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Resonance Tuning in Rhythmic Arm Movements

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ABSTRACT. The hypothesis was tested that the preferred frequency of rhythmic movement corresponds to the resonant frequency of the muscle–limb system, as proposed by the hybrid spring–pendulum model (Kugler & Turvey, 1987). In contrast to previous studies, the resonant frequency and stiffness of the system were estimated independently, which permitted quantitative predictions of the preferred frequency to be made. Human subjects ($N = 5$) were asked to oscillate their forearms in the vertical plane at their preferred frequency under conditions of added mass and external spring loading. Subjects also oscillated their arms at frequencies below and above the preferred frequency, which enabled the investigators to estimate the resonant frequency and stiffness of the elbow joint by using the phase transfer method (Viviani, Soechting, & Terzuolo, 1976). The preferred frequency corresponded to the resonant frequency of the muscle–limb system under each condition, as predicted. The oscillation amplitude varied inversely with the preferred frequency, which was also predicted. Finally, the internal joint stiffness was modulated so that it matched the impedance of the external springs but was unaffected by added mass. The results are consistent with an autonomous oscillator model that incorporates proprioception about the dynamics of the periphery.

Key words: hybrid spring–pendulum model, impedance matching, preferred frequency, resonant frequency, stiffness.

How are stable movement patterns organized and generated by the action system? Bernstein (1967) originally proposed that actors take advantage of nonmuscular forces—the physical dynamics of the musculoskeletal system—to produce efficient, coordinated movements. Such physical constraints may not only allow for the optimization of efficient behavior but also provide anchoring points around which behavior is organized. An important testing ground for this issue has been the domain of rhythmic movements such as walking, hammering, and speech. How are oscillatory movements generated? What determines the preferred frequency, amplitude, and phase of oscillation? In this study, we empirically tested the hypothesis that the preferred frequency of oscillatory limb movement corresponds to the resonant frequency of the system. Also, the hypothesis was tested that the amplitude corresponding to the preferred frequency is proportional to the resonant amplitude, assuming the forcing amplitude is constant.

There are several approaches to the problem of producing rhythmic movements. The centralized control approach assumes a central representation of the movement, including its form, amplitude, and temporal characteristics, that is imposed on the periphery. In this vein, we include impulse-timing theory (Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979; Wallace, 1981), central clock theory (Creelman, 1962; Gibbon, Church, & Meck, 1984; Wing & Kristofferson, 1973), and inverse modeling (Hildreth & Hollerbach, 1985). Although the representations may be as diverse as force profiles, internal clocks, and specific trajectory plans, they all share the feature that the precise timing and spatial extent of the peripheral motor apparatus are centrally dictated.

An alternate approach claims that stable movement patterns emerge from an interaction between the neural dynamics of the central nervous system and the physical dynamics of the musculoskeletal system and environment (Kelso & Tuller, 1984; Kugler & Turvey, 1987). This view emphasizes the role of physical constraints such as the inertia of limbs and external loads, the stiffness of muscles and tendons, and resonant frequencies of the system and argues

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that these properties are exploited and modulated by the actor in the service of adaptive, goal-directed behavior. In particular, the musculoskeletal dynamics do not simply determine a movement but are sensed and complemented by the neural dynamics to shape the intended movement. Recent research has demonstrated that both infants and adults reduce the active muscular contribution as they presumably become sensitive to dynamic constraints (Schneider, Zernicke, Schmidt, & Hart, 1989; Thelen, 1990). Other work within this approach is consistent with this view (Kay, 1986; Kay, Saltzman, & Kelso, 1991; Kelso, DelColle, & Schöner, 1990; Kelso, Holt, Kugler, & Turvey, 1980; Kelso, Holt, Rubin, & Kugler, 1981; Kugler, Kelso, & Turvey, 1980; Kugler & Turvey, 1987; Reed, 1982; Rosenbaum, Slotta, Vaughan, & Plamondon, 1991).

In the present study, we were concerned with the determination of the preferred frequency and amplitude of rhythmic movement. Our thesis was that the resonant frequency of the musculoskeletal system is sensed, modulated by varying joint stiffness, and adopted as the preferred frequency of oscillation. There are two potential advantages for operating at the resonant frequency: The energy required to generate oscillations with a given amplitude is minimized, and such a sensed frequency allows for stable and reproducible movements.

Previous Research

Kugler and Turvey (1987) performed experiments varying the length and mass of hand-held pendula and showed that subjects chose a comfortable frequency of oscillation that was related to the resonant frequency of the wrist–pendulum system. Subjects performed two tasks: (a) swing one pendulum about one wrist, and (b) swing two pendula simultaneously about both the left and right wrists. In the single-pendulum case, the length of the equivalent simple pendulum (referred to as the *equivalent length*) was computed from the mass and moment of inertia of the wrist–pendulum system. The equivalent length is the length of a simple pendulum whose resonant frequency is equal to that of the original pendulum. In the double-pendulum case, the system was treated as two pendula hanging from a common beam, and Kugler and Turvey used Huygen's law to compute the length of an equivalent single pendulum. It was shown that the preferred frequency scaled linearly with the square root of the reciprocal of the equivalent length, as predicted by the resonant frequency of a physical pendulum.

A linearized, driven pendulum is described by the following differential equation:

$$I\ddot{\theta} + c\dot{\theta} + mgl_{cm}\theta = T_{drive}(t). \tag{1}$$

where I is the moment of inertia measured about the axis of rotation, c is the damping coefficient, m is the mass, g is the gravitational acceleration, l_{cm} is the distance from the axis of rotation to the center of mass, θ is the angular position of the pendulum, and $T_{drive}(t)$ is the external, driving torque. Assuming small values for viscosity (Bennett, Hollerbach, Xu, & Hunter, 1992), the angular resonant frequency is

$$w_r = \sqrt{mgl_{cm} / I} = \sqrt{g / L_{eq}}, \tag{2}$$

where L_{eq} denotes the length of the equivalent, simple pendulum. By definition, a simple pendulum has an equivalent length that is equal to its physical length, L, because $l_{cm} = L$ and $I = mL^2$.

Although Kugler and Turvey (1987) demonstrated that the preferred frequency was proportional to the resonant frequency, the preferred frequency was consistently higher than the resonant frequency of the wrist–pendulum, especially under conditions of large moments of inertia.

Because of that discrepancy, Kugler and Turvey (1987) proposed a revised model, which included a pair of springy muscles attached to the wrist–pendulum system (see Figure 1). This model has a resonant frequency that depends on the internal stiffness of the joint, k_{int}, as well as the equivalent length of the wrist–pendulum:

$$w_r = \sqrt{(mgl_{cm} + k_{int}) / I} = \sqrt{(g / L_{eq}) + (k_{int} / I)}. \tag{3}$$

In this model, the stiffness of the muscles about the wrist joint should account for the discrepancy between the preferred frequency and the resonant frequency of the pendulum by increasing the resonant frequency of the system. In other words, the preferred frequency would equal the reso-

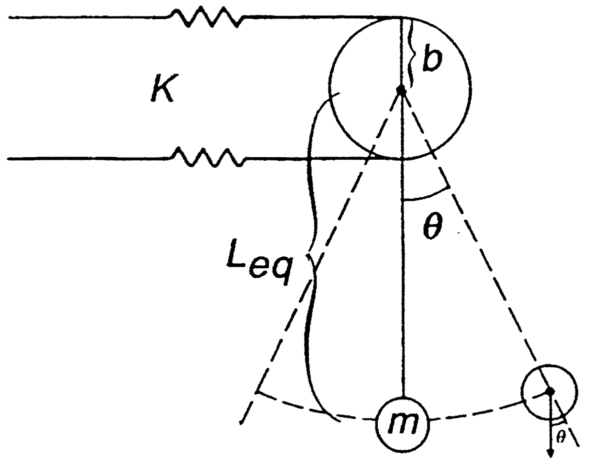

FIGURE 1. The revised model proposed by Kugler and Turvey (1987) in which the limb is represented as a simple pendulum driven by a pair of springy muscles. The linear stiffness of the muscles about the joint is represented by K, and the perpendicular distance between the joint and the line of force from the muscles is represented by b . The torsional stiffness of the joint is, therefore, Kb^2, which is equivalent to k_{int} in the present study. The equivalent length of the limb is L_{eq}, and its mass is m. *Note.* Modified figure from *Information, natural law, & the self-assembly of rhythmic movement* (p. 210), by P. N. Kugler and M. T. Turvey, 1987, Hillsdale, NJ: Erlbaum. Copyright 1987 by Lawrence Erlbaum Associates. Reprinted by permission.

nant frequency of the whole muscle–limb system. In a follow-up article, Bingham, Schmidt, Turvey, and Rosenblum (1991) assumed that the preferred frequency corresponded to the resonant frequency of the hybrid model to calculate the stiffness of the wrist joint. They showed that the estimated stiffness increased with the equivalent length of the wrist–pendulum system.

