

'CLOCK' AND 'MOTOR' COMPONENTS IN ABSOLUTE COORDINATION OF RHYTHMIC MOVEMENTS

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Abstract—Human subjects swung, through motions at the two wrists, hand-held pendulums of variable mass and length. Within a pair, the two pendulums could be of the same or different magnitude. The subjects were required to produce a coordinated state in which the two rhythmic units oscillated at a single common period. Fifty-four conditions of absolute coordination, that is, 54 different pairs of wrist-pendulum systems, were investigated for each of three subjects in the course of six sessions. Each condition of absolute coordination was conducted in the out of phase mode and at the single most comfortable period. The period variances of the right and left systems in the 162 instances of absolute coordination were analysed according to a method that assumes that a timekeeper function and a motor implementation function contribute independently to the variance in the periodic timing of a rhythmic movement. The major findings were that in absolute coordination: (a) a system's 'motor' variance, but not its 'clock' variance, depended on the deviation of the period of absolute coordination τ from the system's characteristic period; (b) right and left 'clock' variances were related and (c) neither the 'motor' variances nor the 'clock' variances were affected by deviations in the mean phase relation from 180 degrees.

The results were discussed in terms of their implications for interpreting von Holst's notions of maintenance tendency and magnetic effect and, more generally, the neural and dynamical basis of absolute coordination.

It is often proposed that two functions underly the rhythmic limb movements typifying locomotion and that these two functions are subserved by different neural elements.^{5,8} A timekeeping function is said to be provided by single central cells or populations of central cells that produce a periodic signal; a motor function is said to be provided by populations of central cells, which under this periodic control, transmit impulses to the muscles. A way of conceptualizing this neural division of labor in terms of the variance of a rhythmic movement's period has been developed by Wing and Kristofferson.¹⁴ Following a suggestion by Ten Hoopen and Reuver,¹⁰ Wing and Kristofferson adopt the strategy of accounting for the sequential dependence of the durations of movement cycles treated as a time series. At a regular interval C the timekeeper is assumed to emit a signal that initiates a response in the motor components. A short delay intervenes between the initiation of this response and the overt, measured behavior. Each period τ_j of rhythmic movement can be viewed, therefore, as the sum of the timekeeper's cycle time (C_j) plus the difference in the motor delays (MD_j, MD_{j-1}) connected with the responses that initiate and terminate the period:

$$\tau_j = C_j + MD_j - MD_{j-1} \quad (1)$$

If the timekeeper intervals and the motor delays are independent random variables with variances of s_c^2

and s_{md}^2 , respectively, then it follows that the period variance s_τ^2 is given by:

$$s_\tau^2 = s_c^2 + 2s_{md}^2 \quad (2)$$

The period variance s_τ^2 can be obtained directly from the rhythmic movement data. The component variances s_c^2 and s_{md}^2 can be estimated from the covariance function of the successive cycle periods. The central predictions of Wing and Kristofferson¹⁴ are that (a) temporally abutting cycles will be negatively correlated and (b) temporally nonabutting cycles, those separated by one cycle or more, will be uncorrelated. The negative sign of the correlation between adjacent cycles means that if one cycle period is by chance shorter than average the next cycle period will be longer than average, and vice versa.¹³ The negative dependence does not point to a fed-back influence (in the form of temporal information) from one cycle to the next. Rather, it is seen more simply as an inevitable result of the inherent delays in the motor system: a large motor delay in the $j-1$ cycle will induce a long $j-1$ cycle period and a short j cycle period. The lag 1 covariance is proposed, therefore, as a measure of the motor delay variance:

$$\text{cov}(\tau_j, \tau_{j-1}) = -s_{md}^2 \quad (3)$$

where

$$\text{cov}(\tau_j, \tau_{j-1}) = \sum (\tau_j - \tau)(\tau_{j-1} - \tau)/(N-1) \quad (4)$$

and N is the number of cycles. Given that the lag 0 covariance is a measure of s_τ^2 (τ being the mean value

Abbreviation: CPG, central pattern generator.

of the periodic time), i.e.

$$\text{cov}(\tau_i, \tau_j) = \sum (\tau_i - \tau_j)^2 / N. \quad (5)$$

then it follows that

$$\text{cov}(\tau_i, \tau_j) = s_i^2 = s_j^2 + 2s_{\text{md}}^2. \quad (6)$$

The lag 1 autocorrelation between adjacent cycle times is expressed most usefully by the ratio of (3) to (6):

$$\text{cor}(\tau_i, \tau_{i-1}) = -1/[2 + s_i^2/s_{\text{md}}^2]. \quad (7)$$

On the average, the predicted negative lag 1 autocorrelation between adjacent cycles is expected to be between 0 (timekeeper variance is very large relative to motor variance) and -0.5 (timekeeper has no variability). Combining the equations for the lag 1 autocorrelation and the period variance s_i^2 yields measures of the 'clock' and 'motor' variances, namely,

$$s_i^2 = s_j^2 + 2[s_i^2 \times \text{cor}(\tau_i, \tau_{i-1})] \quad (8)$$

and

$$s_{\text{md}}^2 = -s_i^2 \times \text{cor}(\tau_i, \tau_{i-1}), \quad (9)$$

respectively.

