Chapter 14
Dynamics of Human Gait Transitions
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Abstract

What is responsible for the organization of complex actions? In this chapter, we address this question by focusing on the transition from walking to running in humans. First, we consider the concept of a motor program as a source of the organization seen in human gait. We then present evidence consistent with a dynamic theory of the shift between gaits. Results from our studies indicate that preferred gaits are attractors that exhibit stable phase relationships between the leg segments, whereas gait transitions are bifurcations characterized by a loss of stability. We conclude that complex behaviors such as locomotion likely emerge from the dynamics of the motor system and task constraints, and that they are not imposed on the system by a motor program.

14.1 Introduction

Complex actions require a large number of degrees of freedom to be coordinated in a precise manner (Bernstein, 1967). For instance, during bipedal locomotion the legs move 180° out-of-phase with each other, and the segments within each leg exhibit specific phase relationships (Diedrich and Warren, 1995b). What is responsible for these complex sequences of limb movements? In this paper, we approach this question by considering the walk-run transition in humans. First, we consider motor programs as a possible source of the organization seen in human gait. We then discuss a dynamic theory of human gait and present supporting evidence from several recent experiments. We conclude that actions such as gait likely emerge from the dynamics of the action system and task constraints.

14.2 The Origin of Organization

It is often assumed that the organization and timing of movements is due to the prior organization of some entity in the motor system. An example from psychology is the motor program, typically defined as a hierarchical memory structure that specifies many aspects of a movement, beginning with the order, phasing, and relative force of its components, and ending
with a sequence of specific muscle contractions (Keele, 1982; Schmidt, 1988). A related example from neuroscience is the central pattern generator (CPG), classically conceived as a neural circuit in the spinal cord that produces a specific pattern of motor neuron activity (Grillner, 1975). According to this view, the organization of behavior is prescribed by a previously organized internal structure, with different modes of movement attributable to different structures. This implies that transitions between movements occur via switching between these internal entities. In the case of human gait, for example, Shapiro and colleagues (1981) proposed that the walk-run transition results from the selection of different motor programs for walking and running.

Although the concept of a motor program addresses the sequencing and timing of limb movements, it leaves a number of questions unanswered. First, the problem of the origin of organization is simply relocated from observable movements to unobservable structures in the nervous system. Even if we grant the existence of motor programs or CPGs, how did they come to be so structured, and why do they have the particular organization they do? This leads us to look to the constraints on movement for a deeper explanation, including the behavioral function or task (e.g., forward progression), the mechanics of the task (e.g., coupled, springy multilink pendula and ground surface characteristics), and the dynamics of self-organization (e.g., the spontaneous behavior of coupled oscillators). Indeed, as currently conceived, CPGs themselves look less like hard-wired structures and more like self-organizing dynamical systems, for interactions among a small network of neurons and neuro-modulators can flexibly generate a variety of patterns, and conversely, the same pattern can be produced by different neural networks (Marder, 1988; Harris-Warwick and Johnson, 1989). We will have to appeal to more general principles to account for the organization not only of movements, but also of the CPGs purported to control them, for the answer is unlikely to be found in the neural structure alone.

A second problem with the motor program concept concerns behavioral transitions. The mechanism responsible for selecting appropriate motor programs or CPGs is unclear. The act of switching between programs or CPGs implies the existence of a central controller, with all its attendant problems (Carello et al., 1984). Further, simply claiming that behavioral transitions are due to the switching of motor programs begs the question of why such transitions occur, that is, why certain action modes are preferred over others under particular conditions.

One way of addressing the question of why behavioral transitions occur when they do is to ask what variables are optimized by the transition. Many optimization criteria have been proposed in the biomechanics literature, including overall energy expenditure and mechanical stresses (e.g., Margaria, 1976; Farley and Taylor, 1991). Although this literature does not address the underlying control processes, the optimization of particular costs can be made consistent with a motor programming perspective if one assumes that the controller is appraised of the cost variable and knows how to evaluate it in order to switch programs. A system can also optimize a cost variable and exhibit stable values as the outcome of a dynamical process, without that variable being explicitly used by a central controller (see later discussion; Kugler and Turvey, 1987).

