

MAINTENANCE TENDENCY IN CO-ORDINATED RHYTHMIC MOVEMENTS: RELATIVE FLUCTUATIONS AND PHASE

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Abstract—Evidence from the oscillatory behavior of fish fins and the crayfish swimmeret system suggests that local rhythmic-pattern generators preserve their characteristic properties over the various locomotory co-ordinations in which they participate. This maintenance tendency, as von Holst termed it, was investigated in an experiment in which human subjects swung, through motions at the wrists, hand-held pendulums of variable mass and length. In the experiment (comprising six sessions over 21 months with the same three subjects) the context for the maintenance tendency was steady-state absolute co-ordination: two rhythmic units oscillating at a single, common period and at a bounded phase relation. The experimental methodology permitted systematic control of (a) the characteristic periods of the individual rhythmic units and (b) the deviations from these periods. Relative fluctuations in periodic timing and amplitude were least when a rhythmic unit's period in absolute co-ordination approximated its characteristic period and increased with departures from the characteristic period. Rates of increase in timing fluctuations were approximately the same for deviations on either side of the characteristic period; the rate of increase in spacing fluctuations was substantially greater for the range in which periods were less than the characteristic period. The phase relation between two co-ordinated rhythmic movement units in absolute co-ordination depended on the difference between their characteristic periods. The intended phase relation of 180° was attained only when the characteristic periods were identical. When the characteristic periods differed, the departure from 180° increased systematically with the difference.

The fluctuation results are discussed in terms of the relation between relaxation and harmonic dynamics in producing rhythmic movements, with particular emphasis on the harmonic tuning of relaxation oscillations. The phase results are discussed in terms of whether or not the very many stable phase relations in absolute co-ordination are reflective of the nervous system or of differences in response latencies in left and right muscle systems induced by different degrees of inertial compensation.

Locomotion is paradigmatic of co-ordinated rhythmic activity. It involves a (possibly large) number of relatively distinct parts of the body gathered into a single functional unit. A widely held opinion is that the rhythmicity of each limb is generated locally. Neurophysiological theories of arthropod and vertebrate walking refer to multiple central rhythmic-pattern generators, at least one per limb^{5,15,19} and possibly one per joint.³ These interconnected local rhythm control centers are modulated by descending tonic neural activity and by each other. Von Holst⁸ chose to use the term automatism for a limb and its local neural source of rhythmic control. His term of choice underscores that the locomotory act is fashioned from interactions among rhythmic units that are independent and self-sufficient.^{4,19}

The interaction among the rhythmic units was referred to by von Holst⁸ as the magnet effect: each rhythmic unit attempts to draw the others to the periodic timing that it exhibits when oscillating alone. Thus, two or more limbs or two or more fins (most of von Holst's work was with fish) of differing preferred periods co-ordinate to settle on a mutual, single period that is between the individually preferred periods. The independent, self-sufficiency of the rhythmic units was referred to by von Holst as the maintenance tendency. Not only does a rhythmic unit

attempt to influence the behavior of other units, but it strives to maintain its characteristic period in the face of the magnet effects of the other rhythmic units.

Three kinds of evidence can be identified for the maintenance tendency. First, whenever one of two coupled rhythmic units is arrested in any way, the other reverts spontaneously to its original, endogenous tempo.⁸ Second, when a rhythmic unit oscillates at a period other than its preferred period, the variance in the duration of the period increases.¹⁴ Third, given two rhythmic units in absolute co-ordination, the unit with the higher characteristic frequency tends to reach the peaks of its cyclic movements before the unit with the lower characteristic frequency.⁸ That is, the inherently faster of two coupled rhythmic units tends to lead in phase with the magnitude of the lead dependent on the size of the difference in the characteristic frequencies.^{16,17} In the coupling of two or more automatisms, von Holst saw the maintenance tendency ("to move at one's own pace") and the magnet effect ("to move at the pace of another") as working in direct opposition. If the maintenance tendency dominated then the co-ordination would be relative—the limbs or fins moving at different tempos. If the magnet effect dominated then the co-ordination would be absolute—the limbs or fins moving at the same tempo. With respect to the latter, however, von Holst⁸ concluded that "the 'struggle' between the

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magnet effect and the maintenance tendency continues in latent form even after attainment of absolute (successful) co-ordination" (p. 65).

The studies to date on the maintenance tendency have been limited to relatively few distinct rhythmic movement units and, therefore, to a restricted number of to-be-maintained characteristic periods. The investigations of von Holst⁸ and Scripture¹⁴ were limited, respectively, to the characteristic periods of individual fins and hands; the investigations of Stein^{16,17} were limited to the degree that the preferred periods of the individual pattern generators associated with the individual swimmerets of *Procambarus clarkii* could be modified by anatomical isolation and electrical stimulation. With respect to the question of how a rhythmic movement unit behaves when absolutely co-ordinated with one or more other rhythmic movement units, the investigations of von Holst and Stein were, of necessity, restricted to a limited number of conditions (couplings) under which a unit's maintenance tendency could be stressed and observed.

A fuller understanding of the maintenance tendency, as indexed by fluctuations and phase, would benefit from a methodology that allows for wide systematic control over (a) the characteristic periods of individual rhythmic units and (b) departures from characteristic periods within the context of stable, absolute, co-ordinations. A methodology introduced by Kugler and Turvey^{9,21} meets these requirements. To begin with, the individual rhythmic movement unit is defined by a hand-held pendulum and the neuromuscular processes by which the pendulum is moved rhythmically about an axis in the wrist at a comfortable tempo. The characteristic period of such a rhythmic unit—a wrist-pendulum system—will be determined primarily by the pendulum's magnitude. Consequently, the systematic variation of pendulum size will result in the systematic variation of characteristic period.⁹

Consider now a left wrist-pendulum system and a right wrist-pendulum system moving rhythmically together under the requirements (instructions to the subject) that the two systems (a) maintain a particular phase relation (0° or 180°) and (b) move comfortably at a single common period. These requirements define the co-ordinated state referred to by von Holst⁸ as absolute co-ordination.^{18,20} For two wrist-pendulum systems of different characteristic periods to meet requirement (b) means that one of the two coupled systems moves, or both of the coupled systems move, at a nonpreferred period. To manipulate the difference between the two coupled wrist-pendulum systems—specifically, to manipulate the size difference—is to control the degree to which the period of an individual wrist-pendulum system will depart from its characteristic period.⁹ In the experiment reported, the wrist-pendulum size is constant for the right rhythmic movement unit in a session and varied for the left rhythmic movement unit. In each session

of the experiment, the characteristic period T_0 of the right unit (the period it exhibits in the uncoupled state) is determined, along with the period T at which the right unit operates when coupled, to provide a dimensionless metric for the right unit's maintenance tendency, namely, operating period of unit (T)/characteristic period of unit (T_0). In each session, the length of the right unit l_{right} relative to the length of the left unit l_{left} determines, for each condition, a difference in characteristic periods to which the phase relation should be sensitive; for absolutely co-ordinated units, $l_{\text{right}} - l_{\text{left}}$ provides a metric of the difference in maintenance tendencies.

EXPERIMENTAL PROCEDURES

Subjects. The same three subjects were used in all six sessions of the experiment. All three subjects were staff members at Haskins Laboratories. The subjects were 21, 41 and 24 years of age at the start of the experiment. Each subject was right handed. The subjects weighed as follows: Subject 1, 73.5 kg; Subject 2, 74.9 kg; Subject 3, 78.0 kg.