Holt, Hamill, and Andres (1990) performed an experiment in which subjects were asked to walk comfortably wearing ankle weights of different masses. They showed that the preferred frequency was proportional to the square root of the reciprocal of the equivalent length of the swinging leg. The preferred frequency was not predicted exactly by the resonant frequency of the pendular leg, however, but was consistently higher by a factor of about $\sqrt{2}$. Again, Holt and his colleagues attributed this discrepancy to the stiffness of the hip joint. Interestingly, Kugler and Turvey (1987; Turvey, Schmidt, Rosenblum, & Kugler, 1988) took previously collected data on the walking frequencies of several mammalian quadrupeds and showed that these walking frequencies scaled linearly with the square root of the reciprocal of the equivalent length of the leg, but these frequencies were higher than predicted by the same factor of $\sqrt{2}$. Moreover, this factor changed for different quadrupedal gaits, being $\sqrt{7}$ for the trot and $\sqrt{10}$ for the canter. That is, the elasticity of the muscles and tendons may increase the resonant frequency of the system by various factors, depending on the particular gait used.

Nevertheless, it remains only an assumption based on the hybrid spring–pendulum model that the stiffness of the joint accounts for the discrepancy between the preferred frequency and resonant frequency of the limb. The stiffness of the joint and the resonant frequency of the whole system have not been determined empirically, but one must do so to test the hybrid model. The present experiment was performed to do just that.

In this experiment, we asked subjects to oscillate their freely hanging arms (i.e., forearms) about the elbow joint in the vertical plane under various added mass and external spring-loading conditions. We performed the experiment to answer three questions. First, how does the preferred frequency chosen by subjects relate to the resonant frequency of the musculoskeletal system? If the preferred frequency is higher than the resonant frequency of the pendular limb alone, does the internal stiffness of the joint account for the discrepancy? Second, is the stiffness of the joint modulated as a function of external loading? Third, how does the amplitude corresponding to the preferred frequency vary with the resonant amplitude?

Method

Subjects

One group of 5 male, graduate students from Brown University was paid to participate in two identical sessions, each lasting about 1½ hours.

Design

A 3 × 4 within-subject design varied added mass and external spring stiffness. We used a weighted wrist cuff to define three levels of added mass: 0 kg (0 lb), 2.27 kg (5 lb), and 4.55 kg (10 lb). Four levels of external spring stiffness were created by attaching metal springs to a second wrist cuff: 0 N/m, 47.34 N/m, 94.68 N/m, and 142.02 N/m.[1] The three dependent variables were (a) the preferred frequency of oscillation; (b) the amplitude of oscillation, which is defined as the full angular excursion of the arm from peak to corresponding trough; and (c) the relative phase between the limb displacement and the joint torque. We made measurements of relative phase at several frequencies about the preferred frequency to estimate the resonant frequency of the muscle–limb complex and the internal joint stiffness (phase transfer method).

Apparatus

Kinematic and electromyographic data were collected. We used a BTS Elite motion analysis system to record the kinematics of the oscillating arm. Infrared reflectors were attached to the distal end of the arm near the wrist joint, to the elbow joint, and to the proximal end of the upper arm near the shoulder joint. Infrared signals were reflected off these three markers, received by two cameras, digitized at 100 Hz, and tracked by computer, using a two-link model of the arm. EMG recordings were made by using two sets of bipolar gold-plated surface electrodes (0.48 in. in diameter) placed over the belly of the biceps and the lateral head of the triceps. These EMG signals were amplified and bandpass filtered between 10 Hz and 3000 Hz, using two Grass EEG amplifiers. The output from the amplifiers was low-pass filtered (3db fall-off at 85 Hz), using an anti-aliasing Bessel filter[2] and digitized at 500 Hz, using a 12-bit A/D converter. Data were collected and analyzed on a Gateway 386 microcomputer.

Procedure

At the beginning of the first experimental session, the subject was asked about age and handedness and was weighed. We measured the length of the arm and hand as well as the circumference of the limb in 5-cm intervals to estimate the moment of inertia of the limb. The volume of the limb was measured by immersing the arm and hand into a graduated cylinder of water and measuring the displacement of liquid. Then, the two sets of electrodes were taped onto the dominant arm. Finally, the subject was asked to sit next to the experimental apparatus and place his arm onto a cushioned arm rest (see Figure 2). The arm rest supported the distal end of the upper arm so that it was fully adducted and extended 90° from the vertical.

Five trials were run in each condition: one *preferred* trial followed by four *synchronizing* trials. The 12 conditions were presented once in the first session and replicated in the second session in a different random order. In the preferred

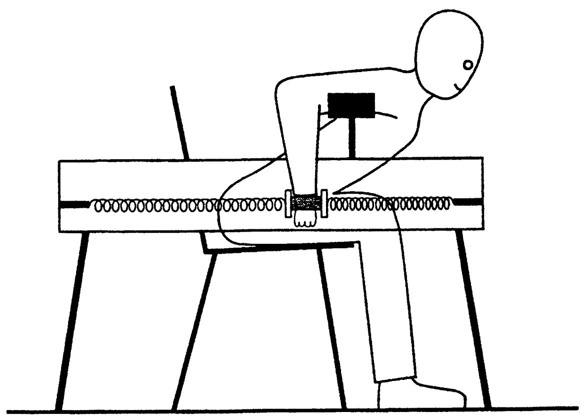

FIGURE 2. A picture of the side view of the experimental apparatus, with a subject swinging his arm.

trials, the subject was asked to swing his arm about the elbow joint at low and high frequencies before settling on a frequency that was most comfortable, whereupon an 8-s data sample was collected. On the synchronizing trials, the subject had to swing his arm in synchrony with a metronome that oscillated at rates approximately 5% and 10% below and above the preferred frequency. As soon as the subject reported that he was moving in synchrony, an 8-s data sample was collected. No instructions were given as to the amplitude of swinging except that subjects were to keep the arm within the bounds of the apparatus. This insured that amplitudes were kept less than 40° so that the arm could be modeled as a linear pendulum (Seto, 1964). Subjects were instructed not to watch the arm oscillate.

Anthropometric Parameters

To test the various theoretical models, we needed to accurately estimate the mass, center of mass, and moment of inertia of the arm and hand. The center of mass of the arm was estimated by Dempster (1955) as 67.7% of the full distance from the elbow to the fingertips, which, as Hatze (1980) argued, is a relatively invariant property. The mass of the arm, on the other hand, varies quite a bit from individual to individual, so information particular to each subject had to be used. We used the immersion method to estimate the volume of the arm. By using an averaged estimate of arm-tissue density of 0.0011 kg/cm^3 (Dempster, 1955), the mass was computed. We measured the moment of inertia by modeling the arm and hand as a series of disks, each 5-cm thick (Hatze, 1975). We calculated and added together the moments of the disks to determine the moment of inertia of the arm and hand, as follows:

$$I = \sum_i m_i (r_i^2/4 + d_i^2), \tag{4}$$

where m_i is the mass, r_i is the radius, and d_i is the distance from the elbow joint of the ith disk. The mass of each of the disks was calculated by multiplying the mass density of the arm by the volume of the disk.