14.3 Gait Transitions

What optimization criteria can account for the transition between walking and running? A first type of explanation proposes that the shift between gaits occurs to minimize mechanical stresses, thereby avoiding injury. For instance, loaded and unloaded horses make the trot-gallop transition at different speeds, but in both cases the transition reduces the peak vertical ground reaction force below a critical level (Farley and Taylor, 1991). In contrast, Hreljac (1993a) measured several kinetic variables in human locomotion (maximum loading rate, braking and propulsive impulses, and braking and propulsive force peaks), and found that none of these measures predicted the walk-run transition. Instead, he proposed that the switch is made to prevent the overexertion of the ankle dorsi-flexors by redistributing the work load to larger muscles in the upper legs (Hreljac, 1995). This analysis does not, however, predict the run-to-walk transition, as this transition likely increases the exertion of the ankle dorsi-flexors.

A second type of explanation proposes that gait transitions occur in order to minimize energy-related costs, such as overall metabolic cost (e.g., Margaria, 1976; Mercier et al., 1994), or mechanical work (Alexander, 1992). Although appealing, these approaches have not been able to predict the transition speed with sufficient accuracy. For instance, Hreljac (1993b) reported that during treadmill locomotion the energetically optimal transition speed (2.24 m/s) is significantly higher than the preferred transition speed (2.06 m/s), and that energy expenditure actually increases from a walk to a run at the transition. These data seem to be inconsistent with the hypothesis of a simple "energetic trigger" for gait transitions, where a trigger is defined as a mechanism that detects when a variable reaches a critical value and initiates a transition. A recent treadmill study did in fact report evidence of a decrease in metabolic cost at the transition (Mercier et al., 1994), but the authors only studied the transition from walking to running, and not the reverse, thus failing to take hysteresis effects into account (see later discussion). This limitation raises the possibility that their estimated transition speed may be too high.
In contrast to these results, measurements of overground locomotion reveal that there are speed jumps at the transition from walking to running (Minetti, Ardigo, and Saibene, 1994), an effect that cannot be observed on a speed-controlled treadmill. Importantly, the metabolic cost at the running speed adopted after the transition is actually lower than the cost would be if walking continued at that speed. This result indicates that energetic costs are minimized by the transition during overground locomotion, despite the small difference between the preferred and energetically optimal transition speeds on the treadmill. Such a minimization of energetic costs is consistent with the dynamic view presented in subsequent sections of this paper, although energetics are not considered to be the proximal cause of the transition.

Finally, one alternative to these optimization criteria is that the walk-to-run transition simply occurs at the mechanical limit of the walking gait. Alexander (1984) predicted this maximum possible walking speed to be about 3.0 m/s. The observed transition speed is significantly lower, however, around 2.1 m/s (Beuter and Lalonde, 1989; Diedrich and Warren, 1995a, 1995b; Hreljac, 1993b; Thorstensson and Roberthson, 1987). Furthermore, participants can maintain a walk at a faster speed than the preferred transition point (e.g., Diedrich and Warren, 1995b, 1998). In addition, this approach does not make a clear prediction for the run-to-walk transition.

In sum, there is little evidence that gait transitions occur in order to explicitly optimize a cost variable or that they occur at the mechanical limit of a gait. Therefore, we turn to an additional class of explanations.

14.4 A Dynamical Approach

The dynamical systems approach to action views behavior as a consequence of the dynamics of the action system within task constraints (e.g., Kelso, 1995; Kugler and Turvey, 1987). In contrast to a motor program imposing organization on the system, the dynamical view seeks to account for stable coordinative patterns and transitions between them as arising from the self-organizing dynamics of the action system. Such principles of self-organization have been observed in a variety of physical systems, as well as in nonlinear mathematical systems (e.g., Haken, 1983; Prigogine and Stengers, 1984), and are increasingly being applied to biological systems. Thus, much of the organization in behavior may come for “free,” rather than assuming prior organization in the nervous system.

