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Descending control of body attitude in the cockroach *Blaberus discoidalis* and its role in incline climbing

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Abstract Unlike intact animals, cockroaches with bilateral circumoesophageal connective lesions have difficulty climbing up smooth inclines. Typically, they slipped badly or even fell over backward before traveling more than 1.5 body lengths up the incline. The major problem involves increased slippage of the front and sometimes middle legs. Periods of front leg slipping are correlated with excess body elevation that pushes the height of the head to 11 mm above the substrate. Intact animals control body attitude very well on the incline, only rarely rearing above 11 mm. Cockroaches with bilateral circumoesophageal connective lesions spend considerable time above this critical amplitude and slipping increases with amplitude above that value. We conclude that circumoesophageal lesion compromises the insect's ability to control body attitude on the incline and this deficit contributes to the inability of lesioned cockroaches to climb steep inclines. A separate body attitude deficit was noted on steps. Upon climbing to the top of a barrier, intact animals bend their body between the first and second thoracic segments. This action maintains good leg mechanics throughout the climb. Cockroaches with bilateral circumoesophageal connective lesions fail to perform this downward flexion. A beneficial role for similar body flexion in simple robots is described in the Discussion.

Keywords Circumoesophageal connective · Cockroach · Incline · Slipping · Walking

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Introduction

Because insects can traverse a wide range of terrains rapidly and efficiently, they draw considerable attention both as models for locomotion control and as inspiration for agile legged robots. However, from a motor control standpoint, most neurobiological studies have focused upon neural circuits in the thoracic ganglia that provide immediate control of foot placement as well as the pattern generation responsible for the basic swing and stance movements in each pair of legs (Bässler and Büschges 1998). While on horizontal flat surfaces, insects may rely primarily upon these local circuits and the advantageous mechanics associated with sprawled posture (Jindrich and Full 2002). However, as they negotiate large barriers that must be climbed over or walked around, the sensors located on their heads become increasingly important to success. For example, cockroaches can climb over blocks in excess of 11 mm in height without making leg contact with the front surface of the obstacle (Watson et al. 2002a). To accomplish this task, they typically evaluate the height of the barrier with sensors such as antennae and then execute a rearing movement that raises the front of the body to an appropriate height at which a normal swing movement of the front legs can place their tarsi directly onto the top of the block. This observation implies that, under these conditions, descending commands from processing regions in the brain are essential to a normal successful climb.

Although decapitated insects do not move in anything like a normal manner, insects with bilateral lesions to the circumoesophageal connectives tend to be hyperactive (Roeder 1937; Roeder et al. 1960; Graham 1979). Members of the cockroach species *Blaberus discoidalis* that have experienced this lesion show spontaneous walking episodes. Indeed, it is difficult to stop them from walking. We refer to these animals as circumoesophageal connective lesioned (CoCL) subjects. As they walk in a natural setting, CoCLs will encounter obstacles in their path and can readily negotiate most of them. As such they provide an excellent model in which to examine the role of neural regions anterior to the circumoesophageal connectives in climbing or turning behaviors.

What is lost by this lesion? CoCLs can climb over blocks and under shelves. However, they do not do so in the planned fashion seen in intact cockroaches (Watson et al. 2002a). Rather they simply keep moving forward, eventually traversing the barrier by brute force. The loss of anticipatory planning is not surprising, since CoCLs lack connections between sensors on the head such as antennae and eyes and the local motor control circuits of the thoracic ganglia. However, one problem that they encounter is less easily explained. We report here that CoCLs experience increased failure in climbing up smooth inclines of 40° or 45°. In these failures, CoCLs will either slip back or even fall over backward shortly after entering the incline. In contrast, this task is readily accomplished by intact animals.

Our data strongly suggest that the immediate problem caused by the CoCL lesion is an inability to control body attitude in a normal fashion. This postural deficit generates a cascade of problems leading to a catastrophic failure on a substantial incline. Body attitude is also compromised on steps, but in a different way. CoCLs can readily climb steps, but fail to bend their bodies at the top of the barrier as intact animals do. The result is an inefficient placement of legs and a high centering movement that raises the body high over the top of the object. We discuss the importance of these postural controls to normal locomotion as well as their role in successful movement of legged robots through complex terrain.

Materials and methods

Animals

Adult *B. discoidalis* cockroaches were housed in small colonies (20-l bucket). These were maintained in a 12/12 h light/dark cycle at 25°C with a relative humidity of 30–60%. Animals had ad libitum access to water and dry food in the form of chicken mash. Both male and female animals were used in these experiments.

Incline climbing apparatus

Cockroaches walked and climbed on a 0.45-m-long×75-mm-wide, stationary, clear acetate belt. The belt was mounted in an apparatus that allowed a pivot axis midway down its length. The climbing arena had vertical sides of rigid clear Plexiglas on both sides of the belt. The belt's transition from 0° (horizontal) was set to 35°, 40° or 45° upwards, as measured by a protractor placed in the field of view. The acetate belt was supported by rigid clear Plexiglas, except for a length of 55 mm in each direction from the pivot axis. The Plexiglas prevented the mass and movement of the cockroach from causing the belt to bounce, since tension alone at both ends of the long belt was not sufficient to support it along its entire length.

Stair climbing apparatus

A 27-cm-long×50-mm-wide×70-mm-high channel was constructed with a glass bottom and sides. Clear acrylic blocks, 50 mm long×50 mm wide×12 mm high, were stacked in the channel to form sets of four steps. The depth of all steps in a single trial was the same. Different trials were taken for step depths of 2.5, 5.0 and 10.0 mm.

Preparation and surgery

Naïve, intact animals were selected by testing them in the climbing arena with the incline set at 45°. Only those animals that demonstrated an ability to climb in the center of the belt (without using the side edges of the belt, or corners where it met the walls) became subjects. Once animals were selected, they were anesthetized with CO_2 gas. Wings were removed and white ink was used to mark the side of the metathoracic body-coxa (T_3 BC) joint as a side view approximation of the insect's center of mass (CoM). Although Nelson et al. (1997) defined a slightly more posterior location, namely, the second abdominal segment, as the CoM, we found that T_3 BC provided a much more distinct side reference point, and it is only a small distance anterior to the true CoM.

Side and ventral video images were recorded for the horizontal walk and climb as intact animals encountered the three incline angles, and step depths. The animals were then re-anesthetized. CO_2 use required the addition of a neck ligation to prevent hemolymph from pumping into the head and obscuring the connectives during surgery. An alternate anesthesia, freezing for approximately 5 min, (until motionless) reduced blood flow eliminating the need for neck ligation. We noted no behavioral differences with the two forms of anesthesia.

