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Dynamics of Human Postural Transitions

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In the present study, the authors examined transitions between postural coordination modes involved in human stance. The analysis was motivated by dynamical theories of pattern formation, in which coordination modes and transitions between modes are emergent, self-organized properties of the dynamics of animal–environment systems. In 2 experiments, standing participants tracked a moving target with the head. Results are consistent with the hypothesis that changes in body coordination follow typical nonequilibrium phase transitions, exhibiting multistability, bifurcation, critical fluctuations, hysteresis, and critical slowing down. The findings suggest that posture may be organized in terms of dynamical principles and favor the existence of general and common principles governing pattern formation and flexibility in complex systems.

One of the major problems facing movement scientists is how humans and other animals coordinate the multitude of degrees of freedom of their bodies, constraining them to act as a single unit in accomplishing behavioral tasks. The great dimensionality of the body (e.g., some 10^3 muscles and 10^2 joints for humans) must be reduced to a controllable system characterized by order, that is, by stable patterns of coordination (Bernstein, 1967). Bipedal stance is one of the most common postures by which humans and other bipeds interact with their environment. Under terrestrial conditions, the human body is unstable during stance (e.g., Yang, Winter, & Wells, 1990), which means that in the absence of continuous muscular control the body would collapse. Successful stabilization of a multisegment, passively unstable system requires that its various components (i.e., segments, muscles, or joints) must be coordinated to preserve balance and achieve functional goals.

In controlling stance, humans' movements of different body segments can be organized in a variety of ways. Researchers have concentrated on two types of organization: one in which the torso and legs move in opposite directions (i.e., rotation around the hips) and one in which the torso and legs move in the same direction (i.e., rotation around the ankles). Postural control actions often co-occur with other movements, such as reaching or leaning. Such movements may bring about a change from one type of postural coordination to another. For example, when a person is standing upright, sway may be concentrated around the ankles, but when leaning forward (e.g., to look at something more closely), sway may be concentrated around the hips. Why does this change occur; that is, why is there a transition from one type of coordination to another? One widely accepted explanation is that basic patterns of postural coordination are centrally represented by a set of motor programs, and postural transitions are behavioral consequences of changes between programs operating at the level of the central nervous system (e.g., Horak & McPherson, 1996; Nashner & McCollum, 1985). Our research is motivated by a different view (cf. Bardy, Marin, Stoffregen, & Bootsma, 1999). We take the position that changes between postural states are consequences of the self-organized nature of the postural system, exhibiting properties of nonequilibrium phase transitions between attractors. The present study tests this hypothesis. In two experiments involving a visual tracking task, we sought to identify the hallmarks of such transitions in human multisegmental control of stance. The results indicate that it is possible and useful to examine the stability and flexibility of postural coordination in a dynamical context. Such coordination reveals general principles governing pattern formation that are shared by many other complex biological systems.

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Theoretical Approaches of Human Postural Transitions

How do humans change from one standing posture to another? This question may seem elementary, but it has received relatively little attention from researchers. At the end of the 19th century, Babinski (1899) showed that in standing humans, movements of the trunk in one direction were accompanied by movements of the knees and the hips in the opposite direction. Contemporary research has concentrated on the existence of postural patterns, focusing on the number and type of patterns and on the conditions under which each pattern occurs (for recent reviews, see Horak & McPherson, 1996; Woollacott & Jensen, 1996). For example, Horak and Nashner (1986) varied the length of the surface of support and found that long surfaces were associated with rotation primarily around the ankles, whereas short surfaces were associated with rotation primarily around the hips. As a result, we know when different patterns can be expected; however, we know very little about how, in a given situation, people shift from one pattern to another. This may be because changes between coordinative states have often been considered as derivatives of the states. If so, then understanding of transitions between patterns may follow from understanding of the states themselves. This view underlies much work in postural control (and in motor control, in general), but it has recently been challenged by the dynamical approach to movement coordination and control (e.g., Kelso, 1995; Turvey, 1990). The dynamical approach has motivated strong interest in phenomena that occur in the vicinity of regions of transition, because these regions may reveal general principles governing pattern formation that are not directly accessible through the study of the patterns themselves (Fuchs & Kelso, 1994).

In the context of stance-related behaviors in humans, four general accounts of changes between postural patterns can be advocated. For clarity, we present these as separate accounts. It should be realized, however, that because of the different levels of analysis invoked, these different accounts should not be regarded as mutually exclusive.

Mechanical Limits

One possibility is that the switch from one postural state to another is determined by the *mechanical limits* of the states involved. Mechanical limits may be characterized in a variety of ways, such as limits of the forces and torques applied at the support surface (Horak & Nashner, 1986; Pai & Patton, 1997) or at the joints (Yang et al., 1990), limits of the intrinsic frequency of postural patterns (Buchanan & Horak, 1999; McCollum & Leen, 1989), or limits of the amplitude of body movements tolerated by these patterns (McCollum & Leen, 1989; Stoffregen & Riccio, 1988). For instance, in healthy adults, body sway around the ankles—the *ankle strategy* in Nashner and McCollum's (1985) terminology—is limited to about 15° of ankle rotation (Bardy, Marin, et al., 1999, Figure 1 and Appendix) and to a maximum rotational frequency of about 0.5 Hz (McCollum & Leen, 1989). Ankle rotations produce body sway primarily by applying torque at the support surface and thus are most effective on extended and rigid surfaces that resist this torque (Horak & Nashner, 1986). According to this explanation, a task requiring body movements in excess of these mechanical limits would produce a change from an ankle-rotation pattern to another pattern, such as a rotation of the trunk relative to the legs (called the *hip strategy,* e.g., Horak & Nashner, 1986). In this pattern, rotations at the hips produce body sway by applying shear force to the support surface. Thus, a shift to a surface with low resistance to shear (e.g., a slippery surface) presumably would produce a change from hip rotation to ankle rotation (e.g., Marin, Bardy, Baumberger, Flückiger, & Stoffregen, 1999; McCollum & Leen, 1989).

There is evidence that mechanical properties of the body or the environment constrain the appropriateness of particular postural patterns. Nevertheless, a theory of postural transitions based solely on mechanical factors would be inadequate. This is because there is not a 1:1 correspondence between mechanical conditions and patterns of postural control. A given set of mechanical properties can give rise to more than one coordination mode (Bardy, Marin, et al., 1999; Krizkova, Hlavacka, & Gatev, 1993; Marin, Bardy, Baumberger, et al., 1999; Stoffregen, Adolph, Gorday, & Sheng, 1997). However, different types of mechanical properties can give rise to a single coordination mode (Bardy, Marin, et al., 1999). These effects occur because posture is not constrained solely by mechanical properties of the animal and its environment but is simultaneously constrained by additional factors (e.g., Marin, Bardy, & Bootsma, 1999). Thus, the formation of postural coordination modes, and transitions between them, cannot be rooted only in Newtonian mechanics (Beek, Peper, & Stegeman, 1995).

Metabolic Cost

Perhaps transitions between postural patterns serve to minimize the metabolic cost associated with control of the body's center of mass (C_M). The rate of energy expenditure required by various postural patterns in a given task has, to our knowledge, not been directly measured (cf. Kita, Sakamoto, & Arita, 1996). Shifts from one postural pattern to another might occur when, as conditions change, the current pattern becomes less efficient than some other pattern, where *efficiency* is defined in terms of the amount of energy expended in achieving the goal (e.g., Sparrow & Newell, 1998). In their geometrical analysis, Nashner and McCollum (1985) argued that in selecting postural strategies people should seek to minimize boundary crossings in the ankle–hip plane.[1] The minimization of boundary crossings would tend to minimize energy expenditure. Consistent with this analysis, Corna, Tarantola, Nardone, Giordano, and Schieppati (1999) reported that participants standing on an oscillating platform switched from a single- to a double-inverted pendulum pattern as platform frequency increased and that this switch reduced the effort required to maintain stability.

Effort minimization may help to shape postural patterns during quiet stance, but for stance, in general, it is not sufficient to trigger changes between patterns. This is because there are many situations in which maintenance of the C_M above the feet is not the sole goal of postural control. In many ordinary situations, stance is not maintained for its own sake but for other behaviors that it affords. For example, lifting and throwing can be done with greater power

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[1] Although Nashner and McCollum (1985) addressed the selection of postural patterns, they did not explicitly address transitions between postural patterns; that is, they discussed relations between individual patterns and different areas of the ankle–hip plane but did not discuss trajectories within the plane that would lead to a change in coordination.

when the muscles of the legs are involved, that is, during stance. Lifting and throwing are examples of what we refer to as *suprapostural* behavior (Stoffregen, Smart, Bardy, & Pagulayan, 1999). During suprapostural behaviors, people do not attempt to minimize overall energy expenditure. Rather, they attempt to maximize efficiency, that is, to produce the lowest metabolic cost that is consistent with achievement of the goals of suprapostural tasks (Newell, 1986; Riccio & Stoffregen, 1988; Sparrow & Newell, 1998). This means that postural transitions are not likely to be caused by attempts to minimize the effort required to control the C_M. Postural transitions might of course be organized in terms of minimization of effort required to integrate postural control with suprapostural activity. Although we do not know of any experimental evidence concerning this hypothesis in the context of postural coordination, studies have demonstrated that transitions between different gait patterns are not governed by energetical considerations only (Diedrich & Warren, 1995). Although preferred states seem to be characterized by minimization of energy expenditure (e.g., Hoyt & Taylor, 1981), in the vicinity of the transition regions there is not a one-to-one correspondence between the different gait patterns adopted and their metabolic cost.

