Phase transitions and critical behavior in human bimanual coordination

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KELSO, J. A. SCOTT. *Phase transitions and critical behavior in human bimanual coordination.* Am. J. Physiol. 246 (Regulatory Integrative Comp. Physiol. 15): R1000–R1004, 1984.—Conditions that give rise to phase shifts among the limbs when an animal changes gait are poorly understood. Often a "switch mechanism" is invoked that has a neural basis which remains speculative. Abrupt phase transitions also occur between the two hands in humans when movement-cycling frequency is continuously increased. The asymmetrical out-of-phase mode shifts suddenly to a symmetrical in-phase mode involving simultaneous activation of homologous muscle groups. The boundary between the two coordinative states is indexed by a dimensionless critical number, which remains constant regardless of whether the hands move freely or are subject to resistive loading. Coordinated shifts appear to arise because of continuous scaling influences that render the existing mode unstable. Then, at a critical point, bifurcation occurs and a new stable (and perhaps energetically more efficient) mode emerges.

modes of coordination; critical values; bifurcation; scaling

IT IS WELL KNOWN that when quadrupeds change their mode of gait from a trot to a gallop, the phase relations of the limbs are altered abruptly from a roughly out-of-phase asymmetric mode to an in-phase symmetric mode. Although such discontinuous changes in coordination are not well understood, it is frequently assumed that central pattern generators exist (often equated with motor programs) with a role that is to select the desired spatiotemporal pattern of muscle activities (1, 4, 12, 19, 25). In the case of so-called stereotypic activities such as locomotion the basic programs are hypothesized to be innately given (5, 31). We report here, however, that under certain conditions phase transitions also exist in voluntary cyclic movements of the two hands. Under instructions to increase frequency of cycling progressively, a sudden and spontaneous shift occurs from an asymmetric, 180° out-of-phase mode in which one wrist flexes as the other extends, into a symmetric in-phase mode, which involves simultaneous activation of homologous muscle groups. When the transition is allowed to occur naturally, the critical frequency is predictable from the preferred frequency regardless of whether the hands move freely or are subjected to resistive loading. We take these data to support the notion (17) that phase transitions in movement may follow the same laws as the phase transitions and critical behavior described for many other natural phenomena (e.g., 3, 6, 7, 10, 24).

The basic experiments reported here required subjects to cycle the hands at the wrist in the horizontal plane in an asymmetical mode, i.e., one in which flexion (extension) of one wrist was accompanied by extension (flexion) of the other. Similar experiments have been conducted by using movements of the index fingers. A preliminary presentation of the finger-movement data, with results that were basically identical to the present studies, has been presented (13, 16). The subjects, seated with forearms firmly supported in a position parallel to the ground, grasped a freely rotating handle with each hand, the positions of which were converted to direct-current voltages by potentiometers mounted over the respective axis of motion (cf. 14). These signals were recorded on FM tape and later subjected to analog-to-digital conversion at a sampling frequency of 200 Hz. Time-domain displacement tracings were obtained that could be displayed and analyzed on a computer graphics terminal. Instructions to subjects were to commence cycling the hands slowly and then to increase rate of cycling either in response to a verbal cue provided by the experimenter at 15-s intervals or by a metronome with an interpulse interval that could be adjusted in 100-ms increments every 15 s. Driving frequencies in the metronome case ranged from 1 to 5 Hz. In another experiment subjects performed a series of trials under identical instructions but with a resistive load applied to both limbs. In this case the vertical rods leading to the potentiometers were clamped between fixed wooden blocks, thus providing a frictional damping force throughout the range of motion for each limb of approximately 5.9 N.

Before the experimental manipulation, base-line measures of subjects' preferred frequency and amplitude in both asymmetric and symmetric modes were obtained under free- and resistive-loading conditions. Subjects were instructed to choose their preferred frequencies and amplitudes in such a way that they "could perform the task all day," if required to do so. Movements of each limb were then continuously sampled at 200 Hz for 30 s. Measures of frequency (in Hertz), amplitude (in degrees) and interlimb phase (in radians) were obtained for each limb on every cycle. In addition, by the assumption of an approximately sinusoidal motion, we estimated the total mechanical energy expended per unit moment of inertia per cycle (proportional to the square of a given cycle's peak velocity).