With either form of anesthesia, the body was stabilized with dental wax in a 5-cm-long×2.5-cm-diameter plastic tube. The head protruded through a small opening at one end of the tube and was secured with wax onto a flat surface end. A corner of a breakable razor blade was held with hemostats and used to create a cuticle incision on the anterior front portion of the head. Extreme care was taken to just penetrate the cuticle and not damage underlying tissue with the razor. An upper lateral incision went across from the edges of the compound eyes, just above the ocelli, without damaging the eyes. The lower lateral incision was parallel to this, and just below the ventral rim of the antennal socket (approximately 2 mm between the incisions). Two angled incisions connected the endpoints of these lines and produced a trapezoidal flap of the front surface that was carefully removed and kept aside. The brain and circumoesophageal connective attachments could be seen once small amounts of connective tissue were deflected. Micro scissors were used to cut the circumoesophageal connectives at the brain. After making the lesion, the front cuticle flap was replaced, and a small amount of dental wax was melted onto a spatula and carefully applied to seal the flap in place. After a 24- to 48-h recovery period, subject animals were re-tested on the three levels of incline and the three depths of steps.

Sham surgeries were performed ($n = 3$ each) for both methods of anesthesia. During the sham operations all procedures were performed except for the lesion of circumoesophageal connectives. All of the sham animals were able to successfully climb 45° inclines. Their climbs were indistinguishable from intact animals.

Kinematic analysis

Two high-speed video cameras (Redlake PCI 1000; San Diego, Calif., USA) were synchronized to record at 125 frames s^{-1}. One was positioned to capture the ventral view of the animal as it climbed the inclined portion of the belt or stairs. The other camera was used to obtain a side view of the animal during both the horizontal walk and the incline or step climb. A mirror, angled at 45°, was positioned under the horizontal portion of the arenas to provide a side view in that region of the belt.

The video images were stored as AVI files directly to the hard drive of a PC. These video files were imported into WinAnalyze3D motion analysis software (Mikromak, Berlin, Germany). *X* and *Y* coordinates were digitized in side view for T_3 BC point, the head (at the junction of the antennal socket), and both prothoracic claws, as well as the belt ends and pivot, or the step edges. Ventral view coordinates were marked for the top of the head and for the pro- and mesothoracic claws (see Fig. 3a). Displacement distances (mm) of each tarsus in the vertical axis were calculated in WinAnalyze and plotted in Origin (Microcal). Perpendicular distances (mm) from the angled belt substrate were calculated using a sine function in Excel.

Results

Cockroaches of the species *B. discoidalis* that received bilateral circumoesophageal connective lesions show some consistent locomotor properties. They have a normal posture and show extended periods of spontaneous walking, often in a tripod gait (Fig. 1). They are, however, characterized by dragging their antennae (Fig. 1a). This property is consistent with the finding that the pattern generator that controls antennal movement during walking resides in the suboesophageal ganglion and projects anteriorly to the protocerebrum where motor neurons for the antennae are located (Horseman et al. 1997). CoCLs can negotiate barriers such as blocks and shelves, but do so without anticipatory adjustments.

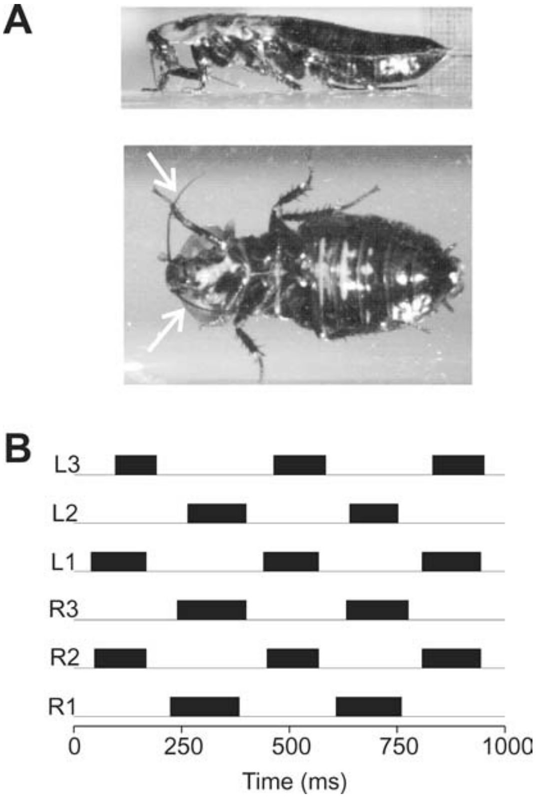

Fig. 1a,b Horizontal walking in a cockroach with bilateral circumoesophageal connective lesions (CoCL). **a** Side and ventral view from high-speed video of a CoCL walking on a horizontal surface. Note posture (*side view*) is normal and ventral view is in tripod gait. Antennae (*arrows*) are deflected backward and dragging on the ground in typical position of a CoCL insect. **b** Swing phase (*black bars*) of each leg during a walking sequence. *R1, R2* and *R3* refer to right legs of the first, second and third thoracic segments. *L1, L2* and *L3* refer to left legs of those segments. Note that L1, R2 and L3 swing together as do the remaining three legs to form alternating tripod gait

Tarsal slip on inclines

When challenged to climb an acetate surface placed at a 45° incline, CoCLs start to walk up the incline, but then slip or fall backward (Fig. 2b). This task poses little challenge for intact cockroaches (Fig. 2a) or cockroaches that have experienced a sham operation, where the head capsule is opened and the circumoesophageal connectives exposed as in the CoCL operation, but the connectives are not severed. The problem faced by CoCLs is linked to the steepness of the incline. All intact cockroaches successfully climbed inclines of 35 and 40°, ($n = 7$) (Fig. 2c). A climb was considered successful if the cockroach moved 1.5 body lengths up the incline before falling back. In some trials intact animals did slip, but always recovered to complete the task. On 45° inclines, 95% of intact trials were successful. CoCLs performed

