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Adaptability of stride-to-stride control of stepping movements in human walking

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ABSTRACT

Humans continually adapt their movements as they walk on different surfaces, avoid obstacles, etc. External (environmental) and internal (physiological) noise-like disturbances, and the responses that correct for them, each contribute to locomotor variability. This variability may sometimes be detrimental (perhaps increasing fall risk), or sometimes beneficial (perhaps reflecting exploration of multiple task solutions). Here, we determined how humans regulated stride-to-stride fluctuations in walking when presented different task goals that allowed them to exploit inherent redundancies in different ways. Fourteen healthy adults walked on a treadmill under each of four conditions: constant speed only (SPD), constant speed and stride length (LEN), constant speed and stride time (TIM), or constant speed, stride length, and stride time (ALL). Multiple analyses tested competing hypotheses that participants might attempt to either equally satisfy all goals simultaneously, or instead adopt systematic intermediate strategies that only partly satisfied each individual goal. Participants exhibited similar average stepping behavior, but significant differences in variability and stride-to-stride serial correlations across conditions. Analyses of the structure of stride-to-stride fluctuation dynamics demonstrated humans resolved the competing goals presented not by minimizing errors equally with respect to all goals, but instead by trying to only partly satisfy each goal. Thus, humans exploit task redundancies even when they are explicitly removed from the task specifications. These findings may help identify when variability is predictive of, or protective against, fall risk. They may also help inform rehabilitation interventions to better exploit the positive contributions of variability, while minimizing the negative.

1. Introduction

People face many locomotor challenges when they walk on multiple surfaces, avoid obstacles, and adapt to different situations. Unpredictable disturbances can induce falls and subsequent injuries, especially in elderly and/or impaired individuals (Maki, 1997). Both external (environmental) and internal (physiological) noise-like disturbances contribute to increase gait variability (Hausdorff et al., 2001). Increased variability of certain gait parameters predicts increased risk of falling (Maki, 1997; DeMott et al., 2007). Conversely, this same variability may indicate humans adaptively use multiple combinations of gait parameters to walk more effectively (Hausdorff et al., 1996; Day et al., 2012; Roerdink et al., 2015). For example, allowing greater variability in robotic gait re-training leads to faster and better improvements (Lewek et al., 2009; Duschau-Wicke et al., 2010; Krishnan et al., 2013).

The neurophysiological processes that control walking integrate multiple sensory inputs to generate coordinated motor outputs (Rossignol et al., 2006). To better understand how these mechanisms function, we must identify what goals the nervous system tries to achieve while walking. Common optimality principles, like minimizing energetic cost (Kuo, 2001; Srinivasan and Ruina, 2006), predict *average* behavior (Collins, 1995; Scott, 2004), but not the *variability* of repeated movements (Körding and Wolpert, 2004; Todorov, 2004; Stein et al., 2005; Faisal et al., 2008), like walking (Winter, 1984; Hausdorff et al., 1995; Dingwell and Marin, 2006; Kang and Dingwell, 2008; Dingwell et al., 2010). Quantifying movement variability may better indicate how movements are controlled (Hausdorff, 2007; Bruijn et al., 2013; Rebula et al., 2013; Roerdink et al., 2015). However, measures of variability (e.g., standard deviations) still only quantify the *average* magnitude of fluctuations. Such measures cannot reveal how each step influences subsequent steps (Dingwell and Cusumano, 2000,

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2015; Dingwell et al., 2010). Determining how fluctuations are actively regulated from each cycle to the next is essential to understand how humans perform skilled movements (Körding and Wolpert, 2004; Todorov, 2004; Cusumano and Cesari, 2006).

Some movement variability arises from inherent noise in the nervous system (Cordo et al., 1996; Osborne et al., 2005; Stein et al., 2005; Faisal et al., 2008). Other variability arises from the control efforts the nervous system makes to regulate movements. Furthermore, this variability is expressed within a context of neuromotor redundancy, which itself creates equifinality (Scott, 2004; Todorov, 2004; Cusumano and Cesari, 2006): i.e., there are an infinite number of ways to achieve the same task or performance goal. Possibly, more variable robotic gait re-training interventions (Lewek et al., 2009; Duschau-Wicke et al., 2010; Krishnan et al., 2013) are more effective because they permit patients to more fully explore many equivalent task solutions.