Phase Transfer Method

The phase transfer method is a technique by which the resonant frequency of a second-order, linear system can be determined. For such a system, the relative phase between input and output signals versus the forcing frequency (the phase transfer function) crosses 90° phase at the undamped resonant frequency of the system. For the hybrid spring–pendulum model, the phase of the displacement of the limb lags that of the sinusoidal force by 90° at the resonant frequency of the system, regardless of mass, length, stiffness, or viscosity. The force–velocity properties of the muscles can be considered a form of viscosity that will affect the relative phase between the displacement of the limb and the force at resonance. They will have no affect on the relative phase at the undamped resonant frequency, however. Once the resonant frequency of the muscle–limb complex is known, one can use Equation 3 to compute the stiffness of the joint. Moreover, one can use the slope of the phase transfer function near resonance to compute the viscosity of the joint.

Viviani et al. (1976) used this method to estimate the stiffness of the elbow joint during voluntary oscillations in the vertical plane. They plotted the phase transfer function at forcing frequencies ranging from 0.5 Hz to 5 Hz and fit the data by using the functional form of the second-order phase transfer function. The theoretical fit failed to match the experimental relative phase points at frequencies above 2 Hz, suggesting that the system cannot be described as a second-order, linear, time-invariant system at higher frequencies. In the current experiment, oscillation frequencies were below 2 Hz, so linearity is a reasonable assumption.

This phase transfer method for determining stiffness has the advantage that it does not disrupt the movement, unlike quasi-static perturbation methods (Feldman, 1980) and time-varying system identification techniques (Bennett et al., 1992; Lacquaniti, Borghese, & Carrozzo, 1992; Latash 1992; Latash & Gottlieb, 1990, 1991; Soechting, Dufresne, & Lacquaniti, 1981). This may be particularly important for preferred movements. On the other hand, it has the disadvantage that it lacks the temporal resolution that other techniques have. That is, it can provide only estimates of average stiffness over a set of trials, not detailed information about temporal variations of this property within a cycle of oscillation. It has been shown that joint stiffness can vary by as much as a factor of five under target-to-target oscillatory movements (Bennett et al., 1992; Latash, 1992). However, in our study we were not interested in detailed variations in internal stiffness over the cycle. We were concerned with the time average of the stiffness over the cycle. The other disadvantage is that the method estimates one resonant frequency and, therefore, one stiffness value by using a number of different frequencies. It is known that average stiffness increases with movement frequency.[3]

To apply the phase transfer method in the present experiment, we estimated the relative phase between the net muscular torque and the displacement of the arm at a number of forcing frequencies. Figure 3 shows an example of the raw data used to compute the relative phase at one frequency: the angular displacement of the arm, the sinusoidal fit of the net muscular activity, and the raw biceps and triceps EMG signals. To compute the phase of the net muscular torque, we performed a series of transformations on the digitized EMG signals from the biceps and triceps. First, the two digitized EMG signals were rectified and low-pass filtered, using a 20-ms window, which was found not to introduce any phase shift. Second, each EMG signal was normalized to its maximum voltage value. Third, an average EMG cycle was generated by binning the voltages into 12 temporal bins, each with a duration of 1/12 of the period of oscillation as computed from the displacement of the arm. This gave a better estimate of the phase because it pooled data over several cycles that occurred during the 8-s sample. Fourth, we subtracted the average, normalized triceps EMG cycle from the average, normalized biceps EMG cycle to generate a signal representing the net muscular activity.[4]

Fifth, a six-component Fourier synthesis was performed on the net muscular activity, using the 12-ordinate scheme (Whittaker & Robinson, 1929; see Figure 3B). The average frequency measured from the angular displacement data[5] was used as the fundamental frequency in the Fourier synthesis. Taking the arc tangent of the ratio of the fundamental sine to fundamental cosine coefficients, the phase was computed. Moreover, we could measure, as follows, the harmonic distortion to see how well the EMG signals fit a sinusoid with a frequency corresponding to the fundamental:

$$\mathit{Distortion} = \sum_{i=2}^{6} (a_i^2 + b_i^2)/(a_1^2 + b_1^2), \tag{5}$$

where a_i and b_i are the ith sine and cosine coefficients, respectively (Viviani et al., 1976).[6] Sixth, we corrected for the phase lags introduced by the analog, anti-aliasing filter and amplifier's band-pass filters. The anti-aliasing Bessel filter had a linear phase transfer function and so introduced a constant time lag of about 4 ms, whereas the amplifier's band-pass filter introduced a time lag that depended on the frequency.

Finally, the net muscle activity phase leads the net muscle torque, so an additional correction was estimated from measurements made by Soechting and Roberts (1975).[7] They asked subjects to voluntarily modulate isometric tension at amplitudes of about 10 to 20% of the mean. Two different mean tension levels were used for each subject, yet

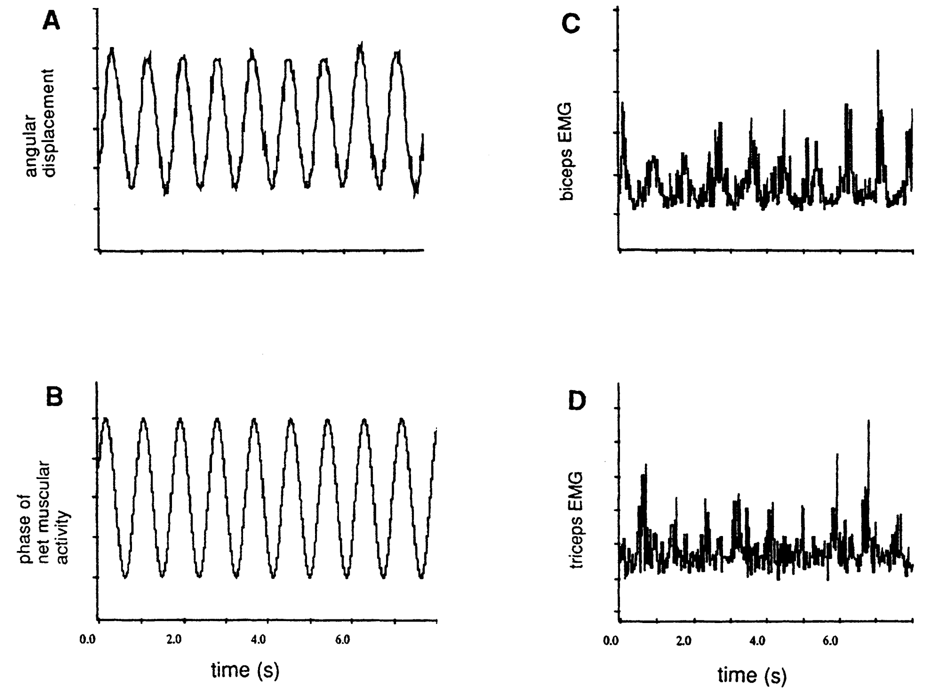

FIGURE 3. Time series plots used to compute the relative phase. **A**. The plot of the angular displacement of the arm. **B**. The phase of the net muscular activity represented as a sinusoidal function, based on the fundamental component of a Fourier synthesis of the difference between the biceps and triceps EMG signals. **C**. The rectified and integrated EMG signals from the biceps muscle. **D**. The rectified and integrated EMG signals from the lateral head of the triceps muscle.

no significant difference in the relative phase was found. We fit logarithmic curves to the biceps and triceps EMG-to-torque phase data between the frequencies of 1 and 2 Hz: Phase = –50.86 – (42.23)ln(frequency) for the biceps, and phase = –57.68 – (39.32)ln(frequency) for the triceps. For both muscles, the relative phase between the EMG signal and the isometric torque varied from about –50° at 1 Hz to about –80° at 2 Hz. On the other hand, the relative phase between the net muscular torque and angular displacement of the arm estimated in the present experiment varied considerably as a function of frequency. These two components of relative phase are plotted in Figure 4. Notice how the EMG-to-torque phase transfer functions are relatively flat as compared with the torque-to-displacement phase data.

