Humans control stride-to-stride stepping movements differently for walking and running, independent of speed

Jonathan B. Dingwell [a,b,*], Nicole K. Bohnsack-McLagan [a], Joseph P. Cusumano [c]

[a] Department of Kinesiology & Health Education, University of Texas, Austin, TX 78712, USA
[b] Department of Kinesiology, Pennsylvania State University, University Park, PA 16802, USA
[c] Department of Engineering Science & Mechanics, Pennsylvania State University, University Park, PA 16802, USA

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ABSTRACT

As humans walk or run, external (environmental) and internal (physiological) disturbances induce variability. How humans regulate this variability from stride-to-stride can be critical to maintaining balance. One cannot infer what is "controlled" based on analyses of variability alone. Assessing control requires quantifying how deviations are corrected across consecutive movements. Here, we assessed walking and running, each at two speeds. We hypothesized differences in *speed* would drive changes in variability, while adopting different *gaits* would drive changes in how people regulated stepping. Ten healthy adults walked/ran on a treadmill under four conditions: walk or run at comfortable speed, and walk or run at their predicted walk-to-run transition speed. Time series of relevant stride parameters were analyzed to quantify variability and stride-to-stride error-correction dynamics within a Goal-Equivalent Manifold (GEM) framework. In all conditions, participants' stride-to-stride control respected a constant-speed GEM strategy. At each consecutively faster speed, variability tangent to the GEM increased ($p \leq 0.031$), while variability perpendicular to the GEM decreased ($p \leq 0.044$). There were no differences ($p \geq 0.999$) between gaits at the transition speed. Differences in *speed* determined how stepping *variability* was structured, independent of gait, confirming our first hypothesis. For running versus walking, measures of GEM-relevant statistical persistence were significantly less ($p \leq 0.004$), but showed minimal-to-no speed differences ($0.069 \leq p \leq 0.718$). When running, people corrected deviations both more quickly and more directly, each indicating tighter control. Thus, differences in *gait* determined how stride-to-stride fluctuations were *regulated*, independent of speed, confirming our second hypothesis.

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1. Introduction

Variability is ubiquitous in human movements (Trommershäuser et al., 2008; Scott, 2012; Chaisanguanthum et al., 2014), including walking (Winter, 1984; Kang and Dingwell, 2008; Collins and Kuo, 2013). Multiple sensory and motor sources of physiological noise contribute to this variability (Stein et al., 2005; Faisal et al., 2008). Variability may be detrimental (König et al., 2016). Increased gait variability predicts increased fall risk in older adults (Verghese et al., 2009; Toebes et al., 2012). Conversely, noise sometimes benefits neural systems and enhances function (McDonnell and Ward, 2011). Facilitating increased variability during robotic gait training can improve outcomes (Lewek et al., 2009; Duschau-Wicke et al., 2010; Ziegler et al., 2010). Understanding how humans regulate variability from cycle-to-cycle in redundant repetitive tasks (Todorov, 2004; John et al., 2016) is critical to understanding the origins of biomechanical variability in locomotion (Dingwell et al., 2010). This is especially relevant because purposefully varying foot placement is a primary means to maintain balance during walking (Townsend, 1985; Wang and Srinivasan, 2014) and running (Peuker et al., 2012). Thus, in walking and running, some variability arises from physiological noise sources. However, movement variability also occurs along with control actions the human nervous system takes in response to this noise-induced variability to maintain balance and forward progression. Simply quantifying variability alone, without regard to disentangling these interwoven processes, cannot yield insights into the motor regulation of gait (Dingwell et al., 2010).

Movement variability is also structured by redundancy, or equifinality (Todorov, 2004; Cusumano and Cesari, 2006; Cusumano and Dingwell, 2013; John et al., 2016). In treadmill walking, equifinality exists between stride length (L_n) and stride time (T_n) because infinite combinations of $[T_n, L_n]$ can either match the treadmill's speed (Dingwell et al., 2010), or maintain position on the treadmill (Dingwell and Cusumano, 2015), or achieve some other goal. Such equifinality can create a "Goal Equivalent Manifold" (GEM) (Cusumano and Cesari, 2006; Cusumano and Dingwell, 2013) in the $[T_n, L_n]$ plane (Fig. 1A) that defines all combinations of $[T_n, L_n]$ that equally satisfy the specified task goal. To determine if humans regulate their movements relative to any proposed GEM, one can define deviations tangent (δ_T) and perpendicular (δ_P) to that GEM and analyze the trial-to-trial (or here, stride-to-stride) fluctuations in these $[\delta_T, \delta_P]$ variables. Fluctuations in δ_T are "goal equivalent" because they do *not* affect the goal, whereas fluctuations in δ_P are "goal relevant" because they directly reflect *errors* with respect to that goal (Fig. 1).

We previously derived computational models to explain how both noise and stride-to-stride control actions contribute to walking fluctuations, and tested these predictions experimentally (Dingwell et al., 2010; Dingwell and Cusumano, 2015). Healthy adults weakly corrected stride-to-stride fluctuations parallel to the constant-speed GEM (δ_T; Fig. 1A), but strongly corrected deviations perpendicular to it (δ_P; Fig. 1A) (Dingwell and Cusumano, 2010; Dingwell et al., 2010). Our primary theoretical predictions and experimental findings were subsequently replicated in several independent studies (Decker et al., 2012; Terrier and Dériaz, 2012; Roerdink et al., 2015). Thus, the GEM framework for analyzing stride-to-stride fluctuations provides a rigorous and coherent basis for showing how variability arises from the interaction of the task definition, intrinsic physiological noise, and stride-to-stride motor regulation.