Materials. The pendulum construction and the recording procedure were as described in Kugler and Turvey⁹ and Turvey *et al.*²¹

A single wrist-pendulum system, when looked at just in terms of the material distribution relative to the point of rotation, is a compound pendulum (a term that applies to any rigid body that is free to oscillate in a vertical plane about a fixed horizontal axis under the influence of gravity⁷). There are three masses, namely, the mass of the pendulum shaft or rod, the mass of the added weights and the mass of the hand, rotating about a point in the wrist joint. The distances of the centers of these masses from the common point of rotation are not equal. Nevertheless, the total mass of a wrist-pendulum system can be characterized as concentrated at a single distance from the point of rotation. This is achieved by computing the moment of inertia of the system by idealizations of the mass shapes and by applications of the parallel axis theorem⁷ and then calculating the simple pendulum equivalent of the compound pendulum in the ordinary manner.^{9,21} The resultant characterization identifies a single length quantity of a wrist-pendulum system (designated here as l_{right} for right units and l_{left} for left units). This characterization can be extended to two coupled wrist-pendulum systems. Even though they are connected neurally rather than connected rigidly they can be treated as if they are connected rigidly. That is, in combination, a right wrist-pendulum system and a left wrist-pendulum system can be conceptualized as a compound pendulum and the total mass of two wrist-pendulum systems, coupled to oscillate at the same tempo, can be characterized as a single point mass at a distance l_{virtual} from a single virtual point of rotation. Thus, $l_{\text{virtual}} = \text{summed moments of inertia of the left and right systems} / \text{summed static moments of the left and right systems}$.^{9,21}

The equivalent simple pendulum lengths for the (constant) right systems and the range of equivalent simple pendulum lengths for the (variable) left systems for each subject in each of the six sessions of the experiment are reported in Table 1. Because the mass of the subject's hand enters into the computation of these lengths and masses, the pendulums' magnitudes differ for the three subjects.

Procedure. Subjects (run one at a time) sat on a stool with their feet planted firmly on a foot-stand. They were given extensive verbal instructions in the first session. Each subject was instructed to hold his forearms parallel to the ground-plane and to gaze straight ahead without looking at either

Table 1. Equivalent simple pendulum lengths of the constant right systems (l_{right}) and the range of equivalent simple pendulum lengths of the variable left systems (l_{left} Range) in meters

Session	Subject					
	l_{right}	l_{left} Range	l_{right}	l_{left} Range	l_{right}	l_{left} Range
1	0.317	0.211–0.455	0.312	0.183–0.453	0.309	0.176–0.447
2	0.317	0.118–0.639	0.312	0.115–0.637	0.309	0.107–0.631
3	0.214	0.118–0.639	0.211	0.115–0.637	0.203	0.107–0.631
4	0.430	0.118–0.616	0.428	0.115–0.614	0.423	0.107–0.609
5	0.153	0.263–0.765	0.149	0.260–0.763	0.142	0.254–0.758
6	0.121	0.246–0.779	0.118	0.261–0.777	0.111	0.255–0.772

wrist-pendulum system. He was asked to oscillate the pendulums forward and backward smoothly using only the wrist joints while gripping the pendulums' handles so as to have complete control over the entire swing. The subject was told to swing the pendulums with a single, most comfortable common period at 180° out of phase. Importantly, before the recording of each trial, the subject was given as long as needed to settle on a tempo that he felt was comfortable and stable. Each recorded trial lasted for 15 s. The set of instructions was repeated to subjects in briefer form for experimental sessions 2–6 and subject behavior was monitored closely throughout the six sessions.

In sessions 2–5 there were eight coupled wrist-pendulum conditions and one single right wrist-pendulum condition. The single right wrist-pendulum condition in each session permitted the determination of T_0 , the preferred or characteristic period of the system that was held constant across the coupling conditions of each session. In sessions 1 and 6 there were 11 coupled wrist-pendulum conditions and one single right wrist-pendulum condition. In sessions 1, 2 and 5 there were eight trials per condition; in sessions 3 and 4 there were four trials per condition; and in session 6 there were six trials per condition. For each session, the total trials were divided into a number of blocks each of which involved one trial of every condition type. Trials within each block were given a random ordering and this ordering was different for each subject. The sessions varied in length from about 1½ to 3½ h (depending on the number of trials involved) including a 15-min break which occurred halfway through each session. The six sessions spanned 21 months with an average interval of 3 months between sessions.

The digitized trials were first analysed by the AngS and Vongraph waveform analysis programs at Haskins Laboratories. The peaks and valleys were "picked" using the criteria of the lowest and highest points of each cycle. Individual and mean peak-to-valley and valley-to-peak durations were used in the calculations pertaining to periodic timing within a trial. Individual and mean peak-to-valley and valley-to-peak distances (in degrees) were used in the calculations pertaining to spacing within a trial. The mean difference of one wrist-pendulum system's peak with respect to the other wrist-pendulum system's peak was used to calculate the mean phase relation within a trial. Exemplary waveforms and phase relation plots are shown in Fig. 1.

RESULTS

Absolute co-ordination

The periodic time for a wrist-pendulum system in a given coupled condition was defined by the mean periodic time of the four, six or eight trials (depending on the session) in which that system in that condition was examined. The periodic times of the left wrist-pendulum systems were regressed against the periodic times of the right wrist-pendulum sys-

tems for each of the three subjects for all 54 couplings of the six sessions. Absolute co-ordination would be identified by a linear regression with an r^2 of unity, a slope of unity and an intercept of zero. For Subjects 1, 2 and 3, respectively, the regression equations were: left period = 0.98 (right period) + 0.020, $r^2 = 0.999$; left period = 0.99 (right period) + 0.016, $r^2 = 0.999$; left period = 1.005 (right period) + 0.006, $r^2 = 0.999$.

Period fluctuation

A modified root mean squared index derived by von Holst⁸ was used. This measure has the form:

$$\Delta T = \sqrt{\left(\frac{\sum (T_{pv} - MT_{pv})^2 / MT_{pv}}{N} + \frac{\sum (T_{vp} - MT_{vp})^2 / MT_{vp}}{N} \right)}$$

where ΔT is the relative fluctuation magnitude for a particular trial; T_{pv} is the peak-to-valley duration of a particular cycle; MT_{pv} is the mean peak-to-valley duration across all cycles of a given trial; T_{vp} is the valley-to-peak duration of a particular cycle; MT_{vp} is the mean valley-to-peak duration across all cycles of a given trial; and N is the number of cycles per trial. The von Holst measure is a relative fluctuation measure that takes into account the fact that the flexion and extension phases of a cycle are often asymmetric. As a consequence, the component durations of a movement cycle (in waveform terms, the peak-to-valley component and the valley-to-peak component) can be unequal. Also, by scaling each variance score to the mean period of the trial from which it was taken, the measure takes into account the fact that from one observation of a given steady-state rhythmic movement unit to the next observation, the mean periodicity will vary. The von Holst relative fluctuation measure was calculated for each trial and these values were then averaged across trials of a given condition to yield a total of 54 such scores for all six experimental sessions for each subject. In the figures presented below, relative fluctuations are expressed as percentages (the above equation is multiplied by 100).

In order to observe how fluctuations changed as a function of a system's departure from its characteristic period, a ratio of coupled period (T) to characteristic period (T_0) was used as the independent variable. Figure 2 shows the relation of relative fluctuations to T/T_0 (a dimensionless quantity) for

