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ORIGINAL PAPER

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Control of climbing behavior in the cockroach, *Blaberus discoidalis*. II. Motor activities associated with joint movement

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Abstract Deathhead cockroaches employ characteristic postural strategies for surmounting barriers. These include rotation of middle legs to re-direct leg extension and drive the animal upward. However, during climbing the excursions of the joints that play major roles in leg extension are not significantly altered from those seen during running movements. To determine if the motor activity associated with these actions is also unchanged, we examined the electromyogram activity produced by the slow trochanteral extensor and slow tibial extensor motor neurons as deathhead cockroaches climbed over obstacles of two different heights. As they climbed, activity in the slow trochanteral extensor produced a lower extension velocity of the coxal-trochanteral joint than the same frequency of slow trochanteral extensor activity produces during horizontal running. Moreover, the pattern of activity within specific leg cycles was altered. During running, the slow trochanteral extensor generates a high-frequency burst prior to foot set-down. This activity declines through the remainder of the stance phase. During climbing, motor neuron frequency no longer decreased after foot set-down, suggesting that reflex adjustments were made. This conclusion was further supported by the observation that front leg amputees generated even stronger slow trochanteral extensor activity in the middle leg during climbing movements.

Keywords Extensor motor neuron · Motor reflex · Load · Joint velocity · Electromyogram

Abbreviations *CoM* center of mass · *CTr* coxa-tro-chanter joint · *Ds* slow trochanteral extensor · *Df* fast trochanteral extensor · *EMG* electromyogram · *FETi* fast extensor of the tibia · *FTi* femur-tibia joint · *SETi* slow extensor of the tibia · T_1 first thoracic (prothoracic) segment or leg · T_2 second thoracic (mesothoracic) segment or leg · T_3 third thoracic (metathoracic) segment or leg · *ThC* thorax-coxa joint · *TrF* trochanter-femur joint

Introduction

In our efforts to understand the kinematics and neural control of legged locomotion, we have begun to concentrate on the transitional behaviors exhibited as an animal shifts from horizontal running to climbing over step-like obstacles. We have found that the strategy used to overcome barriers depends upon the size of the object (Watson et al. 2002). Small barriers (5.5 mm height, or 62.5% body height) are negotiated with little change from the typical horizontal running movement. However, barriers that are higher (≥11 mm) are climbed with a characteristic strategy that includes measurement of the barrier, changes in leg position and body posture followed by a push up and over the barrier, and a return to normal horizontal posture on top of the block.

The companion paper characterized postural adjustments that generate a rearing stage capable of tilting the animal's front end upward to place its legs upon the top of an 11-mm block. However, after these postural adjustments are made, extensions in the coxal-trochanteral (CTr) and femoral-tibial (FTi) joints of the middle and hind legs are very similar to those seen in horizontal running. The similarities in CTr and FTi joint kinematics between horizontal running and climbing raise two more questions (Watson et al. 2002). One issue is whether or not the motor control system for any of the legs is actively compensating during the various stages of climbing for changes such as increased mechanical load. If the animal proceeds through the climbing movements in an open loop manner, it will generate the same muscle forces, but the increased gravitational load will slow

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down its leg movements. However, if the animal compensates for the increased load, it will actively increase motor activity to maintain normal joint movements and speed even during climbing. An analogy can be seen as an automobile begins to climb a hill. If the driver keeps the gas pedal at the same level that was used on the horizontal, the car will slow down. However, if the automobile is equipped with a cruise control, that device will detect the decrease in speed and increase the fuel to the engine so that speed is maintained.

If there is an effective compensation during climbing, the second issue is whether each pair of legs reacts in a similar way. During walking each pair of legs plays a distinct role (Watson and Ritzmann 1998a; Full et al. 1991) and it is likely that they would react differently during climbing. For example, with the front legs detecting the block, middle legs generating body rotation and hind legs extending to lift the center of mass (CoM), the motor adjustments could be distinct for each pair of legs during the various stages of climbing.

There are two ways to estimate muscle activation. Ground reaction forces can be measured using force plates (Biewener and Full 1992) or photoelastic gels (Jindrich and Full 1999). Alternatively, the timing and relative magnitude of muscle activity can be monitored with electromyograms (EMGs). Although a complete view of behavior requires both, the second technique provides a very sensitive measure that allows one to monitor changes in muscle activity during all stages of the behavior and even within specific leg cycles. Although measurement of ground reaction forces was beyond the scope of this study, we did extend our analysis of obstacle climbing by adding EMG recordings from muscles in the middle and hind legs to our kinematic data on the related joint movements. We restricted our recordings to the middle and hind legs because the kinematics of the front legs are more complex than the middle and hind legs. Moreover, recordings from the front legs pose unique difficulties during the climbing movements.

Our observations reveal systematic increases in motor activity during rearing and rising stages of the climbing movement associated with 11-mm obstacles. The pattern of these changes are different for the middle and hind legs and are specific for the middle and last segments of the stance phase bursts.

Materials and methods

Animals, apparatus, and videography

Housing and handling conditions, treadmill apparatus, videography techniques, and kinematic analysis are reported in the companion paper (Watson et al. 2002).

Electromyograms (EMGs)

Equipment and techniques to record electromyograms were reported previously (Watson and Ritzmann 1998a). In order to reduce potential kinematic interference from EMG wires, in each experiment, we recorded from either one middle or one hind leg. In either case, each experiment sought to record motor activity from the main extensor and flexor muscles of the CTr and the FTi joints. The main trochanteral extensor in the middle leg is muscle 135D and the homologous muscle in the hind leg is 177D (Carbonell 1947). These muscles are each innervated by one 'slow' excitatory motor neuron which produces slow graded contractions (Ds), one 'fast' excitatory motor neuron which produces short, powerful twitches (Df) and three inhibitors (Pearson and Iles 1971). Trochanteral flexors (138C in the middle leg and 182C in the hind leg; Carbonell 1947) are each innervated by seven motor neurons including two slow excitors, four fast excitors, and one inhibitor (Pearson and Iles 1971). The tibial extensors (142a in the middle leg and 194a in the hind leg; Nijenhuis and Dresden 1955) are each innervated by one fast extensor (FETi) and one slow extensor (SETi) (Atwood et al. 1969). The tibial flexors (143 in the middle leg and 185 in the hind leg; Nijenhuis and Dresden 1955) are each innervated by nine excitors including fast, intermediate, and slow types, and two inhibitors.

The recording sites are depicted in Fig. 1. These sites were chosen to provide the cleanest recordings of both slow and fast motor activity in the muscles that control joint movement with minimal cross-talk between muscles. From these sites, we could readily distinguish individual activity from Ds and Df in the trochanteral extensor EMGs and SETi and FETi in the tibial extensor EMGs. The flexor motor neuron activity is more complex for both joints. Thus, we did not do extensive analysis of those motor neurons.

Data analysis

Joint movements were recorded with a digital high-speed video system (Redlake) as described in the companion paper. The frame rate was either 125 Hz or 250 Hz. Electromyograms were recorded with a PC-based data acquisition system using a sampling rate of 2.5–10 kHz (Axon Instruments). For each locomotion sequence analyzed, we manually digitized the position of the body and all joints on the leg from which EMGs were recorded. Three-dimensional angles were calculated as described in the companion paper (Watson et al. 2002). The motion data were smoothed using an even weighted moving average of three data points each with a bin width of 4 ms or 8 ms, depending upon the camera frame rate. Smoothed joint angle records were then expanded by the factor necessary to give the same number of data points as the electromyograms. Relevant kinematic and EMG sequences could then be synchronized and merged into a common file using Data-Pac software from Run Technologies. A trigger point was synchronized in the video and electrophysiological records as a square wave in a separately recorded channel. A recording from the video system monitored the exact timing of individual video frames. Thus, we could count frames backward or forward from the trigger event and thereby identify exactly where in the video record any electrical event occurred within 4 ms or 8 ms (the interval between two video frames).

The merged records were analyzed in detail with tools from the Data Pac software package. Criteria for detecting individual muscle potentials and definition of the phases of leg movements were the same as described previously (Watson and Ritzmann 1998a). In general, we used the Data Pac software to mark putative muscle potentials. We then examined each potential visually to assure ourselves that they represented potentials from Ds or SETi and not cross-talk from some other source. Because the muscles that were recorded are innervated by only two excitatory motor neurons and the fast motor neuron potentials are readily distinguished from those of slow motor neurons, we are confident that the analysis identified potentials from single motor neuron sources.

Mean joint angle velocity of the extension phase of the leg cycle was determined as in previous studies (Watson and Ritzmann 1998a) by calculating the regression slope of the joint angle

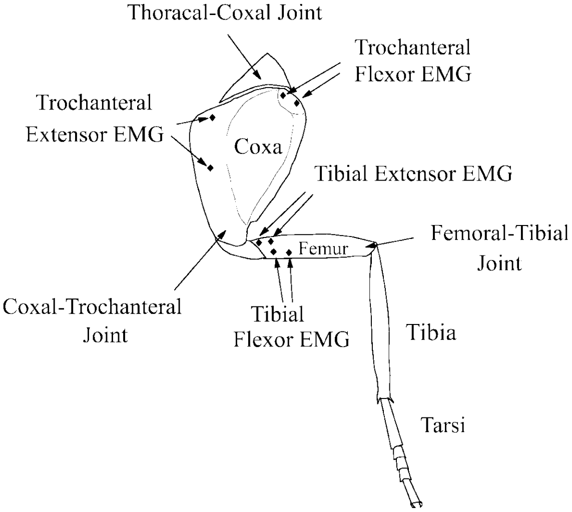


Fig. 1 Leg of *Blaberus discoidalis*, ventral view showing leg segments and recording sites for electromyogram (EMG) wires monitoring trochanteral extensor and flexor muscles in the coxa as well as tibial extensor and flexor muscles in the femur

amplitude for the interval between the first detectable extension and the first detectable flexion. Joint angle velocity was compared to mean EMG frequency for individual step cycles and plotted against each other as described previously for horizontal running (Watson and Ritzmann 1998a). These parameters were compared between different stages of the climbing sequence with one-way analysis of variance followed by pair-wise comparisons with t-tests or rank-sum tests when appropriate. We also compared climbing data to horizontal running data taken from the animals recorded here.