For each subject in each condition and each session, a phase transfer function was found by plotting the relative phase versus the frequency of oscillation. Each phase transfer function consisted of five points, one corresponding to the preferred trial and four corresponding to the synchronizing trials, and a least-squares regression line was fit to these five points (see Figure 5). Because we were using a small range of frequencies about the preferred frequency, a linear approximation to the second-order phase transfer function was justified. We adopted a criterion of $r^2 = .3$ for an estimate to be included in the subsequent analysis. Only four conditions were dropped for failing to meet this criterion, two for Subject 3, one for Subject 4, and one for Subject 6 in both sessions. Over 30% of the conditions had $r^2 \geq .8$. Over 60% had $r^2 \geq .5$.

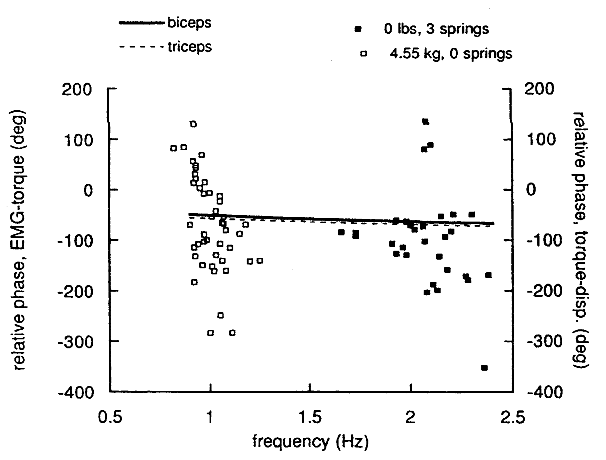

FIGURE 4. A plot of the two components of relative phase that make up the relative phase between the EMG signal and the displacement of the arm measured in this experiment. The EMG-to-torque relative phase curves for the biceps (solid line) and triceps (dashed line) were based on measurements by Soechting and Roberts (1975) under isometric conditions. The torque-to-displacement relative phase data were so scattered because they represented data from all 5 subjects in both sessions in the 4.55-kg, no-springs condition (hollow squares) and in the no-mass, 3-springs condition (solid squares). Notice that a number of phase points fall above the 0° phase level and below the –180° level. This would not occur in a simple, second-order, linear system. One reason for these extreme phase values may be the fact that the biceps signal often exhibited biphasic activity within a cycle. This would have affected the phase estimates.

Estimating Internal Joint Stiffness

To compute the internal joint stiffness, we plugged the resonant frequency into Equation 6, which is a modification of Equation 3, such that the stiffness term of the external springs, $k_{ext}L^2$ was added, as follows, to the equation[8]:

$$k_{int} = \omega_r^2 I - mgl_{cm} - k_{ext}L^2. \qquad (6)$$

Results

Preferred Frequency

Subjects reliably reproduced their preferred frequencies in all conditions, as is evident from the correlation between the first- and second-sessions' preferred frequencies, $r^2 = .90$. A paired t test on the difference in preferred frequency between Session 1 and Session 2 was not significant.

The mean preferred frequency for each added mass and external stiffness condition appears in Figure 6. A two-factor analysis of variance (ANOVA) on preferred frequency revealed significant main effects of external spring stiffness, $F(3, 12) = 271, p < .001$, added mass, $F(2, 8) = 83.87, p < .01$, and a spring–mass interaction, $F(6, 24) = 19.77, p < .001$.

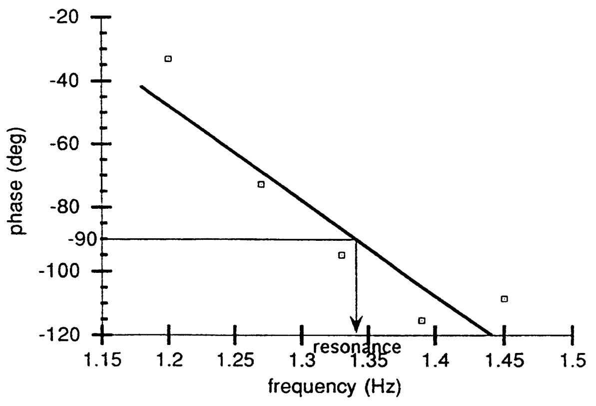

FIGURE 5. A plot and regression line ($r^2 = .89$) of relative phase between the net muscular torque and the displacement of the arm, as a function of oscillation frequency for 1 subject in one session in the 2.27-kg, 2-springs condition. To be consistent with the conventions of Viviani et al. (1976), we allowed a negative relative phase to correspond to a phase lag in the displacement relative to the force and a positive relative phase to correspond to a phase lead. The regression line is, therefore, negatively sloped as frequency increases.

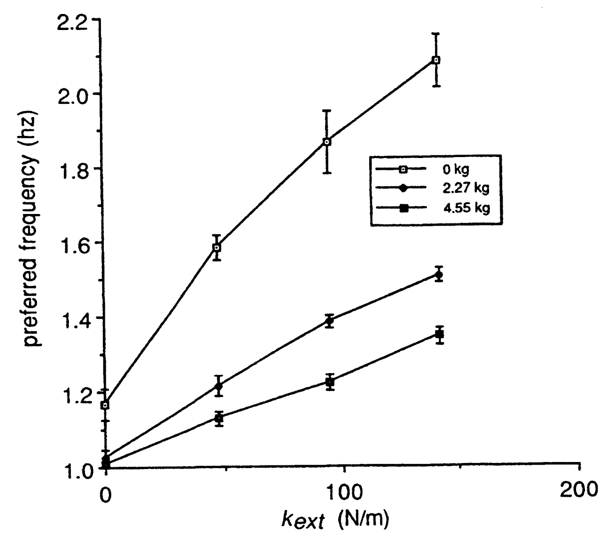

FIGURE 6. A plot of the preferred frequency as a function of external spring condition for each of the three added mass conditions. Data are pooled across sessions and subjects.

Preferred frequency increased with external stiffness and decreased with external mass, as predicted by Equation 3.

The ANOVA was based on a linear statistical model; therefore, an additional two-factor ANOVA was conducted on the squared preferred frequencies, because according to the theory represented in Equation 3, mass and stiffness both fall within a common square root. To linearize this equation, one must square both sides. Again, highly significant main and interaction effects were observed, findings that were consistent with Equation 3.

Resonant Frequency of the Muscle–Limb Complex

The correlation between the resonant frequency of the muscle–limb complex measured in Sessions 1 and 2 was high, $r^2 = .710$. A paired t test showed no reliable difference between sessions. These results supported the reliability of the method by which the resonant frequency was estimated.

Mean resonant frequency of the muscle–limb complex is plotted for each condition in Figure 7. An ANOVA on resonant frequency revealed main effects of added mass, $F(2, 8) = 10.03$, $p < .005$, and external spring, $F(3, 8) = 8.44$, $p < .01$, and a significant interaction, $F(6, 20) = 2.80$, $p < .05$.[9]

Preferred Frequency Versus Resonant Frequency

A linear regression of the preferred frequency on the resonant frequency of the limb alone, modeled as a pendulum without joint stiffness (Equations 1 and 2), resulted in a slope of 2.07 and a y intercept of -1.2, $r^2 = .988$ (see Figure 8A). The correlation was high, and, yet, the preferred frequency was consistently higher than the resonant frequency.

A linear regression of preferred frequency on resonant frequency of the muscle–limb complex, modeled as a hybrid spring–pendulum, was highly significant, $r^2 = .866$, and, more important, the slope of the regression line was 1.096, which is closer to 1.00, and the y intercept was -0.22, which is closer to zero (see Figure 8B). The resonant frequency of the muscle–limb complex incorporating joint stiffness thus more closely predicts the preferred frequency than does the resonant frequency of the limb alone. The decrease in the correlation coefficient was a result of noise in the estimates of muscle–limb resonant frequency, which was absent in calculating the resonant frequency of the limb alone.