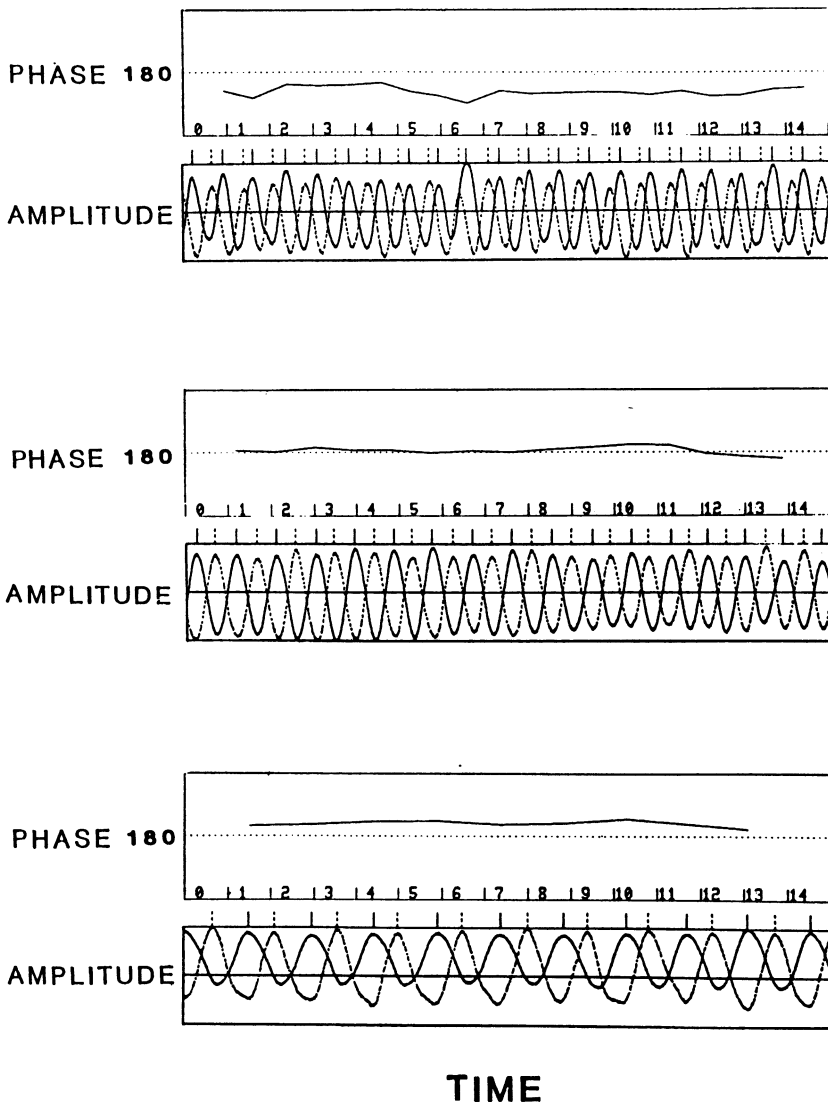


Fig. 1. Examples of phase relation (upper panels of each pair) and time series (lower panels of each pair) for three different experimental conditions. The phase relation panels show phase (in degrees) as a function of time (seconds) (with functions above the 180° mark indicating right hand leading). The time series panels represent the wave-forms for both wrist-pendulum systems with relative amplitude of pendulum swings shown as a function of time. The top pair shows phase relation and time series for a condition in which the right system's characteristic period is less than the left system's characteristic period. The middle pair shows a condition in which the characteristic periods of the two systems are the same. The bottom pair shows a condition in which the right system's characteristic period is greater than the left system's characteristic period.

each subject. Two functions are presented per subject: one showing the pattern of relative fluctuations for $T/T_0 \leq 1$ (system oscillating at, and faster than, the preferred period, left panels), and one showing the pattern of relative fluctuations for $T/T_0 \geq 1$ (system oscillating at, and slower than, the preferred period, right panels). For $T/T_0 \geq 1$, it can be seen that relative fluctuations increased nonlinearly as the ratio increased, leveling off at approximately the same value for each of the three subjects. Despite the obvious nonlinearity, linear regression analysis

suffices to evaluate whether or not the increase in fluctuations was significant. For Subject 1, $r^2(32) = 0.06$, $P > 0.05$; for Subject 2 $r^2(34) = 0.45$, $P < 0.0001$, intercept = 2.28, slope = 1.15; for Subject 3, $r^2(32) = 0.32$, $P < 0.0005$, intercept = 3.54, slope = 0.94.

For $T/T_0 \leq 1$, there is a suggestion that relative fluctuations increased linearly as the ratio decreased, although a significant linear trend was found only for Subject 3 ($r^2(19) = 0.63$, $P < 0.0001$, intercept = 9.66, slope = -6.24). Relative fluctu-

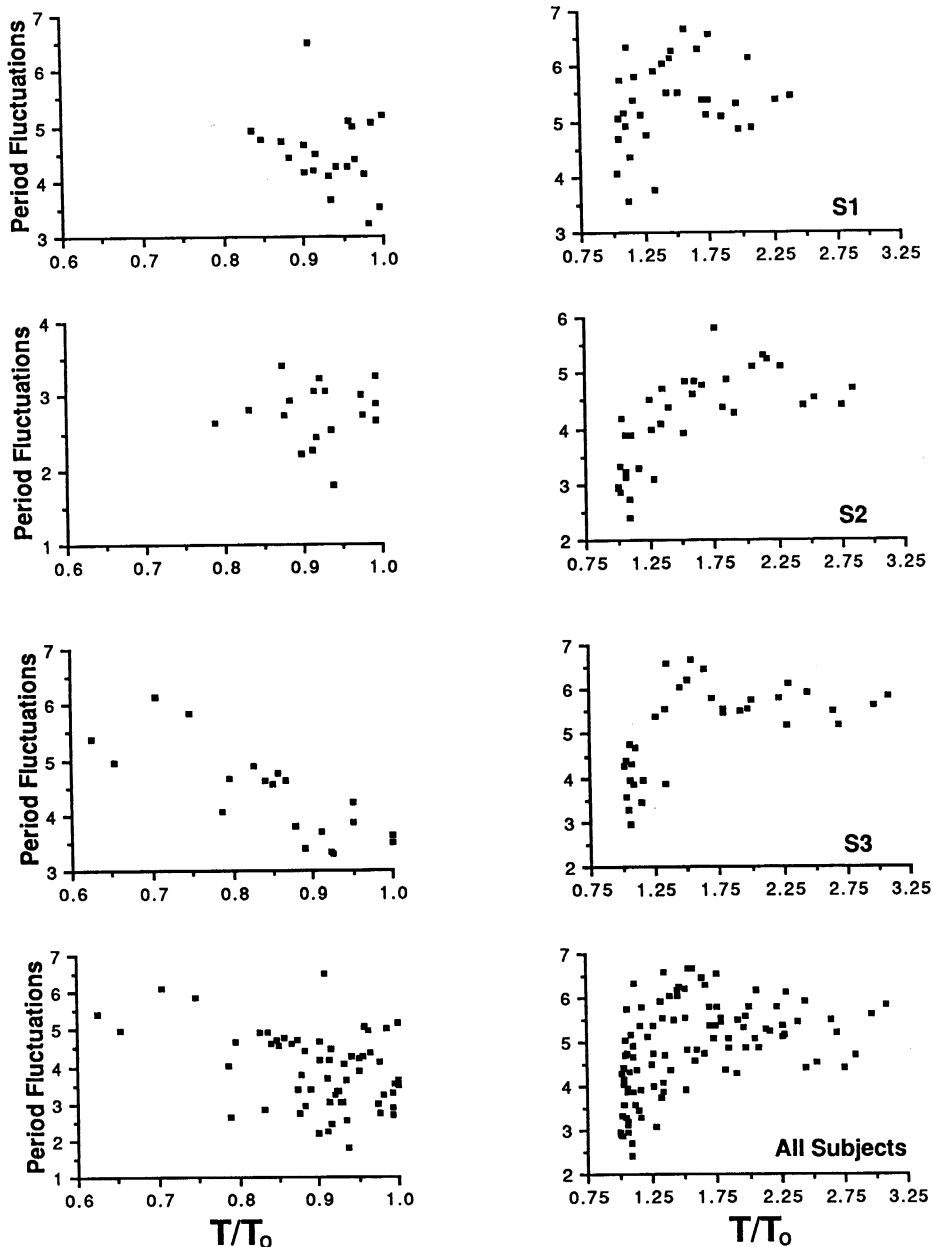


Fig. 2. Right systems' relative fluctuations in periodic time (expressed as percentages) as a function of $T/T_0 \leq 1$ (left panels) and $T/T_0 \geq 1$ (right panels) for each subject and for all subjects pooled (bottom panels). Data are from all six experimental sessions. See text for details.

ations against $T/T_0 \leq 1$ involved fewer observations (than against $T/T_0 \geq 1$) and a smaller range of values. Both limitations are the result of experimental design (the experiment was conducted to investigate simultaneously several aspects of interlimb co-ordination; the maintenance tendency is just one²²).