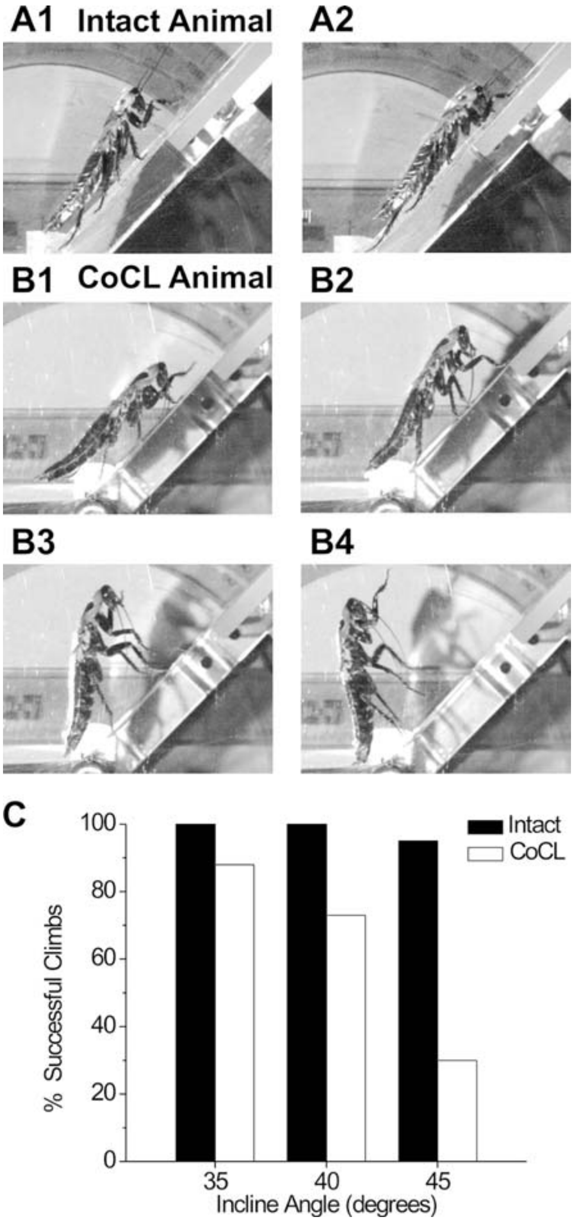

Fig. 2a–c Comparison of intact and CoCL animals on 45° incline. **a** Intact animal starts to slip (*a1*) but rapidly recovers to normal posture (*a2*). **b** As the CoCL animal starts up incline (*b1*), the cockroach is elevated and begins to slip (*b2*). Rather than recovering, this animal rotates its middle leg and pushes insect upward and back (*b3*) until it begins to fall backward (*b4*). **c** Comparison of successful climbs for intact cockroach and CoCL. For intact animals, most climbs are successful. For CoCLs, the percentage successful climbs decreases for increasing incline angles. Data in **c** are from seven animals and between 13 and 20 trials at each angle for both intact and lesioned animals

dramatically worse in the incline task (Fig. 2c). At 35°, 88% of the trials were successful. However at 40°, 73% were successful and at 45° only 33% of CoCL trials made it up the incline for 1.5 body lengths.

When CoCLs fail, the front legs tend to slip and eventually start making very rapid skating movements that do not generate any forward movement. When adhesion is lost, the insect will eventually slide backward. Middle legs may also slip and in some cases the body will start to rotate backwards. If this occurs, the cockroach will rotate the other middle leg to maintain contact with the substrate. This movement is similar to the action associated with rearing movements that precede climbing over large blocks. Although appropriate for block climbing, this leg orientation pushes the body away from the substrate ultimately making it fall over backward (Figs. 2b3, b4).

Tarsal (foot) slippage can be detected by viewing the climbing movements from the ventral surface through the transparent acetate belt (Fig. 3a). With this view, we digitized the movement of each foot and plotted the vertical movement against time (Fig. 3b). The tarsi of intact animals go through a regular cycle where each tarsus moves forward, then contacts the substrate. Upon making contact, the tarsus may slip back slightly before tarsal pads, or pulvilli, adhere to the substrate and maintain a constant position for the rest of stance. Once adhesion occurs the tarsus position remains constant as the leg pushes the body upward until the next swing phase commences. Consistent with normal walking movements, one front leg alternates with the other. We also monitored the position of the head as the cockroach moved up the belt. As long as the head continued upward, we knew that the insect continued to walk. If it stood still, the curve showing movement of each tarsus versus time would be horizontal and flat and the head would also stop progressing upward.

The comparable data for CoCLs clearly show slippage in front tarsi (Fig. 3c). Rather than staying flat when the front legs are in stance, they gradually slip back. When the animal starts skating, the foot cycles simply oscillate. Slippage and oscillation are encountered much more often in CoCLs than they are seen in intact animals. The middle legs of CoCLs tend to slip much less than do the front legs (Fig. 3d). However, middle leg slipping does occur and tends to precede backward falls.

Body attitude on an incline

In addition to slippage, CoCLs also tend to hold their bodies higher, when going up the inclines. We measured body attitude by a factor that we will refer to as ‘‘head height’’. This value is the perpendicular amplitude from the substrate (inclined belt) to the base of the antenna that is closest to the camera. We chose to focus on this point, because it provided a very reproducible feature in the side views of the insect’s head. In our data, a head height of 11 mm appears to be a critical value. Intact animals almost never exceed a head height of 11 mm. In fact, while walking on the incline, they spend very little time above 10 mm (Fig. 4a). They do increase their time above 10 mm on 45° inclines, but not nearly to the degree found in CoCLs. In fact, CoCLs spent more then 50% of their time above 10 mm on 35° inclines and 70%

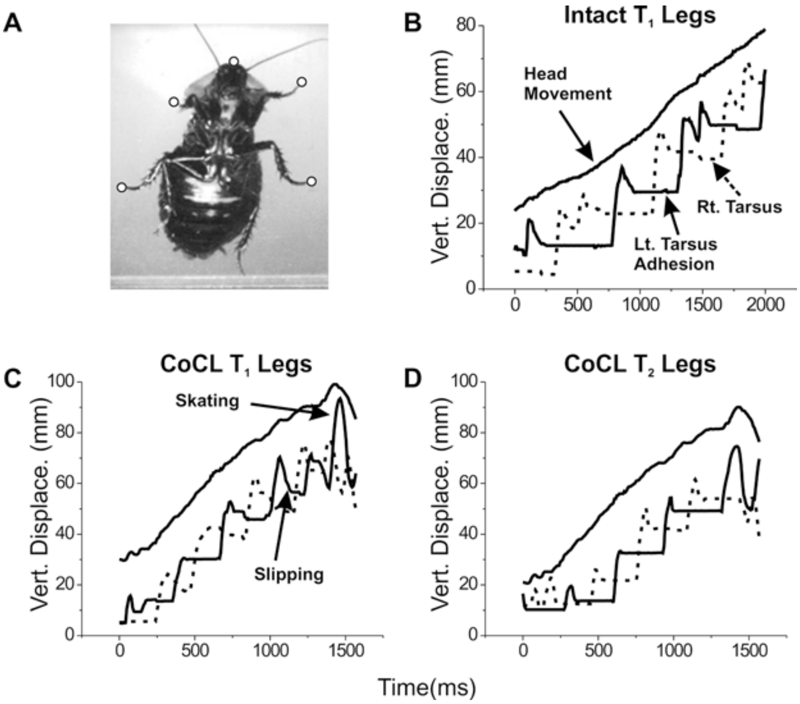

Fig. 3a–d Measurement of vertical displacement of tarsi. **a** *White dots* indicate points that were digitized (*front and middle tarsi and head*). **b** Front leg tarsal and head movements of intact animal. *Solid line* is left tarsus and *dotted line* is right tarsus. *Continuously rising solid line* is movement of head up incline. Note each leg alternates making vertical movement cycle of typical tripod gait. The tarsus swings upward, touches down then begins to move backward. If adhesion occurs, the tarsus becomes stationary generating horizontal straight line until the next swing. During adhesion, that leg contributes to forward head movement. Note, that one left leg cycle and two right leg cycles perform double steps before adhering to the substrate. **c** As in **b** but for CoCL front leg tarsus. Note that unlike the intact animal, upper leg cycles do not flatten out but rather gradually return to rear position indicating continuous slip. At top of climb, the left leg oscillates in skating movement as animal begins to fall back (*downward head movement*). **d** CoCL middle leg tarsi adhere like front leg until the animal begins to fall and left tarsus skates

of their time above that point on 40° and 45° inclines (Fig. 4a).