Internal Joint Stiffness

A correlation between the estimates of internal joint stiffness, k_{int}, in Session 1 and Session 2 yielded $r^2 = .402$, which implies moderate reliability. A paired t test showed no reliable difference in stiffness values between sessions.

The mean joint stiffness in each condition is plotted in Figure 9A, which shows a linear increase in internal joint stiffness as external spring stiffness increased. On the other hand, added mass did not systematically affect joint stiffness. A two-factor ANOVA revealed a main effect of added springs, $F(3, 8) = 4.07$, $p < .05$, but no main effect of added mass nor an interaction.

A linear regression of mean joint stiffness as a function of external spring stiffness (measured in torsional units) was performed by collapsing joint stiffnesses across subjects and added mass conditions (see Figure 9B). A perfect linear relationship was observed (i.e., $r^2 = 1.00$), with a slope of .41 and a y intercept of .743. We computed the external torsional stiffnesses by multiplying the external spring stiffness (mea-

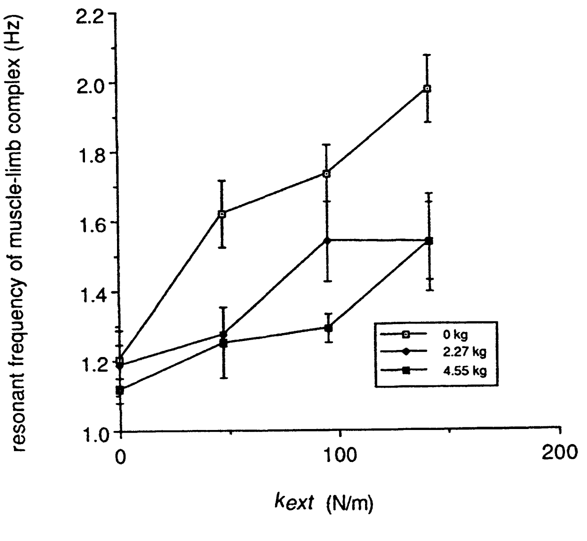

FIGURE 7. Plots of the resonant frequencies of the muscle–limb complex versus the external spring condition for each of the added mass conditions.

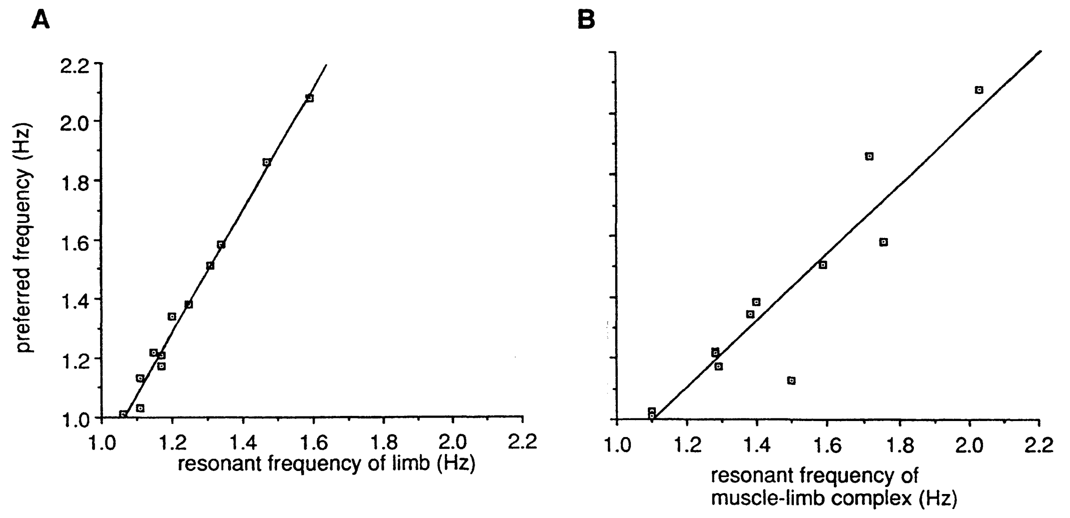

FIGURE 8. **A.** A scatter plot and regression between the preferred frequency and resonant frequency of the pendular limb, pooled over sessions and subjects. **B.** A scatter plot and regression between the preferred frequencies and the resonant frequencies of the muscle–limb complex, pooled across sessions and subjects.

sured in linear units) by the squared length of the subjects' arms and then averaging over all 5 subjects to get a single value for each external spring condition.

Amplitude

The mean amplitude measured in the preferred trials under each condition is plotted in Figure 10. A moderately strong correlation between amplitudes in Session 1 and Session 2 was observed, $r^2 = .388$. A paired *t* test showed no difference in amplitude between Sessions 1 and 2. A two-way ANOVA on amplitude demonstrated main effects of external spring stiffness, $F(3, 12) = 33.59$, $p < .001$, added mass, $F(2, 8) = 7.87$, $p < .05$, and an interaction, $F(3, 12) = 2.70$, $p < .05$. Amplitude decreased monotonically with increasing spring stiffness for each of the mass conditions.

The same mean amplitudes are plotted against preferred frequency in Figure 11A. It is evident that the amplitude varied inversely with the preferred frequency. According to the theoretical amplitude transfer function, the amplitude at resonance depends on the stiffness and inertia of the physical system in the following manner (assuming a constant forcing amplitude):

$$A_r \propto \sqrt{I/(k_{int} + k_{ext}L^2 + mgl_{cm})}\ , \tag{7}$$

where A_r is the amplitude at resonance, I is the moment of inertia about the axis of rotation, k_{int} and k_{ext} are the internal joint and external spring stiffnesses, L is the physical length of the system, m is its mass, g is gravitational acceleration, and l_{cm} is the distance from the axis of rotation to the center of mass. A log–log plot of measured amplitude versus the ratio of I to the quantity $k_{int} + k_{ext}L^2 + \mathrm{mg}l_{cm}$ shows a linear relationship, $r^2 = .71$, with a slope of .45, which is very close to .5, as predicted by Equation 7 (see Figure 11B).

Discussion

These results provide the first direct evidence that the preferred rate of rhythmic movement corresponds to the resonant frequency of the system, as proposed by Kugler and Turvey (1987) in their hybrid spring–pendulum model. Subjects adopted a preferred rate of oscillation of the arm that agreed with the resonant frequency of the muscle–limb complex, which was empirically estimated. This result has significant implications for the control of rhythmic behavior. In particular, it indicates that the timing of preferred oscillatory movements is not simply dictated by the central nervous system but is constrained by the dynamics of the musculoskeletal system.

This suggests that any central timing process, such as a neural oscillator, is not acting as an extrinsic timekeeper to drive the peripheral segments but must be reciprocally modulated by information about the dynamics of the periphery. Preferred motor timing emerges from the interaction of central and peripheral components, rather than from being dictated by either. Presumably, proprioceptive information about variables such as the muscular force required to drive the limb at different frequencies reciprocally influences any potential neural oscillator. Recall that the hybrid spring–pendulum model is a forced, linear system that exhibits no preferred states. Making the forcing frequency dependent upon proprioceptive feedback renders the system autonomous, however, such that the resonant frequency may be preferred and stable as well as efficient (see Hatsopoulos, 1992, 1995, and Hatsopoulos, Warren, & Sanes, 1992, for a neural model of such behavior). Proprioceptive information