Sensory Consequences

A third suggestion is that transitions between postural patterns may result from changes in the information available to the central nervous system. A large body of research on sensory loss, or sensory deficit, has been interpreted as indicating that a change in postural coordination can be caused by changes in available perceptual information (e.g., Allum, Honegger, & Schicks, 1993; Buchanan & Horak, 1999; Corna et al., 1999; Horak, Nashner, & Diener, 1990; Horstmann & Dietz, 1988; Kuo, Speers, Peterka, & Horak, 1998; Nashner, Shupert, Horak, & Black, 1989). Examples include a shift from a pendulum behavior to an inverted pendulum behavior when vision is removed (Corna et al., 1999), the inappropriate use of a hip strategy following somatosensory loss (Horak et al., 1990), and the disappearance of the hip strategy following vestibular deficits (Black & Nashner, 1984; Horak et al., 1990). It is certainly the case that changes in perceptual information contribute to changes in postural coordination. As with the two hypotheses discussed earlier, however, existing studies have not systematically explored transitions between postural patterns. That is, experimental manipulations and analysis have been directed at stable postural patterns and not at the process by which people move from one pattern to another (i.e., transitions occurred between trials rather than within trials).

Other researchers have examined relations between postural control, considered as a response, and the optical consequences of body sway, considered as a stimulus to the postural control system. Body sway relative to an illuminated environment creates optical flow. Flow resulting from sway about the ankles is characterized by low-frequency, small amplitude rotation around a single axis, whereas sway about the hips yields flow of greater complexity. Simulation of the optical consequences of body sway leads to direction-specific postural responses during stance (Van Asten, Gielen, & Denier van der Gon, 1988), during walking (Bardy, Warren, & Kay, 1996, 1999; Warren, Kay, & Yilmaz, 1996), and during running (Young, 1988). Again, however, the methodology used in these studies was designed to test for the existence of functionally specific postural adjustments and not for characterizing the type of transitions between them. Thus, although perceptual information certainly influences the organization of posture, its exact role in the organizational processes underlying the formation of postural patterns is not clear at present. Indeed, the study of postural transitions requires different methodologies.

Self-Organization of Postural Patterns

The account that motivated the present study is that postural coordination modes are attractors in a postural state space and that changes between different modes of postural coordination are nonequilibrium phase transitions between attractors (e.g., Saltzman & Kelso, 1985; Woollacott & Jensen, 1996). The neurophysiological and biomechanical studies described earlier are consistent with the idea that local constraints— central command signals, sensory inputs, or forces—participate in shaping patterns of whole-body coordination. However, we contend that these local constraints operate in the context of more general principles governing the self-organization of dynamic patterns. The principles are general in that they apply not only to posture (as examined in the present study) but also to a wide variety of multijoint movements. The influence of local constraints typically is assessed through the modulation of a given behavioral pattern, but self-organization is revealed in changes between patterns (Haken, 1983). In the next section, we consider the postural system as a dynamical system, characterized by preferred modes of coordination that emerge from various interacting constraints. In this view, transitions between coordination modes are produced by changes in the relative stability of different modes.

Dynamics of Postural Coordination

Emergence of Postural Coordination Modes

We have begun to evaluate the multisegment postural system as a dynamical system, examining modes or types of coordination that may exist between rotations at the hips and ankles. We have focused on the emergence of postural coordination modes that underlie a suprapostural tracking task, as well as on the constraints that shape coordination dynamics (Bardy, Marin, et al., 1999; Marin, Bardy, Baumberger, et al., 1999; Marin, Bardy, & Bootsma, 1999). In these studies, standing participants were asked to use front-to-back movements of the head to track front-to-back oscillations of a target. We measured posture during task performance and found that for movements of the ankles and hips, participants exhibited two preferred coordination modes. Because of its rhythmical nature (e.g., Yoneda & Tokumasu, 1986), body sway could be described in terms of the relative phase, ϕ_{rel}, between the two joints. The ϕ_{rel} variable is valuable in this context because it is a collective variable that captures postural coordination patterns. Two values of ϕ_{rel} consistently emerged: an *inphase* mode, with the two joints moving simultaneously in the same direction (ϕ_{rel} close to 0°), and an *antiphase* mode, with the two joints oscillating simultaneously in opposite directions (ϕ_{rel} close to 180°). The emergence of these phase relations depended on the interaction among environmental constraints (i.e., surface properties, target amplitude, or frequency), intrinsic constraints (i.e., height of the center of mass, length of the feet, or body stiffness), and intentional constraints (i.e., the instruction to track target motion). None of these properties uniquely determined the selection of modes; a given mode emerged in response to particular constellations of different constraints. One consequence of this was that a fixed value of a given constraint was associated with different modes, depending on the values of other independent constraints. It was the simultaneous, interacting,—and sometimes competitive—pressure imposed by these constraints that determined the selective emergence of the inphase and antiphase modes (cf. Newell, 1986).

Transitions Between Modes

Also important for the present study was the repeated observation that a discrete increase in the amplitude or frequency of target motion (across trials) was accompanied by an abrupt shift from the inphase mode to the antiphase mode, and that, conversely, a decrease in target amplitude or frequency produced a shift from antiphase to inphase mode. The findings of Bardy, Marin, et al. (1999), Marin, Bardy, Baumberger, et al. (1999), and Marin, Bardy, and Bootsma (1999) are consistent with a dynamical analysis of coordination modes, with inphase and antiphase patterns being attractors in the postural state space. One limitation of our earlier work is that, as with the majority of research on postural control, our studies evaluated the existence of specific modes of coordination rather than transitions between modes (i.e., transitions occurred between trials and were not recorded or analyzed). Direct observation and study of the act of switching from one coordination mode to another requires new research, in which transitions occur within trials rather than between trials.

The dynamics of an order parameter—a macroscopic, low-dimensional variable that captures the (nonlinear) interactions between the various segments, muscles, or joints of the postural system—can be explored with the help of *potential functions* (e.g., Haken, Kelso, & Bunz, 1985). A potential function represents the energy landscape of the order parameter; it illustrates attractors and their stability, as well as the changes in attractors that result from changes in their parameters. Figure 1 shows an example of such a potential function, used in diverse branches of science, such as fluid dynamics (Araki, Yanase, & Mizushima, 1996), speech production (Tuller, Case, Ding, & Kelso, 1994), human locomotion (Diedrich & Warren, 1995), cognition (Nakahara & Doya, 1998), economics (Barnett & He, 1999), and population systems (Cushing, Dennis, Desharnais, & Costantino, 1998). The potential landscape *V* graphically illustrates the hypothesized dynamics of the postural transition, with ϕ_{rel} being the order parameter for coordination and *k* being a nonspecific control parameter, such as the amplitude or frequency of target motion, which can induce bifurcations in the order parameter. This representation is somewhat generic in the sense that it should not be taken to provide the particular equations of motion that guide the behavior of the postural system, but it has interesting properties for revealing the dynamic signatures of phase transitions (Beek, Peper, & Stegeman, 1995; Haken, 1983; Kelso, Ding, & Schöner, 1992). If changes between inphase and antiphase postural modes of coordination (e.g., Bardy, Marin, et al., 1999) are autonomous and self-organized phase transitions, then the following phenomena should accompany a continuous change in the control parameter *k*: (a) the presence of at least two modes of coordination, or attractors in the phase space for different values of *k*, reflecting the existence of *multistability*; (b) a qualitative change (or *bifurcation*) in the order parameter ϕ_{rel} as *k* reaches a critical value, expressing a sudden reorganization of the postural system; (c) an increase in the variability of ϕ_{rel} when approaching the transition region, reflecting *critical fluctuations* due to a reduction in stability near the transition; (d) a tendency for the postural system to remain in its current basin of attraction as *k* moves through the transition region, or *hysteresis*, yielding different transition values depending on the direction in which *k* is changing (i.e., increasing or decreasing); and (e), *critical slowing down*, which is also an index of stability. This last feature is expressed by the *relaxation time*, that is, the characteristic time of the system in returning to its stable state following a perturbation, which is increased in the transition region because of the shallower gradients in that region.

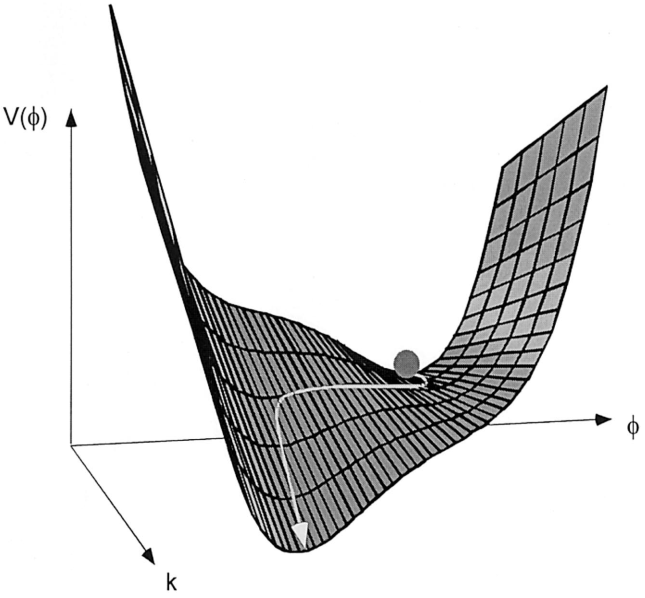

Figure 1. Potential landscape (*V*) exhibiting a bifurcation [$V(\phi) = k\phi - a\phi^2 + b\phi^4$]. As the control parameter *k* approaches a critical point, a previously stable coordination pattern becomes unstable, and the system (represented by an overdamped marble) spontaneously shifts to a new pattern. Loss of stability results in lengthening of the local relaxation time (*critical slowing down*) and, in the presence of stochastic noise, increasing variability of the order parameter ϕ (*critical fluctuations*). As the system becomes unstable, it switches to a new pattern without passing through stable intermediate patterns. The switch between patterns does not occur at the same value of the control parameter *k* when it is increasing as when it is decreasing (*hysteresis*).