These data suggest that CoCLs have lost a capacity to control body attitude while climbing on the incline. This deficit could contribute to the failure of CoCLs on the inclines. Because the cockroach cannot penetrate the acetate surface with its claws, it relies upon adhesion of tarsal pads to generate an effective stance phase. These pads are flexible and must flatten out to develop sufficient surface area for adhesion. The amount of adhesion is thus proportional to the force with which the tarsus impacts the substrate (Jiao et al. 2000). The swing movement of the front leg always goes through a similar arc relative to the pronotum (dorsal side of the thorax) regardless of leg's starting position (Fig. 4b). Therefore, as the insect moves farther away from the substrate, the movement of the tarsus downward goes through longer and longer distances and the force generated upon contact would be expected to decrease. With decreased contact force, the pads would not flatten out as much and adhesion would be reduced (Jiao et al. 2000).

In addition to adhesive forces perpendicular to the substrate, frictional forces that are parallel to the substrate are also important in climbing (Gorb et al. 2002). Indeed, these may be the most critical forces for sticking to the substrate. They are built up when the pads are pulled backward parallel to the substrate, but decline when the leg is pulled upward. This property is critical for allowing the tarsus to release at the onset of swing. However, the raised posture means that the leg is pulled back at a slight upward angle during stance. Thus, the pads will not attach as well as they would in intact animals moving in a normal posture.

Correlation of body attitude and slippage

The data described above indicate that CoCLs are found to slip more and to spend more time elevated away from the substrate. However, neither of these properties occur consistently throughout a climb and indeed, even CoCLs are successful part of the time on the inclines. In order to draw a causal relationship between these two factors, we had to determine whether excess body height occurred at the same time that the tarsi slipped. To accomplish that, we divided each climbing sequence into meaningful time segments. We did this by plotting one middle leg that did not slip along with the other data (Fig. 5). This record then established a series of leg cycles during which effective stance occurred for at least one leg. Within each of those leg cycles, we then measured the percentage of time that each of the front legs was attached to the substrate. This state was established by asking how long the vertical actions of the tarsi remained constant (zero

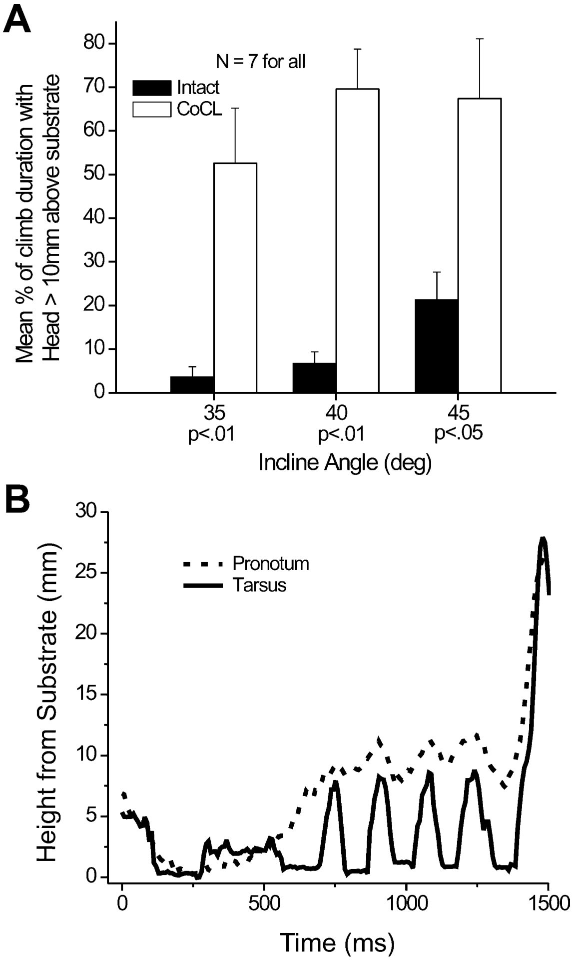

Fig. 4 **a** As intact animals climb up inclines, their head rarely rises above a height of 10 mm from substrate. Percentage time above this height increases with increasing incline pitch, but never reaches the percentage recorded for CoCLs. CoCLs spend much of their time pitched to a point where their head is above 10 mm. Error bars are 1 SE. Significance for a 2-tail, paired *t*-test comparing differences between intact and CoCL animals is indicated *below bars*. **b** Height from substrate of thorax (measured at pronotum) and tarsus during climb. Note that as the body pitches up, the tarsus rises up to same point relative to the pronotum creating a longer move to the substrate

change). We refer to this value as “grip share”. If both of the front legs were attached throughout a leg cycle, the grip share would be 200%. To establish a more normal value, we divided that number by two, so that total adhesion of both legs is in fact 100%.

A grip share of 100% would only be expected when the animal is standing still. As long as the insect is moving, one of the legs should go into swing at some point. In fact in intact animals ($n=7$), the grip shares clustered between 40% and 90%, although some outliers were seen below 40%.