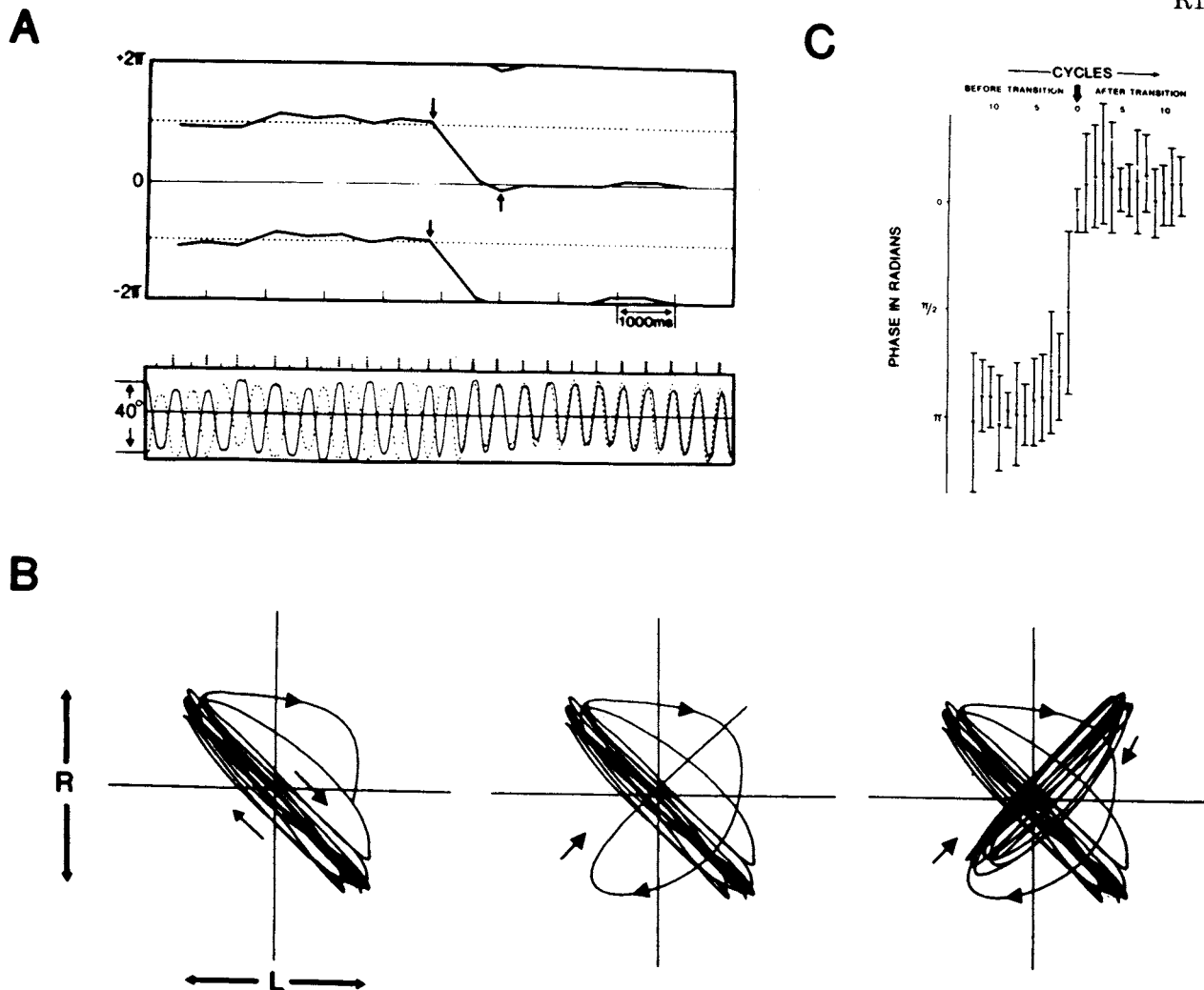The results were unequivocal for all the six subjects' data analyzed. Figure 1A shows the movement trajecto-

FIG. 1. *A*: Computer-generated display of displacement-time profiles of left (*solid line*) and right (*dashed line*) hands plotted against each other and accompanying phase relationship between the two. Peaks of 1 hand movement act as "target" file, and their phase position is calculated continuously relative to peak-to-peak period of other "reference" file. Display repeats phase curve so that phase lags and leads can be noted. Subject in this case is simply increasing frequency of cycling in asymmetric mode in response to verbal cue from experimenter. At critical frequency, abrupt shift occurs to in-phase symmetric mode in which wrists flex and extend synchronously. Asymmetric mode is equivalent to phase difference of π radians (180°); after phase transition phase difference hovers around zero. Downward motion shows wrist flexion; upward motion shows wrist extension. Mean peak-to-peak cycle frequencies of left and right hands before transition (indicated by *downward-pointing arrow*) were 1.852 (period, $\tau = 540$ ms, SD = 30 ms) and 1.852 Hz ($\tau = 540$ ms, SD = 35 ms), respectively.