In this article we used the analysis of Wing and Kristofferson to evaluate the behavior of clock and motor components in absolutely coordinated rhythmic movements. In absolute coordination two or more limbs oscillate at the same frequency. von Holst⁵ interpreted absolute coordination at a freely elected frequency to be the result of two inclinations working in direct opposition, namely, the inclination of an individual rhythmic unit to move at its own characteristic frequency (the maintenance tendency), and the inclination of an individual rhythmic unit to move at the characteristic frequency of another rhythmic unit (the magnet effect). If the maintenance tendency dominated then the units (limbs or fins) would oscillate independently of one another at different frequencies. If the magnet effect dominated then the units would oscillate at one and the same frequency. With respect to the latter condition, however, von Holst⁵ concluded that "... the 'struggle' between the magnet effect and the maintenance tendency continues in latent form even after attainment of absolute (successful) coordination" (p. 65).

A methodology introduced by Kugler and Turvey⁷ permits wide systematic control over both the characteristic frequencies of individual rhythmic units and the departures from characteristic frequencies within the context of stable, absolute coordinations. The individual rhythmic movement unit is defined by a hand-held pendulum together with the neuromuscular processes by which the pendulum is moved rhythmically about an axis in the wrist at a comfortable tempo. The characteristic frequency of such a rhythmic unit—a wrist-pendulum system—will be determined in largest part by the pendulum's magnitude. Consequently, the systematic variation of pendulum

size will result in the systematic variation of characteristic frequency.^{7,12} Absolute coordination is achieved when two wrist-pendulum systems (left and right) move rhythmically together under the requirements (instructions to the subject) that the two systems (a) maintain a particular phase relation and (b) move at the single common period that is most comfortable. For two wrist-pendulum systems of different characteristic periods, meeting requirement (b) means that one of the two systems moves, or both of the systems move, at a nonpreferred period. To manipulate the difference between the two absolutely coordinated 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.

The absolute coordination of two wrist-pendulum systems forms a coordinative structure analysable into three levels.^{7,11} The upper level comprises the constraints the subject brings to bear in accordance with the experimental instructions. The lower level comprises the two individual wrist-pendulum systems. The middle level comprises a cooperative state in which the two systems act together—namely, the state of absolute coordination. The lower level units, in order to satisfy cooperativity, deviate from the rhythmic parameters they would exhibit in isolation; to achieve comfortable absolute coordination with its partner, an individual wrist-pendulum system must oscillate at a frequency that is faster or slower than preferred. One consequence of this deviation ought to be increased variability in the parameters of oscillatory behavior.⁷ It has been observed that when a wrist-pendulum system in absolute coordination oscillates at frequencies other than its characteristic frequency, the fluctuations in the system's frequency and amplitude are magnified.⁹

Returning to the language of clocks and motors, two hypotheses can be advanced about the state of absolute coordination. The first hypothesis is that the lower level comprises two distinct clock/motor complexes with the middle level arising from the mutual adjustment of these two complexes in the sense of von Holst's magnet effect. According to the first hypothesis, both the motor and clock variances of the two systems would be expected to reflect the maintenance tendency, with both kinds of variances increasing as a function of the degree to which the period of absolute coordination differs from the systems' characteristic periods. The basis of the preceding prediction is a particular interpretation of cooperativity, namely, that of component units compromising their preferred states in order to achieve a given effect. The second hypothesis is based on an interpretation of cooperativity as the formation of a unitary process. According to this second hypothesis, the fact that the lower level units oscillate at an identical, or nearly identical, frequency implies a unitary timekeeper—a single, dynamical organization underlying the equal

durations of right and left cycles. That is, absolute coordination is not so much a type of coupling of two local clocking mechanisms as it is the formation of a new, more globally defined clock that provides a reference frame for the intracycle patterning of muscular activities in the lower level units.¹¹ According to this second hypothesis, the clock variances of right and left systems in comfortable absolute coordination should be independent of how far the systems deviate from their characteristic periods. The motor variances, in contrast, should depend on the size of the deviation on the assumption that a characteristic period identifies the preferred pace of the intracycle motor pattern.

In short, we propose and test in the present article two hypotheses about comfortable absolute coordination. The contrast between the two hypotheses may be summarized as follows: (a) the first hypothesis predicts that both clock and motor variances should increase with deviations from a wrist-pendulum system's characteristic frequency; the second hypothesis predicts that only the motor variance should increase; (b) the first hypothesis predicts that the clock variances of right and left wrist-pendulum systems should be uncorrelated; the second hypothesis predicts that the clock variances of right and left wrist-pendulum systems should be correlated.