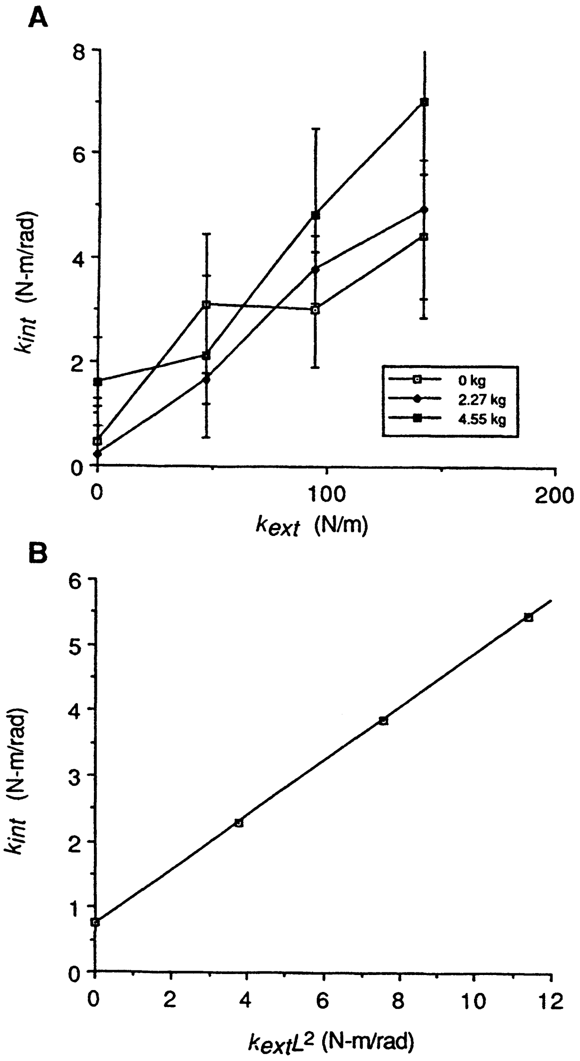

FIGURE 9. A. Plots of internal joint stiffness versus external spring condition for each added mass condition, pooled across sessions and subjects. **B.** A scatter plot and regression between internal joint stiffness and external spring stiffness, pooled across sessions, subjects, and added mass condition. External spring stiffness is represented as torsional stiffness so that its values can be easily compared with those of the internal joint stiffness.

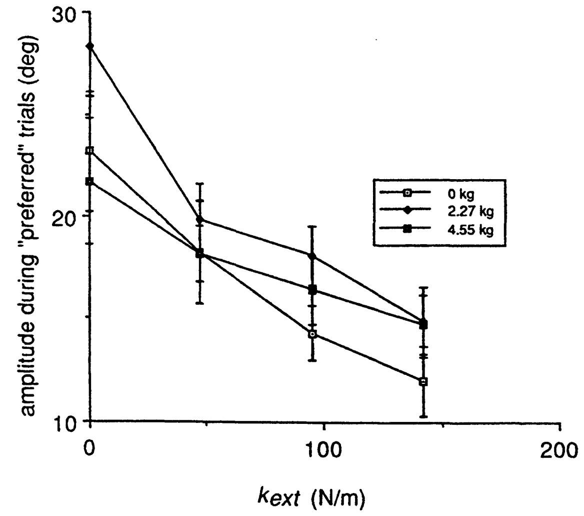

FIGURE 10. A plot of amplitude during preferred trials versus external spring condition, pooled over sessions and subjects.

couples the physical limb to the nervous system. The physical limb becomes, therefore, part of a larger autonomous dynamical system with no explicit time dependence. On this account, the preferred frequency of rhythmic behavior is a product of the intrinsic timing of an autonomous system rather than extrinsic timing of a central clock.

The second major finding of the study is that joint stiffness increased linearly with external spring stiffness but did not vary as a function of added mass. This indicates that the actor has some degree of control in modulating its internal stiffness, as has previously been shown (Cannon & Zahalak, 1982; Feldman, 1980; Greene & McMahon, 1979; Oguztöreli & Stein, 1991). Why do subjects choose to increase the stiffness of the joint as external stiffness increases? After all, increasing joint stiffness involves an increase in contraction of either agonist or antagonist muscles or an increase in cocontraction, all of which are metabolically costly. In fact, the mean EMG activity of either biceps or triceps muscles increased by as much as a factor of 2 from the no-spring condition to the three-spring condition for 2 of the subjects tested. However, maximum energy can be transferred to a load if the impedance of the load (the muscles and tendons) is matched to the impedance of the source (the external springs) (Ogata, 1970). Goldfield, Kay, and Warren (1993) provided indirect evidence that such an impedance-matching strategy is used by bouncing infants. Furthermore, in the context of discrete movements, Hasan (1986) provided theoretical and experimental evidence that increasing joint stiffness may be more cost efficient for short-duration movements. Impedance matching may be a rather general principle of biological motor control.

It is unclear why internal joint stiffness did not vary with added mass. Mass is unique because it has two opposite effects. On the one hand, it affects the force of gravity (gravitational mass) whose component in the direction of equilibrium is a force in phase with the displacement. On the other hand, mass affects the inertial force (inertial mass) which is 180° out of phase with the displacement.

The observed values of joint stiffness were rather low when compared with other estimates during voluntary oscillations in the horizontal plane (6 N-m/rad to 22 N-m/rad estimated by Latash, 1992) and in the vertical plane (average stiffness of 25 N-m/rad estimated by Viviani et al.,1976;

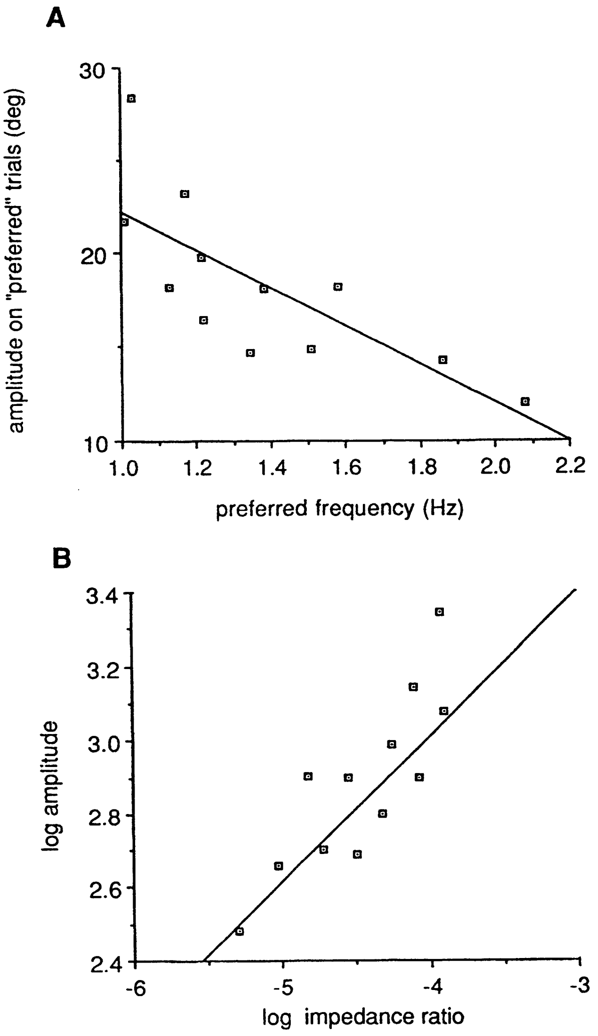

FIGURE 11. A. A plot of amplitude during preferred trials versus preferred frequency, pooled over sessions and subjects. **B.** A plot of the natural log of amplitude versus the natural log of the ratio of I to $k_{int} + k_{ext}L^2 + mgl_{cm}$, which we defined as the impedance ratio.

2 N-m/rad to 18 N-m/rad estimated by Bennett et al., 1992). What accounts for this discrepancy? There are two very important differences between the procedure of the present experiment and the one used in these other studies. First, our subjects were tested near their preferred frequency of oscillation, whereas subjects in the other studies were instructed to move at predetermined frequencies that were generally higher. This reflects the difference in the focus of the present experiment. We were primarily interested in comparing the preferred frequency with the resonant frequency of the system, and estimates of joint stiffness were of secondary importance. Second, subjects were not given any instructions as to the amplitude of oscillation, whereas subjects in the other studies moved between two targets. In addition, it is known that joint stiffness increases linearly with muscle torque (Bennett, 1993). For a given movement frequency, the muscle torques required in this experiment may have been lower than those in other studies.