Results

Coupled kinematics and EMG recording during climbing

As with the kinematic data, motor activity associated with climbing was distinctly different for small and large barriers.

Climbing over 5.5-mm barriers

Consistent with the finding that leg kinematics for climbing over the 5.5 mm obstacle were similar to walking movements (Watson and Ritzmann 1998a; Watson et al. 2002), we found no significant changes in the EMG patterns or frequency as the animal switched from horizontal running to climbing over the 5.5-mm block (Fig. 2a). Both the mean EMG frequencies for all motor neurons that we monitored and the related joint velocities were unchanged. Moreover, the slope of the functions comparing EMG frequency during individual step cycles to related joint velocities for climbing over the 5.5-mm blocks were not discernibly different from the same relationships recorded during horizontal running (Fig. 2b).

Climbing over 11-mm barriers

In the companion paper, we described the kinematic events associated with climbs over an 11-mm block (Watson et al. 2002). After the animal redirected the middle legs in preparation for rearing, rising or leveling, it extended the CTr and FTi joints through their normal excursions. The pattern of motor activity that controls extension of CTr and FTi joints was qualitatively similar to that seen during horizontal walking (Watson and Ritzmann 1998a), suggesting that the animal is using the same neural control circuits in these behaviors. That is, motor activity recorded in the trochanteral and tibial extensor EMGs was dominated respectively by Ds and SETi activity with relatively few instances involving Df and FETi recruitment. Moreover, the relative timing of motor activity was also consistent with running. There was no obvious increase in co-contraction with flexor motor neurons and, as is the case in horizontal running, Ds onset preceded SETi, while SETi activity continued beyond Ds termination (Fig. 3). The timing of activity in both of these motor neurons paralleled extension of their related joints (Ds with CTr and SETi with FTi).

The overall mean EMG frequency of each motor neuron tended to be the same for 11-mm block climbing and running (Table 1), i.e., the firing frequencies recorded during the various stages of climbing for each of the motor neurons that we analyzed (middle and hind Ds and SETi) were not significantly different from that recorded during horizontal running, with one exception in hind leg Ds activity, which was lower for rearing than for climbing. This exception is consistent with the only instance of significant change in joint excursion (hind leg CTr joint) reported in the companion paper (Watson et al. 2002). However, in both the middle and hind legs, the mean joint velocities for the rearing, rising and leveling steps were significantly lower than for horizontal running. Here, the one exception was that the hind leg FTi joint velocity was not significantly different in leveling and running. These two trends were evident whether obstacle climbing was compared to steady-state treadmill running or to the one to two steps as the animal approached the obstacle.

The lower joint velocity relative to EMG frequency indicates that the relationship between motor activity and joint movements is altered during climbing. What is the nature of that change? The change in joint velocity could represent a uniform impediment simply due to increased gravitational load during climbing. Alternatively, there could be velocity dependent effects incorporating motor responses or additional physical properties such as inertia. To begin to address this question we took advantage of the linear relationship between motor activity and joint velocity that exists over a range of horizontal running speeds (Watson and Ritzmann 1998a). In comparing the results from various stages of climbing to horizontal running, a simple offset of the relationship (i.e., change in y-intercept) would

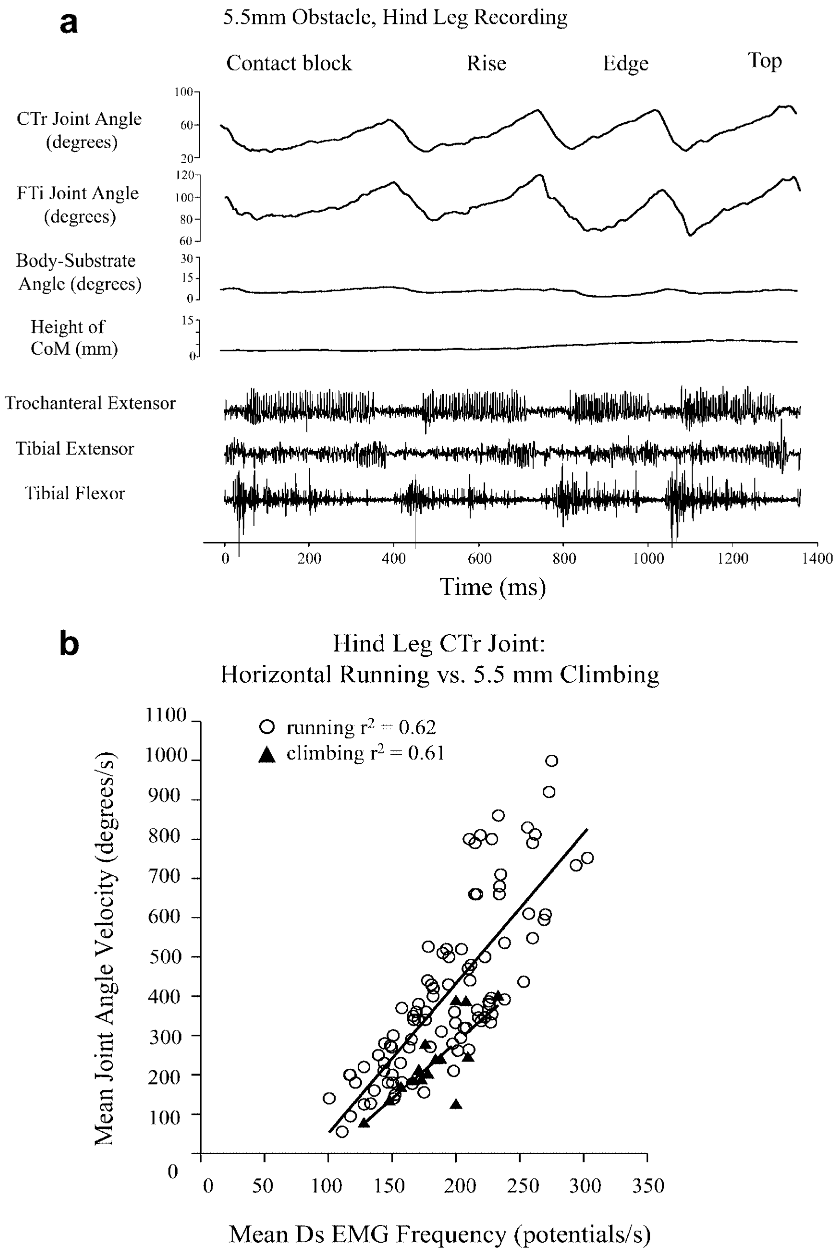


Fig. 2a, b Kinematics and EMG activity of mesothoracic (middle) leg while climbing the 5.5 mm obstacle. **a** Coxal-trochanteral (CTr) and femoral-tibial (FTi) joint angle records, body-substrat angle and height of COM synchronized with trochanteral extensor and tibial extensor EMG records from the middle leg of a cockroach climbing over a 5.5-mm block. **b** Average slow trochanteral extensor (Ds) EMG frequency versus average CTr joint angular velocity for the middle leg during horizontal treadmill running (*circles*) and climbing over 5.5-mm obstacle (*triangles*). Data for running are from seven animals. Data for climbing are from three animals

imply a uniform resistance. However, a change in slope would suggest a more complex effect.

We collected femoral extensor EMG and CTr joint motion data from the middle leg (15 climbs in 4 animals) and the hind leg (15 climbs in 3 animals). We then calculated the regression slope of the EMG-joint velocity function for each animal. The mean of the slopes of the EMG-joint velocity function for the middle legs was significantly lower for the rearing, rising and leveling stages than for horizontal running (Fig. 4). For the hind legs the slopes were significantly lower for rearing and rising stages but not for leveling (Fig. 5), i.e., during climbing, as the frequency of Ds activity increased, joint velocity increased relatively less than during horizontal running. These results suggest that the decrease in effectiveness in joint movement seen during climbing is not a simple uniform change.

We also examined the effectiveness of distal motor neurons. However, because it was very difficult to maintain recordings from the tibial extensor in *B. discoidalis* long enough to collect data during multiple running and climbing sessions, there were insufficient EMG data to test for significant differences in slopes of the SETi EMG frequency versus FTi joint velocity function. Nevertheless, the few animals for which we were able to derive slopes (two animals both for middle and hind leg) showed the same pattern for SETi as for Ds, i.e., the slope of the EMG frequency-joint velocity function was less for climbing steps than for horizontal running (data not shown).