After transition (marked by *upward arrow*) cycle frequencies were 2.400 ($\tau = 417$ ms, SD = 22 ms) and 2.406 Hz ($\tau = 416$ ms, SD = 18 ms). Corresponding mean peak-to-peak cycle amplitudes were 38.65° (SD = 2.64°) and 34.48° (SD = 2.25°) for left and right hands before transition. After transition, cycle amplitudes were 33.39° (SD = 1.41°) for left hand and 35.65° (SD = 2.28°) for right hand. *B*: data identical to those shown in *A*, except displayed on Lissajous plane. Positions of left and right hands are displayed on *ordinate* and *abscissa*, respectively. Viewed from left to right, hands first preserve a quite stable out-of-phase relation that becomes more variable (less stable) over time as evident in widening of Lissajous phase portrait. Eventually hands jump into next mode, which remains quite stable thereafter. *C*: average value of phase plotted over cycles before and after transition. *Bars*, SD. Each *point* is average of 19 different phase transition experiments (11 free and 8 resisted). Abrupt phase shift is apparent.

ries of the two limbs for one subject as the rate increased; the rapid shift in phase is obvious. Figure 1*B* shows the same data on the Lissajous plane with one limb's displacement plotted against the other. It can be seen that the phase relations between the limbs are initially very stable. Were the two motions perfectly sinusoidal with phase equal to π radians, a straight line would be observed. As frequency increases, the phase difference between the limbs becomes more variable, evident in the widening of the Lissajous phase portrait. After the transition, phase becomes stable once again. The overall picture of phasing between the limbs as a function of

cycles is shown in Fig. 1*C*. Each point on the phase diagram corresponds to the mean of 19 different phase-transition experiments (11 free and 8 resisted). In all cases, an abrupt change in phase was observed. Usually the jump from one mode to the other occurred within a cycle; seldom did the transition require more than two or three cycles. On two occasions, both in the same subject, temporary transitions occurred in which the limbs moved from an asymmetric to symmetric pattern and then returned to an asymmetric pattern. Eventually, however, a permanent transition to the symmetric in-phase mode was observed.

Others as well as ourselves have shown that in bimanual finger movement tasks only two modes, symmetric and asymmetric, are stable regardless of whether the subjects are naive or whether they are skilled musicians (15, 32). This is not to say that other phase relations are not possible, only that they tend to be much more variable. Skilled pianists, as well as those who study their motor performance (27), have long recognized the difficulty in performing complex bimanual rhythms. In fact, characteristic "errors" often occur, manifested as tendencies to produce in-phase and out-of-phase patterns, and are avoided only through much practice.

The present data indicate that when cycling frequency is increased, one mode becomes unstable only to disappear and be replaced by another stable mode. In this they share a likeness to studies of locomotion in decerebrate cats (28) that demonstrated that a steady increase in electrical stimulation applied to the midbrain region was associated with increases in rate of locomotion. Moreover, transitions in gait occurred when sufficiently strong current was employed. Like some of our data, unstable regions were also noted in which the animal sometimes trotted and sometimes galloped. Above a certain value of current (80 μA), however, only galloping occurred. Our results, similar to these findings on gait, suggest that changes in coordination may be ordered by changes in the magnitude of a single parameter.

We have some reason to suppose that the "new" stable mode is energetically more favorable at a given frequency than its predecessor. In the free unloaded experiments, cycle frequency increased significantly across the transition [from an average of 2.26 Hz over the 5 cycles before the transient phase to 2.50 Hz averaged over 5 cycles after the transient, $t(10) = 3.45$, $P = 0.006$], but cycle amplitude and energy dropped across the transition [$t(10) = 2.59$ and 2.11; $P = 0.03$ and $P = 0.06$, respectively]. The pattern was similar in the eight resistive-loading experiments: frequency increased significantly across the transition, whereas amplitude and energy dropped slightly but not significantly. It should be emphasized that under both resistive and nonresisted conditions, cycle energy was always substantially greater before the transition than in either of the corresponding preferred mode conditions ($P < 0.01$).

