Contents lists available at ScienceDirect

Human Movement Science

journal homepage: www.elsevier.com/locate/humov



Full Length Article

What factors determine the preferred gait transition speed in humans? A review of the triggering mechanisms



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ARTICLE INFO

Keywords: Biomechanics Energetics Perceptions Triggers

ABSTRACT

Human locomotion is a fundamental skill that is required for daily living, yet it is not completely known how human gait is regulated in a manner that seems so effortless. Gait transitions have been analyzed to gain insight into the control mechanisms of human locomotion since there is a known change that occurs as the speed of locomotion changes. Specifically, as gait speed changes, there is a spontaneous transition between walking and running that occurs at a particular speed. Despite the growing body of research on the determinants of this preferred transition speed and thus the triggering mechanisms of human gait transitions, a clear consensus regarding the control mechanisms of gait is still lacking. Therefore, this article reviews the determinants of the preferred transition speed using concepts of the dynamic systems theory and how these determinants contribute to four proposed triggers (i.e. metabolic efficiency, mechanical efficiency, mechanical load and cognitive and perceptual) of human gait transitions. While individual anthropometric and strength characteristics influence the preferred transition speed, they do not act to trigger a gait transition. The research has more strongly supported the mechanical efficiency and mechanical load determinants as triggering mechanisms of human gait transitions. These mechanical determinants, combined with cognitive and perceptual processes may thus be used to regulate human gait patterns through proprioceptive and perceptual feedback as the speed of locomotion changes.

1. Introduction

Human locomotion is a fundamental skill that is integrated into various activities of daily living. Following the acquisition of bipedal locomotion, healthy adult gait requires little cognitive input (Abernethy, Hanna, & Plooy, 2002). However, the complexity of human locomotion may be overlooked due to the frequency and ease of its use. The ability to constantly adapt gait to various individual and task constraints requires mechanisms to provide continuous feedback about the adopted gait pattern. Gait transitions offer a unique insight into these possible underlying mechanisms that shape human locomotion, as there is a change in the mode of gait as the speed of locomotion changes.

Humans generally either walk or run depending on the locomotive speed; walking is preferred at slower speeds of locomotion whereas running is preferred at faster speeds. As the speed of locomotion changes, there is a spontaneous transition between the

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http://dx.doi.org/10.1016/j.humov.2017.10.023

Received 4 May 2017; Received in revised form 24 October 2017; Accepted 27 October 2017 0167-9457/ @ 2017 Elsevier B.V. All rights reserved.

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walking and running modes of gait. That is, gait transitions are not premeditated or pre-planned actions, but occur naturally without conscious thought. A walk-to-run transition (WRT) occurs with increasing locomotive speeds, while a run-to-walk transition (RWT) occurs as the speed decreases. These gait transitions have been shown to occur over a number of steps, including the steps directly before and after the transition step (Hagio, Fukuda, & Kouzaki, 2015; Li & Hamill, 2002; Li & Ogden, 2012; Segers, De Smet, Van Caekenberghe, Aerts, & De Clercq, 2013; Van Caekenberghe, Segers, De Smet, Aerts, & De Clercq, 2010). While the transition step more closely resembles the post-transition mode of gait, there are still numerous kinematic and kinetic differences (Segers et al., 2013). This set of ordered behaviors does not necessarily reflect a lack of spontaneity when transitioning. Rather, gait transitions occur over a number of steps to maintain balance and upright posture and to prepare the system for the transition between these two mechanically different modes of gait.