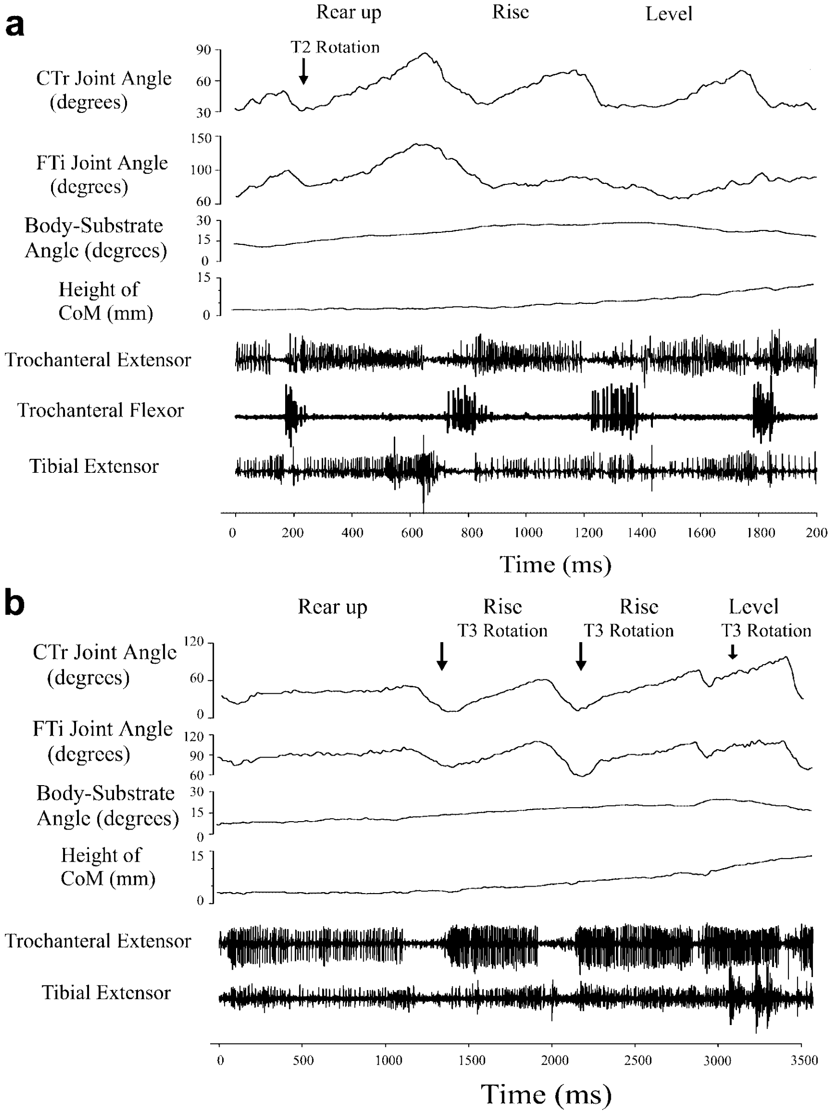


Fig. 3 Kinematics and EMG activity of mesothoracic (middle) leg (**a**) and the hind leg (**b**) while climbing 11-mm obstacles. CTr and FTi joint angle records, body-substrate angle and height of COM synchronized with trochanteral extensor and tibia extensor EMG records from the leg of a cockroach climbing over an 11-mm block. In both figures, the potentials that are recorded during stance phase from the trochanteral extensor muscle are from Ds and those from the tibial extensor are from slow extensor of the tibia (SETi). Occasional fast extensor of the tibia (FETi) spikes are seen, for example at 650 ms in **a** and near the end of the record in **b**. These are readily distinguished from the much smaller SETi potentials. No fast trochanteral extensor (Df) potentials are noted here. There is some cross-talk in the trochanteral extensor record at the outset of each stance cycle in **a**. This was readily distinguished when the record was spread out and compared to the flexor bursts. No such cross-talk was seen in **b**. *Arrows* indicate when the distal segments of the leg are re-oriented to facilitate rearing up (middle leg) or rising and clambering onto the obstacle (hind leg)

Internal Ds burst structure

The shift in EMG versus joint velocity relationships implies that muscle activity is less effective during each of the stages of obstacle climbing. However, while the shift in the slope is clear, it does not distinguish between two possibilities. The animal could be actively generating more motor activity to compensate for mechanical adjustments during climbing such as increased loading or it could simply be generating the same motor activity as it does during horizontal running but with the result that it is less effective during climbing. Because both climbing and running occur over a range of leg cycle frequencies, we cannot distinguish between these two possibilities by simply comparing the mean motor activities in the two behaviors. Our observation that the mean EMG frequency was the same in climbing and running could support the notion that the animal is not compensating during climbing. Alternatively, it could occur because the animal is moving at a slower rate but with an augmented motor response.

The issue could be resolved if the frequency of motor activity changed in a non-uniform fashion within each leg cycle as the animal moves between behaviors. In horizontal running, the Ds and SETi motor bursts show reproducible patterns during leg extension (Watson and Ritzmann 1998a). Ds typically generates a high frequency burst prior to foot set-down, with frequency declining thereafter (Fig. 6a, c). Because this burst occurs while the foot is still in swing, information from that leg about load cannot influence it. If those patterns are maintained during climbing, it would imply that the animal was either making no adjustments to its motor output, or that it compensates by increasing all parts of the stance phase uniformly. For Ds, the latter possibility is unlikely, because loading changes so much during the stance burst (Watson and Ritzmann 1998a; Tryba and Ritzmann 2000) (Fig. 3). If the pattern alters because various phases increase non-uniformly, that would

Table 1 Electromyogram (EMG) and joint velocity values for horizontal, steady-state treadmill running and each of the stages of climbing over an 11-mm block. Data are presented as mean ± SEM. Comparisons show which comparisons were significant ($P < 0.05$) using pair-wise test following one-way ANOVA; NS not significant (*CTr* coxa-trochanter joint, *Ds* slow trochanteral extensor, *FTi* femur-tibia joint, *SETi* slow extensor of the tibia)

Middle leg-CTr joint (*n*)	Running (26)	Rearing (15)	Rising (13)	Leveling (14)	Comparisons
Mean Ds frequency (potentials s^{-1})	237.7 ± 13	209.3 ± 15.5	212.9 ± 19.5	198.2 ± 14.1	NS
Mean Ds duration (ms)	158.7 ± 10.7	305.6 ± 42.3	360.8 ± 93.4	377.9 ± 78.5	All > run
Mean CTr joint velocity (degrees s^{-1})	337.6 ± 23.4	154.5 ± 26.4	169.5 ± 33	125 + 11.7	Run > all
Middle leg-FTi joint	Running (6)	Rearing (14)	Rising (13)	Leveling (14)	Comparisons
Mean SETi frequency (potentials s^{-1})	206.5 ± 8.2	178.6 ± 13.5	173.2 ± 17	172.3 ± 12.2	NS
Mean SETi duration (ms)	171.7 + 12.2	302.4 + 48.7	372.5 + 80.5	380.7 + 87.1	All > run
Mean FTi joint velocity (degrees s^{-1})	279.5 ± 27.6	153.2 ± 30.2	143.3 ± 29.2	102.1 ± 13.8	Run > all
Hind leg-CTr joint (*n*)	Running (31)	Rearing (10)	Rising (15)	Leveling (12)	Comparisons
Mean Ds frequency (potentials s^{-1})	193.3 ± 6.1	146.6 ± 15	172.5 ± 10.9	174.7 ± 9.6	Run > rear
Mean Ds duration (ms)	235.8 + 17.2	565.6 + 114.6	472 + 58.1	321.4 + 40.1	Rear, rise > run
Mean CTr joint velocity (degrees s^{-1})	280.3 ± 16.8	104.4 ± 20	173.2 ± 25.6	174.7 ± 25.2	Run > all
Hind leg-FTi joint	Running (17)	Rearing (9)	Rising (9)	Leveling (7)	Comparisons
Mean SETi frequency (potentials s^{-1})	140.9 ± 10	112.4 ± 13	149.4 ± 16	143 ± 15.2	NS
Mean SETi duration (ms)	282.2 ± 30.7	694.5 ± 150.6	471.3 ± 85.7	406.1 ± 48.4	Rear > run
Mean FTi joint velocity (degrees s^{-1})	291.3 ± 23	95.1 ± 21	157.7 ± 26.7	168 ± 34.2	Run > rear, rise

suggest that motor adjustments are occurring. This rationale led us to look more closely at the pattern of Ds potentials within bursts.

