

ABSOLUTE COORDINATION: AN ECOLOGICAL PERSPECTIVE§

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ABSTRACT

The ecological perspective on the coordination of movement is discussed with regard to the most basic, pervasive form of coordination, namely, absolute coordination. The working hypothesis of the ecological perspective is that coordinations are largely due to general laws and principles. Dynamical explanations of phenomena such as von Holst's magnet effect and maintenance tendency, as well as locomotory time allometries of both large and small organisms, are reviewed. The role of information in the functioning of dynamically based action systems is discussed, where information is understood in the Gibsonian (1979) specification sense.

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INTRODUCTION

In this chapter we illustrate the ecological view of coordination of movement by reviewing research and theory on absolute coordination (von Holst, 1937/1973, 1939/1973). Two or more limbs or two or more body segments are in absolute coordination when they oscillate at the same period and maintain, thereby, a steady phase relation between them. This state has been contrasted by von Holst with relative coordination, in which the period of oscillation of two coupled oscillators is not equal and, hence, the phase relation between the two oscillators is changing constantly. The research and theory in question has focused on the absolute coordination of what might be termed "pendular clocking movements." As instanced in walking and running, the components in absolute coordination are limbs whose individual motions are pendulum-like (they are raised and lowered with respect to gravity) and clock-like (the raising and lowering is done at regular intervals and to approximately the same degree each cycle). This type of absolute coordination is by far the most prevalent. Not only does it characterize terrestrial locomotion but also it is common to many other everyday activities. The principles behind this type of absolute coordination remain, however, largely unknown.

Neurophysiological theories of absolute coordination assume that the nervous system is causally responsible for the coordinating. Theories of arthropod and vertebrate locomotion refer to multiple central rhythmic-pattern generators, at least one per limb (Grillner, 1975; Shik & Orlovskii, 1976; Stein, 1977) and possibly one per joint (e.g., Edgerton, Grillner, Sjogstrom, & Zangger, 1976). In neurophysiology, the problem of absolute coordination is to describe how the central rhythmic-pattern generator of one limb is coordinated with the central rhythmic-pattern generator of another limb. One proposed neural mechanism is a coordinating neuron that sends a neural copy of the motor discharge of one limb to the other (Stein, 1971, 1976, 1977). Another proposed neural mechanism is the mutual inhibition of one rhythmic unit by another rhythmic unit (or every other rhythmic unit), without mutual excitation (Stafford & Barnwell, 1985).

In the ecological approach to absolute coordination, the nervous system is not regarded as solely responsible, in causal terms, for the interaction. Rather, the nervous system is seen as the *medium*

supporting the causal agencies of coordination. The burden of explanation is shifted from modular anatomical units that are ascribed a special causal function a priori to very general physical principles that coordinate both animate and inanimate things. Biological things have not only biological properties but also physical ones, and it would be expeditious for biological things to exploit the organizing that takes place, a posteriori, as a consequence of having physical properties. The purpose of an ecological analysis is to determine the degree to which coordination phenomena can be understood in terms of lawful regularities and principles at the ecological scale, the scale at which the physical entities of animal and environment are defined (Gibson, 1979; Turvey & Carello, 1986).

In this way of proceeding, the high dimensional biological situation (a number of limbs, each with their detailed neural, vascular, and muscular microstructures) can be given a low dimensional, physical redescription. Much work has been done from this perspective in both theoretical (Beeke & Beek, in press; Feldman, 1986; Kelso, 1986; Kugler & Turvey, 1987; Schöner & Kelso, 1988) and empirical (Feldman, 1966, 1980; Kay, Kelso, Saltzman, & Schöner, 1987; Kugler & Turvey, 1987; Turvey, Rosenblum, Schmidt, & Kugler, 1986) domains. This work is aimed at Bernstein's problem of degrees of freedom (Bernstein, 1967; Turvey, 1977; Turvey, Shaw, & Mace, 1978), namely, how components comprising very many degrees of freedom are regulated to yield behaviors of very few degrees of freedom. The many degrees of freedom of an organism are not all controlled by the organism. Many, perhaps most, are controlled by physical constraints that form the context for a movement. In this chapter, we try to illustrate how the presence of physical properties and their functional relations explain many facts about the coordination of limbs in locomotion.

From the ecological perspective, absolute coordination is to be understood in terms of the macroscopic observables of limb complexes (comprising bones, joints, muscular, vascular, and neural components) organized to function as oscillatory units. As such, the individual units of analysis are continuous with the rhythmic "automatisms" identified in von Holst's (1937/1973, 1939/1973) investigations of the interactions among the rhythmically moving fins of the fish *Labrus*. Von Holst discovered three macroscopic phenomena that oscillating fins often exhibit in absolute and rela-

tive coordination, namely, *superposition*, *the magnet effect*, and *the maintenance tendency*. Von Holst noticed that one fin's oscillation sometimes showed up as a second periodicity in another fin's oscillation; the one oscillation was superimposed upon the other. Additionally, he noticed a magnet effect. Each fin oscillator tries to draw the other fin (or fins) to its characteristic period, the tempo it exhibits when oscillating alone. Hence, two coupled oscillators with different endogenous tempos would settle ultimately on a cooperative tempo that was in between the tempos each preferred individually. Further, each oscillator tries to maintain its identity when participating in such a coupling; that is, even though it is operating at the cooperative period, there are residual effects of its preferred period, as indexed by the fluctuations around the mean cooperative period. A physical basis for the latter two features of absolute coordination is suggested later in this chapter.

It must be pointed out that ecological investigations of the physical principles underlying coordination are concerned with biological coordination in general. That is, these investigations are interested not only in the coordination between limbs (as in locomotion) but also in the coordination between an animal and its environment (as in fulfilling an intent). Examples of the latter research are provided by Warren (1984), Lee (1980), and others and are summarized in Turvey and Carello (1986). This chapter is limited to a review of the theory and research within the ecological framework that address the absolute coordination of limbs. We consider how this coordination arises as an emergent property through the operation of physical principles that organize parts into wholes. We then show that this physical modeling has implications for understanding the scalings of locomotory cycles to body proportions found in species as diverse as quadrupeds and insects. Finally, we demonstrate that the linkage of the oscillators in absolute coordination has an informational basis and suggest what form this information might take. We begin with the experimental paradigm used and a physical model for the component pendular clocking movements.

THE "PENDULAR CLOCKING MODE" METHODOLOGY

The pendular clocking movements of a single limb of a human subject have been examined using hand-held pendulums that are swung at the wrist joint with the forearm parallel to the ground (Kugler & Turvey, 1987; Turvey et al., 1986; Turvey, Schmidt, Rosenblum, &

Kugler, 1988). The subject was instructed to swing the pendulum at a comfortable, preferred tempo—the tempo that felt suitable for continuous work. As a rule, people are very good at finding and sustaining the tempo at which they prefer to perform a given task (e.g., Frischeisen-Köhler, 1933; Smoll, 1975a, 1975b). There is evidence to suggest that a preferred tempo corresponds to the working pace that represents a near minimum value of energy per cycle (e.g., Corlett & Mahadeva, 1970). For the task of swinging hand-held pendulums, a person will settle on different characteristic periods for pendulums of different masses and lengths. The smaller the pendulum's moment of inertia, the smaller the period.