Systematic relationships between energy utilization and modal behavior have also been reported in studies of gait in horses (8) and gnus (22). Horses locomoting in a free environment, for example, elect only those ranges of speed within a gait that correspond to regions of minimum oxygen expenditure (8). Moreover, when horses are forced to maintain a given gait at a speed other than that preferred, metabolic costs increase dramatically, until at some threshold value, a shift into the next most economical mode occurs. Shifts in locomotory modes are not hard wired or deterministic (except perhaps at the very limits of stability). Horses can trot at speeds at which they normally gallop or walk, but it is metabolically expensive to do so.

It is also possible to delay the phase transition observed in these experiments consciously. The critical value at which the transition occurs naturally, however (i.e., without a purposeful effort to resist it), is highly predictable. Though the absolute values of frequency, amplitude, and energy (measured over the last 5 consecutive cycles before the transient phase) vary considerably between and within subjects, one relative measure does not. When the frequency at transition is scaled to the individual's preferred frequency in the out-of-phase mode, a highly linear relationship is observed.

This relationship, along with least-squares regression lines, is plotted in Fig. 2 for free- and resistive-loading experiments for five subjects' data (solid lines). The effect of resistive loading was to reduce both preferred frequency and transition frequency in a reliable fashion ($P < 0.01$). The mean preferred frequencies for free and resisted experiments were 1.81 ($\tau = 552$ ms, SD = 30 ms) and 1.37 Hz ($\tau = 730$ ms, SD = 33 ms), respectively. The mean transition frequency for the free case was 2.34 ($\tau = 427$ ms, SD = 48 ms) and 1.83 Hz ($\tau = 546$ ms, SD = 36 ms) for the resisted case. These findings appear to eliminate any simple interpretation in which the redundant symmetric mode (which involves homologous muscles) is chosen when the capacity limit for processing information in the asymmetric mode (which involves nonhomologous muscles) is reached (2).

Although resistive loading systematically reduced transition and preferred frequency, it did not alter the relationship between the two. The slopes of the functions relating transition and preferred frequency were different from zero [$F(1,3) = 84.95$, $P < 0.01$ for the unloaded experiments, and $F(1,3) = 25.80$, $P < 0.02$ for the loaded experiments]. However, the slopes were not different from each other [$F(2,6) = 2.04$, $P > 0.10$]. Moreover, the correlations between preferred and transition frequency (equivalent to normalized regression slopes) were very similar ($r = 0.95$ for resisted and $r = 0.98$ for unresisted conditions). Thus whatever the changes in mean and variance that are introduced by parametric changes in resistance, the critical behavior, manifested in the functional relation between transition and preferred frequency, remains unchanged. In fact, when the transition frequency is expressed in units of preferred frequency, the resulting dimensionless ratio is constant across all preferred frequencies whether loaded or not. Neither of the functions shown as dotted lines in Fig. 2 is significantly different from zero [$F(1,3) = 1.71$ and 2.83, $P > 0.10$ for free and resisted cases, respectively, or from each other, $F(2,6) = 1.67$, $P > 0.1$)]. The mean "critical value" across both conditions, with and without resistive loading, is 1.313, with a coefficient of variation of 0.077.