Evaluating these two hypotheses has significance for recent theorizing about the neuronal networks underlying locomotion. It is usually contended that a single circuit is responsible for both the patterning of motor activity within a limb or fin cycle and the generating of the cycle-to-cycle timing of the locomotory rhythm.³ In contrast, Lennard⁶ has suggested that there is a functional separation of the networks subserving intracycle pattern generation and the timing of the locomotory activity. The oft-cited central pattern generator would be limited to producing the proper phase relations between muscles within each cycle; an independent central timing network would be responsible for initiating each cycle and, therefore, for organizing the locomotor rhythm. Lennard⁶ hypothesizes that the intracycle pattern generator may be conceptualized as an oscillatory network that is entrained by the timekeeping network, or as a heavily damped oscillator (one-cycle pattern generator) driven on a cycle-to-cycle basis by the timekeeping network.

EXPERIMENTAL PROCEDURES

The foregoing predictions are evaluated with the data from a study consisting of six separate sessions (or experiments) conducted over a 21-month interval with the same three subjects. The study was designed to address simultaneously a number of different issues concerning absolute coordination. Some methodological details and results of the study have already been reported.^{9,12} The emphasis in what follows is on the features of the experimental design that bear directly on questions concerning the timekeeping and motor components of rhythmic systems in absolute coordination, for example: How are the clock variances of the two systems related? How are the motor variances of the two systems related? How are the clock and motor variances of a system affected by deviations from the system's characteristic period?

Subjects

The three subjects were 21, 24 and 41 years of age at the start of the study. 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, recording procedure and method for computing the equivalent simple pendulum lengths were as described in Kugler and Turvey,⁹ Turvey *et al.*,¹¹ and Rosenblum and Turvey.⁹

In each session of the study the right wrist pendulum was of fixed magnitude. Different conditions of absolute coordination were produced by varying the magnitude of the left wrist pendulum. The characteristic frequencies of the (constant) right systems considered as strictly gravitational pendulums, and the range of characteristic frequencies for the (variable) left systems considered as strictly gravitational pendulums, are reported in Table 1 for each subject in each of the six sessions of the study. Because the masses of the subject's hands enter into the computations of these simple gravitational pendulum equivalents of wrist-pendulum systems,⁷ the characteristic frequencies 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 wrist-pendulum system. He was asked to oscillate the pendulums forward and backward smoothly using only the wrist joints while gripping each pendulum's handle so as to have complete control over the entire swing. The subject was told to swing the pendulums in alternate fashion (one pendulum moving forward simultaneously with the other pendulum moving backward) with a single, most comfortable common period. 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

Table 1. Characteristic frequencies (in Hz) of the constant right systems, and the range of the characteristic frequencies of the variable left systems, when the systems are considered as strictly gravitational pendulums

	Subject 1		Subject 2		Subject 3	
	right	left range	right	left range	right	left range
Session 1	0.89	1.09-0.74	0.89	1.17-0.74	0.90	1.19-0.75
Session 2	0.89	1.45-0.62	0.89	1.47-0.62	0.90	1.52-0.63
Session 3	1.08	1.45-0.62	1.09	1.47-0.62	1.11	1.52-0.63
Session 4	0.76	1.45-0.64	0.76	1.47-0.64	0.77	1.52-0.64
Session 5	1.27	0.97-0.57	1.29	0.98-0.57	1.32	0.99-0.57
Session 6	1.43	0.97-0.57	1.45	0.98-0.57	1.50	0.99-0.57

lasted for 15 s, except in session 6 in which the trials were of 10 s duration. 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 absolute coordination conditions and one single right wrist-pendulum condition. The single right wrist-pendulum condition in each session permitted the determination of τ_0 , the right system's characteristic period. To reiterate, the right system was held constant across the absolute coordination conditions of each session. In sessions 1 and 6 there were 11 absolute coordination conditions and one single right wrist-pendulum condition. In session 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 the ordering was different for each subject. The sessions varied in length from about 1.5 to 3.5 h (depending on the number of trials involved) including a 15 min break that occurred halfway through each session. The six sessions spanned 21 months with an average interval of three months between sessions.

Analyses

The digitized trials were 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. Peak-to-peak durations were used in the calculations pertaining to periodic timing within a trial. The 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.¹³

For each of the three subjects the mean period and period variance were computed for each trial of each condition. For each subject, the means of these trial values were used as the estimates of a condition's τ and s^2 . Similarly, for each of the

three subjects, the mean lag 1, 2 and 3 autocorrelations were computed for each trial. For each subject, the means of these trial values were used as the estimates of a condition's lag 1, 2 and 3 autocorrelations.

For some of the analyses the period fluctuation measure introduced by von Holst¹ was used. This measure has the form:

$$\Delta T = \sqrt{\left(\left[\frac{\sum (T_{pv} - MT_{pv})^2}{MT_{pv}} \right] + \left[\frac{\sum (T_{vp} - MT_{vp})^2}{MT_{vp}} \right] \right) / N} \quad (10)$$

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 fluctuation 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.