How is the preferred period of oscillation of a single wrist-pendulum system to be understood? Physically speaking, the answer ought to follow from the fact that such a system comprises a body oscillating as a function of two potentials, namely, gravity and the restorative forces formed by the limb musculature and its associated metabolism. There is evidence that these restorative forces in rhythmic movements are based partly upon the inherent elasticity of muscle (Cavagna, 1977). Further, the elastic stiffness assembled in a given movement can be varied by manipulation of the co-contraction of the flexors and extensors at the joint (Feldman, 1980).

The behavior of a wrist-pendulum system can be modeled most simply as a pendulum in the gravitational field with a linear spring attached, the spring corresponding to the restorative contribution of the musculature and the attendant metabolism (Figure 4.1). The equation governing the period of this system is

$$\tau = 2\pi[ML^2/(gML + kb^2)]^{0.5} \quad (1)$$

where M is the mass of the pendulum, L is the length of the pendulum, g is the acceleration due to gravity, k is the elastic stiffness of the attached spring, and b is the distance from the spring to the center of rotation of the pendulum (see Turvey et al., 1988). One can calculate a subject's contribution to the period from this model by measuring the period of oscillation and assuming that the mass and length involved are those of the simple pendulum equivalent of a compound pendulum, consisting of the mass of the

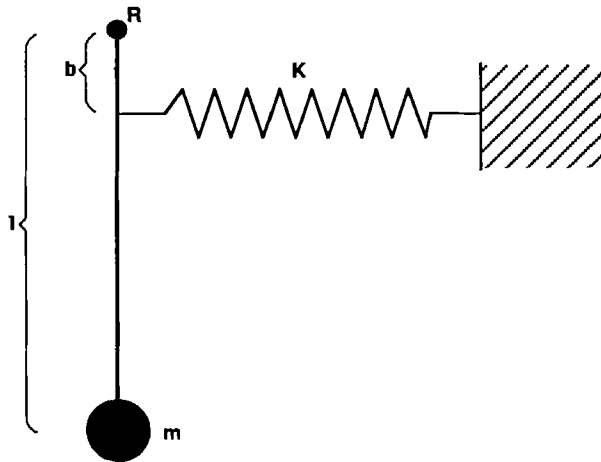


Figure 4.1. The hybrid mass-spring simple pendulum model, where m is the mass of the pendulum, l is the length of the pendulum, K is the elastic stiffness of the attached spring, b is the distance from the spring to the center of rotation of the pendulum, and R is the center of rotation.

wrist, the mass of the rod, and the mass of the attached weight, each at different lengths from the point of rotation.

The value of the elastic contribution is not constant across different pendulums but increases nonlinearly with the pendulum's inertia (Figure 4.2). An increase in the elastic stiffness of the musculature as a function of the load has been observed similarly in the calf muscle of humans landing from a fall without bending their knees (Cavagna, 1970). Assuming that the muscular co-contraction of the flexors and extensors gives rise to the macroscopic physical property of an elastic potential, the characteristic periods (τ) of single wrist-pendulum system movements can then be understood as a consequence of the physical properties comprising the system. A mass is rotating about an axis under the influence of two forces, namely, gravity and an assembled elastic potential whose magnitude depends upon the load involved. This understanding of the basis of a preferred tempo contrasts with the view that preferred tempos in rhythmic tasks are controlled exclusively by physiologi-

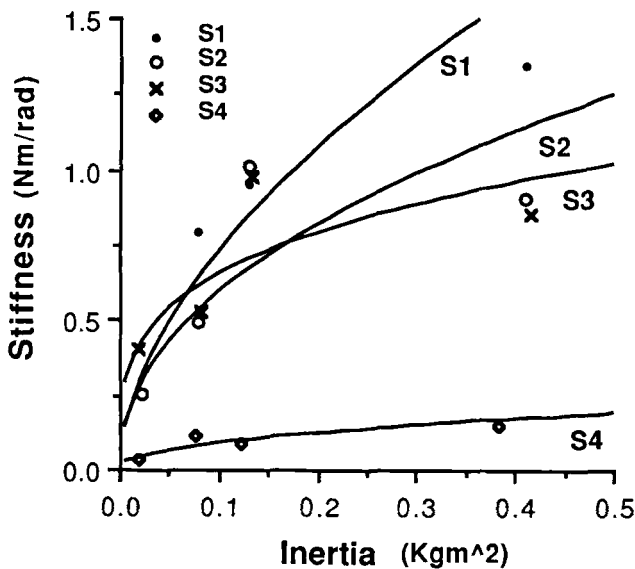


Figure 4.2. Assembled elastic potential (K) versus inertia of a wrist-pendulum system for 4 subjects of Kugler & Turvey's (1987) main experiment (S1: $K = 2.65I^{0.56}$, $R^2 = .92$; S2: $K = 1.728I^{0.46}$, $R^2 = .80$; S3: $K = 1.20I^{0.28}$, $R^2 = .72$; S4: $K = 0.266I^{0.48}$, $R^2 = .83$).

cal or cognitive processes (Smoll, 1982). The only variable that needs to be controlled to produce different characteristic periods in a wrist-pendulum system is the elastic potential provided by the musculature (see Feldman, 1980, for a theory of how the control is effected).

THE MAGNET EFFECT IN THE ABSOLUTE COORDINATION OF WRIST-PENDULUM SYSTEMS

The wrist-pendulum methodology has been used to examine the absolute coordination of pendular clocking movements. The task is to swing two wrist-pendulums (one in each hand) in absolute coordination at the same period and either in the same direction (0° phase difference) or in opposite directions (180° phase difference) (Kugler

& Turvey, 1987; Turvey et al., 1986). These two versions of absolute coordination resemble the organization of symmetric and asymmetric gaits, respectively, in quadrupeds. The subject is asked to find the period that is most comfortable for swinging the pendulums simultaneously. Significantly, the two wrist-pendulum systems to be coordinated can be either identical or different in mass and length parameters. When they have identical parameter magnitudes, the characteristic periods of the wrist-pendulum systems when swung alone are equal; when they have different parameter magnitudes, the characteristic periods of the wrist-pendulum systems when swung alone are different. The ability to manipulate the characteristic periods of the component oscillators to be coordinated permits a replication of the circumstances of von Holst's (1937/1973, 1939/1973) experiments with fish, in which fin oscillators of different inherent periods were coordinated. Given von Holst's work, a central question is whether or not the cooperative period follows from each oscillator drawing the other oscillator toward its own characteristic period. That is, Is there a magnet effect?