Over the past 20 years, experimental and theoretical studies have provided strong evidence for the operation of self-organizational principles in the domain of human interlimb coordination (e.g., Baldissera, Cavallari, Maarini, & Tassone, 1991; Carson, Goodman, Kelso, & Elliott, 1995; Haken et al., 1985; Kelso, 1984; Schöner, Haken, & Kelso, 1986) and intralimb coordination (e.g., Buchanan, Kelso, & DeGuzman, 1997; Diedrich & Warren, 1995; Kelso, Buchanan, & Wallace, 1991), as well as for coordination of limbs with external events (e.g., Dijkstra, Schöner, & Gielen, 1994; Jeka, Schöner, Dijkstra, Ribeiro, & Lackner, 1997). These studies have concentrated on coordination of individual segments, such as fingers, arms, legs, or head. As a result, little is known about the problem of postural coordination, that is, coordination between the trunk and the legs (but see Haken, 1996). The aim of the present study was to test whether shifts between postural modes (expressed by the relative phase between ankle and hip) behave as nonequilibrium transitions between attractors and whether hallmarks of self-organization can be found in the postural coordination that humans spontaneously adopt for the accomplishment of suprapostural goals.

Participants in comfortable, bipedal stance were instructed to maintain a constant distance between their head and a visual target that oscillated along the line of sight. In Experiment 1, the frequency of target oscillation was either increased or decreased. Following our earlier work (Marin, Bardy, & Bootsma, 1999), oscillation frequency was expected to be a control parameter. The relative phase between rotations at the hips and ankles was a dependent variable and was considered as being the order parameter (Bardy, Marin, et al., 1999). Within trials, participants were exposed to stepwise changes (increasing or decreasing) in the frequency of target motion, and we analyzed the effects of these changes on the behavior of the order parameter. This design allowed us to test for the existence of multistability, bifurcation, critical fluctuations, and hysteresis. In Experiment 2, a sudden perturbation in the direction of motion of the visual target was introduced, and we analyzed the time required by participants to recover from the perturbation. Perturbations were timed to occur either close to or far from the value of the control parameter at which postural transitions tended to occur. This design permitted a quantitative analysis of critical slowing down.

Experiment 1: Postural Transitions

Method

Participants

Eleven undergraduate students from the University of the Mediterranean (5 male and 6 female; age = 19–35 years, *M* = 21.8, *SD* = 4.3) volunteered for participation in the experiment. All participants reported normal or corrected-to-normal vision. Their mean height was 1.68 m (*SD* = 0.08), and their mean weight was 65.2 kg (*SD* = 9.3). None of them were informed about the aims of the study.

Task and Apparatus

Participants stood barefoot on the laboratory floor at 1.60 m from a rear projection screen (3.00 m × 2.25 m), with their arms comfortably folded across the chest. A battery-based customized detector (9 V) positioned under the right foot of each participant was used to ensure that toes and heels were constantly kept in contact with the floor. Each trial during which contact was lost more than six times was canceled and immediately repeated. Participants were asked to remain oriented to the screen and to use body movements to track the front-to-back oscillations of a videographic target. Instructions stressed that participants should do their best to move in phase with the target and that the amplitude of their head motion should match the depicted amplitude of target motion. Each knee was strapped with an elastic band to prevent exaggerated flexion at this joint.

The sole source of light was the target display screen; there were no windows in the laboratory, and room lights were extinguished. Displays depicted a frontal surface, simulating a flat, rigid white square (56 cm × 51 cm on the screen) that oscillated in depth with a constant peak-to-peak amplitude of 10 cm. Target frequency depended on experimental conditions. Displays were generated on an INDY 4600 XZ Silicon Graphics, Inc. workstation and presented at eye level using an ELECTROHOME 7500 video projector with an image resolution of 1,350 × 1,100 pixels (see Figure 2).

Design and Procedure

The frequency of target oscillation varied in a stepwise manner in two conditions. In the *up* condition, frequency increased from 0.05 Hz to 0.80 Hz in steps of 0.05 Hz. In the *down* condition, it decreased from 0.80 Hz to 0.05 Hz in similar steps. Each frequency step lasted for 10 oscillation cycles, for a total of 160 cycles/trial. Experimental data were collected in each trial after a warm-up period of 20 s. There were two trials per condition. Participants were given a 5-min rest between trials. Trial order was counterbalanced over participants. Each trial was 12 min long, and each participant was tested in a single experimental session lasting about 90 min.

Data Acquisition and Analysis

The front-to-back displacement of the participant's head was recorded using a potentiometer. A weighted thread was fixed to the back of the head and passed over a wheel attached to the axle of the potentiometer (Bessou, Dupuis, Montoya, & Pages, 1989). Data from the potentiometer were acquired and converted to displacement in millimeters using a Biopac Systems MP-100 A/D converter (Biopac Systems Inc., Santa Barbara, CA). To allow quantification of the performance at the tracking task (gain and relative phase between displacement of the head and displacement of the

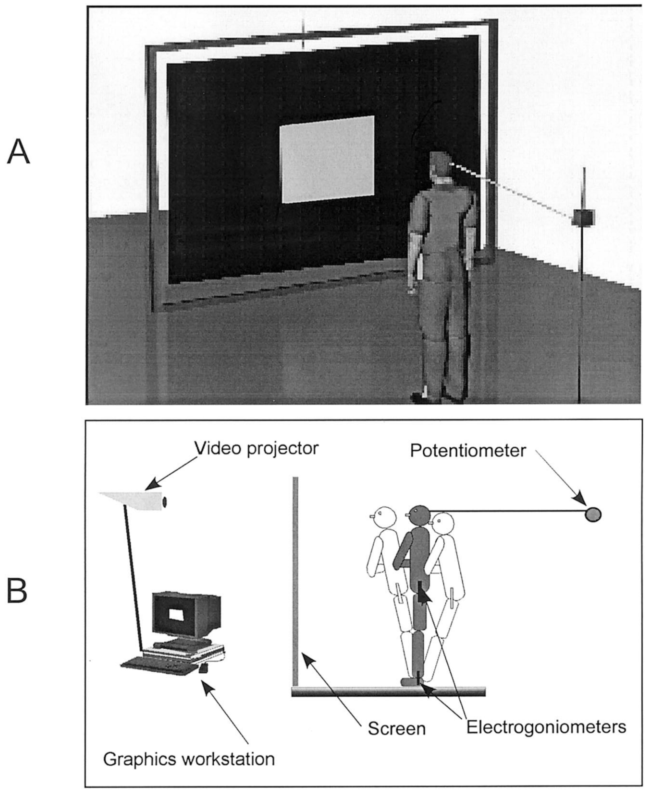

Figure 2. Experimental task and setup. A: Rear view of the experimental situation showing a participant facing the white target on the screen. B: Side view.

target), we used a signal from the graphics workstation to trigger data acquisition for each trial at the onset of a target oscillation cycle.

Postural movements, that is, the angular displacement of hip and ankle, were measured with the help of two electrogoniometers (Biometrics, Inc.). One was attached to the lateral side of the right hip (from the greater trochanter to the iliac crest), and the other was fixed on the anterior side of the right ankle (from the scaphoid to the inferior third of the tibia). Both electrogoniometers were plugged into the Biopac converter and controlled by an Apple Macintosh SE 30. Hip and ankle data were synchronized with the visual target and with data from the head. Angular displacement measurements were accurate to 1° in the anteroposterior (AP) axis. All data were collected at a sampling rate of 20 Hz and were filtered at each frequency step with a recursive, second-order, Butterworth filter, with a cutoff frequency equal to the current frequency step + 0.05 Hz. This procedure was run through twice at each frequency step to negate the phase shift (Wood, 1982).

We expected that a postural transition would occur for each participant. However, on the basis of preliminary findings showing that the transition frequency differed across participants (see Oullier, Bardy, Bootsma, & Stoffregen, 1999; see also Figure 6, which appears later), we adopted the following procedure before computing our dependent variables. First, for each trial 18 segments were defined, 9 before and 9 after the transition. Each segment included the mean values of our dependent variables for four cycles, with an overlap of two cycles (see Kelso, Scholz, & Schöner, 1986, for a similar analysis). The use of 18 segments was imposed by the large variability between participants in the frequency at which transitions occurred and corresponded to the maximal range, including data points from all participants at all frequencies. Second, segments were aligned across each participant on the first cycle following the transition. Overall, this procedure resulted in the analysis of a limited portion of the ascendant or descendant run corresponding to five to six frequency steps. At the same time, the procedure promoted a detailed analysis of the behavioral organization (and its changes) in the transition region, which was the main goal of Experiment 1.

The dependent variables were (a) the mean head–target gain, g, at each frequency segment; (b) the relative phase between oscillations of the visual target and oscillations of the head in the AP direction, $\phi_{\text{t-h}}$; (c) the peak-to-peak amplitude of the angular displacement of the ankle, A_a, and of the hip, A_h; (d) the relative phase, ϕ_{rel}, between ankle and hip motion, which served as the order parameter for characterizing the postural coordination; (e) the standard deviation of ϕ_{rel} for each segment, $SD\ \phi_{\text{rel}}$, which was used to express critical fluctuations; (f) the transition time (TT), that is, the time taken to leave a previously stable mode and to enter a new stable mode; and (g) the transition frequency (TF), that is, the value of the control parameter corresponding to the entrance into the new mode. A change of coordination state was indicated by the last value of ϕ_{rel} not occurring in the interval defined by $\phi_\mu \pm SD\ \phi_\mu$, where ϕ_μ is the mean of the first (for the initial state) or last (for the new state) 25 values of ϕ_{rel}, and $SD\ \phi_\mu$ is the standard deviation of ϕ_μ during the same period (see Figure 3). The last variable, TF, was used to test for hysteresis effects, that is, for the tendency of the postural system to remain in its basin of attraction and delay the transition point. This effect was considered to exist when $\text{TF}_{\text{up}} > \text{TF}_{\text{down}}$. For all variables, the data series for the down condition were inverted, so as to compare up and down conditions.

Both $\phi_{\text{t-h}}$ and ϕ_{rel} were computed using the point-estimate relative phase method (Zanone & Kelso, 1992), with one point estimate per cycle. Because phase is a circular variable, standard circular statistics were used for computing measures of central tendency and variability for relative phase, as well as relevant inferential statistics (cf. Batschelet, 1981).