Additionally, we and others found this constant-speed GEM-aware control strategy remains robust across modest changes in walking speed for both young (Dingwell et al., 2010; Terrier and Dériaz, 2012) and healthy older adults (Dingwell et al., 2017), despite those older adults exhibiting greater gait variability (Kang and Dingwell, 2008). Conversely, less healthy older adults (i.e., who walked at slower preferred speeds) did exhibit altered stepping control (Decker et al., 2012). However, these prior studies only tested unconstrained and unperturbed walking, which may not have adequately challenged participants' locomotor control. Several subsequent independent studies (Terrier and Dériaz, 2012; Roerdink et al., 2015; Bohnsack-McLagan et al., 2016) imposed additional task goals that explicitly specified stride time (using a metronome) and/or stride length (using stepping targets). Each manipulation induced specific changes in stride-to-stride control that were consistent with theoretical predictions. Those studies further validated the GEM framework and demonstrated that healthy humans can flexibly achieve multiple simultaneously specified goals while walking.

Here, we directly extended this line of inquiry to determine how healthy participants alter how they regulate stride-to-stride fluctuations in more challenging contexts that extend from walking to running, and to walking and running at far-from-preferred speeds. Addressing these new questions is critical to establishing the range of contexts across which humans adopt GEM-aware control. Specifically, we asked participants to both walk and run, each at both their comfortable speed for each gait and at their predicted walk-run transition speed. Because infinite combinations of $[T_n, L_n]$ can be used to achieve any number of task goals (Dingwell and Cusumano, 2015) for any of these conditions, participants remained free to choose to regulate stride-to-stride fluctuations in their stepping movements in infinite ways. Performing either gait at speeds near the predicted walk-to-run transition speed can increase metabolic cost (Mercier et al., 1994; Diedrich and Warren, 1995) and the variability of some gait variables (Brisswalter and Mottet, 1996; Segers et al., 2006; Lamoth et al., 2009). Here, we hypothesized that changes in *speed* of locomotion (for either walking or running) would elicit changes in variability, but minimal to no changes in how people regulated stride-to-stride fluctuations (Dingwell et al., 2010) in their stepping movements for either gait. Specifically, we expected that as speed increased (across both walking and running), we would observe tighter alignment (on average) of the relative variability along the GEM, *independent* of changes in stride-to-stride regulation.

Running is very different from walking, exhibiting a flight phase, larger ground reaction forces, and quicker, longer strides (Cavanagh and Kram, 1989; Dickinson et al., 2000). Running is most often modeled as a mass-on-a-spring (Dickinson et al., 2000; Geyer et al., 2005), while walking is often modeled as an inverted pendulum (Kuo et al., 2005) with very different dynamics, although variations of either model can capture both gaits (Geyer et al., 2006; Srinivasan and Ruina, 2006). On average, the biomechanics, muscle function, and energetic cost of steady-state locomotion differ between walking and running, even when participants locomote at the same speeds (Mercier et al., 1994; Li and Ogden, 2012; Pires et al., 2014; Shih et al., 2016). These findings suggest running may be controlled differently than walking. However, those analyses only assessed averages and so cannot address how stepping movements were regulated from stride-to-stride. Here, we hypothesized that adopting different *gaits* (running vs.
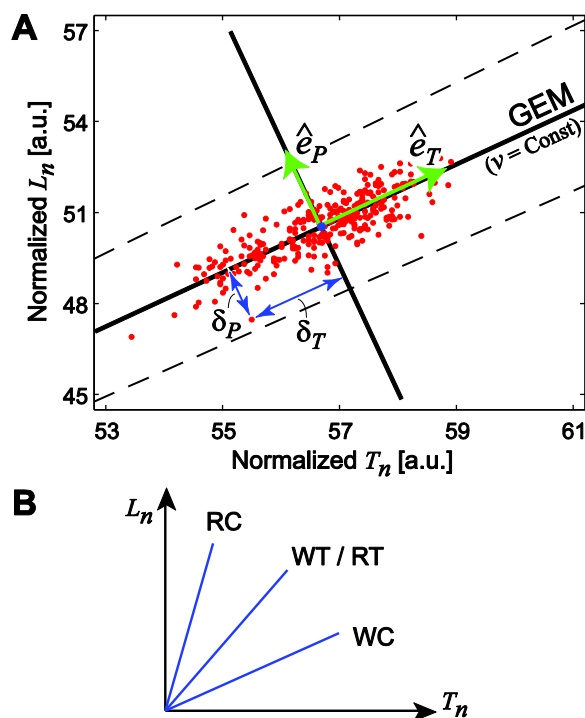
Fig. 1. (A) Schematic of the goal equivalent manifold (GEM) concept for sagittal plane locomotion. Stride lengths (L_n) and stride times (T_n) are plotted in arbitrary units (a.u.) after data for each variable were first non-dimensionalized to unit variance (Dingwell et al., 2010). Red data points show sample $[L_n, T_n]$ data for individual strides from a typical trial. The goal of maintaining constant walking speed, v, forms a straight diagonal line in the $[L, T]$ plane. This line defines a constant-speed GEM because all combinations of $[L_n, T_n]$ that lie on this line (i.e., manifold) 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 showing the relative relationships between the 3 constant-speed GEM's used for the 4 conditions tested here: walk at comfortable walking speed (WC), walk at predicted transition speed (WT), run at predicted transition speed (RT), and run at comfortable running speed (RC). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)