Inspection of all of the graphs in Fig. 2 suggests that, when $T/T_0 \geq 1$, the fluctuations increase up to approx. $T/T_0 = 1.5$ and then level off. A linear regression was conducted on the data of all three subjects in the range $1 \leq T/T_0 \leq 1.5$: $r^2(53) = 0.32$,

$P < 0.0001$, intercept = -0.91 , slope = 4.51 (with lower and upper 95% limits of 2.67 and 6.36, respectively). For the data of all three subjects in the range $T/T_0 \leq 1$, $r^2(59) = 0.17$, $P < 0.001$, intercept = 8.55 , slope = -5.13 (with lower and upper 95% confidence limits of -8.15 and -2.10 , respectively). The rate of increase in relative fluctuations was approximately the same for both ranges $T/T_0 \leq 1$ and $T/T_0 \geq 1$. That is, the growth of relative fluctuations in periodic timing that accompanied departures from the characteristic period was

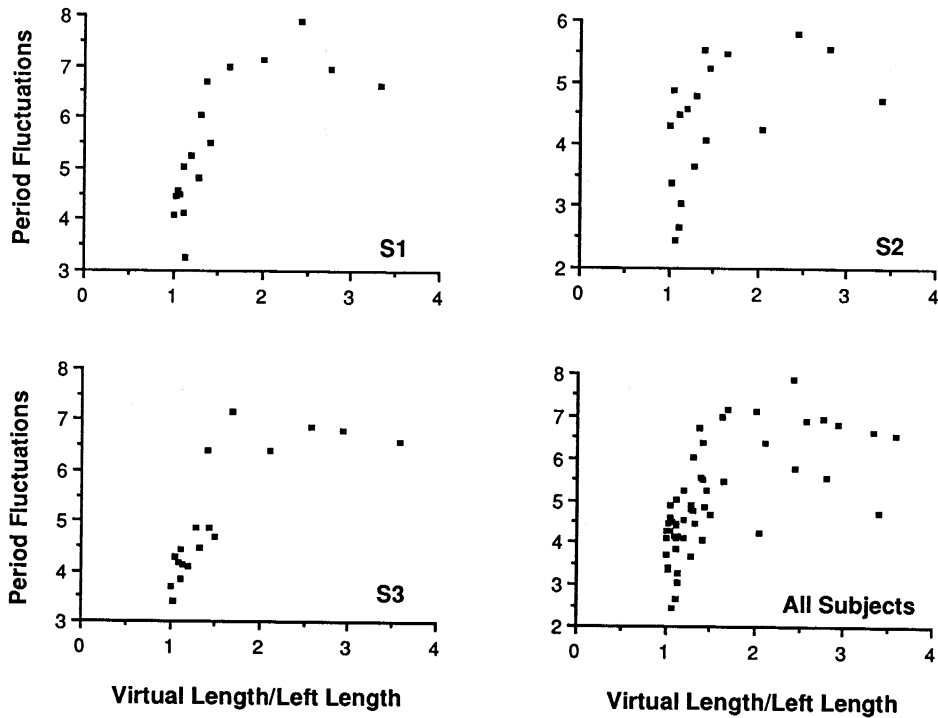


Fig. 3. Left systems' relative fluctuations in periodic time (expressed as percentages) as a function of virtual length/left length ≥ 1 for each subject and for all subjects pooled. Data are from all six experimental sessions. See text for details.

symmetrical within the limits of the experimental conditions, about the vertical axis through $T/T_0 = 1$. For $T/T_0 \geq 1$, the lack of further increases in relative fluctuations with departures from the characteristic period in the range $T/T_0 \geq 1.5$ was verified by a linear regression: $r^2(47) = 0.02$, $P > 0.05$, intercept = 5.76, slope = -0.20 .

In Fig. 3 are plotted the relative fluctuations of the left-hand wrist-pendulum systems. These are included, in part, to show that the dependency evident in Fig. 2 is not restricted to right-hand wrist-pendulum systems. To construct the functions depicted in Fig. 3 a different metric had to be used given that the characteristic periods of left-hand units were not determined experimentally. The metric was the ratio of l_{virtual} (the equivalent simple pendulum length of the compound pendulum defined by the left and right wrist-pendulum systems under the assumption that they are rigidly coupled) to l_{left} (the equivalent simple pendulum length of the compound pendulum defined by the left wrist-pendulum system). This $l_{\text{virtual}}/l_{\text{left}}$ metric ought to approximate T/T_0 in that it represents a mechanical quantity largely responsible for determining the coupled period (l_{virtual}) in ratio with a mechanical quantity (l_{left}) largely responsible for determining a wrist-pendulum system's period in isolation. Figure 3 presents the data for the left units' relative timing fluctuations when $l_{\text{virtual}}/l_{\text{left}} \geq 1$. (There were no significant effects in the range $l_{\text{virtual}}/l_{\text{left}} \leq 1$ which

may be attributed to its small extent, from 0.84 to 1). As is evident from inspection of Fig. 3, the relative fluctuations of left rhythmic movement units augment with departures from $l_{\text{virtual}}/l_{\text{left}} = 1$. Linear regression revealed that for Subject 1, $r^2(17) = 0.52$, $P < 0.0001$, intercept = 3.39, slope = 1.41; for Subject 2, $r^2(17) = 0.24$, $P < 0.05$, intercept = 3.25, slope = 0.75; and for Subject 3, $r^2(17) = 0.61$, $P < 0.0001$, intercept = 2.92, slope = 1.35. For the data of all three subjects taken together, $r^2(53) = 0.39$, $P < 0.0001$, intercept = 3.19, slope = 1.16 (with 95% confidence limits of 0.75 and 1.57). Clearly, the functions for the left units compare favorably with those of the right units. A linear regression on the complete left units' data in the range $1 \leq l_{\text{virtual}}/l_{\text{left}} \leq 1.5$, yielded an intercept of 0.03 and a slope of 3.70 (95% confidence limits, 2.04, 5.37). For the range $l_{\text{virtual}}/l_{\text{left}} \geq 1.5$ there was no significant change in relative fluctuations (intercept = 6.69, slope = -0.14).

Amplitude fluctuation

Relative fluctuations of amplitude were calculated using an amplitude equivalent of the modified root mean square measure for relative fluctuations of period: peak-to-valley and valley-to-peak amplitude values replace the corresponding period values. Relative fluctuations in amplitude of right rhythmic units as a function of T/T_0 are presented in Fig. 4. As with period fluctuations, amplitude fluctuations tend to

