Abstract
An advantage of legged locomotion is the ability to climb over obstacles. We studied deathhead cockroaches as they climbed over plastic blocks in order to characterize the leg movements associated with climbing. Movements were recorded as animals surmounted 5.5-mm or 11-mm obstacles. The smaller obstacles were scaled with little change in running movements. The higher obstacles required altered gaits, leg positions and body posture. The most frequent sequence used was to first tilt the front of the body upward in a rearing stage, and then elevate the center of mass to the level of the top of the block. A horizontal running posture was re-assumed in a leveling-off stage. The action of the middle legs was redirected by rotations of the leg at the thoracal-coxal and the trochanteral-femoral joints. The subsequent extension movements of the coxal-trochanteral and femoral-tibial joints were within the range seen during horizontal running. The structure of proximal leg joints allows for flexibility in leg use by generating subtle, but effective changes in the direction of leg movement. This architecture, along with the resulting re-direction of movements, provides a range of strategies for both animals and walking machines.

Keywords
Climbing • Center of mass • Body-substrate angle • Kinematics • Joint angle

Introduction
Terrestrial locomotion using jointed legs is a complex adaptive behavior. Current understanding of walking and running is based mainly on studies that have recorded kinematic and/or force data from animals on smooth horizontal surfaces (Blickhan and Full 1993; Pearson 1993; Watson and Ritzmann 1998). However, a remarkable quality of legged animals is their agility in traversing diverse terrains. Legged animals readily clamber over obstacles, run on all manners of slopes, pick their way over discontinuous surfaces, and compensate for surface irregularities. The present studies were initiated to examine the specific changes in leg movements that occur as cockroaches of the species *Blaberus discoidalis*, adapt their locomotion to climb over barriers. These alterations provide insight to the mechanisms of control of insect walking and can also indicate effective strategies for limb use in legged robots.

Previous studies have shown that insects walking on a horizontal flat surface use a metachronal gait, in which the legs on each side step in a wave moving from back to front (Delcomyn 1971; Greene and Spirito 1979). Insects increase step frequency primarily by increasing the speed of leg extension during stance phase (Pearson 1976). As the duration of leg retraction decreases relative to protraction, the gait pattern shifts to an alternating tripod gait in which the front and hind legs on one side move as a unit along with the middle leg on the opposite side. This statically stable unit alternates with the tripod formed by the remaining three legs (Hughes 1952; Wilson 1966).

Although the tarsi (feet) of the legs making up a tripod move in synchrony, data on ground reaction

Abbreviations
CoM center of mass • CTr coxa-trochanter joint • FTj femur-tibia joint • Tj first thoracic (prothoracic) segment or leg • T2 second thoracic (mesothoracic) segment or leg • T3 third thoracic (metathoracic) segment or leg • ThCc thorax-coxa joint • Trf trochanter-femur joint
forces as well as electromyograms combined with kinematic analysis clearly demonstrate that each pair of legs plays a unique role in supporting and moving the animal (Full et al. 1991; Watson and Ritzmann 1998). Typically, the rear legs generate propulsive forces that produce much of the forward motion. To generate forces along the long axis of the animal’s body, the two principle distal joints, the coxa-trochanter joint (CTr) and the femur-tibia (FTi) joints extend in near synchrony (Watson and Ritzmann 1998). In the middle legs, the homologous joints also move synchronously, but the excursion of the FTi joint is smaller than that of the CTr joint. The location of the middle leg results in a movement that produces a biphasic ground reaction force consisting of a braking phase followed by an accelerating phase (Full et al. 1991). In the front legs there are large movements at the proximal thoracal-coxal joint(s), which have three degrees of freedom (Tryba and Ritzmann 2000) and the CTr and FTi joints do not always move in strict synchrony. Rather, these legs act like arms reaching forward and to the side to explore the surrounding environment while providing braking ground reaction forces (Full et al. 1991).

In order to climb over substantial obstacles, an animal must ultimately raise its center of mass (CoM) to the height of the obstacle. Most insects run with the body nearly parallel to the ground (Cruse 1976), so climbing over an obstacle might also involve tilting the front of the body upwards to grasp the face or edge with the legs. An insect that encounters an obstacle as it is walking could either climb over it by making minor modifications of the tripod gait, or it could change to a very different set of leg movements. Our data suggest that the deathhead cockroach surmounts obstacles using relatively subtle changes in leg orientation and body posture.