As an example, consider the well-studied case of phase transitions in bimanual coordination (Kelso and Schöner, 1988). In these experiments, participants are asked to oscillate their fingers in an out-of-phase mode and to slowly increase the frequency of oscillation. At a critical frequency, the fingers exhibit a new behavioral pattern, switching to an in-phase mode. According to a dynamical model, this behavioral transition emerges as the system bifurcates from one attractor state (out-of-phase) to another attractor state (in-phase) when frequency reaches a critical level (Haken, Kelso, and Bunz, 1985; Schöner, Haken, and Kelso, 1986). In this case, the relative phase of the fingers is considered to be the order parameter of the system, a low-dimensional collective variable that describes the organizational state of the system and that indexes its stability (Haken, 1983). The control parameter is the frequency of oscillation, a nonspecific parameter that scales the system through the critical value at which a bifurcation between attractor states is observed. An attractor is defined as a subset of the space of possible states the system can occupy, toward which the system evolves as time goes to infinity (Kelso, Ding, and Schöner, 1992). A bifurcation is a sudden jump from one attractor to another that occurs due to a loss of stability.

Could the organization of an ecologically important action such as gait likewise emerge from the self-organizing dynamics of the motor system? An early clue to this question came from work on decerebrated cats (Shik and Orlovskii, 1976; Shik, Severin, and Orlovskii, 1966). In these experiments, a cat was suspended above a motor-driven treadmill after the brain stem and spinal cord were isolated from higher brain centers. At low treadmill speeds, and at low levels of stimulation of particular regions in the brain stem, the cat began to walk. Then, as the speed of the treadmill increased, and as the stimulation increased, the cat began to trot and ultimately to gallop. Surprisingly, these data indicate that a cortical control mechanism that switches between motor programs is not necessary for an animal to switch gaits. Instead, gaits and gait transitions may emerge from the action of coupled oscillators in the spinal cord or brain stem that spontaneously exhibit different patterns of firing when a control parameter is varied (see, e.g., Collins and Stewart, 1993; Taga, Yamaguchi, and Shimizu, 1991; Schöner, Jiang, and Kelso, 1990). This class of explanations therefore views preferred gaits and gait transitions as manifestations of the dynamics of the motor system within a specific context of constraint (see also Diedrich and Warren, 1995a, 1998; Higgins et al., 1995; Thelen and Ulrich, 1991; Turvey et al., 1996; Taga, 1995a,b; Wagenaar and van Emmerik, 1994).

We argue, then, that gait transitions occur as one mode of behavior becomes unstable and the system switches to a new stable mode of behavior (Diedrich and Warren, 1995b). According to this model, the relative phase of the segments within one leg is the order parameter of the system; that is, the relationships between the extensions and flexions of the various leg segments during the gait cycle. Speed of locomotion is considered to be the control parameter of the system. Because speed is the product of
stride frequency and stride length, there are actually two control parameters for human locomotion that can be expressed together as speed. It is important to be clear that this theory does not suppose the existence of a "stability trigger" in the sense of a control mechanism that explicitly senses stability and uses it to regulate the transition. Rather, the transition emerges from the dynamics of the system when the control parameter is scaled past a critical value.

The dynamics of the walk-run transition can be represented by the following potential function (see Tuller et al., 1994), where $x$ is the order parameter and $k$ is the control parameter, as illustrated in figure 14.1.

$$V(x) = kx - x^2/2 + x^4/4.$$  \hspace{1cm} (14.1)

Equation 14.1 is simply the generic form of a potential function that can have two co-existing fixed point attractors and that illustrates transitions between these attractor states (see Kelso, Ding, and Schöner, 1992). Following this model, a phase transition should have the following properties (Kelso and Schoner, 1988). First, there should be a sudden and qualitative reorganization of the system at the transition. Second, the system should show a loss of stability in the transition region. When the system is in a transitory state (i.e., the participants are allowed to switch gaits), stability may be assessed by measuring critical fluctuations and critical slowing down. Critical fluctuations arise near the transition due to a loss of stability that occurs as the potential function $V(x)$ deforms, allowing the system to occupy a greater number states given a constant level of noise. The presence of critical fluctuations is noted by increases in the standard deviation of the relative phase of the limb segments. Critical slowing down is indicated by an increase in the time it takes for the system to recover from a perturbation (relaxation time) in the transition region, due to the shallower gradients of the potential function. An increase in relaxation time is indicative of the loss of stability that underlies the transition. Alternatively, stability may be assessed during steady states (Schmidt, Carello, and Turvey, 1990; Schmidt and Turvey, 1995), in which the system is held in one mode (i.e., one gait). Once again, stability can be measured via fluctuations of phase or responses to perturbations, with larger fluctuations and longer relaxation times indicating lower stability. Third, there should be a tendency for the system to remain in the current basin of attraction as the control parameter moves the system through the transition region, resulting in hysteresis, which is, for gait, the tendency for the walk-to-run transition to occur at a higher speed than the run-to-walk transition.