Figure 4.3 replots data from Kugler and Turvey (1987, main experiment). This new plot gives (a) the difference between the cooperative period ($\tau_{\text{cooperative}}$) and the characteristic period of the left system (τ_{left}) as a function of the difference between the two characteristic periods ($\tau_{\text{right}} - \tau_{\text{left}}$) and (b) the difference between the cooperative period ($\tau_{\text{cooperative}}$) and the characteristic period of the right system (τ_{right}) as a function of the difference between the two characteristic periods ($\tau_{\text{right}} - \tau_{\text{left}}$). To a first approximation, as the absolute difference in the characteristic periods of the component oscillators increases, the deviation of the cooperative period from a component period increases. What dictates the cooperative period and its relation to the characteristic periods of the component oscillators? One answer might be that it is a simple function of the periods of the two pendulums in isolation, as suggested by von Holst (1939/1973) and as suggested by a central pattern-generator analysis. A different answer follows from entertaining the possibility, as Kugler and Turvey (1987) did, that the two wrist-pendulum systems form a common or cooperative period in a manner analogous to ordinary physical pendulums that are coupled rigidly. If the coupling between wrist-pendulum systems were rigid—more exactly, if the nervous system simulated a rigid coupling—then the cooperative

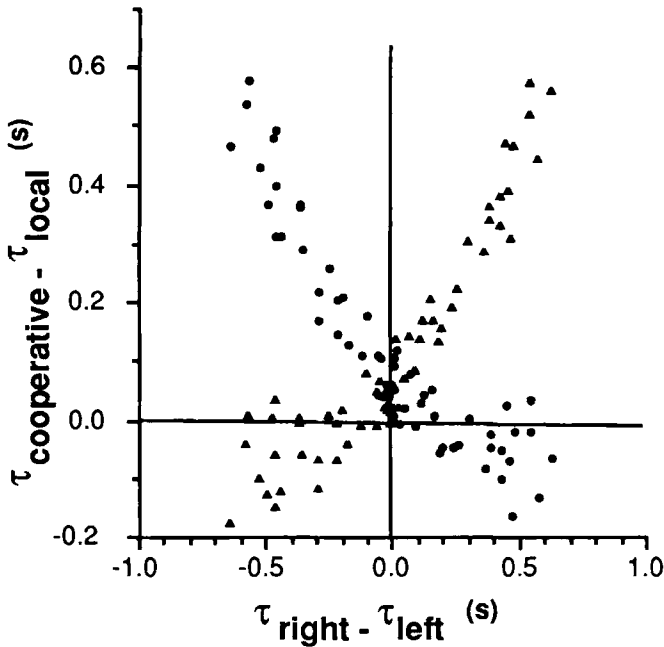


Figure 4.3. The magnet effect in the coordination of wrist-pendulum systems. The triangles represent the deviation of the cooperative period from the preferred period of the left pendulum, and the circles represent the deviation of the cooperative period from the preferred period of the right pendulum. These deviations increase as the differences in the two preferred periods ($\tau_{\text{right}} - \tau_{\text{left}}$) increase.

period at which they settle would follow from the theory of the compound pendulum as advanced by Huygens in the 17th century (Bell, 1950). For two simple pendulums coupled rigidly to form a compound pendulum, the characteristic period of the resultant system depends upon the length

$$L_v = (M_1 L_1^2 + M_2 L_2^2) / (M_1 L_1 + M_2 L_2) \quad (2)$$

where M_1 , L_1 refer to the mass and length, respectively, of one of the simple pendulums and M_2 , L_2 refer to the mass and length, respectively, of the other simple pendulum. The length L_v is the distance to the compound pendulum's center of oscillation (at which the masses are essentially summated and concentrated) from its rota-

tion axis. In the case of so-called rigid coupling of wrist-pendulum systems, the resultant "virtual single system" parameter magnitudes of L_v (distance to center of oscillation) and M_v (total mass of component parts) are physical properties that arise as a consequence of the physical principles behind Huygens's (Bell, 1950) derivation, as those principles are manifest in biological tissue (see Kugler & Turvey, 1987, for the details).

There is a simple test of whether or not the cooperative period is a function of some local linear combination of the periods of the individual oscillators (e.g., some weighted mean of the two) or a function of a physical cooperativity of the individual oscillators as suggested by the Huygens (Bell, 1950) analysis. The test is whether or not the variation of the cooperative period accounted for by the squared virtual length parameter (L_v) is significantly greater than that accounted for by the characteristic periods of the two pendulums (τ_{left} and τ_{right}). As shown in Table 4.1 with the data from Kugler and Turvey's (1987) main experiment, a multiple regression of the cooperative period on L_v , τ_{left} and τ_{right} revealed that L_v accounted for most of the variation of the cooperative period, with the characteristic periods of the individual systems accounting for relatively less overall. In short, the virtual length (which is, roughly speaking, an emergent physical quantity) dictated the cooperative period. This result, it may be argued, points to a lawful basis for the common period, or magnet effect, exhibited by two pendular systems in comfortable, absolute coordination, a basis that depends, presumably, upon purely physical properties of biological systems, under certain boundary conditions.

IMPLICATIONS OF THE VIRTUAL SYSTEM ANALYSIS FOR TIME ALLOMETRIES

The analysis of Kugler and Turvey's (1987) data demonstrates that two limb-like oscillators in absolute coordination can be given a macroscopic redescription as a single virtual oscillator. The cooperative period at which the two limb-like systems settled was linked to the length L_v of this virtual oscillator. As noted, the virtual oscillator has a virtual single concentration of mass defined as the sum of the individual masses and located at the end of this length. Further, it can be assumed that the virtual oscillator has a virtual single restorative potential to represent the contribution of the left and right limb neuromusculatures and metabolisms needed to sustain

Table 4.1

Relative Contribution of Virtual and Local Oscillator Systems to the Cooperative Period

Subject	Multiple regression standardized coefficients (β)		
	Virtual length (L_v)	Characteristic period of left system (τ_l)	Characteristic period of right system (τ_r)
1	.792**	.219*	.062
2	.557**	.149	.453**
3	.495**	.427**	.267
4	.930*	.042	.004

* $p < .05$

** $p < .01$

the oscillation. Hence, with this virtual system analysis, the two wrist-pendulums in absolute coordination can be redescribed as the single spring-pendulum system depicted in Figure 4.1, and the equation $\tau = 2\pi [ML^2/(gML + kb^2)]^{0.5}$ can be predicted to govern them.

Terrestrial locomotion typifies absolute coordination, as noted. An important question to raise is whether or not the physical model depicted in Figure 4.1 can explain the periodic timing of the absolute coordination exhibited in locomotion. Surprisingly, the model rationalizes the different time allometries (that is, how an animal's locomotory cycle time scales to the magnitudes of its body) found over the ranges of different lengths occupied by insects, hummingbirds, small birds, large birds, medium-sized quadrupeds, and large quadrupeds.