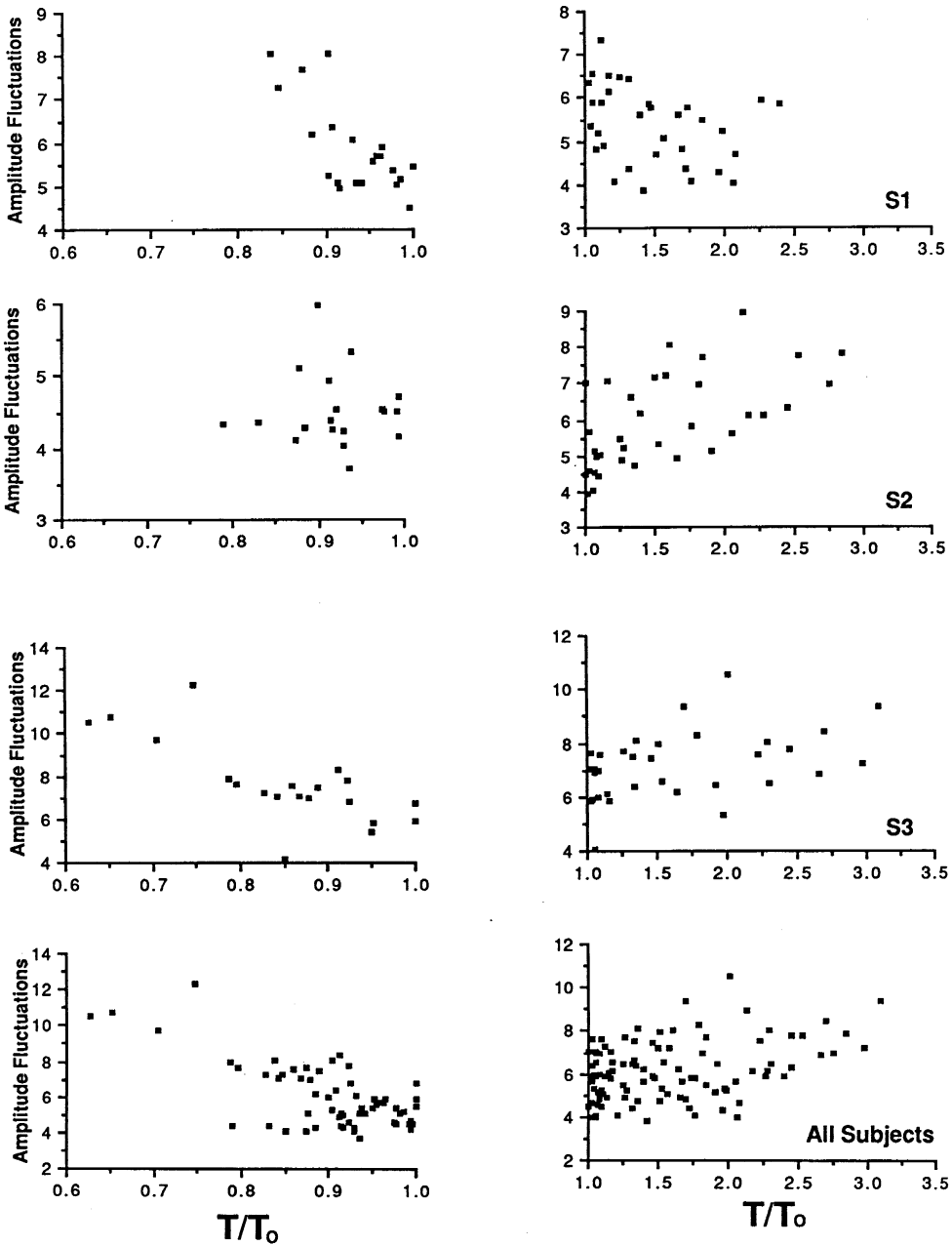


Fig. 4. Right systems' relative fluctuations in amplitude (expressed as percentages) as a function of $T/T_0 \leq 1$ (left panels) and $T/T_0 \geq 1$ (right panels) for each subject and for all subjects pooled (bottom panels). Data are from all six experimental sessions. See text for details.

increase with deviations from $T/T_0 = 1$. Significant linear dependencies of relative fluctuations in amplitude on T/T_0 were observed for Subject 1 when $T/T_0 \leq 1$: $r^2(20) = 0.54$, $P < 0.001$, intercept = 21.15, slope = -16.35 (95% upper and lower confidence limits, -23.66 and -9.04, respectively); for Subject 2 when $T/T_0 \geq 1$: $r^2(34) = 0.36$, $P < 0.001$, intercept = 3.74, slope = 1.40 (95% confidence limits: 0.74 and 2.07); for Subject 3 when $T/T_0 \leq 1$: $r^2(19) = 0.56$, $P < 0.0001$, intercept = 19.36, slope =

-13.79 (95% confidence limits: -19.81 and -7.76); and for Subject 3 when $T/T_0 \geq 1$: $r^2(33) = 0.17$, $P < 0.02$, intercept = 5.82, slope = 0.84 (95% confidence limits: 0.17 and 1.51). The bottom two panels of Fig. 4 pool the data of the three subjects. In the pooled data, relative fluctuations in amplitude varied significantly with T/T_0 for values both less than and greater than unity. For $T/T_0 \leq 1$, $r^2(59) = 0.47$, $P < 0.0001$, intercept = 19.82, slope = -15.30 (95% confidence limits:

−19.57, −11.02); for $T/T_0 \geq 1$, $r^2(101) = 0.13$, $P < 0.0002$, intercept = 4.72, slope = 0.93 (95% confidence limits: 0.45, 1.42). It is evident that, unlike the relative fluctuations in periodic timing, relative fluctuations in amplitude do not grow at the same rate in the two ranges of $T/T_0 \leq 1$ and $T/T_0 \geq 1$. Relative fluctuations in amplitude grow considerably faster in the range in which a rhythmic unit's period is less than its characteristic period. A further difference between the spacing and timing fluctuations is that in the range in which a rhythmic unit's period is greater than its characteristic period ($T/T_0 \geq 1$) the growth of amplitude fluctuations does not reach asymptote.

Looking at the left units' amplitude fluctuations with the aid of the $l_{\text{virtual}}/l_{\text{left}}$ metric, there was no evidence in the complete data set of an increase in the $l_{\text{virtual}}/l_{\text{left}} \leq 1$ range. In the $l_{\text{virtual}}/l_{\text{left}} \geq 1$ range a marginally significant increase was found: $r^2(53) = 0.07$, $P < 0.05$, intercept = 0.43, slope = 0.44 (95% confidence limits: −0.003, 0.89).

Correlated period and amplitude fluctuations

Figure 5 presents, for all three subjects, the relation between relative fluctuations in amplitude and relative fluctuations in period for right systems (upper panel) and left systems (lower panel). The linear regressions are reported with the figures. Both are significant at the 0.0001 level. As is clear from inspection of Fig. 5, the magnitudes of the difference between relative fluctuations in spacing and relative fluctuations in timing, and the rates at which relative fluctuations in spacing increased with relative fluctuations in timing, were closely similar for right and left wrist-pendulum systems.

Summary of period and amplitude fluctuations

A compact summary of the patterning of relative fluctuations in period and amplitude is provided by Fig. 6, in which we collect the complete period fluctuation data (upper panel) and amplitude fluctuation data (lower panel) on the right systems of Subject 3. The major features of relative period fluctuations are an increase in fluctuations when a rhythmic movement unit is either phase delayed ($T/T_0 > 1$) or phase advanced ($T/T_0 < 1$); an increase that achieves asymptote within a small range of departures from steady state (for example, from $T/T_0 = 1$ to $T/T_0 = 1.5$); an increase that occurs at approximately the same rate for phase delay (slope = 5.03 with 95% confidence limits of 2.28 and 7.78) and phase advance (slope = −6.24 with 95% confidence limits of −8.62 and −3.86); and an asymptotic level in phase delay that is between 5.5 and 7% of the mean value. The notable features of relative amplitude fluctuations are that they increase much more rapidly when the system is phase advanced (slope = −13.79, 95% confidence limits of −19.81 and −7.76) than when the system is phase delayed (slope = 0.84, 95% confidence limits of 0.17