Results

In this experiment our main interest was to detect four hallmarks of self-organization in posture when participants performed a suprapostural task. We sought to verify the presence of (a) two stable states or modes of coordination, (b) a sudden jump from one state to the other, (c) an increase in variability when approaching the transition region, and (d) hysteresis. Figure 4 presents a sample trial from a representative participant obtained in the up condition. Displacements over time of target, head, hip, and ankle, as well as relative phase ϕ_{rel} between ankle and hip, are illustrated before and after the transition. We began with an analysis of the participants' performance at the visual tracking task. This was followed by an analysis of the postural states spontaneously adopted by the participants in support of task performance and the changes between postural states that were observed with changes in the control parameter.

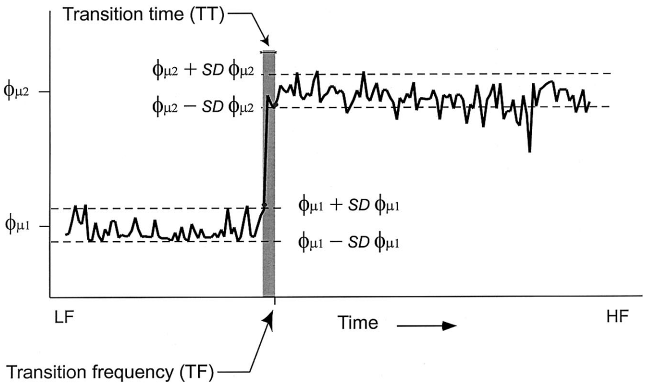

Figure 3. Method for determining the transition frequency (TF) in Experiment 1 (ϕ_μ = mean of the relative phase, ϕ_{rel}; $SD\ \phi_\mu$ = standard deviation of ϕ_μ). The transition time (TT) is indicated by the gray area. The transition frequency is indicated by the tick on the x-axis. LF and HF refer to low frequency and high frequency, respectively.

Tracking Task Performance

For each frequency segment of up and down conditions, mean head–target gain, g, and relative phase, $\phi_{\text{t-h}}$, were calculated and are illustrated in Figures 5 and 6. Optimal performance in this task would produce $g = 1$ and $\phi_{\text{t-h}} = 0$. As the following discussion shows, participants complied with the instruction to track the virtual target, movement of the head was coupled to movement of the simulated target, and the head moved in phase with the target in both up and down conditions.

Mean head–target gain. Gain was calculated for each oscillation cycle and was averaged across the two trials. As a criterion defining acceptable tracking performance, we required that g should fall in the interval $0.50 < g < 1.50$. One participant was excluded from the analysis because he did not meet this criterion (mean $g = 0.24$). Mean gain for the remaining participants ($N = 10$) was 1.07 ($SD = 0.57$) in the up condition and 0.75 ($SD = 0.35$) in the down condition (see Figure 5). A two-way repeated measures analysis of variance (ANOVA; Direction × Frequency Segment) on g revealed no significant main effect for direction, $F(1, 9) = 4.04$, *ns*. A small effect was found for frequency segment, $F(17, 153) = 2.52$, $p < .05$, accounting for 0.80% of the total variance, indicating a decrease in g as target frequency increased. This result may reflect a widely reported inverse relationship between amplitude and frequency of oscillation in cyclical move-

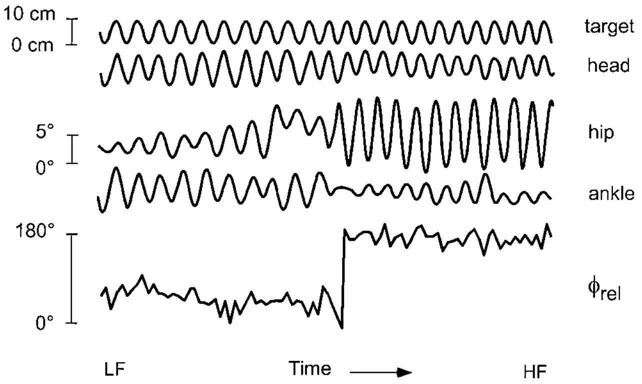

Figure 4. The transition region for one typical record (up condition) showing sustained inphase motion between the target and the head and a transition from an inphase to an antiphase motion of the ankles and hips as target frequency is increased over time. This transition between patterns is highlighted in the change in relative phase, ϕ_{rel}, of the two joints. LF and HF refer to low frequency and high frequency, respectively.

ments (e.g., Kay, Kelso, Saltzman, & Schöner, 1987) rather than specific characteristics of the suprapostural task used here. This interpretation is corroborated by the nonsignificant interaction between direction and frequency segment, $F(17, 153) = 1.25$, *ns*. Overall, *g* was close to unity, confirming that participants satisfactorily tracked the motion of the target.

Target–head relative phase. The mean relative phase $\phi_{\text{t-h}}$ between motion of the head and motion of the target was 10.78° ($SD = 8.19°$) in the up condition and 7.22° ($SD = 15.09°$) in the down condition (see Figure 6). Phase values were clustered around a mean (significant Raleigh tests for nonhomogeneity, $p < .05$), thus indicating a preferred phase angle. The $\phi_{\text{t-h}}$ differed significantly from 0° in both conditions, suggesting that participants' movements were in phase with motion of the target, but with a small lag. This is evidenced by the 95% confidence interval observed for relative phase, which did not contain 0°, in either the up ($10.21° < \phi_{\text{t-h}} < 11.35°$) or the down ($6.07° < \phi_{\text{t-h}} < 8.23°$) conditions. Watson–Williams tests performed on $\phi_{\text{t-h}}$ also revealed significant differences between direction conditions, $F(1, 718) = 7.92$, $p < .05$, indicating a greater phase lag in the up condition. Overall, the data suggest that participants did not anticipate the motion of the target but moved slightly behind it.[2] In short, the tracking task was satisfactorily performed (mean $g = 0.89$; mean $\phi_{\text{t-h}} = 9.02°$) by 10 of the 11 participants.

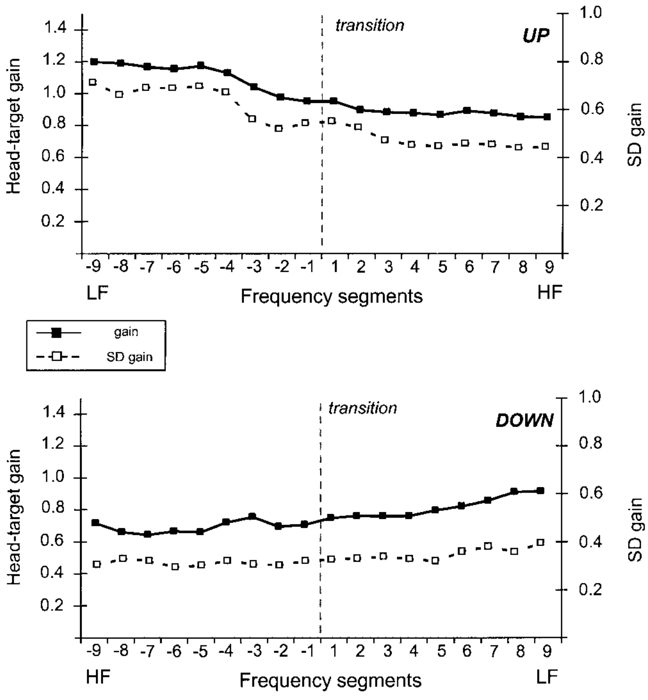

Figure 5. Mean head–target gains (and standard deviations) by frequency segments in up (top) and down (bottom) conditions of Experiment 1. LF and HF refer to low-frequency and high-frequency segments, respectively.

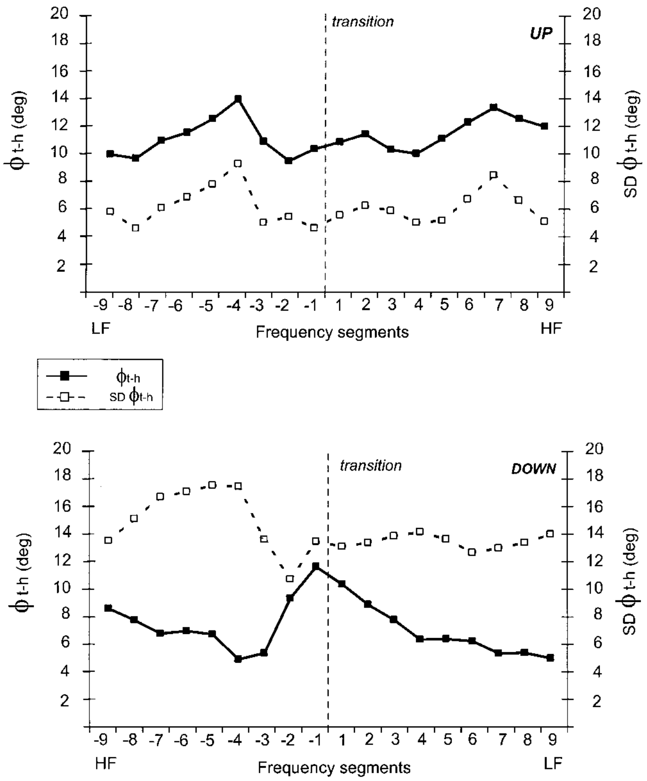

Figure 6. Mean target–head relative phases, $\phi_{\text{t-h}}$ (and standard deviations), by frequency segments in up (top) and down (bottom) conditions of Experiment 1. LF and HF refer to low-frequency and high-frequency segments, respectively. deg = degrees.

Postural Motion and Coordination

We now examine the postural coordination modes adopted during the tracking task. Several points should be noted. First, the

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[2] This phase analysis did not take into account the postural organization that underlies the tracking performance, and it could be argued that the coordination modes adopted before and after the postural transition differentially affected $\phi_{\text{t-h}}$. This was, however, not the case, for $\phi_{\text{t-h}}$ was similar before ($M = 8.91°$, $SD = 12.28°$) and after ($M = 8.75°$, $SD = 11.10°$) the transition in postural modes, Watson–Williams $F(1, 718) < 1$.