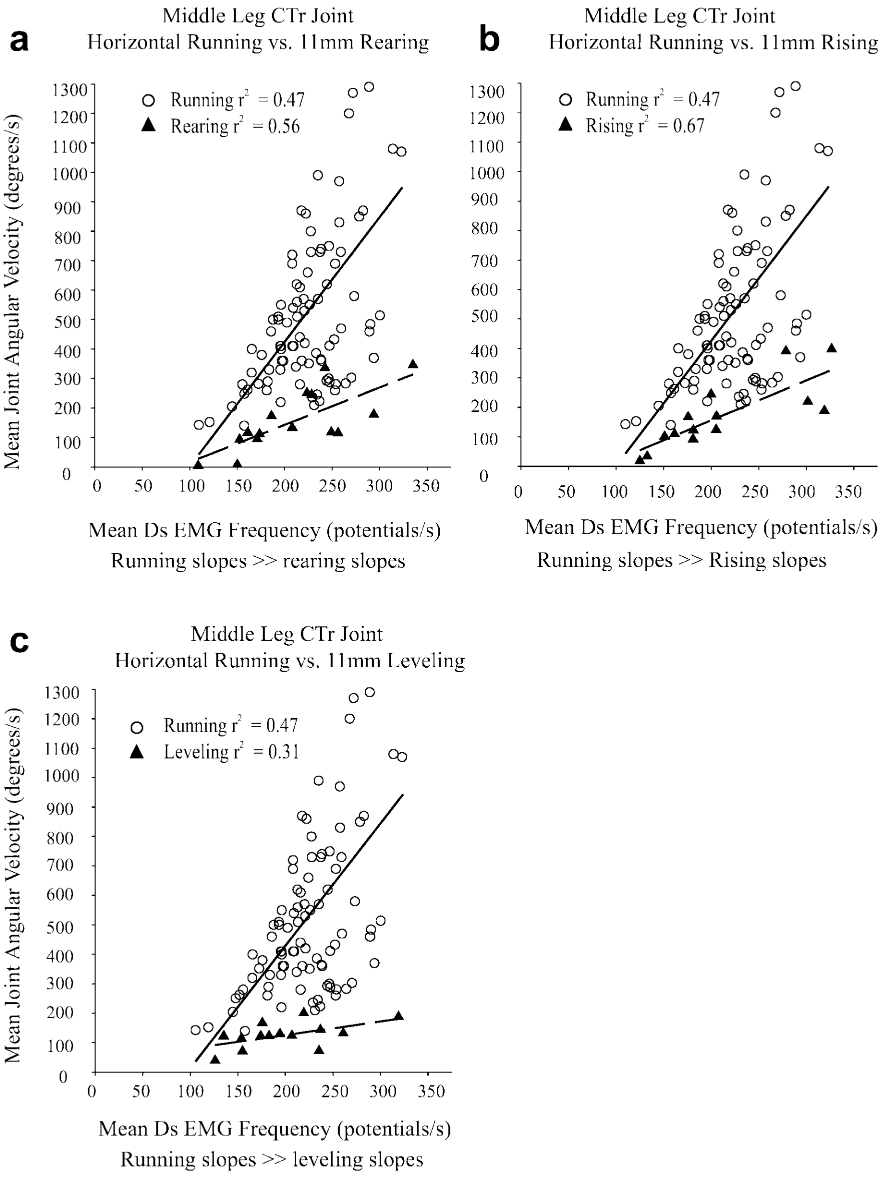
In order to compare regions within each stance burst during the various stages of climbing, we first had to decide on logical places of division. The burst structure during each stage of climbing could be arranged as percentage of bursts and combined into representative histograms. Each burst from 9 to 12 stance cycles was divided into 20 bins and spikes were counted within each bin. Unfortunately, for both walking and climbing, the bursts varied in length from 117 ms to 1062 ms. However, the mean spike frequency did not vary significantly between various behaviors. Therefore, dividing a relatively long burst into 20 bins would capture more spikes per bin than would a shorter burst. To correct for differences in duration, each stance burst was normalized by multiplying the spike counts in the 20 bins by the ratio of the smallest burst duration (117 ms) to the actual duration of each individual burst.

The resultant normalized spike counts were combined and plotted for the three stages of climbing (rearing, rising and leveling) as well as for examples of horizontal running. An initial examination of these histograms did show different patterns for the two leg pairs at various stages of climbing. For horizontal running, the bins segregate into three groups. The initial quartile has the highest level of activity. The middle two quartiles are somewhat reduced and the final quartile is even more reduced. An example of the this pattern is seen for the hind leg in an individual EMG record (Fig. 6a) and a normalized histogram (Fig. 6c). This pattern was not evident for the middle leg during rearing and rising, nor for hind leg during rising (Fig. 6b, d), suggesting a change in motor pattern.

To test whether the apparent changes in pattern in the normalized histograms represented statistically significant effects, we calculated mean EMG frequency for the initial quarter, middle two quarters and last quarter of the bursts from which the normalized histograms were derived (Fig. 7). We then compared the values for the these segments using Kruskall-Wallis one-way analysis of variance (ANOVA) followed by pair-wise comparisons with Student-Newman-Keuls method when appropriate. As expected, the data for running in either middle or hind legs (Fig. 7a, e) showed significant drops between both the first and middle segments and the middle and final segments of the bursts. However, no significant differences were noted among burst segments for middle leg rearing and rising stages (Fig. 7b, c) or for hind leg rising stage (Fig. 7g). In the mesothoracic leg leveling step, the middle burst segment matched the first, but the frequency dropped off in the last segment (Fig. 7d). In the hind leg rearing and leveling steps (Fig. 7f, h), the initial burst segment was still significantly higher than the middle segment (as in running), but the drop off in the last segment was missing.

Thus, the changes in burst structure from the running pattern to a more constant motor frequency occur in specific stages of the climbing behavior. The middle legs appear to be making motor adjustments during rearing and rising stages, while the hind legs are only making significant adjustments during the rising stage. This is consistent with the kinematic data that suggested that the middle legs play important roles in rearing and rising, while the hind legs are primarily used after the postural adjustment to propel the animal to the top of the barrier.

Fig. 4 Average Ds EMG frequency versus CTr average joint angular velocity for the mesothoracic (middle) leg during horizontal treadmill running (*circles*) and various behaviors (*triangles*) exhibited while surmounting the 11-mm obstacle: **a** rearing up, **b** rising, **c** leveling. The means of the slopes of the relationship between average Ds EMG frequency and average CTr joint angular velocity for each of the three obstacle-climbing behaviors were each significantly less than the slope for horizontal running. Data for running are from seven animals. Data for climbing are from four animals



We also examined the burst patterns for SETi, which controls the FTi joint. During each stance cycle of horizontal running the frequency of this motor neuron increases and has a particularly high frequency burst at the end of each leg cycle. In contrast to Ds, the intraburst patterning of SETi, is not substantially altered during any of the climbing stages in either leg (data not shown).

Incline running

Although the analysis presented above indicates that the motor system is actively compensating for mechanical effects during climbing, the exact nature of those challenges is complex. Gravitational load is increased as the animal pushes upward. However, other factors must also be considered. During the various stages of climbing there are postural adjustments that alter the angle between each leg and the substrate (Watson et al. 2002). Also, gait changes occur during climbing in which pairs of legs are both in contact with the substrate for longer periods of time than during the tripod gait used in walking. There are also changes in inertia compared to horizontal running. Since the animal often slowed or stopped moving before rearing and climbing the 11-mm obstacle, additional muscle force might be required to start moving the body mass again.

To begin to examine the relationships between these various mechanical properties and the cockroach's motor response, we can compare our results from climbing over 11-mm obstacles to similar data taken from other behaviors that share some but not all of these challenges. For example, as a cockroach walks up an incline it overcomes additional resistance due to increased gravitational loading that is comparable

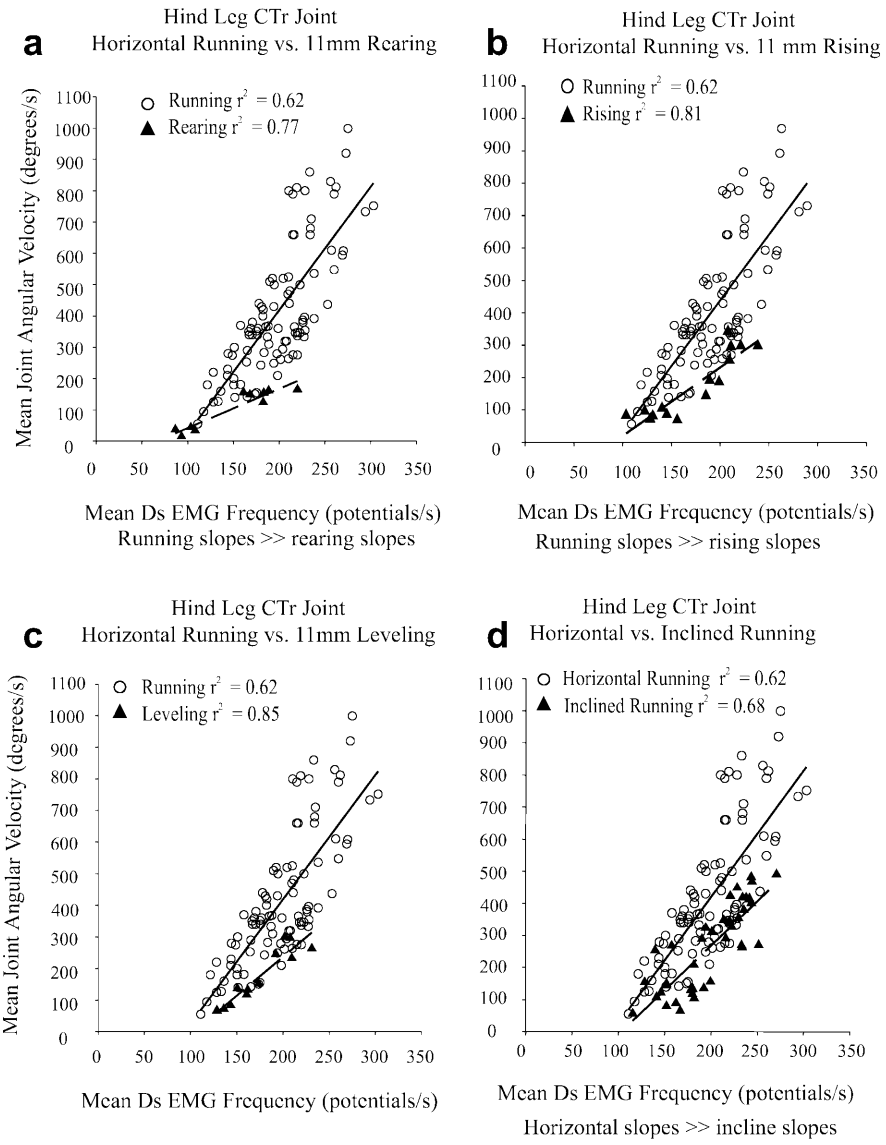


Fig. 5 Average Ds EMG frequency versus CTr average joint angular velocity for the metathoracic (hind) leg during horizontal treadmill running (*circles*) and various behaviors (*triangles*) exhibited while surmounting the 11-mm obstacle: **a** rearing up, **b** rising, **c** leveling, **d** incline running. The means of the slopes of the relationship between average Ds EMG frequency and average CTr joint angular velocity for the rearing rising, and incline running behaviors were each significantly less than the slope for horizontal running. Data for running are from seven animals. Data for climbing are from three animals. Data for incline running are from four animals

to obstacle climbing. However, it still uses a typical tripod gait and maintains running movements for long periods of time. Thus, it does not experience inertial effects associated with transitional behaviors. Finally, the posture is similar to that found in running. Thus, the angle of attack of the legs relative to the substrate is similar to that seen during horizontal running and is, therefore, very different from block climbing movements.