If a quadruped's set of limbs is regarded as a compound pendulum, convertible into a virtual pendulum length L_v , then for quadrupeds in excess of 10 kg, the period found in walking, trotting, and canter-

ing approximates closely the cycle times of a freely oscillating pendulum at length $L_v/2$, $L_v/7$ and $L_v/10$, respectively (Kugler & Turvey, 1987). What this means is that all quadrupeds' cycle times for a particular gait are related regardless of their differences in size and shape. For example, the warthog at 85 kg and the giraffe at 1,000 kg walk at step cycle times (0.784 s and 2.083 s, respectively) that are very much the same proportion of each animal's virtual limb length. How does this empirical result fit with the equation for the pendular clocking mode? The denominator of the equation can be separated into the torsional stiffness due to gravity $G (= gML)$ and the torsional stiffness $K (= kb^2)$ due to the elastic and metabolic contribution from the individual. It proves to be the case (Turvey et al., 1988) that the scalings of the periods of the gaits to L_v follow from the pendular clocking equation if *the elastic restoring torque K assembled by each animal is a constant multiple of the gravitational restoring torque G affecting each animal*, with a different multiple for each gait. If $K/G = 1$ then the equation reduces to $\tau = 2\pi(L/2)^{0.5}$, which characterizes walking; if $K/G = 6$ and $K/G = 9$, then the equation reduces to $\tau = 2\pi(L/7)^{0.5}$ and $\tau = 2\pi(L/10)^{0.5}$, which characterize trotting and cantering, respectively (Turvey et al., 1988). Further, the time allometries exhibited for quadruped locomotion (across all gaits) are $\tau \propto M^{0.125}$ or $M^{0.166}$ and $\tau \propto L^{0.5}$ (see Kugler & Turvey, 1987; Pennycuik, 1975; Turvey et al., 1988). The pendular clocking equation can be translated into biological terms on the assumption that there is geometric similarity in the size and shape of the organism (that is, $L = M^{0.3}$; Peters, 1983). If this is done, and one calculates periodic times for quadruped-sized masses and lengths at constant K/G ratios from the equation, then a simple regression analysis reveals that the scaling of time to mass and length is $M^{0.166}$ and $L^{0.5}$, respectively. This scaling agrees with observation.

The pendulum clocking mode equation $\tau = 2\pi[ML^2/(gML + kb^2)]^{0.5}$ also seems to explain the diverse time allometries found for other creatures across a great range of sizes. This feature is revealed if one takes into account both geometric similarity and the fact that the elastic potential K scales, on the average, to the mass of the animal to the first power (Turvey et al., 1988). The elastic system is constructed in different ways across the range of animals bounded by the smallest insect and the largest quadruped. In insects, it is built from at least three elastic materials: (a) the solid skeletal cuticle of the thoracic box, (b) a typical elastomere in the form of protein re-

silin, and (c) an elastic component in the myofibrils (Buchtal & Weis-Fogh, 1956). Insects have no mechanism for adjusting the magnitude of the elastic potential. Vertebrates, in contrast, can manipulate the magnitude of the stiffness by varying the co-contraction of the flexors and the extensors at the joint.

This difference in elastic structures has behavioral consequences. The mechanism used by insects restricts them to moving their wings at an almost constant period, irrespective of flight maneuvers and speed of travel (Sotavalta, 1952, 1954). The same appears to be true of birds (Greenewalt, 1960, 1975). In contrast, the elastic mechanism used by quadrupeds lets them walk, trot, and canter at a number of different frequencies although each gait does exhibit a preferred period that appears to be metabolically least costly (Hoyt & Taylor, 1981). Various analyses suggest, however, that despite differences in the construction of elastic machinery, there is a constant relation across animals between the elastic potential assembled at the characteristic frequency and body mass; that is, K increases as the first power of body mass (Turvey et al., 1988).

If the pendular clocking equation is translated into biological terms and periodic times are calculated (with length scaling as mass to the one-third power and K scaling as mass to the first power) across the range of lengths from the smallest insect to the largest quadruped, then the regression of log period on log length and log period on log mass exhibit a number of interesting results. The regressions are significantly quadratic and significantly linear (see Figures 4.4 and 4.5). For length < 0.1 m, period scales as length to the 0.913 power and mass to the 0.305 power; for length > 0.1 m, period scales as length to the 0.543 power and mass to the 0.183 power. These are the magnitudes of the time allometries for insects (< 0.1 m) and quadrupeds (> 0.1 m), respectively. The region of the transition between the two slopes, that is, the region of length scales in the vicinity of 0.1 m, is the region occupied by large birds, small birds (passerines), and hummingbirds. Whereas the wing periods of large birds scale to length close to the 0.5 power, those of the small birds scale close to the 1.0 power (Turvey et al., 1988). Moreover, for hummingbirds, the relation in double logarithmic coordinates between period and length is largely quadratic, yielding what has been traditionally an odd scaling (Greenewalt, 1975). Collectively, this pattern of results for large birds, small birds, and hummingbirds is

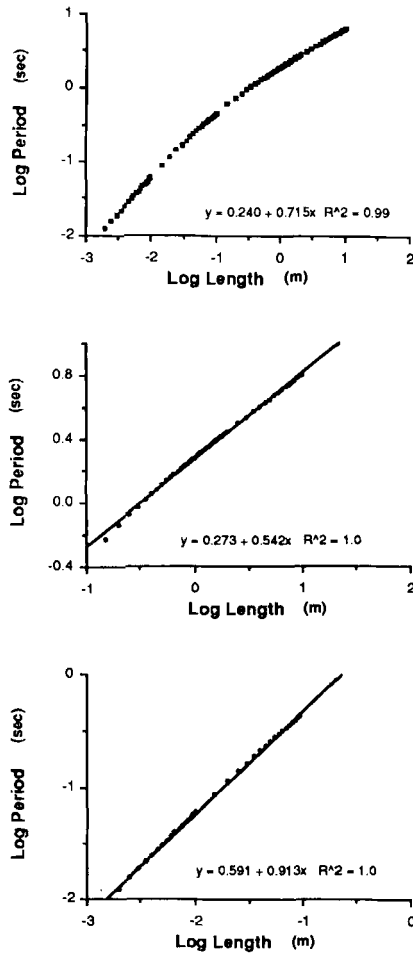


Figure 4.4. Log period plotted against log length for the pendular clocking mode equation over the length scales of insects, birds and quadrupeds. The equation is constrained biologically: $m \propto l^3$, and $K \propto m$. Upper panel is total range of lengths. Middle and lower panels are restricted to length > 0.1 m and length < 0.1 m, respectively. *Note.* From "On the Time Allometry of Coordinated Rhythmic Movements" by M. T. Turvey, R. C. Schmidt, L. D. Rosenblum, and P. N. Kugler, 1988, *Journal of Theoretical Biology*, 130, p. 332. Copyright 1988 by Academic Press. Reprinted by permission.

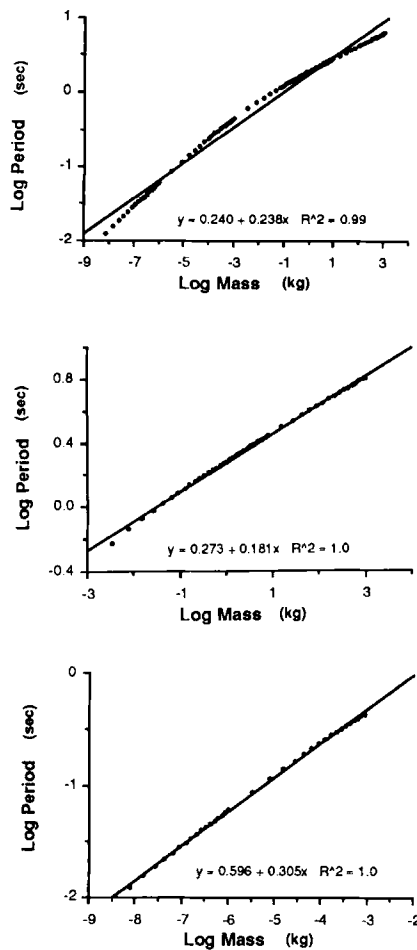


Figure 4.5. Log period plotted against log mass for the pendular clocking mode equation over the length scales of insects, birds and quadrupeds. The equation is constrained biologically: $m \propto l^3$, and $K \propto m$. Upper panel is total range of lengths. Middle and lower panels are restricted to length > 0.1 m and length < 0.1 m, respectively. Top panel regression line shows how the universal biological time scale ($\tau \propto M^{0.25}$) is obtained from the pendular clocking equation. *Note.* From "On the Time Allometry of Coordinated Rhythmic Movements" by M. T. Turvey, R. C. Schmidt, L. D. Rosenblum, and P. N. Kugler, 1988, *Journal of Theoretical Biology*, 130, p. 323. Copyright 1988 by Academic Press. Reprinted by permission.

