PREFLEXIVE AND REFLEXIVE COMPONENTS OF STABILITY: COCKROACH AS A MODEL MUSCULO-SKELETAL SYSTEM.

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INTRODUCTION

During locomotion, animals deal with external perturbations effortlessly. Their ability to maintain stable locomotion results from reflexive actions of the nervous system and the intrinsic mechanical properties of the muscle-skeletal system (preflexes). It has been hypothesized that preflexes act as a first line of defense when dealing with rapid external perturbations (Brown and Loeb, 2000). Due to the complexity of most musculo-skeletal systems, an understanding of the relative contributions to control remains elusive. Cockroaches are ideal subjects to answer such questions, because their musculo-skeletal system and sensory system are well-defined (Full and Ahn, 1995; Wong and Pearson, 1976). This study aimed to determine the presence of preflexes and reflexes in perturbed cockroach legs.

METHODS

The perturbation experiments were performed on the hind-limbs of 10 cockroaches (*Blaberus discoidalis*), using a Single Leg Impedance Measurement device (SLIM). The thorax of the cockroach was rigidly attached to a tether. The left metathoracic limb was attached with a steel rod to the lever arm of a muscle lever system (300B-LR, Aurora Scientific). The animal was positioned in the natural standing posture. Perturbation experiments consisted of sinusoidal oscillations of leg position (amplitude = 1 mm; frequency = 2-25 Hz) roughly in the horizontal plane (Fig. 1). Recording electrodes were implanted into the coxal extensor muscles (177c, 179, and 177d) of the animals while they were immobilized. Force and EMGs responses to the perturbations were recorded.

Digital video was taken from below the animal at 125Hz (Kodak EktaPro, HG imager 2000). The videos were digitized and analyzed (Peak Performance Technologies) to obtain coxa-femoral and femoral-tibial angle changes over the course of the oscillations. Force and displacement data was fitted to a spring - damper model.

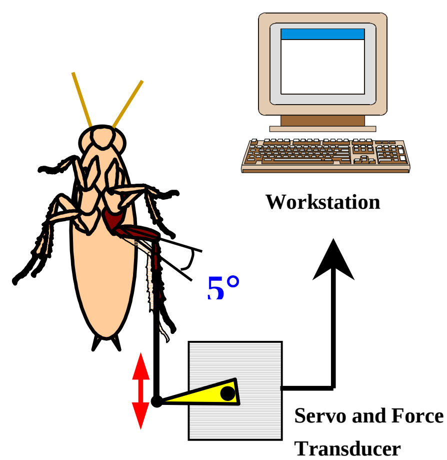

Figure 1. Schematic of our SLIM setup

RESULTS AND DISCUSSION

The positional perturbations of the leg resulted in small, 5-degree angular changes in both the coxa-femoral and femoral-tibial joints. Single legs of cockroaches with relaxed muscles responded to the positional perturbations with a relatively large force (Fig. 2). Forces ranged from 2.8 to 10 mN which is large compared to the average horizontal forces during running on level terrain (4.9 ± 0.7 mN; Full et al., 1991).

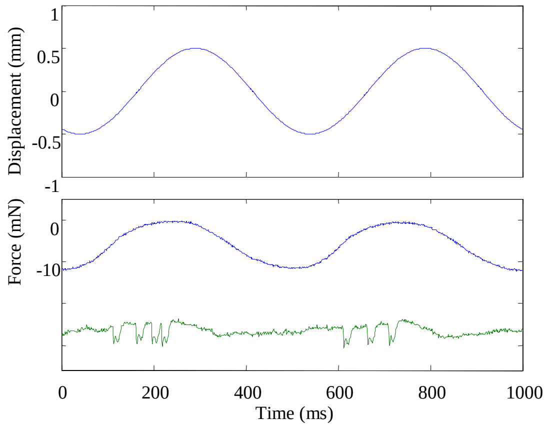

Figure 2. Leg displacement (top); Force and EMG of muscle 177d in response to leg oscillations (bottom)

The mechanical impedance, which was defined as the maximal change in force divided by the maximal change in position, was independent of the frequency at which the perturbation was applied. This suggests that the ability of the cockroach to deal with perturbations is rate-independent. Fitting of the spring-damper model to the data indicated that leg stiffness was independent of frequency, whereas the damping coefficient declined with increasing frequency.

EMG activity in response to the perturbation was found in muscle #177d (Fig. 2), but not in muscles #179 and #177c. Based on this pattern and the amplitude of the EMG signal, the EMG was identified as reflex activity from the slow motor axon in muscle 177d. The reflex activity measured in our experiments probably stems from sensory activity of specialized organs, called hairplates, which are located in the coxa-femoral joint (Wong and Pearson 1976). EMGs had a time delay with respect to the onset of joint flexion. The time delay decreased with increasing frequency and reached a constant value of about 12 ms for frequencies beyond 10 Hz, suggesting that this is the fastest response time possible by the reflex system. The average number of action potentials per perturbation cycle declined from 5 pulses at 2 Hz to less than 1 pulse for frequencies higher than 10 Hz. This suggests that the reflex system contributed less at the higher perturbation rates.

CONCLUSIONS

Our data support the hypothesis that cockroaches use both preflexes and reflexes to deal with external perturbations. The contribution of the reflexive component declines at higher speeds as indicated by changes in EMG signal. The decline is probably related to limitations in the response time of the reflex system. As speed and stride frequency increase, stride period decreases and reduces the time a reflex can produce an effective response. Since the mechanical impedance stays constant with increasing frequency, this means that the contribution of the preflexes becomes more important at the higher perturbation rates.

The behavior of the insect leg is consistent with the hypothesis that intrinsic mechanical properties act as zero order feedback signals, which can respond almost instantly to rapid perturbations (Brown & Loeb 2000). Preflexes can greatly simplify control during rapid gross rhythmic activity.

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