RESULTS

As identified in the introduction, the central predictions of Wing and Kristofferson¹⁴ are that (a) temporally abutting cycles will be negatively correlated with an average lower bound of -0.5 , and (b) temporally nonabutting cycles, those separated by one cycle or more, will be uncorrelated. Application of the clock

Table 2. Serial autocorrelations at lags 1-3 for the three subjects in the six sessions

	Left hand			Right hand		
	lag 1	lag 2	lag 3	lag 1	lag 2	lag 3
Session 1						
Subject 1	-0.245**	-0.056		-0.197**	-0.029	
Subject 2	-0.249**	-0.100*	-0.056	-0.201**	-0.037	-0.002
Subject 3	0.068*	-0.022	-0.073	0.066	0.009	-0.033
Session 2						
Subject 1	-0.217**	0.001	0.008	-0.199**	0.049	0.002
Subject 2	-0.296**	-0.048	-0.067	-0.280**	-0.009	-0.009
Subject 3	-0.133**	0.040	0.015	-0.033	-0.065	-0.060
Session 3						
Subject 1	-0.114*	0.008	0.041	-0.024	0.055	-0.027
Subject 2	-0.213**	-0.077	-0.001	-0.213**	0.033	-0.070
Subject 3	-0.114	0.138*	-0.018	-0.103	0.060	-0.060
Session 4						
Subject 1	-0.136*	-0.077	-0.116	-0.089	0.003	0.051
Subject 2	-0.378**	0.060	-0.125	-0.314**	-0.024	0.104
Subject 3	-0.185*	0.073	-0.035	-0.035	0.002	-0.057
Session 5						
Subject 1	-0.217**	-0.057	-0.004	-0.271**	-0.053	-0.027
Subject 2	-0.291**	-0.027	0.051	-0.286**	0.002	-0.116*
Subject 3	0.001	0.027	-0.021	-0.159**	0.023	0.001
Session 6						
Subject 1	-0.409**	-0.098		-0.328**	0.039	
Subject 2	-0.198**	-0.034	-0.028	-0.342**	-0.010	-0.039
Subject 3	-0.255**	-0.018	0.005	-0.311**	-0.017	-0.020

* $P < 0.05$, ** $P < 0.001$. Empty cells are due to insufficient cycles for computing lag 3.

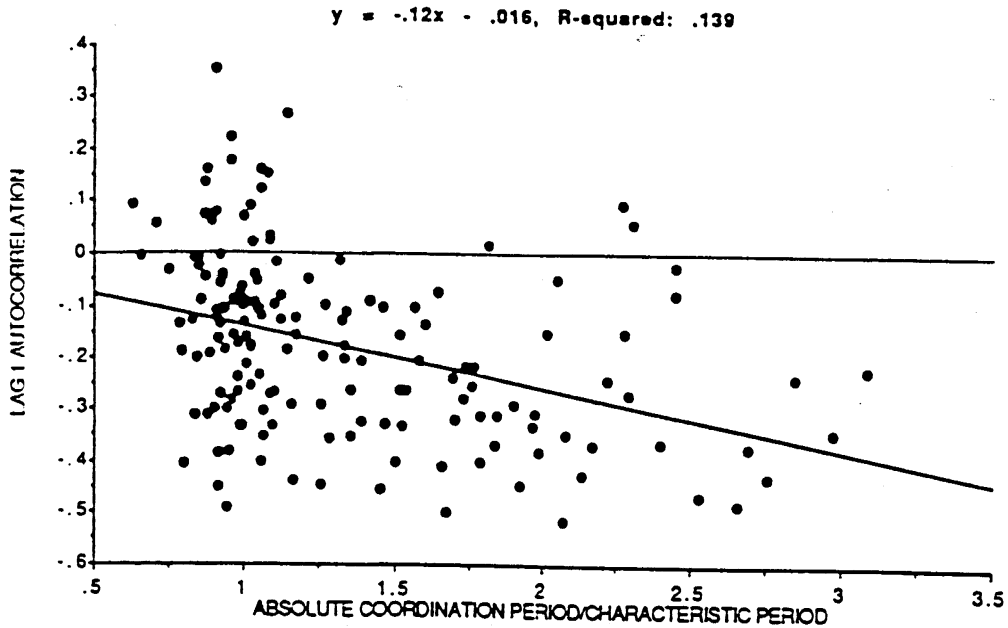


Fig. 1. Lag 1 autocorrelations of the right systems expressed as a function of deviation from characteristic period. The x-axis is the ratio of the period of absolute coordination (τ) to the period a right system oscillates at in isolation (τ_0).

and motor analysis rests on the satisfaction of these two predictions. They follow directly from the central assumption of independent clock and motor processes. To evaluate the two predictions, autocorrelation coefficients were computed for each trial on the durations of cycles at different lags, with the largest lag defined by $N/4$ where N is the number of cycles in a trial (Chatfield²). (Given that trial durations were fixed, the number of cycles observed within a trial varied with the conditions of absolute coordination.) The mean autocorrelation coefficients for the left and right systems of each subject in each session and their significances are presented in Table 1 for lags 1-3. Higher lags under the $N/4$ cut-off criterion were rare and none were significant. The data from the three subjects in the six sessions conform extremely well to the predictions of Wing and Kristofferson's theory (Table 2). Lag 1 autocorrelations were predominantly negative, significant, and less than -0.5 ; higher lag autocorrelations were predominantly insignificant.