rationalized by the biological version of the pendular clocking equation. These creatures are to be found near the inflection of the functional relation (in Figures 4.4 and 4.5). In sum, the pattern of time allometries does not point to shifts in biological design for different creatures but to the physical consequences of the pendular clocking mode at different lengths.

THE MAINTENANCE TENDENCY IN THE ABSOLUTE COORDINATION OF WRIST-PENDULUM SYSTEMS

So far, we have shown how the cooperative frequency exhibited in absolute coordination can be the consequence of very general physical principles rather than specific anatomical devices. In so doing, we have given a physical basis for the time allometries found in animal locomotion and von Holst's (1937/1973, 1939/1973) magnet effect. We now turn to von Holst's (1939/1973) maintenance tendency. We wish to show that the maintenance tendency (a) is found in the absolute coordination of wrist-pendulum systems and (b) can be explained by dynamic modeling of action systems.

Von Holst (1939/1973) saw evidence for the maintenance tendency in the relative coordination of rhythmic fin movements. For example, whenever one fin of a coordinated pair was stopped from moving, the other would move from the cooperative period to its characteristic period. Further, he found that when two fins had different characteristic periods, the faster one would reach its peak excursions before the slower one did. Stein (1973, 1974) corroborated this finding in the interappendage coordination of crayfish swimmerets. He found that the degree of phase lag between the two swimmerets was correlated with the difference between the characteristic periods of the two swimmerets. Other evidence for the maintenance tendency is an increase in the variability of periodic timing of a rhythmic unit as it is moved away from its characteristic period by coupling with another rhythmic unit. This result has been found in human finger tapping (Scripture, 1899) and in human arm movements (Smoll, 1982).

Do wrist pendulum systems show the tendency to maintain their intrinsic steady states when in absolute coordination; that is, do they show a maintenance tendency? A series of six experiments comprising a total of 54 different wrist-pendulum systems was designed to answer this question. The subjects were instructed to

swing the pendulums in an alternating fashion (180° out of phase) and at the most comfortable tempo (see Rosenblum & Turvey, 1988, for a complete description of the methodology.) In each of these experiments, three subjects had to coordinate the same right-hand pendulum (the "target" system) with a number of different-sized, left-hand pendulums. The effect of the different-sized, left-hand pendulums was to pull the target system away from its characteristic period by varying amounts. Because of the magnet effect, a pendulum larger than the target pendulum will cause the target system to move more slowly than its characteristic period whereas a pendulum smaller than the target pendulum will cause the target system to speed up. This design allowed the deviation from preferred period to be indexed by τ_1/τ_0 , where τ_1 is the period of oscillation exhibited by the target wrist-pendulum in a coupling and τ_0 is the period of the target wrist-pendulum when swung alone. To measure fluctuations, von Holst's (1939/1973) relativized root mean square variance measure was used:

$$t_{fluc} = \sqrt{[(\sum(t_{pv} - \text{meant}_{pv})^2 / \text{meant}_{pv}) / (n_{pv} - 1) + (\sum(t_{vp} - \text{meant}_{vp})^2 / \text{meant}_{vp}) / (n_{vp} - 1)]} \quad (3)$$

where *pv* means peak-to-valley half cycles, *vp* means valley-to-peak half cycles, and *n* is the number of cycles. Figure 4.6 shows how the relative periodic fluctuations change as a function of τ_1/τ_0 . As the target pendulum is pulled away from its preferred period ($\tau_1/\tau_0 = 1$), the instability of the period increases. This is true whether the target pendulum is made to slow down ($\tau_1/\tau_0 > 1$) or to speed up ($\tau_1/\tau_0 < 1$). There is a leveling off, however, in the range $\tau_1/\tau_0 \geq 1.5$. Up to this point, the increase of periodic fluctuations with deviation from preferred tempo is symmetrical on both sides of $\tau_1/\tau_0 = 1$. Further, the same basic pattern is true for relativized amplitude fluctuations (computed from the amplitude version of the equation for the variance measure) except that they increase faster when the target pendulum is made to move faster than preferred (Figure 4.7).

The maintenance tendency in coordinated wrist-pendulum movements is indexed not only by fluctuations around the mean states of period and amplitude but also by the phase lag between the wrist-pendulum systems. The phase difference between systems increases with the magnitude of the difference between their charac-

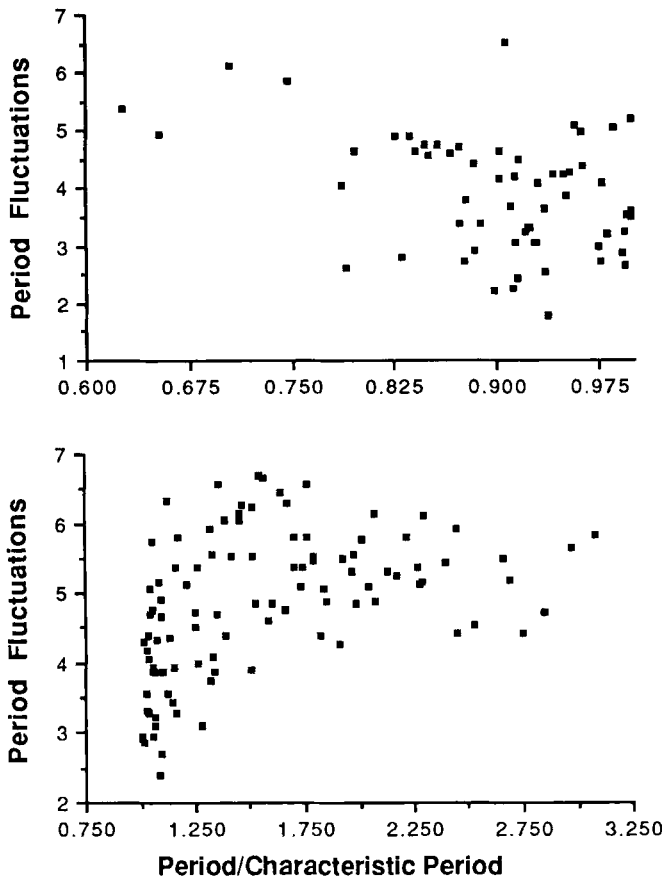


Figure 4.6. The maintenance tendency in wrist-pendulum coordination as revealed by periodic fluctuations (expressed as percentage of mean period). The upper panel shows the fluctuations as a function of τ/τ_0 (period/characteristic period) ≤ 1 , and the lower panel shows them as a function of $\tau/\tau_0 \geq 1$. Data are pooled over the 3 subjects and six experimental sessions of Rosenblum and Turvey (1988). *Note.* From "Maintenance Tendency in Coordinated Rhythmic Movements: Relative Fluctuation and Phase" by L. D. Rosenblum and M. T. Turvey, 1988, *Neuroscience*, 27, p. 293. Copyright 1988 by IBRO. Reprinted by permission.