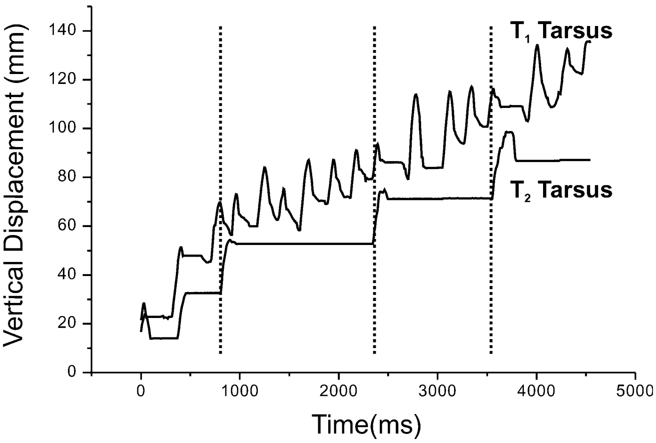

Fig. 5 Measurement of grip share and head height for individual leg cycles in a climbing animal. For clarity, only one T_1 tarsus is plotted. However, in practice both front tarsi were analyzed. A T_2 tarsus that shows normal adhesion, establishes leg cycles (*dotted vertical lines*). Note that in this CoCL climb, relatively few flat periods are found. The percent time that either tarsus trace is flat in the horizontal direction divided by two represents the grip share for that leg cycle. For each leg cycle, the mean distance from the substrate to the point on the head where the near antenna base is located (*head height*) is also determined. These two parameters for each leg cycle can now be plotted against each other

With the grip share calculated for each leg cycle, we then measured the mean head height for the same leg cycles. For these measurements, we used side views that had been taken simultaneously with the ventral view records. We then plotted grip share against mean head height for each leg cycle of climbs by seven cockroaches before (Fig. 6a) and after (Fig. 6b) experiencing the lesion. As noted previously, intact animals rarely went above 11 mm and grip shares tended to be between 40% and 90%. After the lesion, half of the CoCL’s steps were still below 11 mm and at those times their grip share was comparable to the intact values (Fig. 6b). However, they also spent considerable time above 11 mm reaching a maximum of 21 mm. As the head height increased, grip share fell. The differences in grip share values above and below 11 mm for both sets of data were highly significant ($P < < 0.001$, *t*-test).

There are two leg cycles in the intact graph of Fig. 6a that are above 11 mm and those have low grip shares. These points plus the cycles in the CoCLs that are below 11 mm and have normal grip shares, clearly indicate that it was not the surgery that caused slippage. Rather it was the elevated body posture that generated the problem. CoCLs show increased slipping, because they do not control body attitude properly.

We also examined when in a particular climb elevated body attitude and decreased grip share occurred. In an intact animal, the head height remains fairly constant and grip share slightly increases throughout three step cycles (Fig. 7a). After the lesion, head height increases and grip share tends to decrease during leg cycles that just preceded failure (Fig. 7b).

Decapitated cockroaches tend to hold their legs very hyper-extended. Therefore, it is possible that the data on body posture is simply a general result of the lesion rather than reflecting a loss in the insect’s ability to actively control body posture. This conclusion is unlikely since CoCLs only rise above 10 mm half of the

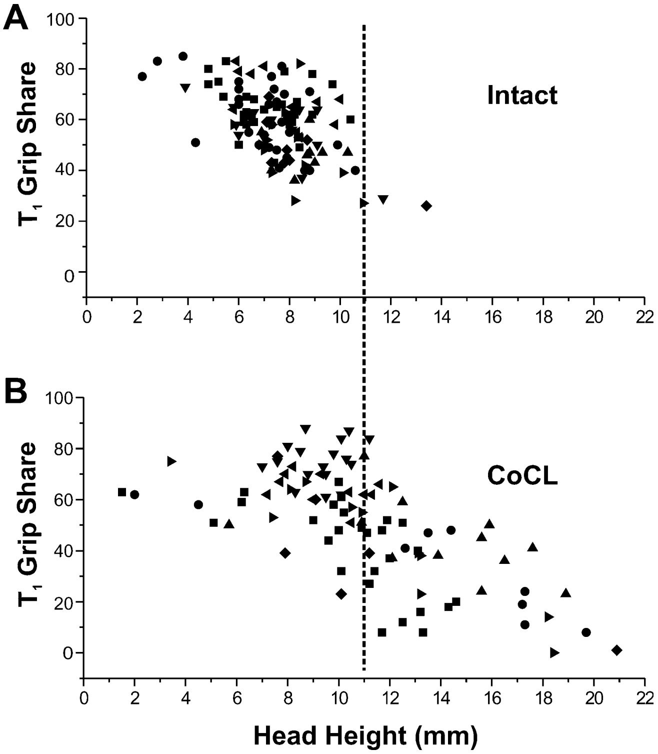

Fig. 6 Plot of grip share versus head height as determined in Fig. 5 for each leg cycle of climbs by seven different animals before **a** and after **b** the lesion. Each animal is represented by a different symbol, at least one climb per animal at each incline level. Note that intact animals tend to stay below 11 mm (*vertical dotted line*) and cluster between grip shares of 40 and 90. However, as CoCLs almost half of their cycles are above 11 mm where grip share falls off to zero

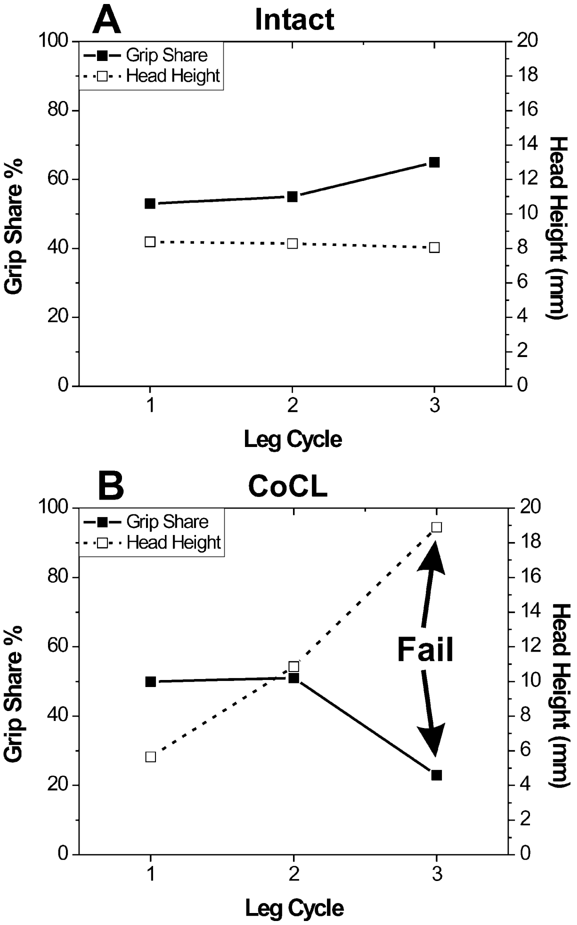

Fig. 7a, b Three leg cycles showing grip share (*solid line*) and head height (*dotted line*) plotted separately. For intact animal (**a**) head height remains constant, while grip share actually rises as the animal proceeds up the incline. For CoCL (**b**) head height increases as the animal proceeds up the incline. After second leg cycle, the head moves above 11 mm and the grip share falls precipitously leading to failure of climb

time. Nevertheless, we tested this possibility by measuring body height as CoCLs walked on horizontal surfaces. Under these conditions, there was a significant increase in height near the CoM (taken as the point where the hind leg connects to the thorax—T_3 BC) (Fig. 8). However, height measured at the head (as was done on the inclines) fails to show a significant increase, probably due to an increase in variability at that place on the body (Fig. 8). In fact, neither measure showed increases above 11 mm as was detected on the inclines. Thus, even the significant change seen at T_3 BC for horizontal walking cannot account for the problems noted on inclines.