In each experiment for each subject, the right system lag 1 autocorrelation coefficients were averaged across the trials for a given condition. The 162 lag 1 values of the right systems in absolute coordination (54 conditions \times 3 subjects) as a function of τ/τ_0 are presented in Fig. 1. This ratio of the period of absolute coordination to the right system's characteristic period defines the deviation of the right system from its preferred cyclic state. Two main features are to be noted. First, the lag 1 autocorrelations are significantly and negatively related to the degree to which a system's period deviates from its characteristic period. The implication of this outcome is that with increasing deviation from the characteristic

period, motor variance was amplified more than clock variance [see Eqn (7)]. Second, although the lag 1 autocorrelations were overwhelmingly negative and in the range of 0 to -0.5 as predicted by the theory of Wing and Kristofferson, some were positive. With the right lag 1 autocorrelations greater than 0 and less than -0.5 removed (a total of 23 cases out of 162), the linear regression remains significant and of negative slope: $r^2(138) = 0.133$, $P < 0.0001$, intercept = -0.098 , slope = -0.089 .

The relationship between the 162 lag 1 autocorrelations of the right systems and the corresponding 162 lag 1 autocorrelations of the left systems is presented in Fig. 2. Again, there are two main observations to be made. First, there was evidently a significant tendency for left lag 1 autocorrelations to be large when right lag 1 autocorrelations were large. The implication from the structure of Eqn (7) is that motor and/or clock variances across the two systems were linked. Second, although the left lag 1 autocorrelations were overwhelmingly negative and in excess of -0.5 , there were a number of violations to the expectation from the theory of Wing and Kristofferson: 30 of the 162 autocorrelations were positive and one was less than -0.5 . With left and right lag 1 autocorrelations in excess of 0 and less than -0.5 excluded, the linear relation between left and right systems remained significant and positive: $r^2(119) = 0.168$, $P < 0.0001$, intercept = -0.134 , slope = 0.39.

For each condition for each subject, motor and clock variances (and standard deviations) were computed for both right and left systems according to Eqns (8) and (9). (By definition, these computations

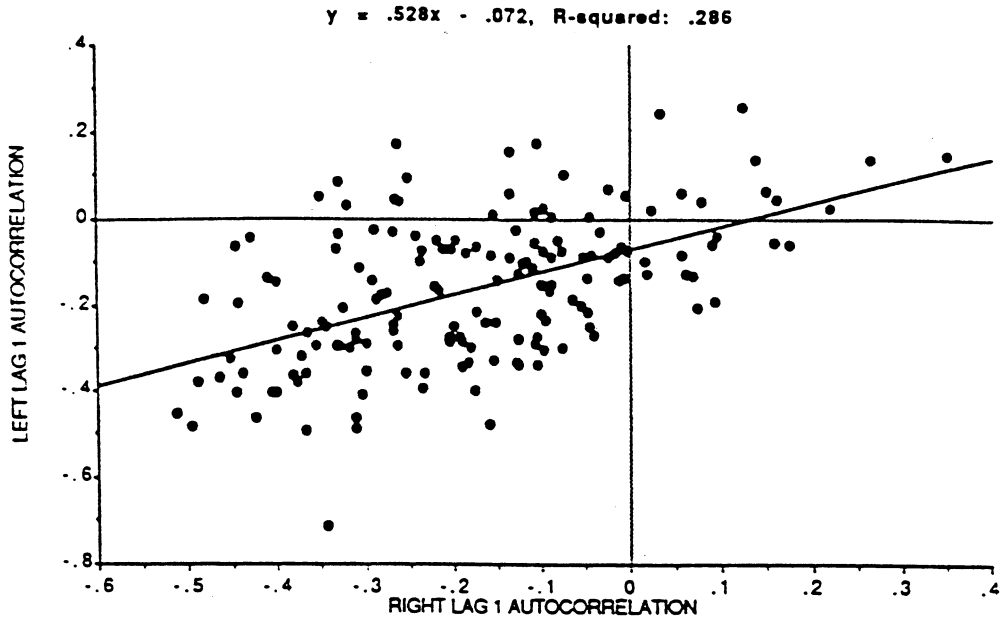


Fig. 2. Linear regression of left systems' lag 1 autocorrelations on right systems' lag 1 autocorrelations.

were restricted to the range: $0 > \text{lag 1 autocorrelation} > -0.5$.) Two multiple regressions, focusing on the motor and clock components of the right systems, were conducted on the overall data and repeated for the individual subject data. In each condition of absolute coordination, the two systems oscillated at a single common period and at a bounded phase relation (these features are documented in Rosenblum and Turvey⁹). The period mean was 1.117 s; the period range was 0.604–1.736 s. The phase mean was 189.4 deg; the phase range was 118–220 deg. Also, in each condition of absolute coordination the right system oscillated at a period other than its measured, characteristic period. The mean ratio of period to characteristic period was 1.32; the range of the ratio was 0.63–3.09. In one multiple regression, the right motor standard deviation (M_R) was regressed simultaneously on distance from characteristic period (τ/τ_0), period (τ), mean phase relation between right and left systems (ϕ), left motor standard deviation (M_L), and left clock standard deviation (C_L). In the other multiple regression, right clock standard deviation (C_R) was regressed on the same five independent variables. The coefficients for the independent variables and their associated probabilities are presented for both regressions on the overall data in Table 3. The r^2 for the motor analysis was 0.601; the r^2 for the clock analysis was 0.413. The total number of degrees of freedom was 111. The attrition from 162 was due to the combination of right and left lag 1 autocorrelations that were outside the theoretically accepted range. Conditions where either the left or right lag 1 autocorrelation was unacceptable were automatically excluded from the analysis. With respect to right motor fluctuations, τ/τ_0 , τ , and M_L made significant,