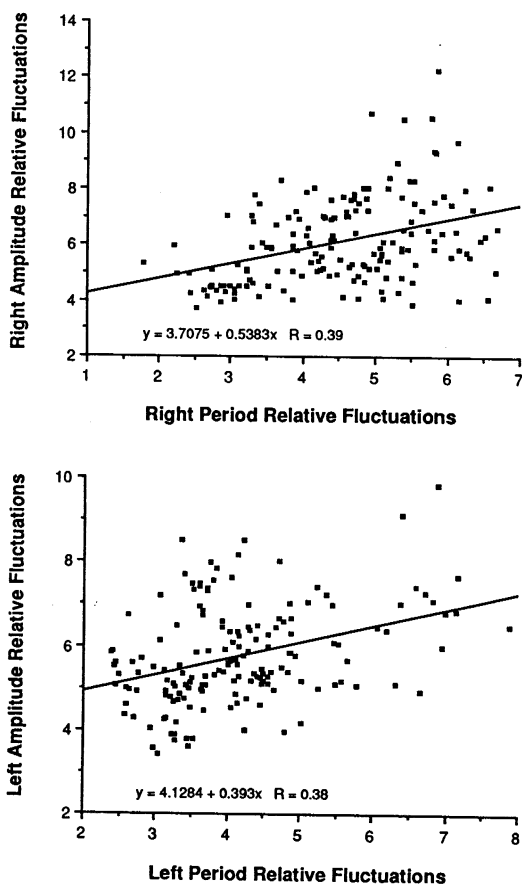


Fig. 5. Upper panel: Linear regression of right system relative fluctuations in amplitude (expressed as percentages) as a function of right system relative fluctuations in periodic time (expressed as percentages). Data are from all sessions and all subjects. Lower panel: Linear regression of left system relative fluctuations in amplitude (expressed as percentages) as a function of left system relative fluctuations in periodic time (expressed as percentages). Data are from all sessions and all subjects. See text for details.

and 1.51) and that they are generally larger than relative fluctuations in periodic timing.

Phase difference

The phase difference data are presented in Fig. 7. The convention is that phase differences greater than 180° indicate that the right wrist-pendulum system is leading the left wrist-pendulum system by $(x - 180)^\circ$; phase differences less than 180° indicate that the right wrist-pendulum system is lagging the left wrist-pendulum system by $(180 - x)^\circ$ (where x is a particular phase value). The independent variable in Fig. 7 is the difference between the lengths of the right and left coupled wrist-pendulum systems (see Table 1). Because the periods of wrist-pendulum systems correlate highly with system length,⁹ and because length and mass were correlated quantities for the experiment, differences in lengths ($l_{\text{right}} - l_{\text{left}}$) ought to be highly correlated with differences in characteristic periods. (Recall that the characteristic periods of

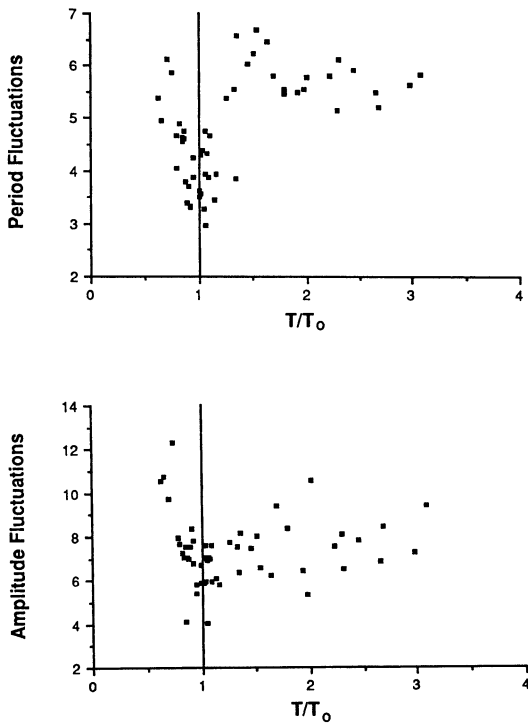


Fig. 6. Upper panel: Relative fluctuations in periodic time (expressed as percentages) for Subject 3 as a function of T/T_0 . Lower Panel: Relative fluctuations in amplitude (expressed as percentages) for Subject 3 as a function of T/T_0 . Data are from all six experimental sessions. See text for details.

the left systems were not determined experimentally.) Consequently, $(l_{\text{right}} - l_{\text{left}}) < 0$ means that the right wrist-pendulum system is the shorter of the two and, therefore, that the characteristic period of the right wrist-pendulum system is shorter; similarly, $(l_{\text{right}} - l_{\text{left}}) > 0$ means that the right wrist-pendulum system is the longer of the two and, therefore, that the characteristic period of the right wrist-pendulum system is longer.

Inspection of Fig. 7 reveals that, for each subject, the phase difference between any two coupled systems depended on the magnitude of $(l_{\text{right}} - l_{\text{left}})$. Inspection of Fig. 7 further reveals that the intended phase relation of 180° was approximated closely when the coupled systems were identical in length (or nearly so) and, therefore, identical in characteristic period (or nearly so). For each subject there appears to have been a limited range of $(l_{\text{right}} - l_{\text{left}})$ values within which the mapping between phase difference and $(l_{\text{right}} - l_{\text{left}})$ was linear, roughly, $-0.2 \text{ m} \leq (l_{\text{right}} - l_{\text{left}}) \leq +0.2 \text{ m}$. Beyond this range, for both $(l_{\text{right}} - l_{\text{left}}) < -0.2$ and $(l_{\text{right}} - l_{\text{left}}) > +0.2 \text{ m}$, phase difference appeared to change little with changes in $(l_{\text{right}} - l_{\text{left}})$, leveling off at approx. $25\text{--}35^\circ$ above and below the intended difference of 180° . A similar limitation on phase differences was noticed by von Holst.⁸

DISCUSSION

As defined by von Holst,⁸ the maintenance tendency refers to the subsistence of a rhythmic move-

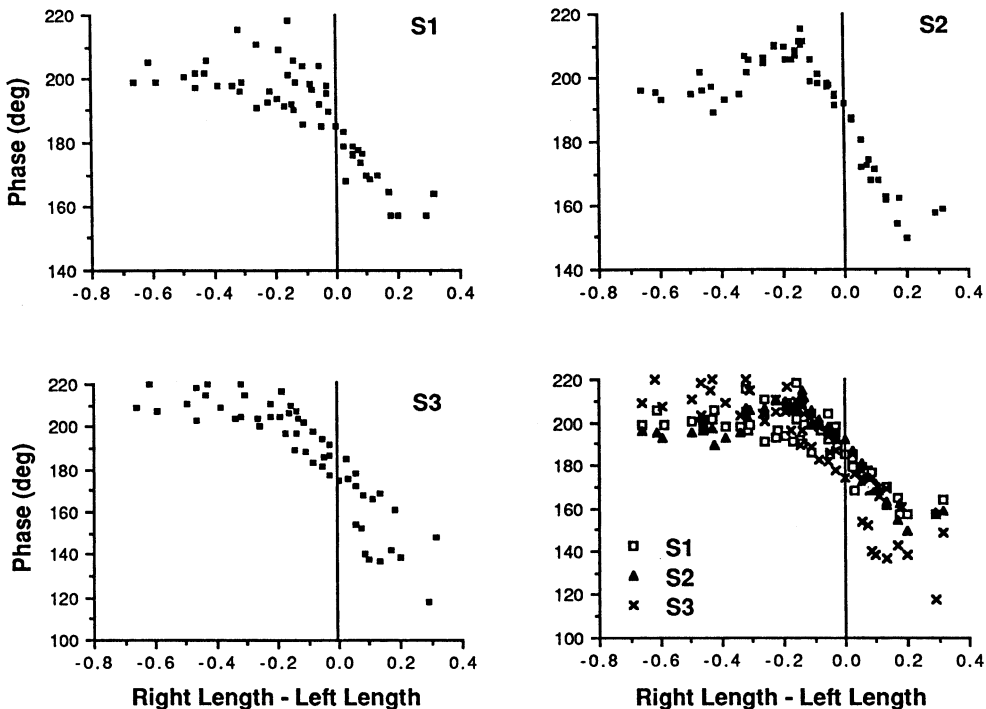


Fig. 7. Phase difference (degrees) as a function of the difference between the equivalent simple pendulum lengths (in meters) of the right and left systems for each subject and for all subjects pooled. Data are from all six experimental sessions. See text for details.

ment unit's intrinsically defined properties, such as its characteristic period, over the various co-ordinations within which it participates. Whereas von Holst's evidence for the maintenance tendency came primarily from investigations of the relative co-ordinations of rhythmic fin movements of medulla-transected fish, the evidence for the maintenance tendency in the present article comes from investigations of the absolute co-ordinations of rhythmic limb movements of normal humans.