The third finding is that the amplitude of oscillation in preferred trials varied inversely with the preferred frequency, in accordance with Equation 7. This inverse relationship between amplitude and frequency (or speed) is consistent with much data on other motor tasks, including arm, wrist, and finger oscillations in the horizontal plane (Feldman, 1980; Kay et al., 1991; Kay, Kelso, Saltzman, & Schöner, 1987; Kelso et al., 1981; Rosenbaum et al., 1991; Wallace, 1989). Kugler, Turvey, Schmidt, and Rosenblum (1990) postulated the existence of an "adiabatic" invariant (Ehrenfest, 1917/1959) in their study of a wrist–pendulum task, which predicts a nonmonotonic, convex relationship between amplitude and frequency. Using this relationship, they were able to predict individual differences in amplitude–frequency data. Interestingly, the power relationship predicted by Equation 7 is similar to the high-frequency portion of the nonmonotonic relationship proposed by Kugler and his colleagues (Kugler et al., 1990).

We used added mass and external springs in this experiment to manipulate the resonant frequency of the system. But the experimental loads are also representative of massive and viscoelastic loads that actors must adapt to in the course of various tasks in the environment. For example, massive loads include implements such as hammers and axes, tennis rackets and golf clubs, and one's own body when on a swing or pogo stick. Examples of viscoelastic loads include stringed instruments, springy levers, pogo sticks, and any compliant object that is pushed or pulled. The ground surface is a viscoelastic load in series with the body, and humans adjust their gait patterns and step frequencies to surfaces such as rubber, sand, and snow (McMahon, 1984). In general, any environmental object that exerts a force proportional to displacement or velocity will have an associated resonant frequency that, if sensed, can be exploited in the control of action. When rocking a car that is stuck in the snow, for example, we take advantage of the resonant frequency of the vehicle to generate large amplitude movements.

In sum, these experimental findings support a view that we believe has important implications for a general theory of motor control. They indicate that one senses and exploits the resonances of the musculoskeletal system to establish the frequency and amplitude of rhythmic movement. Thus, the physical dynamics provide constraints or anchoring points around which motor behavior is organized.

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NOTES

1. Stiffness was increased by adding more springs in parallel. The 0-N/m condition had no springs, the 47.34-N/m condition had one spring on each side of the wrist, the 94.68-N/m condition had

two springs on each side, and the 142.02-N/m condition had three springs on a side.

2. The use of such a low cut-off frequency was justified because this study was concerned with the phasing of muscular contraction at frequencies below 2 Hz.

3. Latash (1992) estimated less than a 5% and 7% increase in average stiffness with a 10% increase in frequency at 1 Hz and 2 Hz, respectively. Unlike Viviani et al. (1976), who used a very large range of frequencies, we used frequencies only 5 and 10% above and below the preferred frequency. Therefore, we expected at most a 7% increase or decrease in average stiffness within one of our conditions, which corresponds to a 1% increase or decrease in resonant frequency in the worst case. For the most part, this was smaller than the change in resonant frequency across loading conditions. Moreover, this small variation should affect only the slope of the measured phase transfer function but not the frequency at which it crosses the 90° phase level.

4. Technically, the brachialis and brachioradialis muscles might contribute to flexor activity. The motor task was set up so that the biceps was the primary flexor muscle by having an average elbow joint angle of about 90° (Kapandji, 1970).

5. The peaks in the angular displacement time series were chosen so that we could estimate the average frequency over the trial.

6. In some trials, a nearly biphasic pattern of activity was observed in the biceps during a complete cycle, which resulted in sinusoidal fits with rather high harmonic distortions. Near the beginning of flexion, there was a burst of activity in the biceps, as expected. However, near the end of extension, a somewhat sharper and stronger biceps burst occurred at about the same time as the triceps burst. This suggests an increase in joint stiffness near the end of extension. Despite this pattern in the EMG activity, we performed the phase analysis but discarded those trials with harmonic distortions greater than approximately 2.00. Seventy percent of the harmonic distortions fell within 0.7 to 2.0. Although this range of harmonic distortions was rather high, it was not unexpected, considering that we had not instructed subjects to generate pure sinusoidal modulations in muscle activity, even if that were possible. Such high harmonic distortions would be expected to affect the reliability of the phase estimates of net muscular torque but would not introduce a bias.

7. The phase data of Soechting and Roberts (1975) were nearly identical below 2 Hz to two other studies that used sinusoidal stimuli. Crochetiere, Vodovnik, and Reswick (1967) used sinusoidal, amplitude-modulated electrical pulse trains to record the EMG-to-torque phase relationship in biceps muscle. Cogshall and Bekey (1970) asked subjects to voluntarily modulate muscular force to measure the phase transfer function in triceps muscle. For 1 of their subjects, tension amplitudes were roughly 50% of the mean tension. The fact that those two studies estimated phase transfer functions that were very similar to the data of Soechting and Roberts within the frequency range in question, despite methodological differences, suggests to us that these EMG-to-torque phase corrections were reliable and robust and, therefore, appropriate in our experimental setting.

8. L is the physical length of the arm. The factor L^2 converts the stiffness of the springs to torsional units, N-m/rad.

9. The degrees of freedom of the error term was decreased from 12 to 8 because 4 stiffness values in both sessions were missing as a result of low correlation coefficients in the linear regressions. By assuming no interaction, a statistical method can provide reasonable estimates of these missing data points (Myers, 1979)

REFERENCES

Bennett, D. J. (1993). Torques generated at the human elbow joint in response to constant position errors imposed during voluntary movements. *Experimental Brain Research, 95,* 488–498

Bennett, D. J., Hollerbach, J. M., Xu, Y., & Hunter, I. W. (1992). Time-varying stiffness of the human elbow joint during cyclic voluntary movement. *Experimental Brain Research, 88,* 433-442.

Bernstein, N. A. (1967). *The coordination and regulation of movements.* London: Pergamon Press.

Bingham, G. P., Schmidt, R. C., Turvey, M. T., & Rosenblum, D. L. (1991). Task dynamics and resource dynamics in the assembly of a coordinated rhythmic activity. *Journal of Experimental Psychology, 17,* 359–381.

Cannon, S. C., & Zahalak, G. I. (1982). The mechanical behavior of active human skeletal muscle in small oscillations.*Journal of Biomechanics, 15,* 111–121.

Coggshell, J. C., & Bekey, G. A. (1970). Emg-force dynamics in human skeletal muscle. *Medical and Biological Engineering, 8,* 265–270.

Creelman, C. D. (1962). Human discrimination of auditory duration. *Journal of the Acoustical Society of America, 34,* 582–593.

Crochetiere, W. J., Vodovnik, L., & Reswick, J. B. (1967). Electrical stimulation of skeletal muscle. A study of muscle as an actuator. *Medical and Biological Engineering, 5,* 111–125.

Dempster, W. T. (1955). Space requirements of the seated operator. *WADC TR 55-159.* Wright Patterson Air Force Base, Ohio.

Ehrenfest, P. (1959). Adiabatic invariants and the theory of quanta. Collected scientific papers. Amsterdam: North-Holland. (Reprinted from *Proceedings of the Amsterdam Academy,* 1917, *19,* 576–597.)

Hatze, H. (1975). A new method for the simultaneous measurement of the moment of inertia, the damping coefficient, and the location of the centre of mass of a body segment Ehrenfest, P. (1959). *Collected scientific papers.* Amsterdam: North Holland.

Feldman, A. G. (1980). Superposition of motor programs. 1. Rhythmic forearm movements in man. *Neuroscience, 5,* 81–90.

Gibbon, J., Church, R. M., & Meck, W. H. (1984). Scalar timing in memory. In J. Gibbon & L. G. Allan (Eds.), *Annals of The New York Academy of Sciences: Timing and time perception* (pp. 52–77). New York: New York Academy of Sciences.

Goldfield, E. C., Kay, B. A., & Warren, W. H., Jr. (1993). Bouncing babies: The assembly and tuning of action systems. *Child Development, 54,* 1128–1142.