Other possible problems with CoCLs

The CoCL deficit certainly causes many problems for the cockroach beyond loss of postural control. In addition to body attitude, we also examined three other factors that might contribute to the problems experienced by CoCLs on inclines; lack of velocity control, failure to adjust gait to patterns appropriate for climbing, and loss of control over tibia–tarsus angle that could further compromise the effectiveness of tarsal pads on the incline.

On horizontal surfaces, CoCLs walk continuously with little or no change in speed. In initial observations, we noted that as they climb vertical Styrofoam walls they remained in a tripod gait and seemed to slip on several steps. This behavior contrasted with intact animals that tended to slow their pace and change to a pattern in which they would rapidly swing one leg at a time. That observation was consistent with previous studies on changes in gait pattern as American cockroaches (Larsen et al. 1995) and Locusts (Duch and Pfluger 1995) walk upside down and on vertical surfaces.

This observation led to an hypothesis that CoCLs could not alter their walking speed and patterns of leg movements in a manner appropriate to walking up an incline. To test this hypothesis, we attempted to compare these parameters before and after performing the lesion.

Although subtle changes could contribute to difficulties on inclines, our observations did not reveal consistent alterations in walking speed or gait pattern that could account in large measure for CoCL failures. Intact

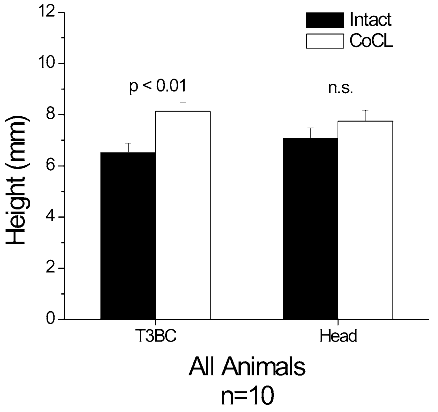

Fig. 8 Comparison of height of ten animals in the intact (*black*) and CoCL (*white*) state as they walked on a horizontal surface. *Error bars* represent 1 SE. When measured using the point where the T_3 BC joint connects to the thorax near the CoM, mean height of all animals was higher as CoCLs than in the intact condition. The difference was found to be significant ($P < 0.01$) according with a 2-tail, paired *t*-test. When measured at the head, as in the analyses for incline climbing, the difference was not significant. Neither measure indicated that the CoCL animals ever rose above the critical value of 11 mm from the substrate

animals tend to move up the incline at a constant speed around 0.04 m s^{-1}. Walking speeds for CoCLs were more difficult to determine. When they slip, they certainly slow down, but that is due to the fact that the tarsi are slipping and they are no longer moving up the incline effectively.

Where CoCLs walked up the incline a substantial distance, we did not detect consistent differences in either walking speed or gait patterns relative to the pre-lesion state. For example, consider the two CoCLs that succeeded in climbing 45° inclines. One was slower after the lesion, changing from a tripod gait in the intact state to individual steps after the lesion. The other went faster after the lesion, changing from individual steps in the intact state to a tripod gait after the lesion. Indeed, intact animals also failed to show a consistent pattern of gait changes on the 45° inclines. Of the intact trials on 45° ($n = 20$), half of the climbs included tripod steps as the insect went up the incline, half did not. The adjustments varied both from animal to animal and from trial to trial within individual cockroaches. Animals that walked using a tripod gait in one climb might show individual leg stepping patterns in the next, and vice versa. Indeed, there were trials where individual steps and tripod steps were observed in the same climb. These kinds of inconsistencies were also noted at 35° and 40°.

The third factor that we examined was the position of front leg tarsi. In some preliminary trials, we noted that one front tarsus was bent back on the tibia when a CoCL attempted to climb a 45° incline and failed. In this position, the pulvilli would not contact the substrate and, therefore, could not generate the necessary traction to climb the incline. This observation led to an hypothesis that the loss of descending activity from the brain weakened activity to the retractor unguis muscle that controls the tarsus. In *B. discoidalis* the default position of the tarsus is bent back on the tibia in a position similar to that seen occasionally in our video records (S.N. Zill, personal communication), i.e., if one cuts the retractor unguis muscle, the tibia springs back into this retracted position.

To test this hypothesis, we examined one intact and one CoCL climb from each of 11 experimental animals as they climbed the 45° incline. We measured the angle between the tibia and the tarsus for three steps of a front leg just prior to set-down. A paired *t*-test on these data found no significant difference in tibia-tarsus angle before and after the lesion.

Examination of a large number of intact animals suggested that the problem with tibia-tarsus angle was probably secondary to the lesion. Intact animals tend to walk in the center of the track, probably using their antennae to avoid contact with the walls. When a tarsus did contact the wall, it bent back just as was noted for the CoCLs. There were more cases where the CoCLs made contact with walls, because they had lost function of their antennae that would normally be used to maintain a distance from walls.

The conclusion that CoCLs may increase tarsal bending due to increased interaction with the wall, could offer an alternative explanation for slipping on the incline. If CoCLs walk into walls often and bend their tarsi more often than intact animals, that could account for the increased slipping in these subjects. However, none of the data reported above comparing CoCL performance to intact animals included trials with bent tarsi. Even in the CoCL cases, we selected for trials where the animal avoided interactions with the wall that would result in bent tarsi.

Step climbing in CoCLs

When challenged with steps of comparable or even greater steepness than the inclines, CoCLs performed much better. Even with very steep steps, the small horizontal surface allowed these animals to get a foothold and push upward. However, at the top of the steps another deficit was detected. Normally, when an intact cockroach reaches the top of a block, it flexes the body joint between the first and second thoracic segments. This flexion allows the cockroach to keep its CoM at an appropriate position relative to the barrier and to maintain an efficient leg angle relative to its thorax. If this joint is fused by gluing a splint over it, the cockroach makes inefficient movements and high centers badly (R.E. Ritzmann et al., unpublished observations), i.e., the animal's CoM rises high above the top of the barrier. On the steps, pre-lesion animals perform this body flexion at the top of the steps generating a fluid efficient movement to the top (Fig. 9a). However, CoCLs do not flex their thorax and, therefore, high center leading to ineffectively spiraling front legs (Fig. 9b).