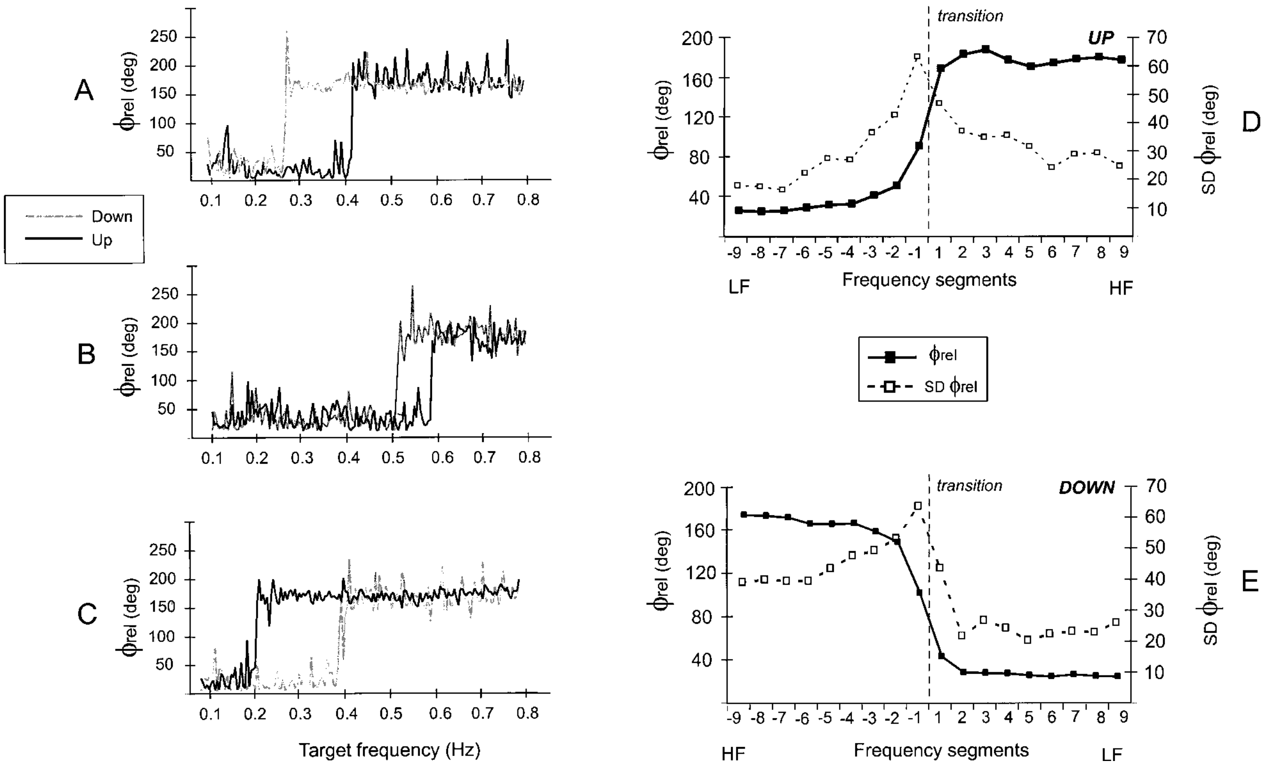

Figure 7. Postural transitions in Experiment 1: Point estimate value of the ankle–hip relative phase, ϕ_{rel}, for three individual trials in the up and down conditions (A, B, and C), and means and standard deviations of ϕ_{rel} for the 10 participants tested in the two conditions (D and E). Each segment includes a temporal average of ϕ_{rel} over four cycles of oscillation, with an overlap of two cycles. LF and HF refer to low-frequency and high-frequency segments, respectively. deg = degrees.

amplitude of ankle motion increased slightly with target frequency (this was not true of hip motion). Second, increasing the target frequency produced a sudden and qualitative change from inphase coordination to antiphase coordination, and decreasing the target frequency produced a similar change in the opposite direction. Third, an increase in variability of ankle–hip relative phase was observed near the transition point. Fourth, the target frequency at which the transition occurred depended on target direction. These results are discussed in turn.

Ankle and hip amplitudes. The mean amplitude of ankle motion (A_a) in the up and down conditions was 3.90° (*SD* = 2.70°) and 4.58° (*SD* = 2.88°), respectively. A Direction × Frequency Segment repeated measures ANOVA on A_a (averaged across the two trials) indicated no main effects for direction, $F(1, 9) = 1.63$, *ns*, or frequency segment ($F < 1$) and no significant interaction ($F < 1$). The mean amplitude of hip motion (A_h) was 3.10° (*SD* = 2.20°) in the up condition and 5.09° (*SD* = 4.12°) in the down condition. A Direction × Frequency Segment repeated measures ANOVA on A_h revealed significant main effects for direction, $F(1, 9) = 4.97$, $p < .05$, accounting for 11% of the total variance, and for frequency segment, $F(17, 153) = 2.60$, $p < .05$, accounting for 0.30% of the total variance. The latter effect indicated a small increase in A_h with increases in target frequency. The Direction × Frequency Segment interaction, however, was not significant ($F < 1$), suggesting that the two effects were independent.

Ankle–hip relative phase. The presence of ankle and hip rotation does not indicate whether, or how, these movements were coordinated. To address these issues, we need to analyze the relative phasing between the two joints. Raw data originating from three different participants in both up and down conditions are illustrated in Figures 7A, 7B, and 7C, and the mean ankle–hip relative phase for the 10 participants is shown on Figures 7D and 7E as a function of frequency segments. We describe in this section the behavior of the order parameter ϕ_{rel} as target frequency increased or decreased.

Two modes. As can be seen in Figure 7, two coordination modes, expressed by two specific values of ϕ_{rel}, emerged consistently: an inphase mode ($\phi_{\text{rel}} \approx 29°$) at low target frequencies, and an antiphase mode ($\phi_{\text{rel}} \approx 171°$) at high target frequencies.[3] Among the 10 participants, there were no exceptions to this finding. Across participants, ϕ_{rel} was significantly clustered around a

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[3] It has to be remembered that because changes in coordination mode were specific to each participant (see the *Method* section and Figures 7A–7C), data were aligned at the transition frequency to compute means and standard deviations across trials and participants; hence what is termed *low* or *high* frequency in this section does not refer to an absolute value of target frequency, and what can be considered as low frequency for one participant may be considered as high frequency for another.

mean in each frequency segment (significant Raleigh tests for nonhomogeneity, $p < .05$), indicating a preferred phase angle for each frequency. In the inphase mode, the 95% confidence interval for ϕ_{rel} did not contain 0° in either the up ($27.5° < \phi_{\text{rel}} < 35.5°$) or down ($24.4° < \phi_{\text{rel}} < 29.9°$) conditions. Overall, in the inphase mode, the ankles tended to lead the hips by approximately 30°. In the antiphase mode, the 95% confidence interval for ϕ_{rel} contained 180° in the up condition ($174.0° < \phi_{\text{rel}} < 181.4°$) but not in the down condition ($158.3° < \phi_{\text{rel}} < 169.4°$). Departures from ϕ_{rel} values of 0° and 180° indicate that the dynamics of multisegment postural coordination of stance differ from the dynamics of natural interlimb coordination (e.g., Kelso, 1984). Similar departures were reported by Bardy, Marin, et al. (1999) and by Marin, Bardy, Baumberger, et al. (1999). The consistency of this finding suggests that coordination patterns observed in multisegment control of stance are task specific. We return to this point in the General Discussion.

Transitions between modes. The series of small increases in target frequency produced a sudden qualitative change, or transition, from the inphase mode to the antiphase mode, and the series of small decreases in target frequency produced the opposite transition. This was observed for all participants, in all trials.[4] Our analysis of transition time TT revealed that these transitions occurred rapidly, within about two cycles after a change in target frequency. The target frequency at which the transition occurred differed among participants; for this reason, TT was calculated for each trial and expressed in cycles. Mean values of TT were 1.50 cycles ($SD = 0.76$) and 1.25 cycles ($SD = 0.71$) for the up and down conditions, respectively. No difference was observed in TT between the two conditions, $t(19) = 1.75$, *ns,* suggesting that similar dynamics underlie transitions in the two directions. Seventy-three percent of the transitions occurred within one cycle, 15% within two cycles, and only 12% within three cycles or more. The rapidity of the transitions, capturing the migration in the probability density of ϕ_{rel}, emphasizes the nonlinear nature of the changes between the two coordination modes (Scholtz, Kelso, & Schöner, 1987; Schöner et al., 1986)

Critical fluctuations. The mean standard deviation of ϕ_{rel}, *SD* ϕ_{rel}, was 32.4° in the up condition ($SD\ \phi_{\text{rel}} = 11.4°$) and 34.7° in the down condition ($SD\ \phi_{\text{rel}} = 11.9°$). Fluctuations in relative phase tended to increase near the transition point (see Figure 7). The profiles of *SD* ϕ_{rel} were similar across participants: A low initial value (near 25°) was followed by an increase in variability near the transition between coordination modes, in both up and down conditions, with a value of about 45° prior to the transition and of 60° during the transition. Following the transition, there was a rapid decrease in phase variability. It is interesting to note that the value of *SD* ϕ_{rel} differed between inphase ($M = 29.4°$, $SD = 7.8°$) and antiphase ($M = 37.6°$, $SD = 13.2°$) modes, Watson–Williams $F(1, 34) = 4.85$, $p < .05$. Thus, there was evidence for a difference in stability between the two modes, with the inphase mode being dynamically more stable than the antiphase mode.

Hysteresis. The values of target frequency (i.e., the control parameter) at which the transition occurred were also used to search for a hysteresis effect. This effect was considered to exist when $\text{TF}_{\text{up}} > \text{TF}_{\text{down}}$. Transition frequency varied across participants, ranging from 0.15 Hz to 0.60 Hz in the up condition and from 0.20 Hz to 0.60 Hz in the down condition. A paired *t* test performed on the (mean) values of TF between the two conditions indicated the existence of a hysteresis effect, with transitions from inphase to antiphase modes occurring at a higher target frequency ($M = 0.43$ Hz, $SD = 0.18$) than transition from antiphase to inphase modes ($M = 0.34$ Hz, $SD = 0.17$), $t(19) = 4.27$, $p < .01$.