independent contributions in the overall data. That is, the motor component of a right system in absolute coordination was affected by the deviation of the period of absolute coordination from the system's characteristic period, by the duration of the period of absolute coordination, and by the motor component of the left system with which it was absolutely coordinated. With respect to right clock fluctuations, only C_L made a significant independent contribution. Importantly, right clock fluctuations in absolute coordination were not affected by the right system's deviation from its characteristic period.

On the basis of the overall analyses it would appear that in absolute coordination, (a) there is a motor subcomponent common to the two oscillatory systems (M_R is linked to M_L); (b) there is a motor subcomponent specific to the right oscillatory system (M_R is affected by τ/τ_0) and, presumably, a motor component specific to the left oscillatory system; and (c) there is a single, common timekeeper (C_R is linked to C_L but is unaffected by τ/τ_0). The analyses of individual subject data are strongly supportive of (b) and (c), and weakly supportive of (a). In the M_R multiple regression, only τ/τ_0 was significant for Subjects 1 and 3; for Subject 2, τ/τ_0 , τ , and M_L were significant. In the C_R multiple regression, only C_L was significant for Subjects 1 and 2; for Subject 3, only the τ beta weight reached significance in an analysis for which the r^2 was insignificant.

The periods of the left systems in isolation were not measured in the six sessions of the study. To analyse the left systems more completely, the periods of these systems considered as strictly gravitational pendulums were used as estimates of their characteristic periods (Table 1). Let a system's gravitational period

Table 3 Multiple regression analysis of component variances of right systems

Independent variable	Variance type			
	Coefficient	Motor Probability	Coefficient	Clock Probability
τ/τ_0	9.36	$P < 0.0006$	-0.09	ns
ϕ	-11.09	ns	6.87	ns
τ	33.65	$P < 0.0001$	14.30	ns
M_L	0.20	$P < 0.007$	0.01	ns
C_L	-0.01	ns	0.60	$P < 0.0001$

ns = nonsignificant at 0.05 level.

be designated by τ_r . Then the ratio τ/τ_r provides a deviation measure comparable to τ/τ_0 . The mean value of τ/τ_r for the left systems was 0.951 with range of 0.781-1.608. Two overall multiple regressions were computed focusing on the motor M_L and clock C_L variances of the left systems, with τ/τ_r , τ , ϕ , M_R and C_R as independent variables. The results reproduced closely the results of the right systems' analyses presented in Table 3. For the M_L regression, the beta weights of τ/τ_r , τ and M_R were significant ($P < 0.02$, < 0.004 and < 0.01 , respectively), those of ϕ , and C_R were insignificant ($P > 0.05$). For the C_L regression, only τ and C_R proved to be significant ($P < 0.02$ and < 0.0001 , respectively).

We present two other analyses for completeness. First, it is possible to gain a more precise impression of the rate of growth in right motor variances as a function of τ/τ_0 by expressing each right system's motor variance in absolute coordination in units of its motor variance in isolation. Normalized motor variance, that is, (motor variance at τ)/(motor vari-

ance at τ_0) as a function of τ/τ_0 in double logarithmic coordinates is presented in Fig. 3. The resulting power function is: normalized motor variance = $1.26(\tau/\tau_0)^{3.89}$ with 95% limits on the exponent of 3.27 (lower) and 4.51 (upper). Second, in the report of Rosenblum and Turvey⁹ the period fluctuation measure was that introduced by von Holst.⁵ The dependencies of right motor and clock variances, in double logarithmic coordinates as calculated with the von Holst relative fluctuation measure [Eqn (10)], on deviation from characteristic period in the region $\tau/\tau_0 \geq 1$ are shown in Fig. 4. Rosenblum and Turvey⁹ observed that the growth of relative fluctuations in period was symmetrical about $\tau/\tau_0 = 1$ but that it was statistically more reliable in the $\tau/\tau_0 \geq 1$ range than in the lower range largely because of the experimental limitation on the number of $\tau/\tau_0 \leq 1$ values. The r^2 values for the motor and clock linear regressions presented in Fig. 4 were 0.252 ($P < 0.0001$) and 0.046 ($P > 0.05$), respectively. That is, motor variance increased with deviations from characteristic period,