**Materials and methods**

**Animals**

Cockroaches (*B. discoidalis*) were housed in 20-l plastic buckets, half filled with aspen shavings, and were held at 27°C in a 12 h light:12 h dark circadian cycle. Commercial dry chicken starter and water were provided *ad libitum*. We used only intact, adult female cockroaches; length of the insects used was 46.1±2.0 mm (mean ± SD) and the body weight was 3.31±0.42 g.

**Preparation and apparatus**

We highlighted the ventral surface of the thoracal-coxal (ThC) joint, CTr joint, the anterior and lateral surfaces of the tibia just distal to the FTi joint and just proximal to the tibial-tarsal joint with white paint to facilitate visualizing them against the dark thorax of the cockroach. We placed each cockroach on a treadmill that allowed us to observe the animals during climbing and horizontal running. A clear acrylic chamber positioned just above the treadmill belt constrained the cockroach to run on the belt in an area of 5 cm x 17 cm. The 5 cm width of the belt was approximately 1.2 times body length and 1.5 times the span of the (middle) tarsi during running; which allowed unhindered running parallel to the belt motion. The treadmill ran at a constant speed during bouts of horizontal running. However, for climbing it was only moved to position cockroaches in front of the camera prior to the climbing movements. Thus, the animal was not subjected to acceleration due to the treadmill changing speed during the recoding period. The treadmill apparatus is depicted in Fig. 1a.

Cockroaches climbed over clear acrylic blocks of 50 mm length x 45 mm width x 5.5 mm height placed on the treadmill belt with one edge perpendicular to the direction of the insect’s motion. A higher barrier was constructed by placing a second block on top of the first for an overall height of 11 mm. As we will show, the choice of block heights was instructive, because each required the animal to use a different climbing strategy.

**Kinematics**

In order to monitor joint movement in three dimensions we recorded two orthogonal views. We recorded video images of the lateral view of the cockroach through the acrylic chamber and the ventral view through the acetate belt via a 19 cm x 7 cm mirror mounted at a 45° angle to the belt and immediately below it. Climbing movements were recorded at 250 frames s⁻¹ with a single camera Redlake digital video system that either downloaded the images to videotape for storage and analysis or stored them directly to digital files on a hard drive. We captured individual fields from videotaped data using a frame grabber card on a PC. Positions of various objects were digitized using the computer’s mouse in conjunction with motion analysis software (MotionTV, DataCrunch Systems, Calif., or MA Studio, Grafoil Imaging, Austin, Tex.). We digitized from each video field the ventral and lateral projections of the ThC, CTr, FTi, and the tibial-tarsal joints of the legs of interest, as well as the anterior tip of the head and the posterior tip of the abdomen, (Fig. 1b, c). We then calculated the true ThC, CTr and FTi joint angles in three-dimensional space from the ventral and lateral projected images (Marx et al. 1993). We defined the second abdominal (A2) segment as the center of mass of the cockroach (Nelson et al. 1997). The x-, y- and z-planes of the animal were defined as shown in Fig. 1b.

**Data analysis**

We smoothed the data on joint angles using an even-weighted, moving-average of three data points. Criteria for definition of the phases of leg movements were the same as described previously (Watson and Ritzmann 1998). We compared kinematic parameters between different stages of the climbing sequence (see below) with one-way analysis of variance followed by pair-wise comparisons with *t*-tests or rank-sum tests when appropriate.

**Results**

An insect that encounters an obstacle as it is walking could do one of three things. First, it could climb over the obstacle by making little or no modifications of the tripod gait. Second, it could change to a completely different set of leg movements. Third, it could use normal walking movements, coupled with postural adjustments to direct the movement of its body over the obstacle. To assess what actually happens, we observed the changes in body attitude and specific leg movements made by animals as they climbed over the two different sized blocks described above.

**Changes in body attitude associated with climbing**

We measured the changes in CoM and body-substrate angle that occurred during stance phase of steps...