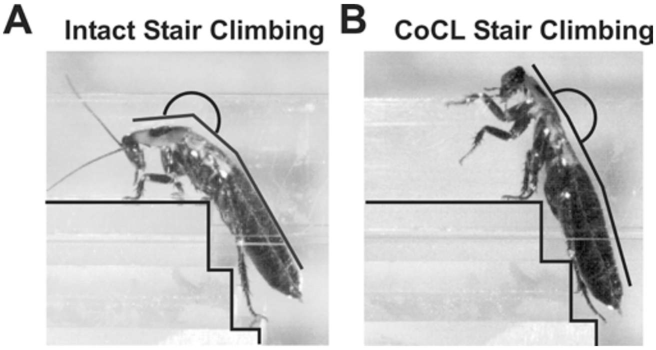

Fig. 9a, b Frames taken from high speed video as animals climbed up steps (*highlighted with black lines*). **a** At top of steps, intact animal flexes its T_1-T_2 joint to keep legs in mechanically efficient postures. Body posture is highlighted with *black line* with body angle indicated with arc. **b** CoCL fails to flex T_1-T_2 joint downward and high centers forcing front legs to flail in air

As with the problems on inclines, this deficit indicates that CoCLs have lost the ability to maintain efficient body attitude while moving over objects. Problems on the incline appear to be associated with actions of the front legs, whereas on the steps, the deficit is associated with body flexion. We will return to this issue in the discussion section and describe how it has influenced some of our robotic designs.

Discussion

Bilateral lesion of the circumoesophageal connectives in the cockroach *B. discoidalis* creates an interesting subject on which to examine the role of brain circuits in locomotion over complex terrain. Unlike cervical lesioned subjects that take at best very few steps, CoCLs show long spontaneous walking episodes. Indeed, casual inspection of walking CoCLs would suggest that descending activity is irrelevant for walking. If all that is necessary for locomotion is forward movement on reasonably level substrates, that may be true. However, relatively few animals spend their lives moving at a constant pace through flat horizontal terrain.

Deficits associated with the CoCL condition

Since the most obvious deficit associated with this lesion is the inability to stop walking, one could conclude that all the brain does relative to legged locomotion is to turn it on or off. This interpretation would relegate all other control to the reflexes and pattern generators found in the thoracic ganglia in association with the sensors of the legs and the mechanical properties of the musculoskeletal systems of the legs. These elements clearly play an important and essential role in legged locomotion. As long as the suboesophageal ganglion is connected to the thoracic ganglia, these cockroaches do, in fact, walk spontaneously as do other insects (Bässler 1986). However, when CoCLs are challenged to walk in more difficult terrain, it becomes clear that this simplistic view is inadequate, because it cannot account for the range of active adjustments made by intact animals as they deal with barriers.

Even tasks that are performed successfully by CoCLs are executed in different and in many cases less efficient ways. Upon encountering a 12-mm block, the CoCL cockroach does, indeed, climb over it. However, close examination finds that the actions are not similar to what is seen in intact cockroaches. When walking slowly, intact cockroaches detect the barrier and evaluate its height, then rear up to an appropriate height so that movements place the front leg tarsi on top of the block (Watson et al. 2002a). Once that is accomplished a forceful push by the middle and hind legs drives the animal up and over the block in a relatively smooth and efficient manner (Watson et al. 2002b). CoCLs climb over the block by ramming into the leading edge and forcing themselves up and over by brute force. In another behavior, a cockroach encountering a shelf in a well lit room will tunnel under the shelf and remain in the dark indefinitely. CoCLs again will force their way under the shelf but then continue to walk, ultimately emerging from the other side.

These changes in climbing behaviors are easily explained by the loss of sensory input to the circuits that generate walking movement in the thoracic ganglia or control by elements in the suboesophageal ganglion. The observation of the cockroach walking out from underneath the shelf is consistent with the notion that the brain simply turns off walking when the insect is in a safe place. Nevertheless, the climbing deficits imply more active control from descending circuits. After an intact cockroach detects a barrier, signals from the brain clearly alter body posture in anticipation of a climb (Watson et al. 2002a). Once the animal rears up, control appears to be returned to the thoracic ganglia where fairly normal stance movements are generated but with some adjustment of foot placement and muscle force that could be attributed to local reflexes (Watson et al. 2002b). The critical difference here is a postural alteration (the rearing movement) that is keyed to the height of the barrier.

The incline and step climbing tasks that we examined in this report add to the motor control events that appear to be lost with bilateral lesion of the circumoesophageal connectives. Here we see a loss of the animal's capacity to control body attitude as it climbs up the incline or reaches the top of a step. Intact cockroaches control body attitude very precisely. Even casual examination of intact animals on the inclines reveals a stable situation where the body is held at a very precise level relative to the substrate, regardless of the pitch of the incline. Previous reports on cockroaches walking on an incline revealed changes in interlimb coordination as the insect experiences the physical changes associated with the incline (Spirito and

Mushrush 1979; Tang and Macmillan 1986). On the steps or at the top of blocks, intact cockroaches flex their bodies between the $T_1$and T_2 body segments. Neither of these properties is observed in the CoCLs. On inclines the CoCL body is seen to rise above 11 mm quite often, something that is rarely seen in intact animals. Although there is a small increase in body angle in intact animals at 45° (Fig. 4a) the effect is much less than that seen after the lesion. Moreover, body flexion is lost causing the CoCL to high center in an inefficient movement at the top of the steps.

These deficits would be considered to be minor effects of a fairly massive lesion, were it not for their consequences, especially on the inclines. Upon losing control of body attitude, a cascade of failures occurs that ultimately result in loss of adhesion on the incline and a catastrophic failure. Were this deficit to occur in nature, the animal might be able to compensate by using its claws. However, it might well limit the places where it could walk efficiently.

How is body attitude controlled?

Body height is ultimately controlled by the angles of leg joints. The lesion could generate an increase in body height by causing chronic hyperextension of all leg muscles. Decapitation is in fact associated with extreme hyperextension of all legs. However, this effect passes after a few days (Ridgel and Ritzmann, in preperation). In the CoCLs a slight amount of chronic elevation is seen. When we measured the body height near the CoM, we did detect a small, consistent elevation even when the cockroach walked on horizontal ground. However, this difference was not large enough to account for the postural changes on the incline. Moreover, when measured at the head, elevation varied in CoCLs walking horizontally. In fact, some subjects had lower head height than intact animals when walking horizontally. In any event, the head height on the horizontal was never found to be as elevated as that occurring during walking on an incline. Finally, even on the incline, more than half of the leg cycles of CoCLs still showed a mean head height that was well below 11 mm, placing them in the intact range. It was simply the case that CoCLs pitch upward above critical heights so often that failure is common.

In particular, the front legs appear to be very important. Pushing down on the substrate with front legs will push the front of the animal upward, causing the increase in head height that ultimately compromises front tarsus adhesion. Attitude control could be accomplished by employing proprioceptive reflexes associated with the front legs to maintain the appropriate joint angles for the correct body posture. If body attitude was solely controlled by front leg proprioceptors, lesion of circumoesophageal connectives should not affect posture. However, it is entirely possible that front leg reflexes control body attitude in association with descending activity. In other words, the immediate reflexes may require some baseline activity from head ganglia in order to function properly. This organization could allow the animal to use information from sensors on the head to modulate those reflexes, for example, during normal rearing movements associated with block climbing.