It may not simply be chance that if a similar normalization procedure is applied to Hoyt and Taylor's (8) locomotion data and a ratio is calculated between the horse's preferred speed in a given gait and the speed at which the transition occurs from one gait to another, a critical value of approximately 1.33 results for both walk-trot and trot-gallop transitions. As in our data, regardless of what the preferred speed is, the transition appears to occur at some constant proportion of the preferred value. Stride frequency at the trot-gallop transition in animals ranging from mice to horses has been shown to scale to total body mass (M) raised to the power of −0.14 (9). This exponent is in close agreement to that of $M^{-\frac{1}{8}}$ predicted by McMahon's (20) model of elastic similarity
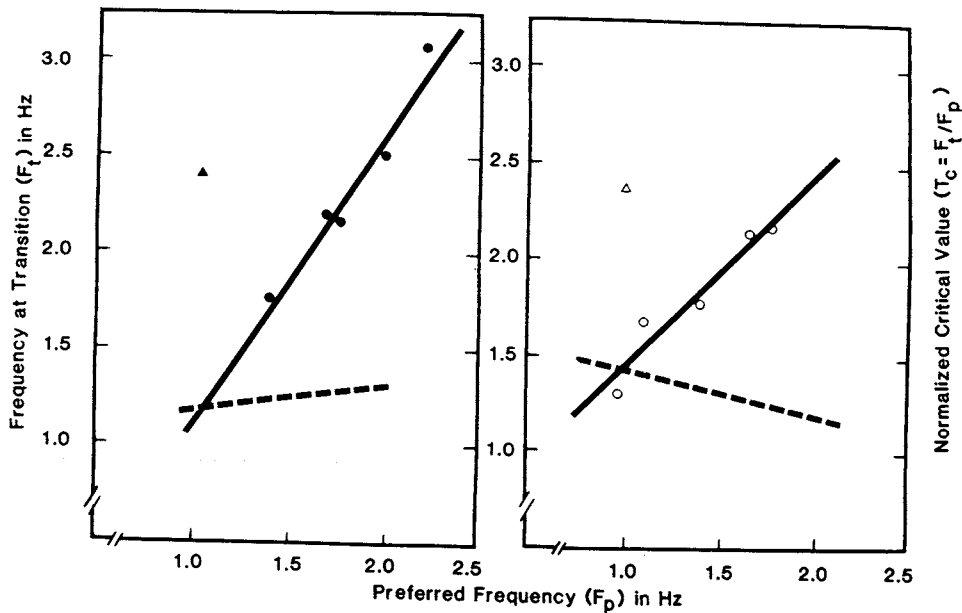
FIG. 2. *Solid lines*: relationship between subjects' mean preferred frequency (F_p) in asymmetric out-of-phase mode and mean transition frequency (F_t) calculated over last 5 consecutive cycles before phase shift. *Solid dots*, free unresisted conditions; *open dots*, resistive-loading experiments. For free case, least-squares linear regression line was $F_t = 1.55 F_p - 0.48$. For loaded case it was $F_t = 1.02 F_p + 0.43$. *Solid* and *open triangles*, data from 1 subject who made deliberate effort to prevent phase transition from occurring. In this case subject's transition frequency is about 2.5 times greater than her preferred frequency. In unresisted case, for which estimates of mechanical energy per unit moment of inertia per cycle are most valid, subject shows by far largest energy drop across transition of all subjects (mean of 30.49 "energy units"/cycle before transition to 20.51 energy units/cycle after transition, compared with group average of 19.38 energy units before and 17.33 energy units after transition). *Dashed lines*: same data replotted for subjects' F_p against ratio of F_t over F_p, i.e., proposed critical transition point (T_c). Least-squares regression line for free case is $T_c = 0.13 F_p + 1.04$; mean value of T_c is 1.284 (SD = 0.057). For the loaded case, regression function is $T_c = -0.23 F_p + 1.66$ with mean T_c of 1.342 (SD = 0.132). Combining both experiments, overall regression equation is $T_c = -0.09 F_p + 1.46$, mean T_c of 1.313 (SD 0.10).

in which muscle stress (tension per unit cross-sectional area) is hypothesized to be the same at gait transitions in homologous muscles in animals of different size. In the present experiments, when the proposed critical value (T_c) is scaled to a preferred frequency (F_p) for all observations, an exponent of -0.12 results ($T_c = 0.14 F_p^{0.12}$). If further work shows preferred frequency to be tightly coupled to M, then it may be that the elastic similarity model can be applied not only to gait transitions but also to the modal shifts observed here.

We would be remiss if we did not mention the possibility that the pattern of results observed for hand movements here (and perhaps for gait changes as well) shares common features with other critical phenomena in nature (3, 6, 7, 10, 21, 23, 24, 29). Systems at many scales of magnitude and varying widely in material properties appear to be qualitatively similar with respect to their behavior at critical points (3, 7). For example, our findings seem consistent with certain aspects of phase transition theory in physics (11, 30), one of which is that parameters adjusted in an experiment may shift the critical point (as resistance does to frequency here) without altering the critical behavior itself (e.g., see Ref. 3). Moreover, a major characteristic of many physical and biological systems is that new "modes" or spatiotemporal orderings arise when the system is scaled on certain parameters to which it is sensitive (e.g., 7 and 10). In the present experiments, continuous scaling on frequency resulted in the initial modal pattern becoming unstable, until, at a critical value, bifurcation occurred and a different modal pattern appeared.

The present approach, if pursued rigorously, may rationalize currently available neurophysiological accounts of transitions in coordination that assume a "switch mechanism" mediated by "coordinating fibers" (5) (neither of which has a neural basis that is well defined; see Ref. 26 and commentaries). Instead a careful elaboration of the conditions that give rise to switching may constrain possible neural explanations of the emergence of new spatiotemporal pattern.

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