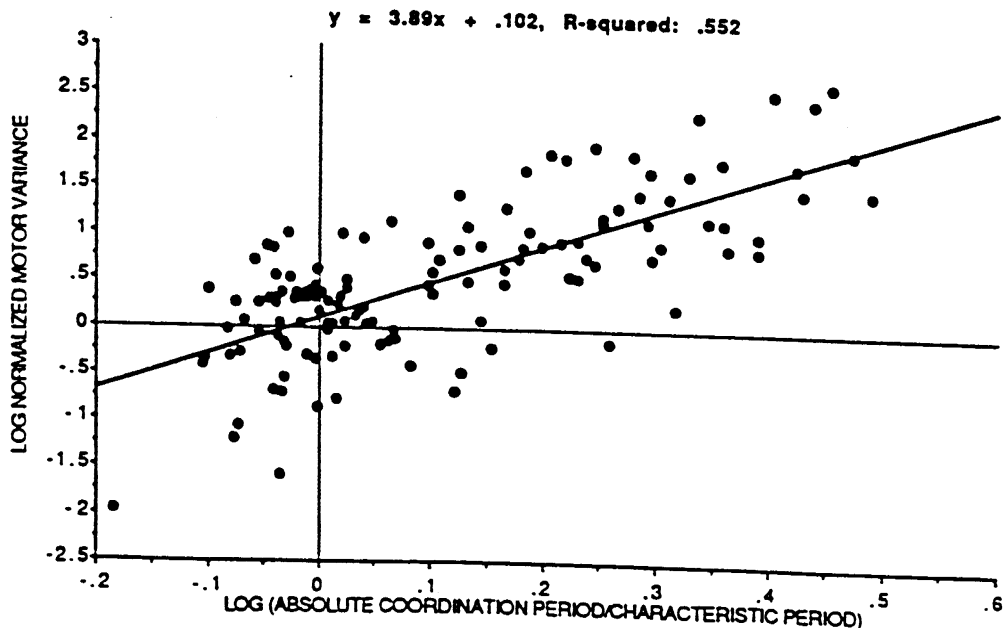


Fig. 3. Plot in double logarithmic coordinates of the ratio of motor variance at period of absolute coordination/motor variance at characteristic period (y -axis) against the ratio of period of absolute coordination/characteristic period (x -axis).

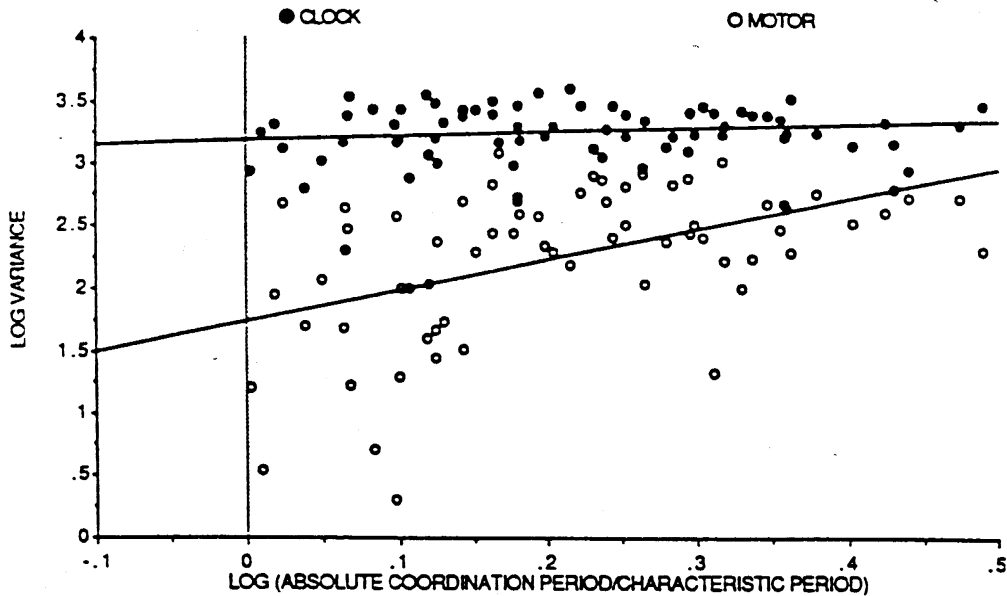


Fig. 4. Plot in double logarithmic coordinates of right systems' clock and motor variances as a function of deviation from characteristic period. Clock and motor variances represented in this figure are computed from the von Holst period variance measure (see text for details).

but clock variance did not, confirming the main observation with motor and clock variances computed conventionally.

DISCUSSION

The present results support the second of the two hypotheses proposed in the introduction: the clock variances of right and left systems were correlated, and only the motor variance was affected by a wrist-pendulum system's departure from characteristic frequency. The implication is that absolute coordination is to be understood as the assembling of a single common clocking process and not as the linking of already established clocks. Additionally, the present results complement those of an experiment by Turvey *et al.*¹¹ in which absolute coordination of wrist-pendulum systems moving forward simultaneously (in phase, symmetric) was compared with absolute coordination of wrist-pendulum systems moving in opposite directions simultaneously (out of phase, asymmetric). The Turvey *et al.*¹¹ experiment revealed that the contrast of phase symmetry affected right and left clock variances (out of phase clock fluctuations were largest) but did not affect right and left motor variances. When the results of the two experiments are combined a clear cut double dissociation emerges: clock variance is affected by phase symmetry but not by deviation from characteristic frequency; motor variance is affected by deviation from characteristic frequency but not by phase symmetry.