We inclined the treadmill to an angle similar to that which the animal assumes during rearing in an 11-mm obstacle climb and acquired both joint angle and EMG data from hind legs (summarized in Table 2). The CTr joint excursion was smaller during inclined running than for horizontal running. The mean Ds EMG frequency was not significantly different between these two conditions, but the CTr joint angle velocity was significantly lower during incline running than during horizontal running. When we compared the EMG frequency versus joint velocity data among horizontal running, obstacle climbing and incline running (Fig. 5d), we found that the relationship for incline running resembled the rearing and rising data more than it did the horizontal running data. The mean of the slopes for the incline running data was not significantly different from the means for rearing and rising data but was significantly less than the mean of slopes for the running data.

In spite of the change in mean EMG versus joint velocity relationship, the burst pattern during incline running was in fact similar to the pattern seen during horizontal running (Fig. 8). As with horizontal running, Ds frequency decreased after the initial phase, and the frequency during the middle phase was, again, higher than the frequency during the last phase. This result suggests that the changes in mean Ds activity versus joint velocity during incline running are more due to a decreased effectiveness for muscle activity associated with Ds, than to an increased Ds motor activity in the response to

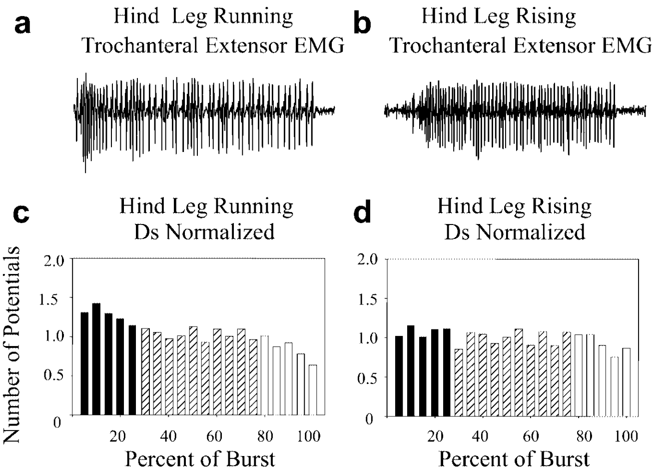


Fig. 6a–d Intra-burst pattern of Ds EMG frequency during running and the rising stage of climbing. **a** and **b** are examples of Ds activity during a running sequence (**a**) and the rising stage of a climb (**b**) taken from the same animal. Both records are 600 ms long. Note that the frequency declines from an initial high-frequency burst during running but that it remains uniform in the climb. **c** and **d** are normalized histograms of several instances of these cycles to demonstrate how we analyzed the data. The cycles were broken up into quartiles with *black bars representing the first quartile*, *hatched the middle two, and open bars the last*. The values for these segments were averaged and presented for both legs in all stages of the climbs and running in Fig. 7

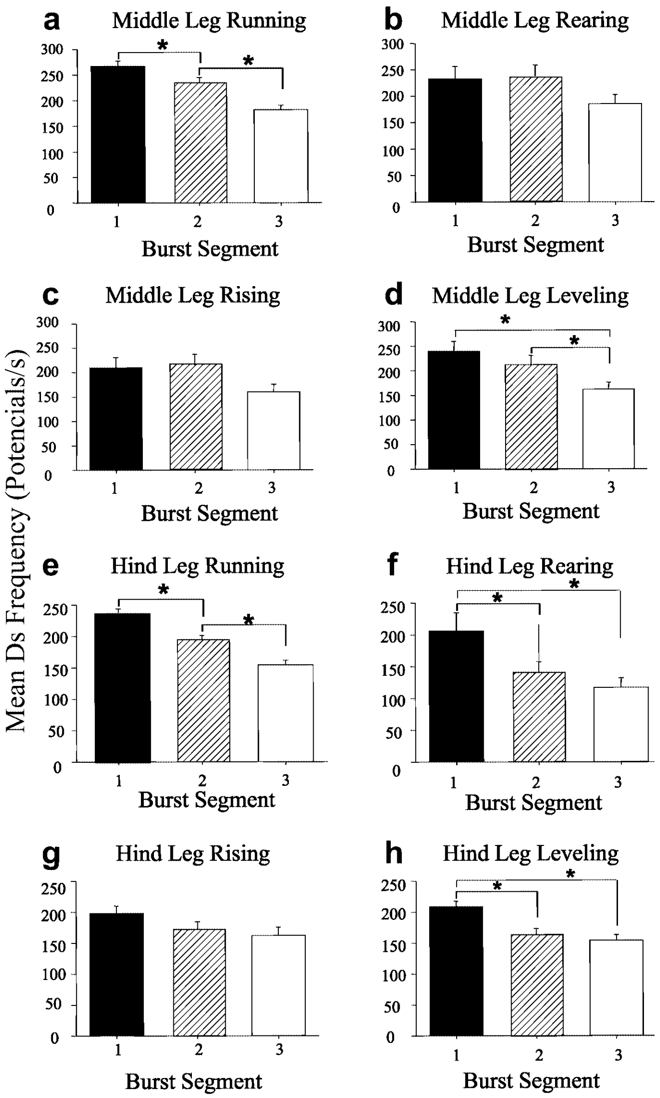


Fig. 7 Ds patterns in the middle leg during **a** horizontal running, **b** rearing, **c** rising, and **d** leveling, and in the hind leg during **e** horizontal running, **f** rearing, **g** rising, and **h** leveling. Each figure shows the mean Ds spike frequency for the first quarter of the burst (*black bars*), the middle two quarters of the burst (*hatched bars*) and the last quarter of the burst (*open bars*). The *shading* is consistent with that used in Fig. 6. An *asterisk* indicates a significant difference ($P < 0.05$) between burst segments. In **a** and **e**, first segment ≫ middle segment ≫ last segment. In **d**, first and middle segments ≫ last segment. In **f** and **h**, first segment ≫ middle and last segments. Each graph represents the mean of 9–12 bursts recorded from 3–4 animals

increased gravitational load. The contrast between intra-burst effects seen in incline running and climbing further suggests that Ds burst patterning seen during rearing, rising and leveling are not simply a direct effect of the greater resistance imposed by overcoming gravity.

Effects of front leg amputation on motor activity to middle leg CTr and FTi joints

Experimentally altering leg loading by amputation of pairs of legs can also shed light upon the cues that influence motor control during climbing. As reported in the companion paper, we found that cockroaches could climb the 11-mm barrier even with either the front or middle legs amputated. This suggests that intact animals utilize both sets of legs to produce rearing movements. If the front legs contribute substantially to rearing up, their removal should force the middle legs to play a greater role in lifting the animal upward than would be the case in the intact condition. The middle legs would then have to generate even greater motor responses relative to joint velocity during rearing than we saw for intact animals.

We examined motor activity combined with leg kinematics in the middle legs of two animals before and after the front legs were amputated. During rearing and rising, both of these front leg amputees made similar movements in middle leg joints. That is, the CTr and FTi joint velocities and excursions were not significantly different from the values noted prior to amputation. After amputation, however, both animals demonstrated increased motor activity during rearing. The data in Fig. 9a, derived from one animal, show a significantly higher frequency of Ds activity during rearing (seven climbs) than was seen in the same animal prior to amputation (eight climbs) even though the joint velocity was the same (Fig. 9a). Figure 9b, c show climbs made by another animal before and after amputation. After amputation the fast trochanteral extensor (Df) was recruited and fired seven muscle

Table 2 Kinematic variables compared between horizontal and inclined running. Data are presented as mean ± SEM. *P* shows the probability of the indicated difference based on the Student's *t*-test or Mann-Whitney Rank-Sum test, as appropriate

Hind leg	Horizontal running	Incline running	*P*
Number of steps	49	39	
Mean CTr joint velocity (degrees s^{-1})	376.3 ± 28.7	261.2 ± 21.4	0.012
Mean Ds frequency (potentials s^{-1})	209 ± 6.3	197 ± 6.3	NS
Minimum CTr joint angle (degrees s^{-1})	23.8 ± 1.0	23 ± 1.4	NS
Maximum CTr joint angle (degrees)	85.1 ± 1.7	72.5 ± 1.4	<0.0001
CTr excursion (degrees)	61.2 + 2.1	49.4 ± 1.6	<0.0001
CTr extension duration (ms)	206.1 ± 14.0	267.2 ± 24.6	NS
N for FTi joint	22	39	
Mean FTi joint velocity (degrees s^{-1})	387.7 ± 30.7	271.8 ± 23.2	0.031
Mean SETi frequency (potentials s^{-1})	147.2 ± 8.1	184.5 ± 7.9	0.0034
Minimum FTi joint angle (degrees)	65.2 ± 0.9	68.9 ± 1.7	NS
Maximum FTi joint angle (degrees)	128.3 ± 3.0	122.1 ± 2	NS
FTi excursion (degrees)	63.1 ± 3.4	53.2 ± 1.6	NS
FTi extension duration (ms)	197.0 ± 12.8	262.1 ± 24.2	NS

potentials, a rare occurrence in intact animals (4 of 31 climbs showed any Df activity with a maximum of three Df muscle potentials in each climb). These data suggest that the animal responds to the loss of the front legs by generating greater motor activity in the middle legs to rear up the front of the body again through similar joint excursions.