Diedrich and Warren (1995b) reported evidence consistent with this dynamic theory. First, the transition is sudden and is characterized by a qualitative reorganization of the relative phase of the segments within a leg. Figure 14.2 shows the ankle-knee phase relationship and the ankle-hip phase relationship during a typical transition trial (speed increases with time along the X-axis). The peak extensions of the joints near the end of the stance phase (near toe-off) were used in the calculation of point estimates of relative phase. During walking, the ankle-hip phase is about 45° and the ankle-knee phase is about 85°. In contrast, both phase relationships are close to 0° for running. These results indicate that the ankle extends after both the knee and hip during walking (more out-of-phase), but that the joints extend together during running (more in-phase). Furthermore, this plot shows that the switch between gaits occurs rapidly.
within one stride, consistent with the presence of a bifurcation between attractors, each with its own characteristic phase relationship. Note that the change in phase coincides with the presence of a flight phase, which is the traditional indication of a running gait.

We also measured stability during steady-state trials in which the participants performed particular gaits at a variety of speeds below, at, and beyond the transition (Diedrich and Warren, 1995b, 1996). Using this method, we observed that fluctuations of the relative phases of the leg segments are enhanced in both gaits when speed is scaled away from preferred values, and that in general, these fluctuations begin to increase in the typical transition region for both gaits. In particular, figure 14.3 indicates that for both phase relationships, the SD of phase is a U-shaped function of speed for walking, and a declining exponential for running. Note that the SD of phase is plotted as a function of Froude number $F$, where $v$ is speed, $L$ is the leg length, and $g$ is the acceleration due to gravity (Alexander and Jayes, 1983):

$$F = \frac{v^2}{L^2g}.$$  \hfill (14.2)
By normalizing speed to leg length, we can average data across participants (or animals) of different sizes. Thus, although the absolute speeds at which particular activities occur across participants may be different, they are the same relative to the participants' anthropometric characteristics. Because speed increases as Froude number increases, for simplicity we can consider Froude number to be speed.

In sum, these data on phase fluctuations demonstrate that the control parameter (speed) weakens the dynamics as it is scaled, consistent with the claim that relative phase indexes different attractor states for walking and running. Furthermore, because there is a sudden, nonlinear change in relative phase at the transition from values that define a walk to values that define a run (figure 14.2), we have evidence that the transition behaves as a bifurcation between two relative phase attractors caused by a loss of stability. Formal measurements of critical fluctuations and critical slowing down are planned for future work.

In general there is also evidence for the presence of hysteresis, as the walk-to-run transition speed is often higher than the run-to-walk transition speed, although this effect depends on the rate at which the control parameter (speed) is scaled (Beuter and Lalonde, 1989; Diedrich and Warren 1995a, 1995b, 1998; Hreljac, 1993b; Thorstensson and Robertsson, 1987). Diedrich and Warren (1995a) tested for the presence of hysteresis using trials in which speed was changed "continuously" (in a smooth manner), in steps of 0.083 m/s each lasting 10 s, or in steps of 0.083 m/s each lasting 20 s. Significant hysteresis was found only in the continuous condition, with a hysteresis trend in the 10-s condition, and a reverse hysteresis trend in the 20-s condition (figure 14.4). Reverse hysteresis, or enhanced contrast, means that the run-to-walk transition actually occurred at a higher speed than the walk-to-run transition. Such a dependence of hysteresis on the scaling of the control parameter can be anticipated from the dynamic theory (Kelso, 1995). Near the transition the system is not deterministic as there is a bistable region (speed 4 in figure 14.1) characterized by the presence of multiple attractors and noise. Significant hysteresis is observed in the continuous condition because the system is moved through this bistable region quickly enough that it remains in its current basin of attraction until the attractor actually disappears. In contrast, for long plateaus in the transition region, it is likely that one will see spontaneous shifts between gaits due to random fluctuations, reflecting a decrease in the system's equilibration time (see, Kelso, Ding, and Schöner, 1992; Schmidt, Carello, and Turvey, 1990). Such spontaneous shifts would eliminate any strong hysteresis effects. It is interesting to note that the degree and amount of hysteresis also depends on the individual participants, although the hysteresis pattern is predominant (Diedrich and Warren, 1995a, 1995b, 1998). Some participants do show significant reverse hysteresis, which is further evidence for a bistable transition region, because both gaits are possible over a range of speeds (Tuller et al., 1994). At this time, however, the specific reasons for these individual differences remain unclear.

