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Domestic cat walking parallels human constrained optimization: Optimization strategies and the comparison of normal and sensory deficient individuals



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ABSTRACT

To evaluate how fundamental gait parameters used in walking (stride length, frequency, speed) are selected by cats we compared stride characteristics selected when walking on a solid surface to those selected when they were constrained to specific stride lengths using a pedestal walkway. Humans spontaneously select substantially different stride length–stride frequency–speed relationships in walking when each of these parameters is constrained, as in walking to a metronome beat (frequency constrained), evenly spaced floor markers (stride length constrained) or on a treadmill (speed constrained). In humans such adjustments largely provide energetic economy under the prescribed walking conditions. Cats show a similar shift in gait parameter selection between conditions as observed in humans. This suggests that cats (and by extension, quadrupedal mammals) also select gait parameters to optimize walking cost-effectiveness. Cats with a profound peripheral sensory deficit (from pyridoxine overdose) appeared to parallel the optimization seen in healthy cats, but without the same level of precision. Recent studies in humans suggest that gait optimization may proceed in two stages – a fast perception-based stage that provides the initial gait selection strategy which is then fine-tuned by feedback. The sensory

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deficit cats appeared unable to accomplish the feedback-dependent aspect of this process.

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1. Introduction

Although normal gait can be recognized and described, it is currently not entirely clear why specific features, such as stride length and frequency, are selected over other possible options. Recent studies, comparing subject responses to different testing conditions that mimic possible real-life constraints on gait options, support the constrained optimization hypothesis of gait control. This hypothesis proposes that the locomotion strategies employed by subjects are developed largely to optimize the metabolic cost of locomotion within given physical or physiological limitations. This perspective provides substantial novel insight into how gait parameters are functionally determined in humans, but there has previously been little indication that other mammals utilize similar control strategies. It is important to extend the observations made in humans to other mammals, as they may act as models that allow investigation of the underlying mechanisms responsible for the gait determination processes observed. First, in order to understand how walking control can be inferred from another species' response to experimental manipulation of a given gait parameter (our experimental results), we briefly explain constrained optimization in humans.

1.1. Constrained optimization in human walking

It has long been held that stride length (d) and stride frequency (f) are selected to provide the required speed of progression (v) at a minimum metabolic cost (Elftman, 1966; Molen, Rozendal, & Boon, 1972; Ralston, 1958). Minimizing metabolic energy during treadmill testing results in a relatively consistent relationship between speed and step frequency under normal conditions. This relationship was thought to be a fundamental characteristic of natural gait. For humans normal walking fits the relation $v = C f^b$ (v ms⁻¹, f strides s⁻¹, C m stride⁻¹ and $b = 1.72$ appears to be a good fit over commonly used walking speeds, Kuo, 2001).

If the v - f relationship is a fundamental characteristic of economical walking, we might reasonably expect that the combination of values that minimizes metabolic cost when one factor is specified (e.g., v) would hold when one of the other factors that determine the gait are specified (f or d), since v is the product of f and d . This, however, is decidedly *not* the case in human locomotion. Different v - f relationships are expressed depending on which of the three determinant parameters are controlled in both human walking and running (Bertram, 2005; Bertram & Ruina, 2001; Gutmann, Jacobi, Butcher, & Bertram, 2006). That is, for an individual walking on a treadmill at constant speed the v - f relationship differs from that for an individual walking overground at a constant frequency (as in walking to a metronome beat where the individual selects stride length and speed), and both these v - f relations differ from that selected when stride length is set by floor markers, stepping stones, etc., but where the individual is free to select stride frequency and speed.

Indeed, as anticipated, the different v - f relationships for walking under these conditions are largely a result of selecting those walking parameters that minimize metabolic cost of transport. However, it is necessary to consider the global structure of the cost 'surface' involved in order to understand how metabolic cost is minimized under different testing conditions and how this results in three distinct, but naturally selected, gait parameter relationships (Bertram, 2005).

For human walking plotted on the axes f (x axis, strides s⁻¹), v (y axis, m s⁻¹) and *metabolic cost of transport* (z axis, J kg⁻¹m⁻¹) an obloid bowl-shaped surface is formed (Fig. 1). Due to the inter-relationship of these parameters (where $v = d \cdot f$), each of the walking parameters, f , v , and d , influences where on the cost surface the individual operates. The position on the surface is specified by any two walking parameters and the height of the surface corresponds to the metabolic investment needed to progress

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