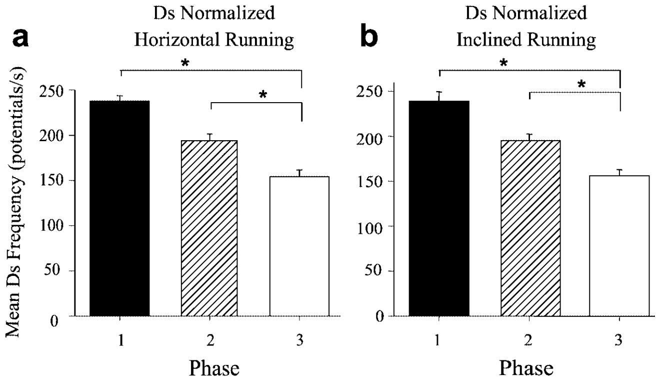


Fig. 8a, b Intra-burst pattern of Ds EMG frequency is modified during incline running. Ds EMG patterns in the hind leg during **a** horizontal running and **b** during inclined running. Each figure shows the mean Ds spike frequency for the first quarter of the burst (*black bars*), the middle two quarters of the burst (*hatched bars*) and the last quarter of the burst (*open bars*). Each graph represents the mean of 9–12 bursts recorded from 4 animals. An *asterisk* indicates a significant difference ($P<0.05$) between segments. In both, first segment ≫ middle segment ≫ last segment

Discussion

This study examined the changes that are associated with transitional behaviors. In the companion paper, we compared the leg joint movements that cockroaches use to traverse blocks of two different heights to movements used in horizontal running (Watson et al. 2002). Although small barriers pose little problem to the animal and it uses the same leg movements to traverse them, larger barriers require alterations as the animal rears up to place its front legs on top of the barrier then push up and over it. Changes were noted for the middle leg thorax-coxa (ThC) and trochanter-femur (TrF) joints that re-orient the leg so that extension now rears the front of the body upward. Similar changes in orientation of the hind legs allow for more efficient placement as the animal pushes its CoM upward. In contrast, the CTr and FTi joints, which are primarily responsible for leg extension during horizontal running, move through the same excursions during all stages of climbing.

Does the motor system compensate during climbing?

Because the CTr and FTi joint excursions were unchanged in going from running to climbing, we wondered if the associated motor activities were also unchanged. The simplest possibility is that the animal generates the same motor pattern in Ds and SETi and that pattern results in similar joint excursion. The alternative is that mechanical properties change substantially as the animal pitches up, moves upward and levels off on top of the block, but the motor system compensates for these changes in order to maintain consistent joint movements. Given that each pair of legs plays distinct roles at various stages of the climb, such adjustment might not be uniform among all six legs at all times during a climb.

The EMG recordings that we reported on in this paper in conjunction with joint kinematics provide an answer to this question. The relationship between joint velocity and EMG frequency was significantly different from running during each stage of climbing. This in itself was not sufficient to conclude that the motor system compensated during climbing, because both running and climbing occur over a range of leg velocities. The data could mean that during climbing the animal evokes the same motor activity, but that under the mechanical loads associated with climbing, this activity is simply less effective and, therefore generates less joint velocity. But these graphs would have also occurred if the animal actively evoked stronger motor responses in order to generate the same joint velocity.

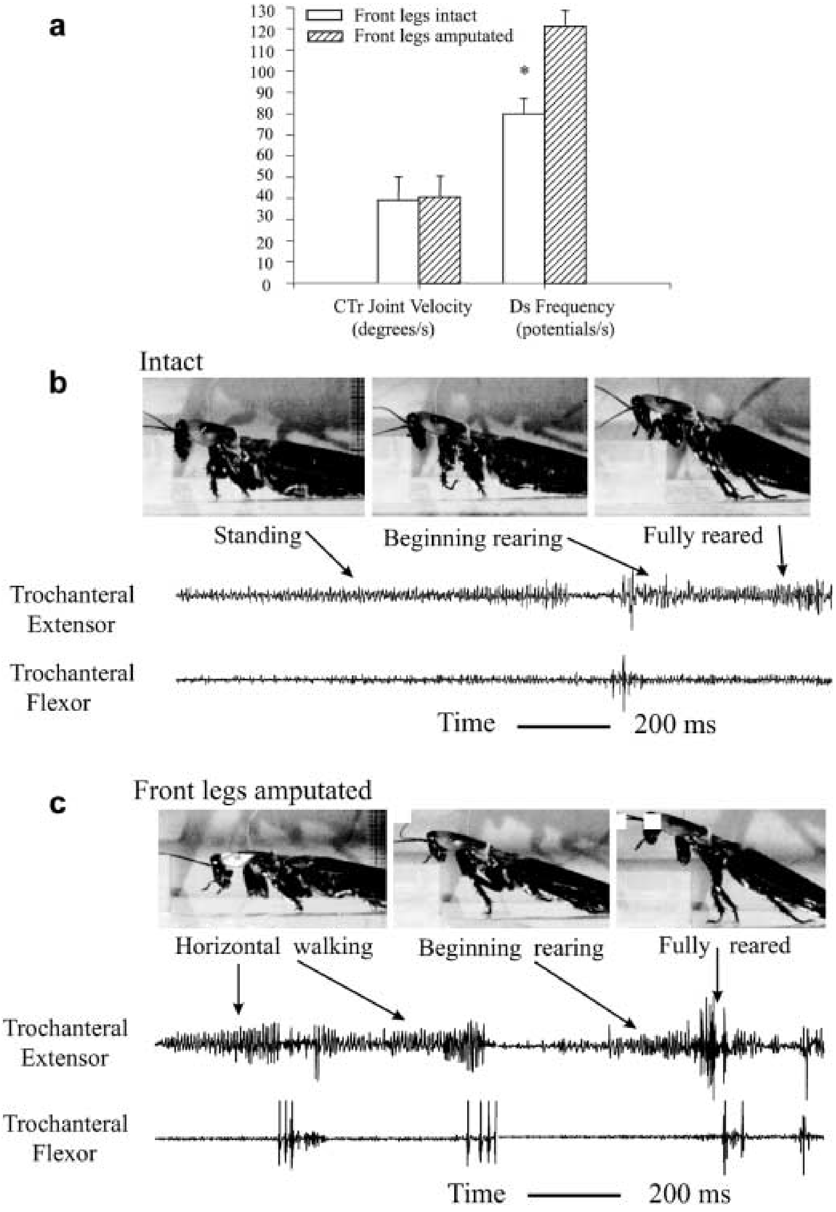


Fig. 9a–c Amputation of front legs changes motor activity in middle legs during climbing. **a** Mean middle leg CTr joint velocity and Ds frequency during the rearing step in one animal before and after bilateral front leg amputation. **b**, **c** Representative video frames showing rearing movements and EMG recordings from one middle leg of another cockroach before (**b**) and after (**c**) amputation of both front legs. Note recruitment of fast trochanteral extensor motor neuron (Df) in the amputee during the rearing step

The fact that overall mean motor activity was not significantly different between running and climbing may have been a coincidence, i.e., the animal may have simply been moving slower when it was climbing. Of course, the answer could lie somewhere between these extremes. The animal may be trying to compensate for altered mechanics, but not completely succeeding.

To resolve this dilemma, we compared the internal Ds burst structure of running to that which occurs during the rearing, rising and leveling stages of climbing. During horizontal running, Ds has a reproducible initial high-frequency component followed by a significant decline in frequency (Watson and Ritzmann 1998a). A similar initial high-frequency burst is seen also in cats and may be a fundamental property of legged locomotion. In cats, the initial burst is invariant whether the animal walks on a solid substrate or steps in a hole (Gorassini et al. 1994). In contrast the remainder of the stance cycle is altered by loading and muscle force (Hiebert and Pearson 1999).

In the current study, the burst pattern was altered but only in specific stages of climbing. During rearing and rising stages, the Ds activity for the middle leg no longer showed significant differences among the burst segments, i.e., the latter three-quarters of the burst now matched the initial quarter which normally contains the distinct high-frequency burst. This was also true in the hind leg for the rising stage of the climb. We believe that these changes indicate that the animal's motor system compensates for mechanical changes during those stages of the climbing behavior where specific legs are doing extra work. The most obvious explanation for the changes that we observed was that the animal increased Ds activity in either the middle or hind legs in specific stages of the climbing behavior in response to increased mechanical load.