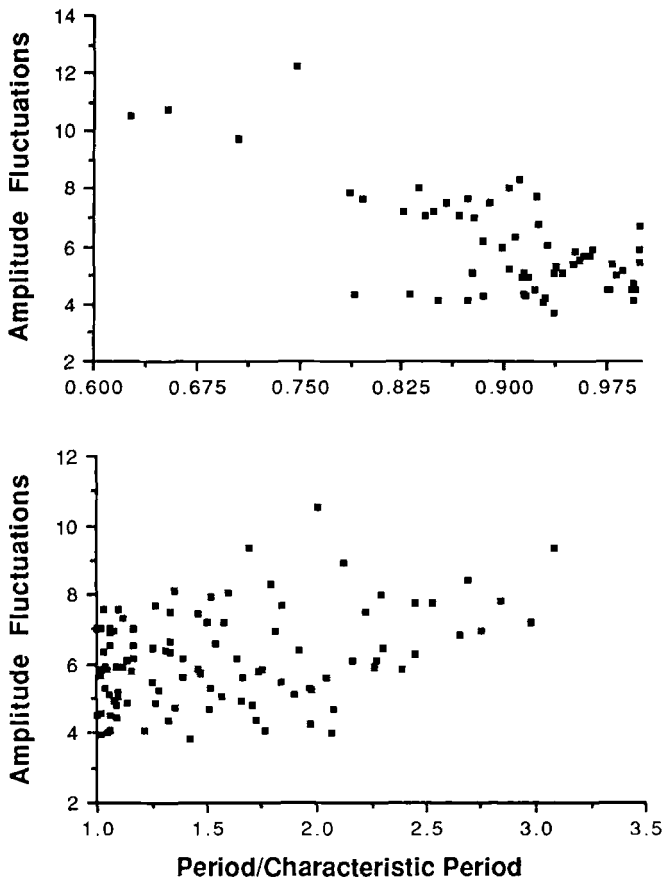


Figure 4.7. The maintenance tendency in wrist-pendulum coordination as revealed by amplitude fluctuations (expressed as percentage of mean amplitude). The upper panel shows the fluctuations as a function of τ/τ_0 (period/characteristic period) ≤ 1 , and the lower panel shows them as a function of $\tau/\tau_0 \geq 1$. Data are pooled over the 3 subjects and six experimental sessions of Rosenblum and Turvey (1988). *Note.* From "Maintenance Tendency in Coordinated Rhythmic Movements: Relative Fluctuation and Phase" by L. D. Rosenblum and M. T. Turvey, 1988, *Neuroscience*, 27, p. 295. Copyright 1988 by IBRO. Reprinted by permission.

teristic periods. Because the preferred period (τ_0) was not measured for each pendulum in a wrist-pendulum pairing (it was measured only for the right-hand system), the metric used for the difference between the left and right pendulums' characteristic frequencies was $L_T - L_l$ (that is, the length of the right system minus the length of the left system). The mean phase difference between the two oscillating systems was calculated with a point estimate at the peaks of each cycle (Yaminishi, Kawato, & Suzuki, 1979):

$$\phi = 360 [\Sigma [(\tau_{1i} - \tau_{2i})/(\tau_{2i} - \tau_{2i+1})]/n] \quad (4)$$

where τ_{1i} is the time of peak i of the target pendulum, τ_{2i} the time of peak i of the reference pendulum, and n is the number of cycles in a trial. Hence, phase differences greater than 180° indicate that the right pendulum is leading the left pendulum, and phase differences less than 180° indicate that the left pendulum is leading the right pendulum. Figure 4.8 demonstrates that when L_T is less than L_l (and L_T is the faster pendulum in isolation), the target pendulum leads the left pendulum; when L_T is greater than L_l , the target pendulum lags the left pendulum. This result is just what one would predict for a system demonstrating the maintenance tendency; namely, the intrinsically faster pendulum always leads the intrinsically slower pendulum in phase.

What kind of physical system would manifest these characteristics? It can be argued that the physical system formed in the absolute coordination of two wrist pendulums is a stratified system with three levels of stratification (Kugler & Turvey, 1987; Turvey et al., 1986). The highest level is the intentional level at which the subject has chosen to perform a pendular clocking behavior. Intentional states act as extraordinary boundary conditions on the dynamical principles underlying human movements (Kugler & Turvey, 1987). The middle level, the cooperative level, is a coordinative structure or functional unit (Kugler, Kelso, & Turvey, 1980) formed as a consequence of the interaction of the individual's intentional state and the dynamical principles governing rhythmic limb movements. This formative process consists, in part, of the freezing out of biomechanical degrees of freedom (for example, setting the postural context for the movement and setting the antagonist co-contraction) to allow the harnessing of dynamics so that absolute coordination can be obtained with minimal moment-to-moment intervention.

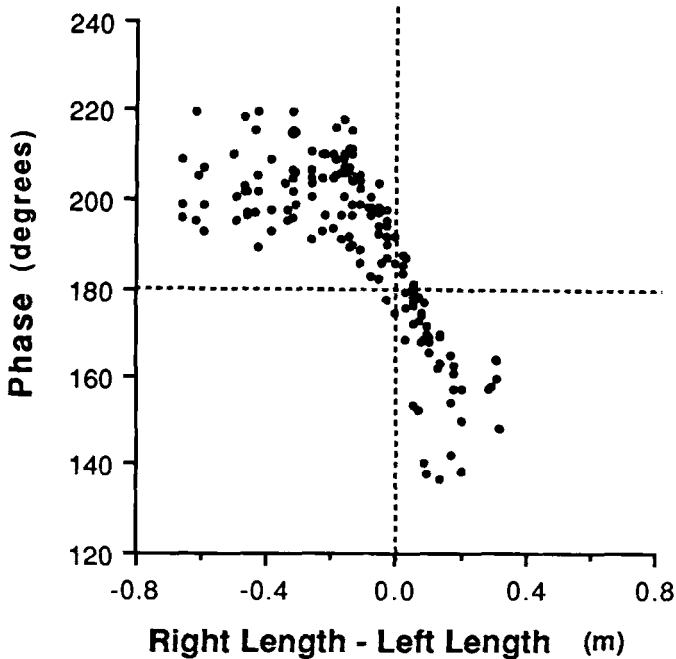


Figure 4.8. The maintenance tendency in the coordination of wrist-pendulum systems as revealed by phase differences (in degrees). Phase differences are presented as a function of the difference between the lengths of the right and left systems. Data are pooled over the 3 subjects and six experimental sessions of Rosenblum and Turvey (1988). *Note.* From "Maintenance Tendency in Coordinated Rhythmic Movements: Relative Fluctuation and Phase" by L. D. Rosenblum and M. T. Turvey, 1988, *Neuroscience*, 27, p. 297. Copyright 1988 by IBRO. Reprinted by permission.