Greene, P. R., & McMahon T. A. (1979). Reflex stiffness of man's anti-gravity muscles during kneebends while carrying extra weights. *Journal of Biomechanics, 12,* 881–891.

Hasan, Z. (1986). Optimized movement trajectories and joint stiffness in unperturbed, inertially loaded movements. *Biological Cybernetics, 53,* 373–382.

Hatsopoulos, N. G. (1992). *The coupling of neural and physical dynamics in motor control.* Unpublished doctoral dissertation, Brown University, Providence, RI.

Hatsopoulos, N. G. (in press). Coupling the neural and physical dynamics in rhythmic movements. *Neural Computation.*

Hatsopoulos, N. G., Warren, W. H., & Sanes, J. N. (1992). A neural pattern generator that tunes into the physical dynamics of the limb system. *International Joint Conference on Neural Networks '92, Baltimore MD, 1,* 104–109.

Hatze, H. (1975). A new method for the simultaneous measurement of the moment of intertia, the damping coeffieient, and the location of the centre of mass of a body *in situ. European Journal of Applied Physiology, 34,* 217–226.

Hatze, H. (1980). A mathematical model for the computational determination of parameter values of anthropomorphic segments. *Journal of Biomechanics, 13,* 833–843.

Hildreth, E. C., & Hollerbach, J. M. (1985). *The computational approach to vision and motor control* (A. I. Memo 846, C. B. I. P. Memo 014). Cambridge, MA: Massachusetts Institute of Technology, Artificial Intelligence Laboratory and Center for Biological Information Processing.

Holt, K. G., Hamill, J., & Andres, R. O. (1990). The force-driven harmonic oscillator as a model for human locomotion. *Human Movement Science, 9,* 55–68.

Kapandji, I. A. (1970). *The physiology of the joints: Vol. 1. The upper limb.* Edinburgh & London: Churchill Livingstone.

Kay, B. A. (1986). *Dynamic modeling of rhythmic movements: Converging on a description of he component oscillators.* Unpublished doctoral dissertation., University of Connecticut, Storrs.

Kay, B. A., Kelso, J. A. S., Saltzman, E. L., & Schöner, G. (1987). Space-time behavior of single and bimanual rhythmical movements: Data and limit cycle model. *Journal of Experimental Psychology: Human Perception and Performance, 13,* 178–192.

Kay, B. A., Saltzman, E. L., & Kelso, J. A. S. (1991). Steady-state and perturbed rhythmical movements. A dynamical analysis. *Journal of Experimental Psychology: Human Perception and Performance, 17,* 183–197.

Kelso, J. A. S., DelColle, J. D., & Schöner, G. (1990). Action-perception as a pattern formation process. In M. Jeannerod (Ed.), *Attention and performance XIII* (pp. 139–169). Hillsdale, NJ: Erlbaum.

Kelso, J. A. S., Holt, K. G., Kugler, P. N., & Turvey, M. T. (1980). On the concept of coordinative structures as dissipative structures: II. Empirical lines of convergence. In G. E. Stelmach & J. Requin (Eds.), *Tutorials in motor behavior* (pp. 49–70). Amsterdam: North-Holland.

Kelso, J. A. S. , Holt, K. G., Rubin, P., & Kugler, P. N. (1981). Patterns of human interlimb coordination emerge from the properties of non-linear limit cycle oscillatory processes: Theory and data. *Journal of Motor Behavior, 13,* 226–261.

Kelso, J. A. S. & Tuller, B. (1984). A dynamical basis for action systems. In M. S. Gazzaniga (Ed.), *Handbook of cognitive neuroscience* (pp. 319–356). New York: Plenum Press.

Kugler, P. N., Kelso, J. A. S., & Turvey, M. T. (1980). On the concept of coordinative structures as dissipative structures: I. Theoretical lines of convergence. In G. E. Stelmach & J. Requin (Eds.), *Tutorials in motor behavior* (pp. 3–47). Amsterdam: North–Holland.

Kugler, P. N., & Turvey, M. T. (1987). *Information, natural law, and the self-assembly of rhythmic movement.* Hillsdale, NJ: Erlbaum.

Kugler, P. N., Turvey, M. T., Schmidt, R. C., & Rosenblum, R. D. (1990). Investigating a nonconservative invariant of motion in coordinated rhythmic movements. *Ecological Psychology, 2,* 151–189.

Lacquaniti, F., Borghese, N. A., & Carrozzo (1992). Internal models of limb geometry in the control of hand compliance. *The Journal of Neuroscience, 12,* 1750–1762.

Latash, M. L. (1992). Virtual trajectories, joint stiffness, and changes in the limb natural frequency during single-joint oscillatory movements. *Neuroscience, 49,* 209–220.

Latash, M. L., & Gottlieb, G. L. (1990). Compliant characteristics of single joints: Preservation of equifinality with phasic reactions. *Biological Cybernetics, 62,* 331–336.

Latash, M. L., & Gottlieb, G. L. (1991). Reconstruction of shifting elbow joint compliant characteristics during fast and slow movements. *Neuroscience, 43,* 697–712.

McMahon, T. A. (1984). *Muscles, reflexes, and locomotion.* Princeton, NJ: Princeton University Press.

Myers, J. L. (1979). *Fundamentals of experimental design* (3rd ed.). Boston: Allyn & Bacon.

Ogata, K. (1970). *Modern control engineering.* Englewood Cliffs, NJ: Prentice-Hall.

Oguztöreli, M. N., & Stein, R. B. (1991). The effect of variable mechanical impedance on the control of antagonist muscles. *Biological Cybernetics, 66,* 87–93.

Reed, E. S. (1982). An outline of a theory of action systems. *Journal of Motor Behavior, 14,* 98–134.

Rosenbaum, D. A., Slotta, J. D., Vaughan, J., & Plamondon, R. (1991). Optimal movement selection. *Psychological Science, 2,* 86–91.

Schmidt, R. A., Zelaznik, H. N., Hawkins, B., Frank, J. S., & Quinn, J. T. (1979). Motor output variability: A theory for the accuracy of rapid motor acts. *Psychological Review, 86,* 415–451.

Schneider, K., Zernicke, R. F., Schmidt, R. A., & Hart, T. J. (1989). Changes in limb dynamics during the practice of rapid arm movements. *Journal of Biomechanics, 22,* 805–817.

Seto, W. W. (1964). *Theory and problems of mechanical vibrations.* New York: Schaum.

Soechting, J. F., Dufresne, J. R., & Lacquaniti, F. (1981). Time-varying properties of myotatic response in man during some simple motor tasks. *Journal of Neurophysiology, 46,* 1226–1243.

Soechting, J. F. & Roberts, W. J. (1975). Transfer characteristics between EMG activity and muscle tension under isometric conditions in man.*Journal of Physiology (Paris), 70,* 779–793.

Thelen, E. (1990). Coupling perception and action in the development of skill: A dynamic approach. In H. Bloch & B. I. Bertenthal (Eds.), *Sensory-motor organization and development in infancy and early childhood* (pp. 39–56). Dordrecht, The Netherlands: Kluwer.

Turvey, M. T., Schmidt, R. C., Rosenblum, D. L., & Kugler, P. N. (1988). On the time allometry of co-ordinated rhythmic movements. *Journal of Theoretical Biology, 130,* 285–325.

Viviani, P., Soechting, J. F., & Terzuolo, C. A. (1976). Influence of mechanical properties on the relationship between EMG activity and torque. *Journal of Physiology (Paris), 72,* 45–58.

Wallace, S. A. (1981). An impulse-timing theory for reciprocal control of muscular activity in rapid, discrete movements. *Journal of Motor Behavior, 13,* 144–160.

Wing, A. M., & Kristofferson, A. B. (1973). Response delays and the timing of discrete motor responses. *Perception and Psychophysics, 14,* 5–12.

Whittaker, E. T., & Robinson, G. (1929). *The calculus of observation: A treatise on numerical mathematics.* London: Blackie & Sons.

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