It is particularly interesting that we only observed changes in the burst pattern in certain legs during specific stages of the climb, i.e., the middle legs during rearing and rising stages and the hind legs during the rising stage. This observation addresses the second question posed in the introduction of this paper. During climbing, each pair of legs plays a distinct role (Watson et al. 2002). The middle legs are important in pitching the animal upward during the rearing stage and then continue to act as the animal's CoM is raised up in the rising stage. The hind legs on the other hand appear to be the main source of power during rising, but do not play a major role in pitching the animal upward during rearing. Thus, our observations are consistent with the conclusion that the alterations in motor pattern are specific to the mechanical changes that occur during climbing over 11-mm or larger blocks.

Of course, the pattern that we observed could also occur if the initial burst segment was reduced. Indeed, the histograms shown in Fig. 6 suggest that this may have occurred. We believe that this is not the case, because during running the initial segment tends to be the most unchangeable region of the stance burst, due at least in part, to the fact that it occurs prior to foot set-down (Watson and Ritzmann 1998a). It is more likely that the latter segments of the burst are affected by loading as the animal begins to change its posture and push up and over the barrier. The apparent reduction in mean activity in initial segments is probably due to inherent variability between leg cycles or the process of normalization that was described in the Results section, either of which makes global comparisons tenuous. For this reason we restricted our analysis to comparisons within individual bursts. Because we analyzed the data within bursts, the important conclusion is simply that the pattern goes from one in which there is a significant decline to one in which there no longer is any change. If this is due to a decrease in the initial segment, that would be equally interesting, although it is difficult to understand how that would come about.

The notion that load affects the magnitude of Ds activity was supported by the observations made on front leg amputees. In intact animals both the front and middle legs contribute to rearing actions that tilt the front of the animal upward. Without the front legs, the upward movement of the front of the body is performed solely by the middle legs. The increased Ds activity in the middle leg or recruitment of Df is consistent with a reflex motor compensation for increased load carried by those legs. The trochanteral and proximal tibial campaniform sensilla have been shown to excite Ds in restrained preparations (Bässler 1977; Zill 1990). If those reflexes are active during stance (as suggested by Bässler 1977) any additional or more prolonged strain in the cuticle would lead to increased Ds activity.

What mechanical properties is the animal reacting to?

During climbing the animal certainly experiences differences in loading as it moves upward against gravity. As the animal rotates the middle leg, it pushes down more vertically than during horizontal running. Moreover, pairs of legs tend to extend in tandem more during climbing movements than during the tripod gait associated with running, and this would alter loading characteristics on each leg. However, the animal also experiences different inertial properties during running and climbing. During running the cockroach is moving forward and that forward momentum certainly could affect motor activity. In the 11-mm climbs that we observed, the animal often paused at the block before rearing up, as was the case in the example shown in Fig. 2. In the climbs over 5.5-mm blocks, the cockroach typically did not break stride and there the motor response was unchanged.

Full and colleagues also studied the deathhead cockroach as it climbed over barriers of varying heights. However, they concentrated on behaviors where the animals moved at continuous rapid speeds. Under those conditions, the animals simply scrambled over even large barriers without first stopping. To do this they apparently take advantage of the dynamics and sprawled posture found in cockroaches (Full et al. 1998). Even under these conditions the cockroaches do not simply rely upon kinetic inertial energy to get over the barriers. Indeed, they use a relatively small amount (13%) of their kinetic energy during approach to assist them in climbing over obstacles (Full et al. 1997).

Inertial properties are also very important in escape movements where survival requires that the animal go from a standstill to very fast speeds in a remarkably short time. In the American cockroach, *Periplaneta americana*, escape from a standstill involves reproducible extension movements of all six legs (Nye and Ritzmann 1992; Levi and Camhi 1996), typically using fast motor neurons (Levi and Camhi 1996; Schaefer and Ritzmann 2001). The gait changes and recruitment of fast motor neurons during escape is reminiscent of some of our observations on climbing.

The incline running that we observed in this paper presented an interesting set of mechanical properties. It required the cockroach to move against gravity in a manner similar to that which it experiences during obstacle climbing. However, because the animal did not change speed during ascent, the inertial properties were closer to horizontal running. Although the EMG versus joint velocity relationship for incline running was identical to that seen during the rising stage of climbing, the burst pattern was similar to that associated with running, suggesting that in this case no motor adjustment was made. The differences in motor activity between incline running and climbing further suggests that gravitational load may not have been the primary cue to which the motor system responded during climbing.

Inertial effects, that were unchanged during incline running may be a more significant factor.

Where is the source of control for changes in leg movement and motor activity?

The postural adjustments associated with middle leg rotation presumably require input from higher centers. The cockroach rears up sufficiently to place the front legs on the top of the block with little or no contact with the front plane of the block. It appears that the animal measures the block, probably using sensory structures on the head such as compound eyes and antennae. It then either uses this information to rear up ballistically or moves up in a closed loop fashion, using head sensors to monitor the rise of the front of its body. Certainly these two forms of control are not mutually exclusive and elements of both could occur. In any case, higher centers are probably involved in these postural adjustments.

After the rotation of the middle legs, the remainder of the motor events could well be the result of local control reflexes. Indeed, higher control may not be practical for the subtle and rapid compensatory reactions, which are much more suited to local reflexes. Position of each joint can be provided by hairplates at the extremes of joint excursion (Büschges and Schmitz 1991; Schmitz et al. 1991; Kuenzi and Burrows 1995) and by chordotonal organs throughout the range of joint movement (Bässler 1977, 1993). Position information can be used to provide consistent joint excursion. One characteristic of the CTr and FTi joints that was altered in climbing was the duration of stance phase motor activity. The duration of the Ds burst is typically longer during climbing (Table 1). This change may occur because it takes longer to work against gravity to reach the appropriate joint angles, which are then detected by the joint angle detectors that terminate extensor motor activity.

As mentioned earlier, leg sensors also provide information on load. Numerous campaniform sensilla are found in strategic regions of the cuticle (Zill 1990) and they respond directionally to cuticular strains (Zill and Moran 1981). In addition to the observations on campaniform sensilla in restrained preparations that is discussed above (Bässler 1977; Zill 1990), Ramasubramanian et al. (1999) and Kaliyamoorthy et al. (2001) used finite element analysis to model the strains occurring in the exoskeleton of the trochanter during walking and climbing. Their models predict that there are large strains in the locations of some groups campaniform sensilla that can enhance extensor activities. Moreover, Ridgel et al. (2000) recorded the activities of the tibial campaniform sensilla during walking and climbing. They showed that similar patterns of activity occur in both behaviors and that increases in the maximum firing frequency of the proximal receptors (that are active after foot down) occur in some climbing sequences. Later, Ridgel et al. (2001) found that dynamic responses occurred in the tibial sensilla in freely standing animals associated with changes in leg loading when the limb was in contact with the substrate. They showed that similar patterns of activity occur in both behaviors and that increases in the maximum firing frequency of the proximal receptors (that are active after foot down) occur in some climbing sequences. We observed that although the CTr and FTi joint kinematics are unaltered, there are active modifications of the intra-burst extensor motor patterns and those modifications occur after foot set-down. Therefore, it is probable that the extensor responses seen in the climbing movements utilize feedback reflexes from campaniform sensilla due to the changes occurring in loading of the leg.

During complex postural control tasks such as obstacle climbing, several mechanical properties are altered simultaneously. Again thoracic control circuits can handle adjustment to such complex sensory events. In stick insects, position and load information converge on retractor motor neurons. The strength of the position feedback response is dependent upon the sign and amplitude of the load feedback and vice versa and the two responses interact non-linearly (Schmitz and Stein 2000).

Finally, we also noted changes in interleg coordination, that increases the probability that two legs in a segmental pair extend in tandem for increased support (Watson et al. 2002). As described in the previous paper, Cruse and his colleagues (Cruse et al. 1995; Schmitz et al. 2001) have shown interleg influences among local control centers that contribute to gait patterns. Taken together, the literature suggests that the Ds motor modifications during obstacle climbing do not require any control scheme other than local leg reflexes.

Can anything be learned about horizontal running from observing obstacle climbing?

In the course of this study, we have drawn upon the running literature to help us interpret our results on climbing. Can we use our climbing results to say anything about the simpler horizontal running behavior? We believe so. In previous studies of horizontal running the varying frequency of Ds and SETi activity within stance phase bursts has been an enigma. The basic pattern in burst structure persists across a wide range of running speeds and fast motor neurons tend to be recruited at the phase of the burst when the highest frequency of slow motor neuron activity occurs (Watson and Ritzmann 1998a, 1998b). In our earlier studies on treadmill running, we tentatively concluded that the mechanics of the leg and/or leg musculature change over the course of stance phase, and the muscle activity is sculpted to mechanical requirements. The EMGs recorded during obstacle climbing in the current study further support this notion. The obstacle climbing task, which imposes mechanical requirements that change between and within individual steps, alters the pattern of Ds activation within stance phase bursts. It is reasonable to assume that such control schemes are active during horizontal running to produce the varying EMG frequency associated with smooth, monotonic joint movements. Obstacle climbing may highlight these effects simply because it is an extreme variation in the mechanics of stepping.

A hierarchical control scheme for locomotion

The scheme that unfolds from our observations on climbing points to an interaction between higher centers and local reflex control leading to efficient movement through a range of natural terrains. The brain does not micromanage all adjustments in motor control of leg movements, nor can the local reflexes account for all postural adjustments to complex terrain. Rather the higher centers dictate postural adjustments to solve a problem and these generate a cascade of mechanical effects to which local reflex circuits respond.