The lowest level is that of the component oscillators. When two wrist pendulums are in absolute coordination, neither of the component oscillators is at its preferred period. Each is pulled towards the cooperative period defined by the natural laws underlying the virtual system. The interaction between the coordinative level and the component level is very much like that of self-organizing sys-

tems found elsewhere in nature (Kugler & Turvey, 1987). An example is the oft-cited Bénard convection. Here, a vat of oil is heated from the bottom and cooled from the top. The energy injected into the system by heating causes the component oil molecules to collide randomly with one another. At a critical temperature of heating, the molecules that have been pulled far from their equilibrium states form hexagonal columns which, upon further heating, begin to roll vertically. This type of self-organizing system has been called a dissipative structure (Prigogine, 1980) because the new macroscopic, coordinative level is formed in response to the need to dissipate the energy injected into the system. The conditions forming the cooperative virtual system are not only the metabolic energy put into the system to create the movements but also the informational-functional linking of degrees of freedom as designated by the subject's intentional state. As a consequence of forming a cooperative level of organization, the component microstructures (the individual molecules in the oil convection experiment and the component pendulums in the wrist-pendulum experiment) are driven far from the state they would settle at if left to their own exigencies and not subject to external influences. The individual wrist-pendulum systems in absolute coordination index the maintenance tendency through fluctuations because they have been marshalled temporarily to cooperate in an organization that has a dynamical basis. In order for stability to be in evidence at the cooperative level, the components must be made unstable temporarily. One can then expect the kinematics (period and amplitude) of the components to index their unstable states. The more the cooperative state demands that the components compromise their preferences, the larger will be the fluctuations seen in their behavior.

In sum, the fluctuations that index the maintenance tendency can be explained by the supposition that the system formed to produce the coordinated movement has a dynamical basis and a stratified structure of cooperating levels in common with many self-organizing systems in nature. In order to explain the phase difference result, Rosenblum and Turvey (1988) presented two hypotheses. The various phase differences between the wrist-pendulum systems are: (a) consequences of neural innervations of the musculature at those phase difference, or (b) consequences of a single phase difference of neural innervation (in this case 180°) and resultant pendulum phase differences produced by a self-organizing property of the musculature comprising each component system (Partridge, 1966,

1967). The second hypothesis is a strong candidate from the ecological point of view. Loaded muscle, for a given frequency of neural innervation, varies the force of its output with the load it carries very much as a spring would. This property leaves amplitude of contraction constant across different inertial loads but produces a variable phase lag between the input neural signal and the output movement for pendulums of different inertial magnitudes. On the assumption that a neural signal is sent to the coordinated limbs exactly at a 180° phase difference, the observed deviation in phase difference from 180° between the two pendulums can be attributed to this compensatory property of the component musculature. The degree of this compensation depends upon each wrist-pendulum system's moment of inertia (I_1 or I_2), which correlates with its length (L_1 or L_2). If the wrist-pendulum systems have the same inertial loadings ($I_1 = I_2$), then the phase lag between innervation and movement is equal for both, and their phase relation when coupled will be the intended 180° (out of phase). The wrist-pendulum system with the lower moment of inertia will always lead, and the wrist-pendulum system with greater moment of inertia will always lag, as is seen in Figure 4.8.

THE INFORMATIONAL BASIS FOR ABSOLUTE COORDINATION

The physical interactions between limbs that underly absolute coordination must be nonstandard from a physical point of view. At issue here is the fact that the two oscillating wrist-pendulum systems are not interacting in a classical mechanical way by a transportation of mechanical energy from one unit to the other. The reason is simply that they are not forcefully linked as would be the case if the two pendulums were connected by a metal rod. Patently, the physical linkage, or medium for the interaction, is the nervous system. The problem that this fact poses for a physical account is that nervous system interactions are *informational*. That is, even though an electromagnetic potential is the basis for the function of the nervous system, it is not the electromagnetic energy transported over the nervous system that is the basis for interactions among limbs. Rather, it is the *patterning* of action potentials (e.g., rate) over neural lines, not the amount of energy each line contains, that supports these interactions. When a patterning of some medium is the basis for the interaction of units (e.g., an animal and its environment via structured ambient light), rather than energy transported along this medium, then the

interaction may be termed informational (Kugler, Turvey, Carello, & Shaw, 1985; Kugler & Turvey, 1987). If physical principles indeed shape absolute coordination, and if they are functioning across the nervous system, then some physical principles may apply equally in either energy or informational interactions. This intriguing possibility is corroborated by experimental results.

If it is true that the principles of organization underlying the magnet effect and the maintenance tendency are physical and operational across an informational medium, then the magnet effect and the maintenance tendency should be manifest in absolute coordination across an informational medium different from the central nervous system. In research now underway, the wrist-pendulum system methodology is being used to study the *visual* absolute coordination of movements between two people. In this research, two people sit facing the same direction but turned slightly towards each other to enable each person to see the other's outside wrist. Each person swings a wrist-pendulum with the outside hand in two conditions: (a) coordinated synchronously with the other person at 180° out of phase; and (b) with the eyes closed. Four wrist-pendulum systems of different sizes (the same pendulum magnitudes and coupling as in Kugler & Turvey, 1987) are combined in 16 ways. The characteristic periods of the individual pendulums are measured in the eyes closed condition. With this design we can investigate whether or not the phenomena of absolute coordination that were found in the within-person or neuro-anatomical coupling of wrist-pendulum systems will be found in the between-person or visual coupling of wrist-pendulum systems.

Preliminary analyses suggest that both the maintenance tendency and the magnet effect occur. The analyses are complicated, however, by the heterogeneity of the elastic potential brought to the task by different subjects (see Figure 4.2). (In the within-person case, the elastic stiffness seems to be uniform across the two wrists.) The data for the magnet effect are presented in Figure 4.9 for two pairs of subjects and replicate the within-person coupling data presented in Figure 4.3. The period of a pendulum decreases when that pendulum is coupled with a faster pendulum but increases when the pendulum is coupled with a slower pendulum. The virtual system analysis, which assumes that a lawful cooperative state is formed to dictate the coupled period, seems to apply equally well to this visual instance of the magnet effect. Under the assumption that the coupled

