Toward a New Theory of Quadrupedal Animal Locomotion

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The Problem: Why do animals run the way they do? We are developing a new theoretical framework that explains and integrates the mechanics and energetics of quadrupedal locomotion. With dynamic computer simulations, we can identify plausible control mechanisms behind such fundamental behaviors as speed and gait changes. Our goals are (a) to formulate the simplest models capable of predicting available biological data, and (b) to generate testable hypotheses that relate body design and locomotory performance.

Motivation: Our broad aim is to understand the biomechanical control principles of legged locomotion. We focus on quadrupedal animals because of their diversity in size and shape and the extensive availability of animal data. There is a strong need for theoretical models to integrate these data to explain how control strategies are selected. How stiff should an animal make its legs and back for economical running? How are stride rates and stride lengths chosen? At what speed should an animal switch from a walk to a trot? How does body size influence these strategies? By answering these scientific questions, we also hope to improve the performance of legged robots and prostheses.

Previous Work: A number of general principles have emerged from the literature. Experiments show that mammals operate within a narrow range of leg stiffness values even as they change speeds [1]. Gait transitions in horses can be explained by minimizing metabolic energy [2]. Moreover, running performance varies systematically with body size; on a per gram basis, larger animals use more compliant legs and less metabolic energy to travel a given distance [1, 3].

Some basic mechanics of running are captured by simple spring-mass models [4]. More detailed computational models give us ways to think about interactions between body design and locomotory control [5]. However, no model to date has integrated full-body mechanics and energetics to test control strategies for running. Recently, a running-horse model was shown to predict biological data including stride length, stride rate, and limb angle as functions of speed [6]. This model serves as a starting point for this research.

Approach: Our modeling approach is to manipulate properties of the body (size, shape, stiffness) as well as the control (leg speed, timing). As a first step, we have performed computational experiments with a trotting- horse model. The model's structure consists of rigid segments linked by rotary joints (hips, shoulders, back, neck) and telescoping joints (elbows, knees); body mass is distributed realistically. Motion is restricted to the sagittal plane, and running is controlled by torques applied to the hip and shoulder. Torques are adjusted so that tangential foot speeds during ground contact and aerial time before limb retraction are constants. This scheme produces biologically realistic simulations without vestibular inputs.

To test ideas about how animals modulate stiffness, we simulated a horse trotting with a wide range of leg stiffnesses. We varied the stiffness by adjusting individual joint stiffnesses, foot speeds, and aerial time. Genetic algorithms were used to map out regions of periodic trotting solutions in speed-stiffness space (Fig. 1). For each speed, smooth trotting occurs if and only if leg stiffness exceeds a minimum value (21-24 kN/m); otherwise, stride-to-stride fluctuations in body height and pitch make the animal fall down. We also found that for each speed, the predicted metabolic costs (computed from [7]) are lowest at the minimum stiffness values. These minimum values are in striking agreement with experimental values of stiffness from trotting horses [1]. Therefore, we hypothesize that animals minimize stiffness to keep metabolic costs low while maintaining a smooth gait. In addition, the walk-trot transition speed in animals may be influenced by stability, as suggested by the paucity of smooth trotting solutions at the lowest speed (Fig. 1).

A control strategy that is critical for biologically realistic predictions is that the hind limbs (hips) thrust whereas the forelimbs (shoulders) brake. This strategy is implemented by controlling foot speeds during ground contact. With this file=figures/Herr3.eps,width=4in

Figure 1: Stable solutions in speed-stiffness space based on simulations of a trotting horse. Leg stiffness, computed as in [1], ranged from 10-35 kN/m in simulations. The speeds plotted are biological trotting speeds except below 1.5 m/s, where real horses prefer to walk [2].

strategy, the simulation results point to a mechanism that is fundamental to why animals select particular gaits and stiffnesses: maintaining stability in body pitch. This idea should be tested across body size and shape.

Difficulty: The model's parameter space (foot speed, leg angle, joint stiffness, aerial time) is large, which requires a computationally intensive scheme. Stability of the model is difficult to quantify; we use a combination of smoothness of gait, minimum number of successful strides, and linearized analysis of state variables.

Impact: This work is a first step toward a new theory of animal locomotion that unifies structure, mechanics, energetics, and control. More generally, it will broaden our understanding of stability in legged locomotion. Applications include treatment of musculoskeletal diseases, design of size- and speed-adaptive prostheses and orthoses, and improvement of control algorithms for legged robots.

Future Work: We hope to explain why stiffness and metabolic cost scale with body size, and what role the body's shape (e.g., ratio of leg length to body length) might play. Further down the road, morphologically realistic legs with virtual muscles could be included in the model to capture energetics and postural effects. Regardless of the model's sophistication, new experiments with animals and/or robots will be needed to test new hypotheses of locomotory control.

Research Support: A Shaffer Foundation fund for rehabilitation research (Account 2732345).

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