Because legged animals evolved to traverse complex terrain rather than flat, horizontal continuous treadmill belts, it is probable that local control circuits that manage much of the leg activity expect inputs from higher centers and, if those inputs are absent, thoracic synaptic gains and connections may not function in a normal way. Although many of the requirements for control have been elucidated at the local level, decapitated insects or insects that have had cervical connectives lesioned fail to walk in a normal fashion (Zill 1986). Moreover, spinal cats that can walk on a treadmill after recovery do so much better after a period of training, which may reorganize local control circuits (Edgerton et al. 1997; de Leon et al. 1998, 1999). In much the same way that deafferented animals can generate fictive motor patterns but require peripheral sensory input to generate accurate natural movements (Pearson and Wolf 1987), realistic locomotory patterns may require the close interaction between postural adjustments from higher centers and reflex control from local circuits. That is not to detract at all from the insights gained from reduced preparations. However, one should be cognizant of the important interplay between higher and lower centers that is particularly well brought out in complex movements such as obstacle climbing.

Implications for control of legged vehicles

Our observations also have important implications for control of legged robots. Several groups have had considerable success using simple distributed schemes to control hexapod robots as they walk on horizontal surfaces and over small barriers (Espenscheid et al. 1993, 1996; Pfeiffer et al. 1994). However, the ultimate goal of legged robotics is to develop machines that can readily traverse very complex terrains. Indeed, wheeled vehicles can easily outperform all current legged robots on smooth terrain even if small barriers are present. It is in environments where irregular barriers exist that wheeled vehicles fail and legged robots show great promise. However, control of legged vehicles in such terrain can be complex. If one had to largely reconfigure or override the distributed lower control system to execute agile movements dictated by higher centers, the control architecture could become very cumbersome.

Our results on climbing imply that such major changes are not necessary. A hierarchical system in which higher centers utilize information from head-based sensors to alter posture and then turn over controls to local reflex systems could readily solve such problems of locomotion. The reflex responses from local control will optimize movements of actuators and skeletal systems (musculo-skeletal systems in animals) in the face of changing mechanical effects and create efficient locomotion over virtually any barrier.

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References

Atwood HL, Smyth T, Johnston HS (1969) Neuromuscular synapses in the cockroach extensor tibia muscle. J Insect Physiol 15:529–535

Bässler U (1977) Sense organs in the femur of the stick insect and their relevance to the control of position of the femur-tibia joint. J Comp Physiol 121:99–113

Bässler U (1993) The femur-tibia control system of stick insects–a model system for the study of the neural basis of joint control. Brain Res Rev 18:207–226

Biewener A, Full RJ (1992) Force platform and kinematic analysis. In: Biewener A (ed) Biomechanics: structures and systems. A practical approach. Oxford University Press, New York, pp 45–73

Büschges A, Schmitz J (1991) Nonspiking pathways antagonize the resistance reflex in the thoraco-coxal joint of stick insects. J Neurobiol 22:224–237

Carbonell CS (1947) The thoracic muscles of the cockroach *Periplaneta americana* (L.). Smith Misc Coll 107:1–23

Cruse H, Bartling C, Brunn DE, Dean J, Dreifert M, Kinderman T, Schmitz J (1995) Walking: a complex behavior controlled by simple systems. Adapt Behav 3:385–418

Edgerton VR, Leon RD de, Tillakaratne N, Recktenwald MR, Hodgson JA, Roy RR (1997) Use-dependent plasticity in spinal stepping and standing. Adv Neurol 72:233–47

Espenscheid K, Quinn R, Chiel H, Beer R (1993) Leg coordination mechanisms from stick insect applied to hexapod robot locomotion. Adapt Behav 1:455–468

Espenscheid K, Quinn R, Chiel H, Beer R (1996) Biologically-based distributed control and local reflexes improve rough terrain locomotion in a hexapod robot. Robot Autom System 18:59–64

Full RJ, Blickhan R, Ting LH (1991) Leg design in hexapedal runners. J Exp Biol 158:369–390

Full RJ, Glasheen J, Autumn K, Jagger AE, Yamauchi A (1997) Dynamics of cockroach climbing: vaulting, bouncing or powering over a step? Am Zool 37:177A

Full RJ, Autumn K, Chung JI, Ahn A (1998) Rapid negotiation of rough terrain by the death-head cockroach. Am Zool 38:81A

Gorassini MA, Prochazka A, Hiebert GW, Gauthier MJA (1994) Corrective responses to loss of ground support during walking. I. Intact cats. J Neurophysiol 71:603–610

Hiebert GW, Pearson KG (1999) Contribution of sensory feedback to the generation of extensor activity during walking in the decerebrate cat. J Neurophysiol 81:758–70

Jindrich DL, Full RJ (1999) Many-legged maneuverability: dynamics of turning in hexapods. J Exp Biol 202:1603–23

Kaliyamoorthy S, Zill S, Ritzmann RE, Choi J, Quinn RD (2001) Finite element analysis of exoskeletal strains and discharges of force receptors during walking and climbing. Soc Neurosci Abstr 27:518.12

Kuenzi F, Burrows M (1995) Central connections of sensory neurons from a hair plate proprioceptor in the thoraco-coxal joint of the locust. J Exp Biol 198:1589–1601

Leon RD de, Hodgson JA, Roy RR, Edgerton VR (1998) Locomotor capacity attributable to step training versus spontaneous recovery after spinalization in adult cats. J Neurophysiol 79: 1329–40

Leon RD de, Tamaki H, Hodgson JA, Roy RR, Edgerton VR (1999) Hindlimb locomotor and postural training modulates glycinergic inhibition in the spinal cord of the adult spinal cat. J Neurophysiol 82:359–69

Levi R, Camhi JM (1996) Producing directed behaviour: muscle activity patterns of the cockroach escape response. J Exp Biol 199:563–568

Nijenhuis ED, Dresden D (1955) On the topographical anatomy of the nervous system of the mesothoracic leg of the American cockroach (*Periplaneta americana*). I. Proc Kon Ned Akad Wetensch Ser C 58:121–136

Nye SW, Ritzmann RE (1992) Motion analysis of leg joints associated with escape turns of the cockroach, *Periplaneta americana*. J Comp Physiol A 171:183–194

Pearson KG, Iles JF (1971) Innervation of coxal depressor muscle in the cockroach, *Periplaneta americana*. J Exp Biol 54: 215–232

Pearson KG, Wolf H (1987) Comparison of motor patterns in the intact and deafferented flight system of the locust. I. Electromyographic analysis. J Comp Physiol A 160:259–268

Pfeiffer,F, Eltze J, Weidemann H (1994) The TUM Waking machine. In: Jamshidi M, Nguyen C, Lumia R, Yuh J (eds) Intelligent automation and soft computing. TSI Press, Albquerque, pp 307–323

Ramasubramanian S, Flannigan WC, Nelson G, Quinn R, Zill SN (1999) Modeling of load sensing during the stance phase of cockroach walking. In: Virk GS, Randall M, Howard D (eds) Climbing and walking robots. Engineering Publishing, London, pp 17–28

Ridgel AL, Frazier SF, Zill SN (2000) Effects of cockroach force receptors in freely moving animals: dynamic signals of leg loading during walking and climbing. Soc Neurosci Abstr 26:1724

Ridgel AL, Frazier SF, Zill SN (2001) Dynamic responses of tibial campaniform sensilla studied by substrate displacement in freely moving cockroaches. J Comp Physiol A 187:405–420

Schaefer PL, Ritzmann RE (2001) Descending influences on escape behavior and motor patterns in the cockroach. J Neurobiol 49:9–28

Schmitz J, Stein W (2000) Convergence of load and movement information onto leg motoneurons in insects. J Neurobiol 43:424–436

Schmitz J, Dean J, Kittmann R (1991) Central projections of leg sense organs in *Carausius morosus* (Insecta, Phasmida). Zoomorphology 111:19–34

Schmitz J, Dean J, Kindermann T, Schumm M, Cruse H (2001) A biologically inspired controller for hexapod walking: simple solutions by exploiting physical properties. Biol Bull 200:195–200

Tryba AK, Ritzmann RE (2000) Multi-joint coordination during walking and foothold searching in the *Blaberus* cockroach. I. Kinematics and electromyograms. J Neurophysiol 83: 3323–3336

Watson JT, Ritzmann RE (1998a) Leg kinematics and muscle activity during treadmill running in the cockroach, *Blaberus discoidalis*. I. Slow running. J Comp Physiol A 182:11–22

Watson JT, Ritzmann RE (1998b) Leg kinematics and muscle activity during treadmill running in the cockroach, *Blaberus discoidalis*. II. Fast running. J Comp Physiol A 182:23–33

Watson JT, Pollack AJ, Zill SN, Ritzmann RE (2002) Control of climbing behavior in the cockroach, *Blaberus discoidalis*. I. Kinematics. J Comp Physiol A (DOI 10.1007/s00359-002-0277-y)

Zill SN (1986) A model of pattern generation of cockroach walking reconsidered. J Neurobiol 17:317–328

Zill SN (1990) Mechanoreceptors: exteroceptors and proprioceptors. In: Huber I, Masler EP, Rao BR (eds) Cockroaches as models for neurobiology: applications in biomedical research. CRC Press, Boca Raton, pp 247–267

Zill SN, Moran DT (1981) The exoskeleton and insect proprioception. I. Responses of tibial campaniform sensilla to external and muscle-generated forces in the American cockroach, *Periplaneta americana*. J Exp Biol 91:1–24