Although these data suggest that speed is a control parameter for gait because speed is the product of stride frequency and stride length, in theory either stride frequency, stride length, or speed (their combination) could act as the actual control parameter. To empirically identify the control parameter, Diedrich and Warren (1995b) dissociated these variables by pacing participants with a metronome. This pacing caused participants to use different combinations of stride frequency and length at equivalent speeds. When the treadmill was accelerated or decelerated, the participants made the transition at a constant speed, while allowing stride frequency and length to vary. This indicates that speed likely acts as the control parameter for locomotion when on a flat treadmill, because it reflects a tightly coupled relationship between stride frequency and stride length. Under other circumstances, however, these variables can be
decoupled, such as when wearing ankle weights (see later description; Diedrich and Warren, 1998). Therefore, one should always consider the dual actions of stride frequency and length when considering different locomotor tasks.

In summary, there is evidence for a dynamic interpretation of the transition from walking to running in humans. The evidence is consistent with a change in the relative phase of the leg segments at the transition, accompanied by a loss of stability and the presence of hysteresis.

14.5 Energetics of Locomotion

In addition to the results reported previously, an additional step in the analysis of the dynamics of human locomotion is to ask more about the nature of the attractors for each gait. For instance, how do the attractors reflect the costs of locomotion? In an initial attempt to address this question, Diedrich and Warren (1995b) suggested that increases in total metabolic energy expenditure roughly reflect the costs of driving the locomotor system away from its attractor or resonant states, along with other metabolic factors. To understand this idea, recall that a linear oscillator requires a minimal amount of force to sustain oscillation when driven at its natural frequency (see Holt, Hamill, and Andres, 1990; Kugler and Turvey, 1987). As the driving frequency moves away from the natural frequency, more force is required to sustain oscillation, leading to increases in energy costs. If these costs are specified by proprioceptive information and the system follows the information gradient back toward the natural frequency, then the natural frequency can be considered an attractor (Bingham, 1995; Hatsopoulos and Warren, 1996; Kugler and Turvey, 1987). Consistent with this claim, it has been shown that the walk-run transition reduces the internal mechanical work that reflects the costs of accelerating the limb segments (Minetti, Ardigo, and Saibene, 1994). Also, it is clear that proprioceptive information could play a role as perceived exertion is minimized by the transition, although it is unclear what variables influence this perceived exertion (Hreljac, 1993b; Noble et al., 1973). These results illustrate that the dynamics are inherently informational (Kelso, 1995).

Following this logic, it is informative to take a closer look at the energetics of human locomotion (figure 14.5; see Diedrich and Warren, 1995b, for notes on the calculations and previous data used to construct this figure, following Molen, Rozendal, and Boon, 1972a, 1972b). For walking there is a preferred combination of stride frequency and length (a speed) at which energy expenditure per unit distance is minimized at approximately 0.79 cal/kg/m (smallest circle, figure 14.5). Any change in stride frequency or length away from this preferred combination results in increases in energy expenditure (larger circles, figure 14.5). In contrast, for running there is no single speed that minimizes energetic costs, as energy expenditure per unit distance is constant at approximately 1.0 cal/kg/m across a wide range of running speeds (inner set of parallel lines, figure 14.5). Nevertheless, at any given speed a departure from the preferred combination of stride frequency and stride length results in increases in energy expenditure (outer sets of parallel lines, figure 14.5). These data suggest that there is a round "basin" of attraction for walking (concentric circles in figure 14.5) and an elongated "valley" of attraction for running (parallel lines in figure 14.5) in stride frequency-stride length space. There is also evidence for an equal-energy separatrix (a boundary at which the system is pulled toward either walking or running) between the attractors.
Dynamics of Human Gait Transitions