What might be inferred from the different dependencies of the motor and clock variances? In swinging a hand-held pendulum, radial flexion opens the wrist

joint and ulnar flexion closes the wrist joint. This intracycle pattern of muscle activations can be said to comprise the motor component of the Wing and Kristofferson analysis. Wing and Kristofferson's motor component, therefore, is conceptually close to what is commonly termed a central pattern generator (CPG). Functional models of the neural networks underlying locomotion typically ascribe to a single circuit, namely, the CPG, the responsibility for both (a) producing the proper phase relations between muscles within a cycle and (b) generating the cycle-to-cycle timing.³ The identification of (a) as the source of motor variance, and the different dependencies of clock variance, suggest that (a) and (b) are separate functions and only function (a) should be assigned to the CPG. This conclusion comports with the separation of timing and pattern generating functions suggested by Lennard⁶ and described in the introduction.

Positive lag 1 autocorrelations

Although the lag 1 autocorrelations in the present study were overwhelmingly negative and in the range of 0 to -0.5 as predicted by the theory of Wing and Kristofferson, some were positive. These positive values were mainly in the vicinity of periods equal to or less than the characteristic period (see Fig. 1). The analysis of Wing and Kristofferson attributes period variance wholly to neural factors. There is good reason to expect, however, that where a body segment is oscillating relatively fast, additional non-neural factors enter into the determination of period variance. One such additional non-neural factor is an elastic recoil, specifically, the storage of mechanical energy that occurs when contracted muscles are stretched forcibly immediately before shortening.¹ If

this factor is exploited in the performance of a rhythmic movement, and if its magnitude is variable from cycle-to-cycle, then the variance in period will be due partly to the variance in elastic recoil. Adding further sources of variance to the model of Wing and Kristofferson can be expected to affect the equation set in non-trivial ways, resulting, perhaps, in predictions of positive lag 1 autocorrelations under certain conditions of oscillation.

Component variances and phase deviations from 0 and 180 degrees

In the present study, subjects executed their absolutely coordinated motions out of phase. As noted, however, they usually produced a phase relation greater or smaller than 180° . If any given movement phase relation of x° reflects a neural activation phase relation of x° , and if 0 and 180° identify highly preferred phase relations in the sense of 'attractors',⁴ then effects of deviations from 0 and 180° on the component variances should have been observed. The absence of such effects suggests that the different phase relations exhibited in the absolute coordination of wrist-pendulum systems may not be indicative of different neural processes—e.g. a right-left movement phase relation that deviates from 180° may not identify a right-left neural activation phase relation that deviates from 180° .⁹

CONCLUSIONS

Absolute coordination is perhaps the most basic of all movement coordinations (it typifies walking, running, hopping, swimming, and flying), yet the principles behind it remain largely unknown. In the present article we have applied an analysis developed by Wing and Kristofferson^{13,14} to data on the absolute coordination by human subjects of hand-held pendulums. The analysis assumes an independence of timekeeping and motor implementation functions. The major expectations from this assumption with respect to a time series treatment of sequential cycle durations were confirmed. Moreover, the results reported in this article and elsewhere¹¹ identify in absolute coordination reliable and theoretically interesting differences between the two functions as they are

measured by the method of Wing and Kristofferson. One major overarching conclusion, therefore, is that the independence assumption and the details of its interpretation may map onto real aspects of rhythmic movement.

Other conclusions follow from the preceding and bear on efforts to describe absolute coordination in neural and dynamical terms. First, there appear to be two isolable and independent aspects of the motor implementation component. One aspect can be linked to the intracycle phasing of muscle contractions. This aspect is sensitive to the characteristic period and becomes increasingly more variable with increasing deviations of the operating period from the characteristic period. It expresses the maintenance tendency as defined by von Holst.⁵ The other, perhaps less prominent aspect of motor variance, may be linked to intentional modifications in rhythm designed to maintain a particular constraint (e.g. "move the two limbs together at the most comfortable frequency"). Unlike the first motor aspect, which is specific to each of the units in absolute coordination, the second motor aspect is common to the two units. Second, it appears that absolute coordination is characterized by a single timekeeping function. This function expresses the magnet effect of von Holst but its apparently unitary nature contrasts with his original formulation of a compromise of two or more clocks. A notable feature of the timekeeper is that it is confined to the cycle-to-cycle timing of the rhythm. Within-cycle phasing of events is the duty of the first motor aspect. The timekeeping function, therefore, is probably not captured by the familiar neural concept of CPG. The first motor aspect provides a better fit to the traditional 'CPG role'. These conclusions agree with a recent suggestion⁶ that the neuronal underpinnings of the patterning of activity within a cycle are functionally distinct from the neuronal underpinnings of the cycle-to-cycle timing of locomotory activity.

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