In summary, Experiment 1 provided insight into the self-organizing properties of the postural system. First, participants complied with the instructions to track the moving target, with a gain close to unity and a phase lag of about 10°. Second, two (and only two) coordination modes were found to emerge out of the interplay of intentional, behavioral, and environmental constraints: inphase (30°) and antiphase (170°). Third, a frequency-induced loss of stability occurred as target frequency increased or decreased, yielding critical fluctuations in the vicinity of the transition region. Fourth, an abrupt transition was observed between modes, with no intermediate values. Fifth, a hysteresis effect was found in the data, with inphase to antiphase transitions occurring at a higher target frequency than antiphase to inphase transitions.

Experiment 2: Perturbation of Stance

In Experiment 2, we pursued our dynamical analysis of postural pattern formation by examining more closely the stability of the two postural coordination modes. We addressed changes in stability related to changes in the frequency of target motion, measuring (a) the number of transitions provoked by a perturbation in target motion and (b) the local relaxation time following each perturbation. If the increase in variability of ϕ_{rel} obtained in Experiment 1 near the transition region is caused by loss of stability, then the number of provoked transitions due to the imposed perturbations should increase in that region. Moreover, the local relaxation time should be smaller when the system is far from the transition and larger when it is near the transition.

Method

Participants

Eight participants from the University of the Mediterranean (4 female and 4 male; age = 19–34 years, $M = 21.4$, $SD = 4.1$) took part in Experiment 2. With one exception, all had already participated in Experiment 1. All reported normal or corrected-to-normal vision.

Task and Apparatus

The task and apparatus were the same as in Experiment 1. The novel feature of Experiment 2 was in the motion of the target to be tracked. In experimental conditions, the frequency of target oscillation was held constant during the course of each trial, and a transient visual perturbation was introduced. The perturbation consisted of a sudden, 180° shift in the AP displacement of the target. The perturbations occurred at the position of maximum velocity in the cycle of target oscillation. The direction of switch (from far to close, and from close to far) was counterbalanced between perturbations for each participant (see Figure 9, which appears later). Participants were instructed to move their heads to track the AP motion of the target, tracking whatever motion occurred during the course of the trials. Participants were informed that there would be sudden changes in

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[4] In almost all trials (38 out of 40), the transitions resembled those illustrated in Figures 7A–7C, with a single and abrupt shift from one pattern to the other and no intermediate state.

target motion. The amplitude of the target motion was kept constant at 10 cm.

Design and Procedure

Four conditions of perturbation were tested. An initial control trial was used to determine TF, that is, the frequency at which the transition from inphase to antiphase coordination took place. This trial was similar to the up condition of Experiment 1. TF was determined separately for each participant. In the four experimental conditions, the frequency of target oscillation was set at a constant value, either far from the participant's TF (TF − 0.30 Hz, TF + 0.30 Hz) or close to it (TF − 0.15 Hz, TF + 0.15 Hz). Thus, in the two low-frequency conditions (TF − 0.30 Hz and TF − 0.15 Hz), participants were expected to exhibit inphase coordination, whereas in the high-frequency conditions (TF + 0.15 Hz and TF + 0.30 Hz), participants were expected to exhibit antiphase coordination. Each condition included 110 target cycles. The first perturbation, which occurred after 20 oscillation cycles, was not analyzed. Subsequent perturbations occurred every 10 cycles, for a total of eight perturbations (i.e., trials) analyzed in each condition. Each condition was tested once, and the order of conditions was counterbalanced between participants.

Data Acquisition and Analysis

The data acquisition system was similar to the one used in Experiment 1. To determine whether the visual perturbation had an effect on postural coordination, we computed ϕ_β, the mean value of the (point estimate) ankle–hip relative phase ϕ_{rel}, over 20 cycles preceding the first perturbation. Following the method used in Experiment 1, an interval around ϕ_{rel}, bounded by $\phi_\beta \pm SD\ \phi_\beta$, was created (see Figure 8). Posture was considered to be perturbed if the value of ϕ_{rel} left this interval during the course of a trial. Because these 20 values of ϕ_{rel} were not affected by the perturbation, the $\phi_\beta \pm SD\ \phi_\beta$, interval was considered to reflect a stable phase relation between the two joints.

Dependent variables included (a) the number of trials affected by the perturbation, (b) the occurrence of *provoked transitions* in perturbed trials (i.e., transitions from one coordination mode to another induced by the perturbation), (c) the relative phase ϕ_{rel} between ankles and hips, and (d) the *relaxation time* τ_{rel}. The τ_{rel} was calculated only for the perturbed trials in which there were no provoked transitions (see Table 1). Relaxation time was estimated using the exponent a of the decay rate of ϕ_{rel}, expressed by

$$\phi_{\text{rel}} = \phi_{\text{rel,f}} + (\phi_{\text{rel,0}} - \phi_{\text{rel,f}}) \cdot e^{-at},$$

where $\phi_{\text{rel,f}}$ is the final value of ϕ_{rel} after its return to its stable state (i.e., into the interval $\phi_\beta \pm SD\ \phi_\beta$), and $\phi_{\text{rel,0}}$ is the maximal value of ϕ_{rel} after the perturbation. The value of a in each trial was estimated by fitting the above equation with the time series of ϕ_{rel} following the perturbation. The τ_{rel} was defined by the ratio $1/a$ (e.g., Beek, Peper, Post, & Reijnen, 1995; Post, Peper, & Beek, 2000). As a consequence of fitting the decay function to point estimates of relative phases, τ_{rel} was scaled to cycle duration.

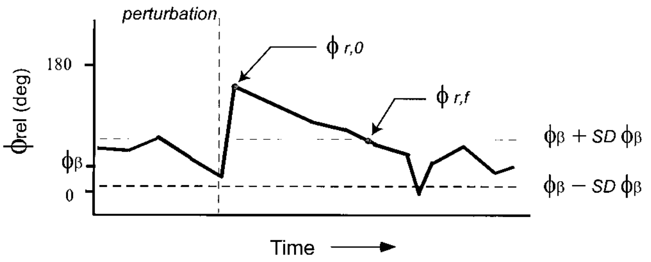

Figure 8. Method used in Experiment 2 to assess the relaxation time, τ_{rel}. deg = degrees.

Table 1
Number of Trials Analyzed and Affected by the Visual Perturbation in Experiment 2, by Frequency Condition

	Transition frequency (Hz)				
Trial	−0.30	−0.15	0.15	0.30	Total
Analyzed	56	56	53	53	218
Affected	53	51	37	45	186
Provoked transition	19	23	0	0	42
Computation of τ_{rel}	34	28	37	45	144

Finally, we also computed (e) the head–target gain g and (f) the relative phase $\phi_{\text{t-h}}$ between target and head for these affected trials. These variables were calculated for each oscillation cycle following each perturbation and were averaged across perturbations before performing statistical tests.

Results

Figure 9 presents a typical record from Experiment 2 showing motion of target, head, hip, and ankle during two perturbation trials, and mean results are illustrated in Tables 1 and 2. Perturbations affected postural coordination in 85% of the trials. Provoked transitions were more common when the visual perturbation occurred at frequencies below the TF, and the relaxation time τ_{rel} was higher in the vicinity of the TF. These results are discussed below.

Affected Trials

The perturbation in oscillation of the tracking target affected postural organization in 85% of the total number of trials analyzed (N = 218, see Table 1), according to the criterion illustrated in Figure 8. Of the total of 256 trials (8 participants × 8 perturbations × 4 conditions), 38 were not included in the analysis because of technical problems with one goniometer, and 32 trials were not affected by the perturbation, leaving 186 affected trials. The affected trials were differentially distributed among the four condi-

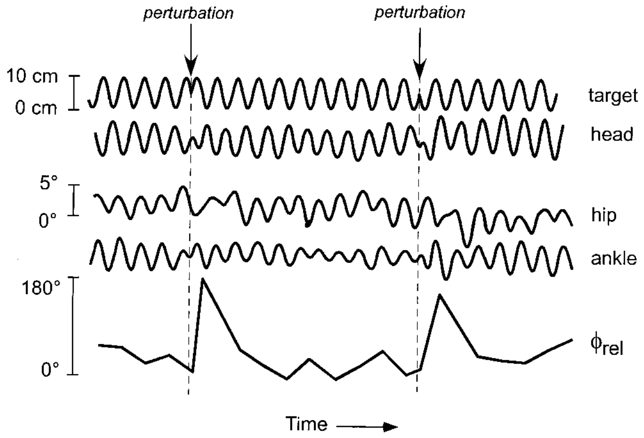

Figure 9. A typical record from Experiment 2, showing motion of target, head, hip, and ankle, as well as ankle–hip relative phase, ϕ_{rel}, during two consecutive visual perturbations.

Table 2
Means (and Standard Deviations) for Ankle–Hip Relative Phases (ϕ_{rel}), Relaxation Times (τ_{rel}), Head–Target Gains (g), and Target–Head Relative Phases ($\phi_{t\text{-}h}$) in Experiment 2, by Frequency Condition

	Transition frequency (Hz)			
Measure	−0.30	−0.15	0.15	0.30
ϕ_{rel} (deg)	21.82 (19.82)	28.31 (27.20)	181.21 (28.18)	177.12 (21.71)
τ_{rel} (cycles)	0.90 (0.48)	2.54 (0.98)	1.94 (1.01)	1.39 (0.49)
g	0.84 (0.33)	1.05 (0.57)	1.25 (0.66)	0.95 (0.38)
$\phi_{\text{t-h}}$ (deg)	8.28 (10.49)	16.49 (16.77)	12.64 (11.20)	6.89 (8.73)

Note. Values are reported for only the affected trials in which there were no postural transitions.

tions, $\chi^2(3, N = 186) = 12.25$, $p < .01$, occurring mainly in the two low-frequency conditions.