The evidence in question is two-fold. First, relative fluctuations in timing (and relative fluctuations in spacing) were least when a rhythmic movement unit's period in co-ordination approximated its characteristic period; fluctuations increased with departures from characteristic period. Second, the phase relation between two absolutely co-ordinated rhythmic movement units depended on the relation between their characteristic periods. An intended phase relation of 180° was attained when the characteristic periods were identical. When the characteristic periods differed, the departure from 180° increased with the difference. We examine, in turn, the nature and the implications of the two types of evidence.

Fluctuations

In the present experiment the variances in periodic timing and amplitude can be conceptualized as the variances of hybrid oscillators. It can be argued, following suggestions by Beek and Beek,¹ that the behavior of a wrist-pendulum system (and the rhythmic behavior of limbs, fins, and wings more generally) is composed of a harmonic oscillatory dynamic associated with the pendulum and a relaxation oscillatory dynamic associated with the neuromuscular machinery that maintains the rhythmic wrist-pendulum motion through an energy flux (chemical-to-mechanical). The two kinds of oscillatory dynamics differ in important ways. They differ, for example, in the stability of period and amplitude.^{1,23} In harmonic or pendulum oscillations the period is stable and independent of external influences; amplitude, on the other hand, varies with variations in external conditions. In relaxation oscillations the reverse holds: amplitude is stable but variations in external conditions can alter period significantly. When coupled, the two oscillatory dynamics affect each other.¹ Thus, the pendulum is likely to be "detuned" by the relaxation dynamic, oscillating at a period other than its characteristic period; the neuromuscular oscillator is likely to be "tuned" by the harmonic dynamic, oscillating at one well-defined period. The characteristic period of the harmonic dynamic T_h can be calculated from $T_h = 2\pi(l/g)^{1/2}$, where l is the length of the simple pendulum equivalent of a wrist-pendulum system. The observed preferred periods of the right wrist-pendulum systems of the six sessions (the periods they exhibited in the uncoupled state) differed from the periods expected from the harmonic dy-

namic alone. The mean difference between T_h and T_0 was +66 ms, $t(17) = 10.64$, $P < 0.001$. In short, detuning occurred.

The relative contributions of the harmonic and relaxation dynamics to the hybrid harmonic/relaxation oscillatory motion should vary with the size of the pendulum. Intuitively, the harmonic dynamic should be more prominent when the pendulums are very large and the relaxation dynamic should be more prominent when the pendulums are very small. This prediction is clearest with respect to period fluctuations: if the fluctuations in periodic timing are associated primarily with the relaxation dynamic of the neuromuscular processes, then smaller pendulums should be associated, on the average, with larger timing fluctuations. In corroboration of this hypothesis, period fluctuations regressed simultaneously on right system lengths and mean periods (over the three subjects and the six sessions) revealed a significant ($P < 0.001$) inverse dependence on length: period fluctuations = $4.89 - 5.51 l_{\text{right}} + 0.88 T$; $r^2(161) = 0.35$. That is, fluctuations were greater on the average for smaller pendulums regardless of their actual periods of oscillation. Repeating the analysis with left system lengths produced a similar outcome: period fluctuations = $4.28 - 6.89 l_{\text{left}} + 2.21 T$; $r^2(161) = 0.40$. Apparently, pendulum size as well as the maintenance tendency metric T/T_0 affected the timing fluctuations reported in Fig. 2. It is important to establish whether or not the two variables made independent contributions. Period fluctuations regressed on l_{right} and T/T_0 , for all of the data in the range $1 \leq T/T_0 \leq 1.5$, yielded $r^2(53) = 0.48$, with the two variables significant, respectively, at the 0.001 and 0.01 levels. In the range $T/T_0 \leq 1$, the multiple regression yielded $r^2(59) = 0.17$ with only T/T_0 contributing significantly ($P < 0.001$).

Consider now the relation between period fluctuations and T_0 . Each T_0 is the preferred period of a given right wrist-pendulum system. Under the present interpretation, it is the characteristic period of a hybrid oscillatory system comprising coupled harmonic and relaxation dynamics. Through the multiple regression technique we can determine how variations in T_0 affect period fluctuations when the harmonic component and the actual periods of motion are held constant statistically. Regressing period fluctuations simultaneously onto T_0 , T_h and T for the data of all three subjects and all six sessions yielded the equation: period fluctuations = $6.84 + 4.24 T_0 - 6.84 T_h + 0.432 T$; $r^2(161) = 0.44$. The positive beta weight of T_0 was significant at the 0.001 level, indicating that period fluctuations increased systematically with T_0 . Given the significant ($P < 0.001$) negative beta weight for T_h (again, smaller pendulums exhibit, on the average, larger timing fluctuations), the significant positive beta weight for T_0 would appear to indicate that the more prominent the role of the relaxation dynamic in the

oscillatory behavior of a wrist-pendulum system, the larger, on the average, are its timing fluctuations.

The sum of the foregoing analyses is that relative fluctuations in period are most likely due to the relaxation dynamic. Variability in this dynamic arises from two sources—one macroscopic, the other microscopic. The macroscopic source is the degree to which the harmonic dynamic tunes the relaxation dynamic. It may be hypothesized that, for any given rhythmic unit, the preferred period T_0 represents that state in which the tuning is maximal. With departures from T_0 the relaxation dynamic becomes less tuned and, therefore, more variable in its periodicity. The microscopic source is the neuromuscular processes over which the relaxation dynamic is defined. The domain of these processes comprises very many 'atomistic' components, for example, functional motor units,² whose states can vary independently in one or more ways. Spontaneous deviation from some average regime is a universal phenomenon of atomistic (usually molecular) origin and is always present in a system with many degrees of freedom. Fluctuations are to be expected, therefore, in the timing and spacing properties of rhythmic movements given the 'atomistic' basis in the functional units of mammalian muscle. These fluctuations will be amplified to the degree that a rhythmic movement unit is (a) 'soft-molded' (meaning, approximately, that the neural and metabolic flows underwriting the relaxation dynamic are not constrained to precisely determined kinematic paths); (b) assembled afresh each cycle;^{9,21} and (c) not operating at the period at which the assembled relaxation dynamic is tuned maximally by the coupled harmonic dynamic.

Phase

The present data show that, in absolute co-ordination, two limbs can co-ordinate at very many phase relations. The subject's goal was to oscillate the two wrist-pendulum systems comfortably at a common period and at a phase relation of 180° . Actual phase relations were less than or greater than the phase relation intended in accordance with the difference in magnitude of the two wrist-pendulum systems (Fig. 7). Two hypotheses can be entertained. One hypothesis is that an observed movement phase relation of x° reflects a neural phase relation of x° ; that is, the neural activation of the right ulnar flexors, say, leads or lags by x° the neural activation of the left radial flexors. According to this first hypothesis, the neural processes governing co-ordination of limbs of the same girdle can assume very many stable phase relations in absolute co-ordination. Given any particular pair of wrist-pendulum rhythmic units, the neural states governing left limb and right limb motions, respectively, settle onto a stable phase relation tailored to the difference between the characteristic periods of the two units.^{13,22}

The other hypothesis is that an observed movement phase relation of x° , as depicted in Fig. 7, is not

to be equated with a neural phase relation. Rather, it reflects a phase relation of 180° in neural processes and a difference in the response latencies of loaded muscles to neural activation. That is, although the neural activations of the right and left muscle systems are 180° out of phase, the contraction of the right ulnar flexors leads or lags by x° the contraction of the left radial flexors. According to this second hypothesis, the neural processes governing the co-ordination of limbs of the same girdle can assume only two stable phase relations in absolute co-ordination, namely, 0 and 180° .^{6,21}

Behind the second hypothesis are the results of investigations demonstrating that loaded muscle self-adjusts to loading variations so as to preserve invariant, over a reasonable physiological range, the magnitude of its contraction for a given frequency of neural activation.¹⁰⁻¹² The constancy of contraction amplitude is accompanied by variable latency; roughly, the greater the inertia to be overcome by the muscle, the greater the lag between neural activation and muscular response. This characteristic of muscle would come into play in the present experiment as follows.