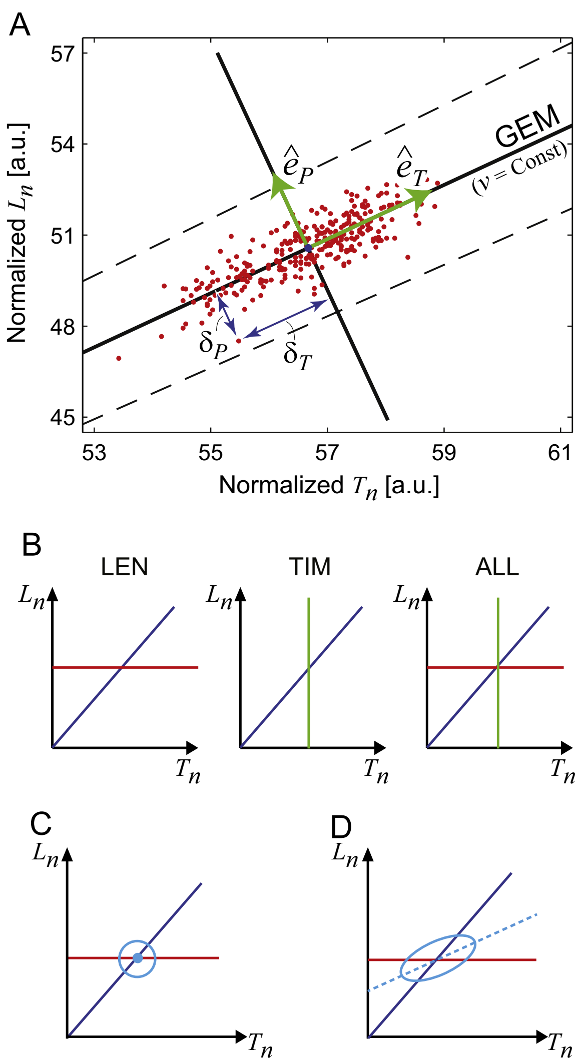

Fig. 1. (A) Schematic of the goal equivalent manifold (GEM) concept for walking. The red data points show sample stride data from a typical subject, where stride lengths (L_n) and stride times (T_n) were first non-dimensionalized to unit variance (Dingwell et al., 2010). The goal of maintaining constant walking speed, v, forms a straight diagonal line in the [L, T] plane. This line defines the constant-speed GEM because all combinations of [L_n, T_n] that lie on this line achieve the exact same speed. Unit vectors indicate directions tangent to ($\hat{e}_T$) and perpendicular to ($\hat{e}_P$) this constant-speed GEM. (B) Schematic representations of the three task conditions involving multiple simultaneous goal functions. Blue lines indicate the constant-speed goal function. Red lines indicate the constant stride length goal function. Green lines indicate the constant stride time goal function. (C) One possible strategy to resolve the conflict introduced be the multiple task goals given in part B would be to try to constrain all variability to the intersection between the two goal functions: i.e., to the single point in the [L, T] plane that equally satisfies both goals simultaneously. (D) An equally plausible alternative would be to adopt some "intermediate" strategy that tries to balance errors with respect to each additional goal function, but does not fully satisfy either. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

During walking, humans must adapt their movements at each individual step and not just on average. However, the basic underlying goal(s) the nervous system tries to achieve when making these stride-to-stride corrections remain largely unknown. Even less well understood is how adaptable humans are at modifying these goals when circumstances change. Understanding how control is enacted across sequential strides requires quantifying the temporal sequencing of stride-to-stride fluctuations (Dingwell and Cusumano, 2010).

There are infinitely many equally successful strategies for walking on a treadmill (Dingwell and Cusumano, 2015). During normal walking, humans naturally choose to exploit the task-level redundancy between stride length (L_n) and time (T_n) to try to maintain approximately constant stride speed ($S_n = L_n/T_n$) (Fig. 1A) (Dingwell et al., 2010). However, few studies have sought to determine how subjects respond when asked to simultaneously satisfy multiple, competing (possibly even contradictory) task goals. Two recent studies manipulated step timing by introducing different types of metronome signals (Terrier and Dériaz, 2012; Roerdink et al., 2015) and obtained results consistent with our previous theoretical predictions (Dingwell et al., 2010; Dingwell and Cusumano, 2015). However, neither study manipulated either stride length or length and time in combination.

Here, we directly manipulated the task goals of walking by presenting to subjects different combinations of L_n, T_n, and S_n conditions that systematically varied the nature of the available redundancies (Fig. 1B). Removing the redundancy between L_n and T_n (Fig. 1A) by adding additional task goals (Fig. 1B), allowed us to directly and quantitatively test competing hypotheses about how participants resolve the problem of trying to satisfy multiple competing task goals. On one hand, if humans attempt to equally satisfy both (or all) goals, their movement fluctuations should converge around the single [T_n, L_n] combination that simultaneously satisfies both goals (Fig. 1C). However, this is not the only strategy subjects could choose. For example, subjects might instead attempt to achieve some "intermediate" goal that only partly satisfies each individual goal (Fig. 1D). In this case, we predict movement fluctuations should be structured in a very different, but still systematically predictable, way. Here, we directly tested these competing hypotheses to determine how humans changed how they regulated their stepping parameters when additional, multiple competing tasks goals were introduced.

2. Methods

2.1. Subjects

Fourteen healthy adults participated (Table 1). Participants were screened to ensure they had no history of lower limb injuries, surgeries, or cardiovascular,

Table 1
Participant characteristics. All values except Sex are given as Mean ± Standard Deviation.

Characteristic	Value
Sex	5M/9F
Age (years)	24.14 ± 4.22
Body height (m)	1.70 ± 0.13
Body mass (kg)	65.75 ± 11.75
Leg length (m)	0.93 ± 0.07