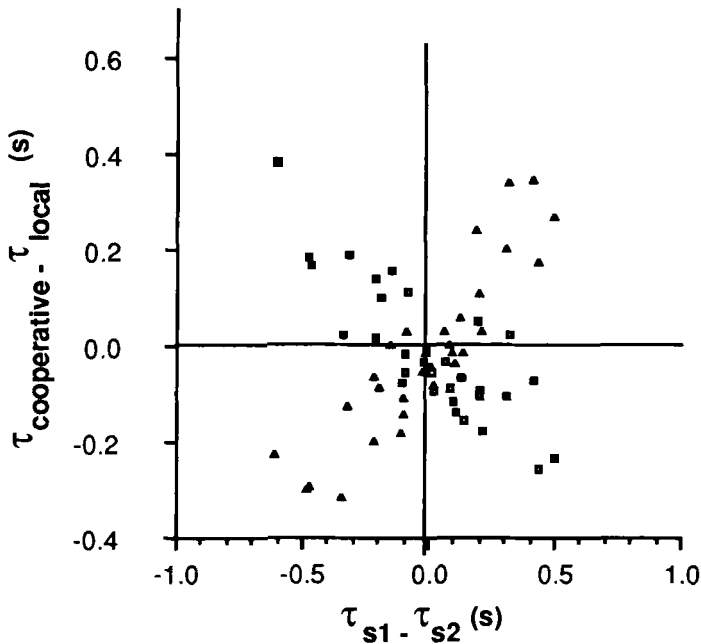


Figure 4.9. The magnet effect in the visual coordination of wrist-pendulum systems between two people. The squares represent the deviation of the cooperative period from the preferred period of the 1st subject's pendulum and the triangles represent deviation of the cooperative period from the preferred period of the 2nd subject's pendulum. These deviations increase as the differences in the two preferred periods ($\tau_{\text{first}} - \tau_{\text{second}}$) increase.

wrist-pendulums are performing as if rigidly coupled, the length to the center of oscillation L_v (the length of the virtual simple pendulum) can be calculated. In a multiple regression of the cooperative period on L_v , τ_{s1} and τ_{s2} (where s1 refers to the first subject of a pair and s2 refers to the second), the virtual length L_v was found to account for more variation in the cooperative period than did either of the individual pendulums' characteristic periods (Table 4.2).

In the visual case of absolute coordination, the cooperative period cannot be a consequence of signals from a central pattern generator interacting via interneuronal connections because there is no nervous system connecting the two individuals. It can, however, be the result of a very general physical organizing strategy—one that

Table 4.2

Relative Contribution of Virtual and Local Oscillator Systems to the Visual Cooperative Period

Subject pair	Multiple regression standardized coefficients (β)		
	Virtual length (L_V)	Characteristic period of left system (τ_l)	Characteristic period of right system (τ_r)
1	.542*	.306	.379*
2	.644*	.016	.185

* $p < .05$

confines the comfortable period of absolute coordination to that determined by the coupled systems' center of oscillation—that is manifest equally in energy and information contexts. How is it possible for information to link the dynamical states of two components of a physical organization? To answer this question, we must say something about J. J. Gibson's notion of information and its function in the behavior of wrist-pendulum systems.

In Gibson's (1979) ecological theory of optical information, the light ambient to a point of observation, light that has been structured by multiple reflections from surfaces, is referred to as the optic array. Gibson argued that macroscopic qualitative properties of the optic array and, in particular, the transforming optic array, are unique and specific to surface layout, changes in surface layout, and displacements of the point of observation. As such, the transforming optic array is a low-energy field that contains information about the environment and about movements of the perceiver, by virtue of its kinematic form (Kugler et al., 1980). Visual perception studies by Runeson and Frykholm (1981) and Bingham (1987) have demonstrated that dynamical properties of an event (for example, momentum and mass) are perceivable from merely the kinematic

morphologies in the optic array. They referred to this phenomenon as the *kinematic specification of dynamics*.

Kugler and Turvey (1987) suggested that the subject discovers the preferred period of wrist-pendulum behavior through a process similar to kinematic specification of dynamics. They maintain that the deformation of tissue during a movement induces a patterning of mechanoreceptors that is unique and specific to the dynamical properties of the movement. The dynamical property that needs to be perceived is the minimum of the potential energy function associated with a particular single or coupled wrist pendulum system. Finding the most comfortable period of oscillation is tantamount to finding the period at which the subject contributes as little energy to the cycle as possible. By exploring different tempos at the initiation of the behavior, the subject is exploring the potential space of that wrist-pendulum system. Where he or she is in the space with respect to the potential minimum is specified by the gradient of the space (that is, the magnitude and direction of the rate of change of the potential). The gradient of the potential needs to be perceived in order for the subject to lengthen or shorten his or her cycle to obtain the preferred period. Kugler and Turvey (1987) suggested that there is information for this dynamical property in the patterning of the deformation of tissue produced by the movement. Biomechanically, the shortening or lengthening of a cycle can be understood as the varying of the assembled neuromuscular elastic potential, previously discussed. In short, the physiology is being tuned by the perceived dynamical properties of the activity.

Armed with this ecological notion of information, we are in a better position to try to understand how "virtual" quantities emerge from an interaction defined across an informational medium such as the optic array or the nervous system. The dynamics of each wrist pendulum's movement creates a neural patterning and an optical patterning that are unique and specific to the dynamics. The subject's task (or each subject's task, in the visual case) is to find the period that is dynamically least costly for coordinating both pendulums isochronously and 180° out of phase. The solution that emerges is interpretable as the harnessing of the two different dynamics by means of *the period dictated by the center of oscillation of the two components*. At this period, the potential energy function of the cooperative state comprising the two wrist-pendulum systems

is at its minimum. In sum, for single wrist-pendulum systems, and for two wrist-pendulum systems connected neuroanatomically or visually, the basis for perceiving the dynamical state of an oscillatory system in order to find the least energetically costly cycle period is identical.

CONCLUDING REMARKS

The ecological perspective on coordination maintains that one should look for a low-dimensional redescription of the high-dimensional (*viz.*, neural, vascular, etc.) system in question and see whether the patterning of the macroscopic components can be explained by physical principles at the macroscopic scale. Special anatomical mechanisms that are posited to explain a particular phenomenon should be proposed only after more general forms of explanation have been proved unusable.

The magnet effect is such a patterning of the macroscopic components that can be explained by physical principles. It is a general characteristic of coordinated rhythmic movements: It is observed for limbs, fins, and wings; it is observed for rhythmic units that relate neuroanatomically, as in the within-person coordination of wrist-pendulum systems, and for rhythmic units that relate visually, as in the between-people coordination of wrist-pendulum systems. The commonalities among these very different circumstances must be the result of laws operating over the physical properties that all the circumstances share. The implication is that organisms use the natural organizing dispositions of their physical attributes to facilitate the coordination of their movements. Thus, the predictions from the pendular clocking mode equation, concerning the time allometries involved in the locomotion of animals of all sizes, are evidence for the operation of physical constraints in the coordination of wrist-pendulum systems and in the coordination of limbs in locomotion generally. Further, the fluctuations that are the hallmark property of the maintenance tendency can be understood as an index of the tension between two levels of the dynamical organization formed to coordinate two or more rhythmic units.

A major assumption behind the arguments in this chapter is that absolute coordination is a lawful process involving information. This assumption is in keeping with the understanding that organ-

isms are physical entities that relate to their surroundings through informational contact, an understanding that poses significant challenges for the development of a physical biology (Kugler et al., 1985; Kugler & Turvey, 1987; Yates, 1987). An organism's ability to perceive the dynamical properties of its limbs on the basis of information about those dynamics underlies the operation of physical strategies of organization in locomotion. The surprising outcome of this fact is that physical laws are manifest in situations that are governed more by information than by forces. A thoroughgoing ecological perspective necessitates exploring in detail the role of information in the dynamical constraints on coordinated movements, where information is understood in Gibson's (1979) specification sense.

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