Mechanical Properties Of The Support Tripod In Running Insects: The Role Of Preflexes In Dynamic Stabilization

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INTRODUCTION

Despite variations ranging from leg number and shape to type of skeleton employed, terrestrial runners from mammals to arthropods produce ground reaction forces that can be modeled as a spring-mass system with the same dimensionless stiffness (Blickhan and Full, 1993). There are two major beneficial consequences of bouncing while running: 1) the ability to use springs to store and return elastic strain energy (Alexander, 1988) and 2) passive self-stabilization resulting from a well tuned mechanical (musculo-skeletal) system (Seyfarth *et al*, 2002; Schmitt *et al*, 2002).

The mechanisms which produce and control this amazingly stable bouncing behavior remain a mystery. Neural control relying on negative feedback is one obvious and important means of maintaining stability (Cruse, 1990), but without knowledge of the animal's musculo-skeletal system, such control can be counterproductive and even destabilizing (Full *et al*, 2002). This is due to preflexes, or the "zero delay, intrinsic response of a neuromuscular-skeletal system to a perturbation" (Brown and Loeb, 2000), which produces forces that could counteract the neural response.

The running deathhead cockroach, *Blaberus discoidalis*, can be modeled as a spring-mass system in both the horizontal and sagittal planes. It has been shown to be dynamically self-stabilizing in the horizontal plane (Kubow and Full, 1999) and capable of recovering from large lateral perturbations without a step transition (Jindrich and Full, 2002). Results from dynamic oscillations of the hind limb in the sagittal plane predict that the cockroach is under-damped during the stance phase of locomotion and over-damped during the swing phase (Dudek and Full, 2001). This leaves open the possibility that cockroaches possess a damped spring capable both of elastic energy storage during stance and perturbation rejection during swing. It remains to be seen whether the preflexes of live, actively running cockroaches are properly tuned in the sagittal plane to simplify control of locomotion via dynamic self-stabilization. The goal of this study was to determine the preflexive properties of the tripod of support of a running insect.

METHODS

Deathhead cockroaches, *Blaberus discoidalis* (2.56±0.32 g, N=4), were tethered to the arm of a servomotor by epoxying a candle (0.63±0.11 g) to the third thoracic tergum. The candle tether was shaved down to the wick at its center and therefore acted as a universal joint, providing the roach with a complete range of motion. They were then positioned above a Styrofoam ball (20 cm diameter, 6.61 g) that was floating on an air bearing and allowed to run freely. The rotational inertia of the ball is designed to match the translational inertia of the cockroach and therefore serves as an inertial treadmill.

Leg joint angles and body kinematics (yaw, pitch, and roll) were recording using 3 digital cameras at a frame rate of 500 Hz. Running speed was measured by two optical encoders aimed at the ball's surface, directed 90° apart. Roaches ran at their preferred speed (17.78±4.16 cm/s) and stride frequency (8.89±1.56 Hz) with the servomotor arm deflecting passively. The servomotor, acting in the sagittal plane, then imposed sinusoidal force oscillations ranging from 10-50 mN in amplitude (25 or 40 Hz) and the induced displacements were recorded. The resulting hysteresis loops were modeled as a spring and damper in parallel.

RESULTS AND DISCUSSION

Mechanical impedance (the time-dependent resistance of a material to deformation) of the support tripod varies with the magnitude of the imposed force and ranges from 25-100 N m^{-1}. This is 2-4 times the impedance of a single, ablated limb (Dudek and Full, 2001). The stiffness component of the impedance ranges from 20-60 N m^{-1}. This gives a dimensionless stiffness of 14.03±1.56, close to the 16.7 estimated from force plate data (Blickhan and Full,1993). The damping component of impedance ranges from 0.05-0.55 N s m^{-1} and is larger at a perturbation frequency of 40 Hz compared with 25 Hz.

Previous data from forced oscillations of individual limbs predicts that cockroaches should be underdamped during running, with a damping ratio (ζ) between 0.1 and 0.2. These data show that during low frequency perturbations the roach is underdamped ($\zeta = 0.63 \pm 0.15$), but at high frequency perturbations the roach is actually overdamped ($\zeta = 1.59 \pm 0.57$). This supports the hypothesis that for slow, small-scale perturbations, the cockroach relies on neural reflexes for control but for fast, large-scale perturbations the passive dynamics of the mechanical system play a larger role in controlling energy.

SUMMARY

Animals from humans to cockroaches bounce like a pogo-stick during running. These dynamics have the benefits of increasing mechanical efficiency by storing and returning elastic strain energy and also simplifying control using a well-tuned, springy musculo-skeletal system. The mechanical properties of the support tripod of running cockroaches appear to be well suited for both of these functions.

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