01 (large) and differed significantly \( F(2,6) = 32.65, p < 0.001 \). The rate of increase of \( c_{03} \) with decreasing amplitude was more dramatic for the larger pendulums \( F(10,30) = 4.39, p < 0.001 \), while pendulum size by itself also led to a significant increase in \( c_{03} \) \( F(5,15) = 6.36, p < 0.05 \). A similar pattern of results was found for \( c_{21} \) (the van der Pol term). The interindividual means of \( c_{21} \) increased with decreasing amplitude \( F(2,6) = 4.40, p < 0.05; 3.10 \) (small), 0.58 (comfort), and 0.36 (large) and with increasing rotational inertia, while the interaction between these two effects was significant, \( F(10,30) = 4.27, p < 0.001 \), because the increase in \( c_{21} \) in the small-amplitude condition was particularly strong for the larger pendulums. It might be inferred, therefore, that the observed systematic variations in the Rayleigh and the van der Pol dynamic in the present experiment were due to the requirement of precise amplitude control. The increase of the nonlinear friction terms with decreasing amplitude was matched by a significant decrease of the linear damping coefficient \( c_{01}(P) \) \( F(2,6) = 5.92, p < 0.05 \).

As in Experiment 2, \( c_{01}(P) \) also decreased significantly with increasing moment of inertia \( F(5,15) = 14.12, p < 0.0001 \).

5 General discussion

The focus of the present article has been the question: What kind of oscillator is a rhythmic limb movement? Wherever a source of non oscillatory excitation is converted within a system to oscillatory excitation the system is referred to as a self-induced or self-sustained oscillator. Rhythmic movements, therefore, can be viewed as expressing a self-sustained oscillator given that they are achieved by a non oscillatory energy source (the chemical fuel contained within the muscles). In general, an auto-oscillator can be divided into four distinct components: (i) an oscillatory component, comprising a linear and/or nonlinear elastic property that guarantees a return to equilibrium and an inertial property that guarantees overshoot; (ii) an energy source that makes up for the loss of energy through friction; (iii) a gate that admits energy to the oscillatory component in the right amounts and at the right instants; and (iv) a feedback component that controls the gate, using the properties of the oscillatory system itself. A force acting in the same direction as the oscillatory component's velocity does positive work (impacting, overcoming damping); a force opposed to velocity does negative work (withdrawing energy, increasing damping). Because negative feedback is normal friction that suppresses oscillations and positive feedback is inverse friction that excites oscillations, (iv) is described most usefully as a friction function.

The question of the oscillatory nature of a rhythmic limb movement is, therefore, the question of what kinds of elastic and friction functions comprise this type of self-sustained oscillator. In addressing this question we have applied the \( W \)-approach (2) introduced by Beek and Beck (1988). The ideal oscillator (constant total energy and an inverse linear relation between kinetic and potential energy) is defined solely by component (i), constituted by an inertial property and a linear elastic property. Its phase portrait (velocity against displacement) is a perfect circle. Adding components (ii), (iii), and (iv), together with a nonlinear elastic element, would change the shape of the phase portrait. It would no longer be circular. The \( W \)-function captures these deviations from circularity. Behind its application is the understanding that the sources of the deviations from circularity fall into restricted classes. Any oddly shaped phase portrait that resists description through a single continuous function can be described by piecing together a number of simpler, basic functions. It has been hypothesized that the five kinds of functions identified in Table 1 enter into the approximation of the continuous description (Beek and Beck 1988). By this hypothesis, there are more types of elements with which to construct oscillators than previously considered, but the number of elemental types is still limited.

The \( W \) quantity at any point of a phase portrait is the derivative, with respect to displacement, of the total energy of the oscillator at that point. For each such point the elementary elastic and friction terms can be calculated and the question posed (via stepwise multiple regression) of how \( W \), the measure of deviation from a circular orbit, depends upon them. This analysis applied to the data of experiments 1–3 in the form of (3) suggests that for rhythmic pendular movements the friction function tends to be assembled from properties identified in the Rayleigh and van der Pol series – as suggested by Haken et al. (1985) and Kay et al. (1987) – and the elastic function from properties identified in the Duffing series and in the new elastic series (see Table 1). Perhaps not surprisingly, the evidence from the \( W \)-analysis is that rhythmic movement oscillators are compositionally rich, braiding a variety of linear and nonlinear friction and elastic functions in a manner that depends on the particular nature of the rhythmic task. To summarize the main results: experiment 1 revealed that,
The larger the rotational inertia, the greater the extent to which the pendular oscillations were dominated more by the springs (linear and cubic stiffnesses) and less by the dissipative and restorative energy flows (normal linear friction and inverse nonlinear frictions as expressed by Rayleigh and van der Pol terms). Experiment 1 revealed that, as oscillatory frequency deviated from the eigen-frequency, neuromuscularly assembled linear and cubic springs contributed subtractively or additively to the gravitational stiffness depending on the direction of the deviation, with the magnitude of the Rayleigh and van der Pol frictional components depending on the interaction between the pendulum’s moment of inertia and the degree of detuning relative to its eigenfrequency. Experiment 3 revealed that, as the magnitude of prescribed limits on the angular excursion increased, both Rayleigh and van der Pol components changed systematically, as did the velocity-dependent stiffness identified in the odd n-mix series (see Table 1). In all three experiments the coefficients derived from the W-approach provided reasonable models (in the form of ordinary differential equations) of the empirically observed sustained oscillations.

One potentially important contribution of these results concerning the W-approach is an appreciation of the nonlinearity of the stiffness underlying biological rhythmic movements. For the most part, analysis and modeling of oscillatory movements has been limited to linear springs (e.g., Cavagna 1977; Bingham et al. 1991; Schmidt and Turvey 1992), although nonlinear spring characteristics of muscles at a joint have been noted (Kol et al. 1985; Vatikiotis-Bateson and Kelso 1993). Another potentially important contribution is the identification of the nonconservative mechanisms that are responsible for the stability of an oscillatory movement. Previous modeling had suggested mixtures of Rayleigh and van der Pol escapements (Haken et al. 1985; Kay et al. 1987) and the present research appears to bear this out. Future applications of the W-approach will be aimed at understanding the dynamical basis of fluctuations in the elastic and friction terms occurring during the adduction and abduction phases of pendular rhythmic movement (i.e., half-cycle to half-cycles variations; see Beek et al. 1992) under a variety of conditions, including those studied in the present article. The W-method may also be useful in the context of studying the properties of the coupling between two oscillating limbs or limb segments. Given the identification of the linear and nonlinear stiffness and friction properties of two rhythmic movement units, it can then be determined how these properties are affected by the coupling between them needed to achieve the 1:1 frequency locking that typifies many biological rhythmic movement patterns.

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References