Given two coupled rhythmic units oscillating at a common period T and at a phase relation ϕ , the interscillator latency¹⁸ is given by $IOL = (\phi/360^\circ) T$. If the intended phase is 180° , then $IOL_{\text{neural}} = (180/360) T$. However, if there are muscle latencies t_r and t_l proportional approximately to the inertial loadings on the right and the left muscle systems, respectively, then $IOL_{\text{actual}} = IOL_{\text{neural}} + t_r - t_l$ (where, for sake of argument, $t_r > t_l$). Consequently, for $\phi_{\text{intended}} = 180^\circ$ and a common period T , $\phi_{\text{actual}} = 360 (IOL_{\text{neural}} + t_r - t_l)/T$. In words, for coupled wrist-pendulum systems, an intended phase of 180° should exhibit variation that depends on the difference between the magnitudes of the left and right systems, as observed, and on the coupled period.

Two analyses demonstrate the feasibility of the second hypothesis. One analysis focuses on the equation $IOL_{\text{actual}} = IOL_{\text{neural}} + t_r - t_l$. The magnitude of the difference between t_r and t_l can be calculated from the observed value of IOL_{actual} and the easily computed value of IOL_{neural} . By this procedure, the mean difference between right and left muscle latencies was found to be -0.035 s, with a minimum of -0.171 s and a maximum of 0.165 s. The foregoing would seem to be physiologically reasonable differences. The other analysis focuses on the coupled period's contribution to ϕ . The equation for ϕ_{actual} identifies the common period as a significant determinant of the phase relation in addition to l_{right} and l_{left} . For completeness, two common periods are considered—the observed coupled period T and the harmonic coupled period as predicted from l_{virtual} . Multiple regression shows that the independent variables l_{right} and l_{left} account for 55% of the amount of variance in phase. Adding T to the regression analysis raises this amount to 61%. Adding, instead, the harmonic

coupled period raises the variance in phase accounted for to 71%. Importantly, the beta weight on either coupled period is significant (at the $P = 0.001$ level) and negative, indicating that when the composition of wrist-pendulum systems is held constant statistically, phase gets smaller as the period (actual or harmonic) of absolute co-ordination gets longer, in accordance with the equation $\phi_{\text{actual}} = 360 (IOL_{\text{neural}} + t_r - t_l)/T$.

Electromyographical data would, of course, help to distinguish between the two hypotheses. In their absence we conclude with the following comments. The second hypothesis could accommodate von Holst's⁸ data insofar as his main observations were of phase relations between coupled fins that differed in size and, thereby, differed in the degree to which they imposed loads on their respective muscles. The second hypothesis seems ill suited, however, to Stein's¹⁶ observations on the swimmeret system, observations that match those depicted in Fig. 7. (Stein¹⁶ produced oscillators with different characteristic periods by cutting the crayfish's lateral axons in the ipsilateral connective between ganglia. That is, he induced variations in the characteristic periods

of the oscillators to-be-coupled through a neural manipulation rather than an inertial manipulation, as was the case in the present experiments). The first and second hypotheses differ, as noted, in the capabilities ascribed to the nervous system with respect to achieving absolute co-ordination between limbs (viz. very many stable phase relations can be defined on the nervous system vs only two stable phase relations can be defined on the nervous system). Resolving the two competing hypotheses, therefore, has implications for understanding the principles that generate the locomotory pattern.

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REFERENCES

1. Beek P. J. and Beek W. J. (1987) Model choice and parametric sensitivity in quantifying rhythmical movement. Presented at the 4th Int. Conf. Event Perception and Action, Trieste, 24–28 August 1987.
2. Bloch E. H. and Iberall A. S. (1982) Toward a concept of the functional unit of mammalian skeletal muscle. *Am. J. Phys., Reg. Integ. comp. Physiol.* **242**, R411–R420.
3. Edgerton V. R., Grillner S., Sjöstrom A. and Zangger P. (1976) Central generation of locomotion in vertebrates. In *Neural Control of Locomotion* (eds Herman R. M., Grillner S., Stein P. S. G. and Stuart D. G.), pp. 439–464. Plenum Press, New York.
4. Gallistel C. R. (1980) *The Organization of Action: A New Synthesis*. Erlbaum, Hillsdale, NJ.
5. Grillner S. (1975) Locomotion in vertebrates: central mechanisms and reflex interaction. *Physiol. Rev.* **55**, 247–304.
6. Haken H., Kelso J. A. S. and Bunz H. (1985) A theoretical model of phase transitions in human hand movements. *Biol. Cybern.* **51**, 347–356.
7. Hartog J. P. den (1948/1961) *Mechanics*. Dover Publications, New York.
8. Holst E. von (1937, 1939/1973) *The Behavioral Physiology of Animal and Man*. University of Miami Press, Coral Gables, FL.
9. Kugler P. N. and Turvey M. T. (1987) *Information, Natural Law, and the Self-Assembly of Rhythmic Movement*. Erlbaum, Hillsdale, NJ.
10. Partridge L. D. (1966) Signal-handling characteristics of load-moving skeletal muscle. *Am. J. Physiol.* **210**, 1178–1191.
11. Partridge L. D. (1967) Intrinsic feedback factors producing inertial compensation in muscle. *Biophys. J.* **7**, 853–863.
12. Partridge L. D. (1981) Muscular properties. A problem for the motor physiologist. In *Posture and Movement* (eds Talbot R. E. and Humphrey D. R.), pp. 189–229. Raven Press, New York.
13. Pavlidis T. (1973) *Biological Oscillators: Their Mathematical Analysis*. Academic Press, New York.
14. Scripture E. W. (1899) Observations on rhythmic action. *Stud. Yale Psychol. Lab.* **7**, 102–108.
15. Shik M. L. and Orlovsky G. N. (1976) Neurophysiology of locomotor automatism. *Physiol. Rev.* **56**, 465–501.
16. Stein P. S. G. (1973) The relationship of interlimb phase to oscillator activity gradients in crayfish. In *Control of Posture and Locomotion* (eds Stein R. B., Pearson K. G., Smith R. S. and Redford J. B.), pp. 621–623. Plenum Press, New York.
17. Stein P. S. G. (1974) The neural control of interappendage phase during locomotion. *Am. Zool.* **14**, 1003–1016.
18. Stein P. S. G. (1976) Mechanisms of interlimb coordination. In *Neural Control of Locomotion* (eds Herman R. M., Grillner S., Stein P. S. G. and Stuart D. G.), pp. 465–487. Plenum Press, New York.
19. Stein P. S. G. (1977) A comparative approach to the neural control of locomotion. In *Identified Neurons and Behavior of Arthropods* (ed. Hoyle G.), pp. 227–239. Plenum Press, New York.
20. Stein P. S. G. (1977) Application of the mathematics of coupled oscillator systems to the analysis of the neural control of locomotion. *Fedn Proc. Fedn Am. Socs exp. Biol.* **36**, 2057–2059.
21. Turvey M. T., Rosenblum L. D., Schmidt R. C. and Kugler P. N. (1986) Fluctuations and phase symmetry in coordinated rhythmic movements. *J. exp. Psychol. hum. Percept. Perf.* **12**, 564–583.
22. Turvey M. T., Schmidt R. C., Rosenblum L. D. and Kugler P. N. (1988) On the time allometry of coordinated rhythmic movements. *J. theor. Biol.* **130**, 285–325.
23. Wever R. (1965) Pendulum versus relaxation oscillation. In *Proc. Feldafing Summer School, September 1964: Circadian Clocks*, pp. 74–83. North-Holland, Amsterdam.