Evidence consistent with a link between stability and energetics also comes from experiments that manipulated the properties of the attractors by investigating the effects of changes in the task dynamics (Diedrich and Warren, 1998). These experiments tested the prediction that movement of the attractors will result in corresponding changes in the transition. For example, if both of the attractors shift down in speed, then the system will lose stability at a lower speed, and as a result, the walk-run transition will occur at a lower speed. Specifically, because any movement along a speed axis implies some combination of changes in stride frequency and stride length, the dynamic theory predicts that movement of the attractors to new stride frequency-stride length combinations will result in a corresponding shift of the transition.

One way to manipulate the task dynamics, and thereby shift the attractors, is to manipulate the grade of the treadmill. From previous data, we know that the walking speed at which energy expenditure per unit distance is minimized decreases from 1.30 m/s on a 0% grade to 1.26 m/s on a 10% grade, and that the speed at which the equal-energy separatrix is located drops from 2.32 m/s to 1.90 m/s (fits on Margaria’s 1938 data using equations developed by Inman, Ralston, and Todd, 1981). Therefore, given the link between energetics and stability, it is likely that these changes in metabolic cost reflect changes in the location of the attractor states. In fact, as predicted by the dynamic theory, a change in the inclination of the treadmill does act to move the attractors and the transition (Diedrich and Warren, 1998). Consistent with the energetic data, an increase in grade affects both the stable walking attractor and the transition by moving them down along a speed axis, as measured by the ankle-hip phase relationship (figure 14.6, top, see arrows). These data, along with the observation of changes in the preferred stride frequency-stride length combinations used at any given walking speed (crossing lines in figure 14.6, top), suggest that the attractor layout rotates in stride length-stride frequency space when going uphill, leading to corresponding changes at the walk-run transition (figure 14.6, top).

A second way to manipulate the location of the attractors is to load the participants’ legs with ankle weights (Diedrich and Warren, 1998). Previous data indicate that there are increases in energy expenditure when participants wear loads on their ankles or feet (e.g., Claremont and Hall, 1988; Inman, Ralston, and Todd, 1981). Although data are not available that assess directional shifts in energy expenditure, the preferred walking frequency drops when loads are added to the ankles (Holt, Hamill, and Andres, 1990). As predicted, the addition of load does in fact reduce both the most stable walking speed and the transition speed through reductions in stride frequency, with no significant changes in stride length (figure 14.6, bottom, see arrows). These results indicate that the attractor layout translates down along a frequency axis in stride length-stride frequency space when load is added to the ankles (figure 14.6, bottom), as predicted by a drop in the natural frequencies of each gait (Diedrich and Warren, 1998; see also Holt, Hamill, and Andres 1990).

As predicted by the dynamic theory, these data are generally consistent with the claim that movement of the attractors is accompanied by corresponding changes at the walk-run transition. Importantly, these experiments make it clear that the precise nature of the attractors is a product of the dynamics of the task, which includes support surface characteristics and external loads, as well as the state of the motor system itself. Given these results, it is also clear that there are strong links between measures of stability and energetics. In many ways, overall metabolic cost per unit distance and measures of stability closely correspond to each other. For both gaits the overall metabolic cost predicts the patterns of changes in stability that occur with speed manipulation, and these energetic measures
also correspond to the directional shifts seen for the grade manipulation. It is also clear that the measures of the most stable speed (1.65 m/s; Diedrich and Warren, 1998) do not exactly match the energetically optimal speed (1.3 m/s; Margaria, 1938), although direct comparisons between the experiments cannot be made due to unspecified differences in the participants' leg lengths. In addition, recall that when on a treadmill the optimal energy transition speed is slightly different than the actual transition speed (Hreljac, 1993b). Thus, the energy and stability measures closely, but not exactly, correspond to each other. This relationship between stability and energetics needs to be explored more fully by using the same participants to measure both stability and energy expenditure across the whole space shown in figure 14.5. These relationships have already been explored for participants walking along a single frequency axis at a constant speed (Holt et al., 1995). As expected, the ankle-knee phase relationship accurately predicted the energetic minimum, but the minimum for the ankle-hip phase relationship was slightly different. This experiment indicates that there is still a need to fully explore the attractor space using multiple stability measures as well as energetic measures. Nevertheless, the general pattern of results is consistent with the idea that overall changes in total metabolic cost roughly reflect the costs of driving the system away from its attractor states.