There are a number of theories about why humans transition between walking and running, particularly as the preferred transition speed (PTS) in healthy adults has consistently been reported to occur within a narrow range of speeds around $2 \,\mathrm{m \, s^{-1}}$ (Brisswalter & Mottet, 1996; Diedrich & Warren, 1995; Hreljac, 1993b; Hreljac, Imamura, Escamilla, & Edwards, 2007b; Prilutsky & Gregor, 2001; Thorstensson & Roberthson, 1987; Tseh, Bennett, Caputo, & Morgan, 2002; Ziv & Rotstein, 2009). These theories include anthropometric characteristics (Alexander, 1984) and efficiency or protective mechanisms (Cavagna & Kaneko, 1977; Farley & Taylor, 1991; Hreljac, 1993b; Prilutsky & Gregor, 2001). Previous studies have demonstrated that humans tend to use the most metabolically efficient gait pattern, especially in terms of adopting the optimal combination of stride length and stride frequency (Cavanagh & Williams, 1982; Hogberg, 1952; Holt, Hamill, & Andres, 1991; Zarrugh, Todd, & Ralston, 1974). Deviations from this preferred combination of stride length and stride frequency have increased oxygen consumption during both walking (Zarrugh et al., 1974) and running (Cavanagh & Williams, 1982; Hogberg, 1952), thus reducing the efficiency of the gait pattern. Therefore, the transition may be a response to the change in the combination of stride length and stride frequency rather than locomotive speed itself, as the speed of locomotion is the product of these spatiotemporal variables. Altering these spatiotemporal parameters may have important implications on the efficiency and effort required at the cellular and musculoskeletal levels, especially when considering the differences in the mechanics of walking and running (i.e. inverted pendulum model of walking versus the spring-mass model of running (Farley & Ferris, 1998)). At the PTS, it would seem that the body experiences either unfavorable or unstable patterns of coordination that are difficult to maintain. This instability is demonstrated by greater variability in gait patterns (Brisswalter & Mottet, 1996; Diedrich & Warren, 1995), as well as greater muscle activity (Li & Ogden, 2012; Prilutsky & Gregor, 2001) and energy expenditure (Mercier et al., 1994). Thus, a single gait determinant, or a combination of determinants, may reach a critical value at the PTS, thereby triggering the transition between the modes of gait.

Numerous determinants of the PTS have been investigated, but there is not a clear consensus regarding the triggering mechanisms of gait transitions and thus the underlying control mechanisms of gait. The previously proposed efficiency and protective mechanisms that trigger gait transitions are thought to help conserve metabolic (Hreljac, 1993b) and mechanical (Cavagna & Kaneko, 1977; Minetti, Ardigo, & Saibene, 1994) energy and to reduce musculoskeletal stress and minimize the risk of injury (Farley & Taylor, 1991; Hreljac, 1993a; Prilutsky & Gregor, 2001). Accordingly, the determinants that reflect these efficiency and protective mechanisms have been used to form hypotheses about the triggering mechanisms of human gait transitions (Diedrich & Warren, 1995; Mohler, Thompson, Creem-Regehr, Pick, & Warren, 2007). Specifically, these proposed triggers of gait transitions have included energetic (i.e. *metabolic efficiency*), efficiency (i.e. *mechanical efficiency*) and mechanical (i.e. *mechanical load*) triggers, respectively. These triggers presumably work through proprioceptive feedback; however, cognitive or perceptual feedback must also be considered. Therefore, there may also be a *cognitive or perceptual* trigger that would assist the mechanical load trigger in reducing musculoskeletal stress and the risk of injury through cognitive and perceptual feedback. These proposed triggers and their accompanying determinants are presented in Fig. 1.

While the aim of each of the proposed triggers are different, the determinants that fall within each trigger are highly correlated, thus presenting a challenge when identifying which determinants drive the transition between walking and running as task constraints change. The *dynamic systems theory* provides a foundation from which the determinants of the PTS can be analyzed, particularly regarding their role in triggering gait transitions (Diedrich & Warren, 1995; Kelso, 1984; Kelso & Schöner, 1988). The dynamic systems theory was initially used to identify transitional behavior during hand and finger coordination activities (Kelso, 1984; Kelso & Schöner, 1988). When applied to gait transitions, walking and running are considered as two separate organizational states of the system, or 'attractors,' while gait transitions resemble phase transitions. As the task constraints change, accompanying changes in the determinants of the PTS would trigger a gait transition. The purpose of this article is to review (a) the dynamic systems theory as a basis from which gait transitions are analyzed; and (b) the determinants of the PTS and their role in triggering gait transitions in humans.

2. How does the dynamic systems theory apply to human gait transitions?

Dynamic systems theory applies principles of self-organization to understand how low dimensional (i.e. ordered) behavior arises in human coordination (Kelso, 1997). In particular, it proposes that orderly behavior arises out of the nonlinear interaction between different components (e.g. limbs, perceptual variables, neurons in the brain) without reliance on a centrally controlled or stored pattern. Using this theory, coordination between effectors can be captured by a collective variable, which undergoes a qualitative shift (i.e. a phase transition) as a control parameter is varied. In the classic example of bimanual finger coordination (Kelso, 1984), both in-phase (where both index fingers perform the same action at the same time) and anti-phase (where when one finger abducts, the other adducts, and vice versa) coordination is possible at slow movement frequencies. As the control parameter of movement frequency is increased, anti-phase coordination becomes more difficult, and at a critical value of the control parameter a shift from anti- to in-phase coordination is observed (Kelso, 1997).

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