Provoked Transitions

The transient increase in the frequency of target motion caused by the perturbation provoked postural phase transitions in 42 of the affected trials (see Table 1). Each of these transitions occurred during low-frequency motion of the target; accordingly, the transitions were from inphase to antiphase coordination. This asymmetry may be understood as the consequence of the type of perturbation used; that is, a sudden and transient increase in target frequency that produces, consistent with the findings of Experiment 1, a postural transition from inphase to antiphase coordination. This is addressed in the General Discussion.

Postural Modes

In the remaining 144 trials (77% of the affected trials), postural coordination was altered by the perturbation in target motion, but there was not a transition between modes. As in Experiment 1, two coordination modes, expressed by two specific values of ϕ_{rel}, were observed: an inphase mode ($\phi_{\text{rel}} = 25.4°$, $SD = 12.8°$) at low target frequencies, and an antiphase mode ($\phi_{\text{rel}} = 178.5°$, $SD = 22.4°$) at high target frequencies.[5] The ϕ_{rel} was significantly clustered around a mean (significant Raleigh tests for nonhomogeneity, $p < .05$), indicating a preferred phase angle at each frequency. The 95% confidence interval for ϕ_{rel} did not contain 0° for the inphase mode, either far from ($18.7° < \phi_{\text{rel}} < 24.4°$) or close to ($22.33° < \phi_{\text{rel}} < 34.6°$) the transition. Overall, in the inphase mode, the ankles tended to lead the hips by approximately 25°. In the antiphase mode, results were different. The 95% confidence interval for ϕ_{rel} contained 180° both close to ($174.6° < \phi_{\text{rel}} < 186.0°$) and far from ($173.3° < \phi_{\text{rel}} < 182.0°$) the transition in postural mode, suggesting the ankles and the hips were moving purely out of phase. Finally, the variability of postural modes (expressed by the standard deviation of ϕ_{rel}; see Table 2) was higher near the transition region (about 27°) than far from it (about 20°), Watson–Williams $F(1, 142) = 10.31$, $p < .01$, consistent with the results from Experiment 1.

Relaxation Time

For each of the 144 affected trials, we calculated the relaxation time τ_{rel}, that is, the time characterizing the recovery from the perturbation. Overall, the fit between the exponential decay rate of ϕ_{rel} and the values of ϕ_{rel} following the perturbation was reliable (mean $r^2 = .63$); we therefore proceeded with the comparison of τ_{rel} between conditions. Means and standard deviations of τ_{rel} in each condition are given in Table 2. The table reveals that τ_{rel} was smaller than 3 cycles in each condition; that is, τ_{rel} was less than one third of the number of cycles (10) separating consecutive perturbations. Inspection of the data demonstrated that the postural system was always stable (i.e., had returned to the tolerance interval) when a new perturbation arrived. A one-way (between-trials) ANOVA performed on τ_{rel} revealed a significant effect of TF, $F(3, 140) = 24.02$, $p < .01$. We had predicted a loss of stability in the vicinity of TF and, consistent with this, τ_{rel} was smaller for the frequencies far from *TF* (± 0.30 Hz; $M = 1.18$ cycles) than for the frequencies close to TF (± 0.15 Hz; $M = 2.20$ cycles, Newman–Keuls $p < .01$). Hence, when the basin of attraction becomes shallower in the region of transition, there is an increase in the time it takes the postural system to relax to its stable state. A significant difference was found to exist between the two frequencies far from TF (TF − 0.30 Hz and TF + 0.30 Hz, Newman–Keuls $p < .01$), suggesting a more rapid decrease in τ_{rel} for the inphase mode than for the antiphase mode. This is also consistent with the results from both Experiment 1 and Experiment 2 for the standard deviation of relative phase, also showing a difference in stability between the two modes.

Head–Target Gain and Relative Phase

Mean gain and relative phase between head and target as a function of condition for the affected trials are shown in Table 2. The mean gain ($M = 1.02$, $SD = 0.18$) fell between 0.50 and 1.50 in each condition, indicating that the amplitude of the head was relatively close to the amplitude of the target. The top panel in Figure 10 illustrates the evolution of g for each cycle following the perturbation in the four experimental conditions. Each data point represents the average of gain values across participants and perturbations (see Table 2). A two-way (Frequency × Cycles) repeated measures ANOVA performed on g revealed a main effect for frequency, $F(3, 21) = 45.20$, $p < .01$, with all frequency conditions different from each other (Newman–Keuls $p < .05$). A

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[5] The affected trials in which there was a transition from inphase to antiphase were not included in this analysis to avoid undesirable values of ϕ_{rel} due to the transition.

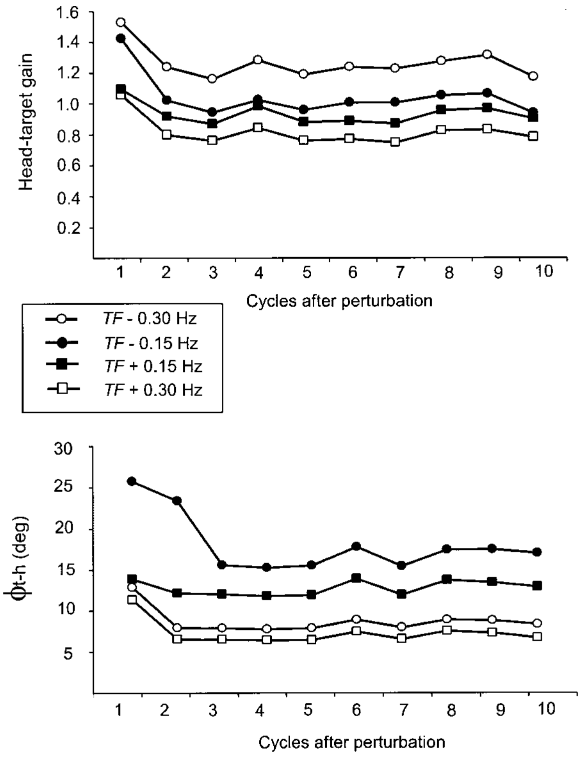

Figure 10. Mean head–target gain (top) and mean target–head relative phase, $\phi_{\text{t-h}}$ (bottom), by oscillation cycle, following the perturbation in each frequency condition of Experiment 2 ($N = 144$). TF = target frequency; deg = degrees.

significant effect was also found for cycles, $F(9, 63) = 4.84$, $p < .01$. This last effect is due largely to a higher gain in the first cycle after a perturbation (Newman–Keuls $p < .05$; see the top panel in Figure 10), suggesting that the perturbation brought about a transient increase in the amplitude of head motion. The Frequency × Cycles interaction, however, was not significant ($F < 1$), suggesting that these effects were independent.

The mean relative phase between target and head as a function of condition is shown in Table 2. In each condition phase was significantly clustered around a mean (significantly Raleigh tests for nonhomogeneity, $p < .05$), indicating a preferred phase angle, $\phi_{\text{t-h}}$. In addition, phase was significantly different from 0° in each condition. Participants moved in phase with the target with a small but consistent lag of about 10° (see the bottom panel in Figure 10), similar to the results of Experiment 1. This is confirmed by the 95% confidence interval observed for $\phi_{\text{t-h}}$, which did not contain 0° for any of the conditions (confidence intervals ranged from 6.08° to 18.45°). At the same time, $\phi_{\text{t-h}}$ was different between far and close conditions, Watson–Williams $F(1, 1438) = 117.20$, $p < .01$, suggesting a greater phase lag of the head with respect to the target close to the transition.

These results indicate that performance at the tracking task was satisfactory, with the amplitude of the head matching the amplitude of the target in all conditions. However, the perturbation temporarily affected the amplitude of head motion, and a greater phase lag of the head was observed when the perturbation was introduced close to the transition region.

Taken together, results of Experiment 2 provide additional knowledge of the dynamics underlying postural coordination in human stance. Whereas the tracking task was performed satisfactorily in each condition (i.e., gain close to unity and phase close to 10°), the visual perturbation temporarily affected the head–target coupling as well as the relative stability of inphase and antiphase patterns. Postural modes were found to be less stable when the perturbation was applied close to the transition region than when it was applied far from it, as evidenced by the larger relaxation time values in the latter situation. In addition, differential stability was found between the two modes, with the inphase mode being more stable than the antiphase mode.

General Discussion

In the two experiments reported here, we examined the self-organized properties of postural coordination patterns. In Experiment 1, a control parameter (the oscillation frequency of the target to be tracked) was increased or decreased in a stepwise manner, and we analyzed the behavior of the order parameter characterizing postural coordination (the relative phase, ϕ_{rel}, between ankle and hip). Two postural modes were observed (inphase and antiphase), and we found that changes between modes exhibited characteristics of nonequilibrium phase transitions, including multistability, critical fluctuation, bifurcation, and hysteresis. In Experiment 2, we investigated the stability of postural coordination both close to and far away from the region in which transitions between coordination modes occurred. We introduced a perturbation in the motion of the target to be tracked, and we varied the location of the perturbation relative to the transition region. We calculated the time needed by the postural system to relax to its stable state as a function of the location of the perturbation and found that the relaxation time was shorter for perturbations that occurred when the system was farther away from the transition region. The results of the two experiments are consistent with a dynamical theory of pattern formation in the multisegment control of stance, according to which postural states behave like attractors in the postural space and changes between states behave like self-organized, nonequilibrium phase transitions between attractors.

Are Changes Between Postural Modes Continuous or Discrete?

Our results provide new insight into the mechanisms underlying transitions between patterns of postural coordination. Some previous research has suggested that changes between postural patterns follow a continuous, progressive migration from one state to another. In the seminal work of Horak and her colleagues (e.g., Diener, Horak, & Nashner, 1988; Horak & Moore, 1993; Horak & Nashner, 1986), standing participants were exposed to a sudden horizontal perturbation of the support surface. Across trials, the support surface decreased in length; this was associated with a progressive shift from an ankle strategy to a hip strategy, as measured by changes in muscle activation patterns (i.e., a progressive decrease in the activity of the quadriceps accompanied by a corresponding increase in the activity of the hamstrings). By contrast, in the present study, our measurement of hip–ankle relative phase revealed an abrupt, qualitative reorganization of the postural components, from inphase to antiphase and from antiphase to inphase. This discontinuous, sudden change in coordination occurred despite the fact that, as in previous studies, changes in the independent variable (the frequency of target oscillation) were gradual. What might account for the difference between our results and those of Horak and her colleagues?