14.7 Conclusions

What is responsible for the complex coordinative patterns that comprise actions such as gait? Evidence from a wide range of motor tasks suggests that, rather than motor programs imposing organization, stable patterns of behavior and transitions between them arise from the self-organizing dynamics of the motor system and task constraints (e.g., Kelso, 1995). Apparently, as reviewed here, the walk-run transition in humans also behaves as a bifurcation between attractors (Diedrich and Warren, 1995a, 1995b, 1998). The transition is characterized by a sudden and qualitative reorganization of the relative phase of the segments within a leg, by a loss of stability, by increases in energetic costs, and by hysteresis. Furthermore, as predicted by the dynamic theory, movement of the attractors is accompanied by corresponding movement of the transition, indicating that the attractor layout is a product of the dynamics of the task. Although it is unclear if a theory of motor programming could account for the full range of results presented in this paper, motor programming theories have been proposed for some phase transition phenomena (e.g., Rosenbaum, 1991). Dynamic systems theory offers the advantage that it can account for pattern formation across a wide range of systems and tasks without assuming prior organization in the nervous system.
Although these experiments have provided substantial evidence in support of the dynamic theory, several aspects of gait remain to be tested. First, all of the experiments conducted so far on the dynamics of locomotion have been performed on a motorized treadmill. Although it is likely that most aspects of overground locomotion are similar to those observed for treadmill locomotion (e.g., Arsenault, Winter, and Marteniuk, 1986; Elliot and Blanksby, 1976), it is necessary to see how the present results generalize to overground locomotion given small differences reported for behavior at the transition (Minetti, Ardigo, and Saibene, 1994).

Second, it is necessary to further evaluate the stability of gait by exploring the prediction of critical slowing down. It should take longer for the system to recover from a perturbation when in the transition region due to a loss of stability. Such experiments could be accomplished through the use of mechanical perturbations and would enable us to determine whether external perturbations influence the internal rhythm of the system, thus providing information about the coupling between the central oscillator and the limbs (Kay, Saltzman, and Kelso, 1991).

A third investigation will focus on independent changes in stride frequency and stride length. Under normal circumstances, increases in speed derive from simultaneous increases in stride frequency and length. The dynamic theory predicts that independent variation of these variables away from their preferred values will also lead to a loss of stability and ultimately to a transition. Consistent with this idea, there are changes in stability when stride frequency is varied at one speed during walking (Holt et al., 1995). Yet, stability has not been measured across the complete variety of stride frequencies and stride lengths in both gaits (figure 14.5), and the predicted transitions have yet to be explored.

Finally, there is still some question as to whether we have in fact identified “the” order parameter. Our measures reveal a change in relative phase and a loss of stability at the transition. In brief, the ankle extends after the knee and hip during walking, and the joints extend simultaneously during running. These changes in phase may, however, simply reflect the movement of the center of mass of the body, as they are consistent with an inverted pendulum model for walking and a bouncing ball model for running (e.g., Margaria, 1976; McMahon, 1984). During walking, the center of mass of the body rotates over the support foot acting to extend the hip and knee prior to the push-off at the ankle. In contrast, during running, the joints accept (flex) and release weight (extend) together, much like a bouncing ball. This distinction is important, as the potential and kinetic energy cycles are out-of-phase during walking (inverted pendulum), but in-phase during running (bouncing ball). Phase thought of in this way could act as the order parameter, and should be investigated with respect to changes in stability.

In conclusion, the experiments that have been conducted so far provide evidence in support of a dynamical interpretation of human locomotion. Although many questions remain to be asked, these experiments lend further support to the claim that much of the organization of behavior arises from the dynamics of the action system and task constraints.

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