One area of difference is in the dependent variables used in different studies. In most studies, postural coordination has been measured and characterized (i.e., modeled) in terms of muscular activation patterns, concentrating on the degree to which individual muscles or muscle groups were implicated in the production of movement. Because many different activation patterns may exist, the state space of muscular activation is, by definition, high dimensional. By contrast, we concentrated on a higher order collective variable (ϕ_{rel}) that captures the behavior of the whole system (i.e., including but not limited to muscles) in a low-dimensional state space. The ontological motivation for this choice of variables relies on the *equivocality principle* first raised by Bernstein (1967), who pointed out that there is not a 1:1 correspondence between movement and muscular or neural activity: A given pattern of muscular activity can give rise to different movements of the body and, conversely, different patterns of muscular activity can produce the same movement (e.g., Bardy, Marin, et al., 1999; Buchanan & Horak, 1999). The abrupt changes that exist at the level of relative phase may not exist at the level of lower order components of the postural system, such as those revealed by muscle activity. Consonant with this interpretation is the finding (e.g., Horak & Nashner, 1986) that gradual changes in the length of the support surface lead to abrupt changes in phasing between individual muscle responses, despite the existence of continuous changes in the amplitude of muscular activity. Another interpretation of the difference in results between this study and previous research is that most previous research had used designs that were not appropriate for investigating properties of postural transitions (e.g., Bardy, Marin, et al., 1999; Black & Nashner, 1984; Buchanan & Horak, 1999; Horak & Nashner, 1986).

In addition to differences in dependent variables, our work differs from that of other researchers in the independent variables used. Studies of multisegmental postural control typically evaluate postural responses to punctate movements of the surface of support. We evaluated postural responses to continuous, periodic movements of a visual target. In Experiment 2, we included a punctate perturbation, but this was embedded in the continuous, periodic stimulus, and it was of interest to us only insofar as it influenced postural responses to the periodic stimulus. Our experiments were designed to facilitate the observation of dynamical aspects of posture, but our argument is that such dynamics are general to posture across situations. It should accordingly be possible to observe the relevant dynamical properties in the context of a wide variety of manipulations.

Theories of Postural Transitions

Our results (and the methodology that made it possible to obtain these results) have implications for theories of postural coordination. Consider the theory that postural patterns (and changes between them) are behavioral expressions of centrally programmed neural strategies (e.g., Alexandrov, Frolov, & Massion, 1998; Nashner & McCollum, 1985). Some of our results might be explained by this view. For example, inphase and antiphase relations between the ankles and hips could be understood as resulting from two different neural plans for action. In a similar manner, abrupt transitions between phase relations could be explained in terms of a sudden shift, in the central nervous system, between these plans. However, other aspects of the present results may not be so easily explained. Consider for instance our findings of hysteresis and of critical fluctuation effects. Experiment 1 showed that different patterns of posture can occur for a single value of target frequency. In addition, the variability of ϕ_{rel} increased when approaching the region of transition, irrespective of the direction of changes in the frequency of target motion (up or down). It would be difficult for a pure prescriptive theory of postural transitions to account for these effects. Why would the central nervous system choose different coordination modes for identical environmental conditions? How would centrally programmed changes in posture produce an increase in the variability of relative phase when approaching the transition? This type of result suggests that a general theory of postural transitions cannot be rooted in central mechanisms such as motor programs nor, for that matter, solely in mechanical, energetic, or perceptual mechanisms. None of these components can easily account for the hysteresis, critical fluctuation, and critical slowing-down effects. This does not of course imply that biomechanical, metabolic, or informational properties have no influence on the emergence of postural coordination modes (e.g., Bardy, Marin, et al., 1999; Buchanan & Horak, 1999) or on transitions between modes. After all, the dynamics of the order parameter ϕ_{rel} enslaves, in a way that remains to be determined, the dynamics of more local components (and the interaction between them), including the mechanical, metabolic, or informational levels reviewed separately in the introduction (e.g., Haken, 1996). Rather, our methodology and results suggest that the causes of transitions are not to be found in each of these properties alone (Diedrich & Warren, 1995). At a more general level, we would like to suggest that any theoretical approach to posture could benefit from the present results, because the production and regulation of movement could take advantage of the self-organized properties outlined here (e.g., Rosenbaum, 1998).

Multistability and Postural Modes

Multistability refers to the existence of multiple, qualitatively distinct patterns in a state space, each of which is stable over some range of values of a control parameter. Consistent with this, our measurements revealed two consistent values of hip–ankle relative phase, each of which tended to predominate in a certain region of the control parameter space. At low frequencies of target oscillation, the ankles and hips moved in phase, whereas at higher frequencies of target motion, antiphase motion was observed. These results replicate our earlier findings (e.g., Bardy, Marin, et al., 1999).

For the inphase mode, the value of ϕ_{rel} differed from 0° in both up and down conditions of Experiment 1 ($\phi_{\text{rel}} \approx 30°$), indicating that the ankles tended to lead the hips. It also differed from 180° for the antiphase mode in the down condition of Experiment 1 ($\phi_{\text{rel}} \approx 170°$). This departure from pure inphase and antiphase mode-locking has not been observed in two more or less identical components (e.g., Kelso, 1984; Schöner et al., 1986), but it has been observed in the context of whole-body coordination (Bardy, Marin, et al., 1999; Buchanan & Horak, 1999). This observation could have implications for modeling of postural states and transitions. Why does phase-related motion in posture differ from phase-related motion in other movement domains? An explanation may be found in the frequency competition $\Delta\omega$ between the individual oscillators involved. Following the pioneering work of Von Holst (1937/1973) indicating that the coordination between fins of the *Labrus* fish was a combination of the *maintenance tendency* effect (the tendency of the two fins to oscillate at their preferred frequency) and the *magnet* effect (the tendency for each fin to be attracted to the other fin's frequency), much work in interlimb (e.g., Rosenblum & Turvey, 1988; Schmidt, Shaw, & Turvey, 1993; Sternad, Turvey, & Schmidt, 1992) and interorganism (e.g., Amazeen, Schmidt, & Turvey, 1995) coordination has demonstrated a systematic shift in the location of basins of attraction when $\Delta\omega$ differs from zero (this shift is referred to as *fixed point drift*). Similarities in eigenfrequency favor symmetrical couplings between fingers, between arms, or between people. By contrast, the upper and lower parts of the body differ substantially in length, mass, and moment of inertia, and these differences, in turn, produce differences in frequency between the torso and the legs (e.g., McCollum & Leen, 1989). This nonidentity in eigenfrequency may be responsible for the different value of relative phase, and for the variability of ϕ_{rel}, during inphase postural coordination (e.g., Sternad, Amazeen, & Turvey, 1996). This hypothesis could be evaluated using a systematic manipulation of $\Delta\omega$, for example, by changing the distribution of mass of the torso or legs.

Another candidate explanation is related to the type of coupling between oscillators. Previous research on biological coordination has focused on limbs that had no mechanical influence on one another. In studies of finger coordination, for example (e.g., Kelso, 1984), the links between the fingers of different hands have been neural or informational, but not mechanical. In a similar manner, in studying pairs of people, Schmidt, Carello, and Turvey (1990) observed stable coordination that was mediated solely by information (vision). By contrast, the limbs involved in postural control are linked not only in neural and perceptual terms but also in mechanical terms. The two-segment inverted pendulum that has been used to characterize the postural system is composed of oscillators that are coupled together inertially. This inertial coupling might underlie the phase lag observed between the two oscillators in the inphase mode.

Mode Stability and Asymmetry

Two measures of mode stability were used in this study. In Experiment 1, changes in the variability of relative phase over the course of a trial showed a decrease in stability as the transition point was approached. This was confirmed in Experiment 2 by introducing a visual perturbation either close to or far from the individual transition frequency and by analyzing the local relaxation time τ_{rel} following perturbations. As predicted, τ_{rel} was greater close to the transition. Hence, changes in postural behavior were accompanied by loss of stability of the order parameter (expressed by critical fluctuations and critical slowing down). This finding supports a dynamical interpretation of postural transitions. At the same time, these two behavioral expressions of (loss of) stability also captured interesting differences between the two coordination modes. The standard deviation of ϕ_{rel} was smaller for the inphase mode, and so was τ_{rel}, suggesting that the inphase mode is more stable than the antiphase mode. This may indicate that the local slopes at the bottom of each well in the potential function (Figure 1) are not identical. Similar effects have been reported in classical work on interlimb coordination (Haken et al., 1985). At the same time, the greater stability of the inphase mode appears to be at variance with the finding from Experiment 2 that provoked transitions due to the perturbation were exclusively from inphase to antiphase. The possibility of modeling the dynamics of the postural system while taking into account the coexistence of these two observations remains an open question, which may be addressed in future research. We note, however, that the two findings may be mutually consistent. It may be that the asymmetry in the direction of provoked transitions observed in Experiment 2 was caused by the asymmetry in the visual perturbation rather than by an asymmetry in postural dynamics. The perturbations consisted exclusively of transient increases in the frequency of target motion. For this reason, the observed transitions from inphase to antiphase, and not from antiphase to inphase, might have resulted from a sudden destabilization of the inphase mode, as evidenced by the data obtained in Experiment 1. To evaluate this possibility, in future research there should be manipulation of the type of perturbation (e.g., increase vs. decrease in target frequency). For the present, we believe that these results offer converging evidence for the existence of self-organized phenomena operating at the level of whole-body coordination and that they encourage examination of the possibility that the interactions between the various components of the postural system might be addressed through the physics of nonequilibrium processes.

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