An observation that is consistent with this notion is seen in the effect of decapitation upon escape responses in the American cockroach (Schaefer and Ritzmann 2001). Although the escape circuit is located in the abdominal and thoracic ganglia and these animals still escape, the details are affected. In particular, the front legs fail to move much at all. Electromyograms of decapitated cockroaches demonstrate that the loss is associated with a failure of fast motor neurons to the front legs—without descending activity, fast motor neurons do not reach threshold, so that movement is reduced to slow motor activity that does not provide the rapid forceful movements normally developed by fast motor neurons. A similar event associated with proprioceptive reflexes in CoCLs could compromise control of body attitude.

Although our observations point to sensors on the head as the source of body attitude control, we have not identified the actual source. Nevertheless, there are some obvious choices to examine in future studies. In walking insects, antennae continually move up, down and laterally examining the terrain immediately in front of the head (Dürr 2001; Dürr and Brenninkmeyer 2001). Preliminary observations in block climbing clearly implicate antennal contact in identifying a barrier to forward locomotion and in measuring the height of that barrier (Ritzmann et al. 2001). However, other sensors are also available.

Video records of walking cockroaches consistently show the maxillary palps touching and examining the substrate beneath the head. When close to a block, intact cockroaches will often ‘‘walk’’ up the leading edge of the block with their maxillary palps. These appendages could readily keep the head at the appropriate level relative to any substrate. Interestingly, sensory nerves from the maxillary palps project to the suboesophageal ganglion, so it is not clear that information from them is actually lost to the motor centers in CoCLs.

Visual information is available from both the compound eyes and the ocelli. Ocelli are often associated with horizon detection in flying insects (Stange 1981). Similar information may be provided on edges of barriers for walking insects. Compound eyes could provide detailed images of barriers or simply cues regarding objects or distance from substrate.

It is, of course, possible that all of the sensors that are available to the insect combine in sensory association regions of the brain to create an image of the surroundings relative to the body posture. The output of these brain regions could descend to the thoracic ganglia where they modulate reflexes and pattern generation activity.

Is descending control only present in association with barriers?

Because CoCLs do walk very well on horizontal terrain or where barriers are limited, one might conclude that descending control only turns on when needed. This on-demand control of body attitude would certainly work and brings us back again to the notion of the brain circuits as switches. The switches would go beyond simply starting or stopping walking to now turning on body attitude control when necessary.

We feel that this notion is unlikely. Rather, we suspect that the descending intervention is there all of the time. However, the effect is minor when the cockroach is walking on flat, horizontal terrain or even over minor barriers. It is only when large barriers are encountered that modifications in the basic walking pattern are sufficient to be detected in our assays. The fact that the cockroach *can* negotiate some obstacles without descending intervention and that we cannot readily detect changes, does not necessarily mean that descending activity is unimportant even on level terrain. The observations of CoCLs climbing over barriers and up inclines demonstrates that seemingly minor changes can have important consequences under the right conditions.

Mechanical effects of body attitude in robotic vehicles

Insects and other animals have served as inspiration for a number of robotic vehicles. In many cases, these efforts allow one to test the mechanical importance of properties that were identified in the animals and implemented in the robots. One of our authors (R. D. Quinn) has developed two series of robots based upon data from the laboratory of another of our authors (R.E. Ritzmann). In one of those series, leg designs attempt to capture the joint angles and movements found in the cockroach as it walks and climbs (Nelson et al. 1997). They represent a long-term project with vehicles that are only now beginning to walk on their own. However, the other line of robots, called Whegs (R.D. Quinn), is a simplified type of robot that uses abstracted data from cockroach locomotion to capture biologically inspired strategies, but ignores the details of implementation (Allen et al. 2003; Quinn et al. 2003). Whegs follows several other simplified robots that were developed under a similar strategy, including Prolera (Martin-alvarez et al. 1996) and Rhex (Saranli et al. 2000).

In particular, Whegs uses six three-spoke appendages that rotate at the same speed and can, therefore, be driven by a single motor (Fig. 10). The three-spoke design provides for a mechanical advantage in that the effect on the ground mimics the slow stance and rapid swing of a single limb. Each limb or wheg is essentially a hybrid of wheels and legs (hence the name "wheg"). They move rapidly like a wheel, yet have the advantages of legs in reaching up and gripping the top of a barrier. Turning is accomplished by servo motors that steer the front and rear whegs to different directions. The vehicles can be constructed in a range of scales. We have manufactured large hexapod Whegs and smaller four "whegged" mini-vehicles. All of these robots are rapid and agile devices that are very capable of climbing over a range of objects.

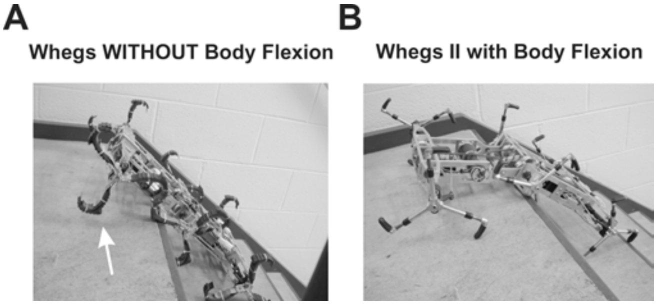

Fig. 10a, b Two versions of Whegs robot climbing up stairs. **a** Whegs robot lacking body flexion high centers, causing front feet to spin in air (*arrow*). **b** Whegs II robot with body flexion joint bends down to keep feet in contact with stair and make efficient movement. Compare to cockroach images in Fig. 9

The speed and agility of these devices allowed us to examine the importance of controlling body attitude from a mechanical standpoint. Our first generation Whegs vehicle had a rigid body. Because whegs appendages cannot change orientation for rearing movements, body attitude was totally passive. Although it was a very successful robot, Whegs I high centered badly as it climbed over a curb or other tall object (Fig. 10a). The high centering reduced foot adhesion causing the robot to spin its whegs inefficiently. The effect is very reminiscent of what is seen in CoCLs on inclines and steps. Whegs II includes a flexion joint in its body that allows the driver to pitch the front pair of whegs upward simulating a rearing movement (Allen et al. 2003). It can also flex the body downward after it reaches the top of a barrier to avoid high centering and keep the feet on the front whegs in good contact with the top of the barrier (Fig. 10b).

These changes greatly improve the robot's agility. The rearing movements allow it to climb over much higher barriers. Body flexion results in much more animal-like and efficient movements over large objects. Spinning of whegs is greatly reduced. In more recent versions, we have experimented with a range of foot designs to generate better adhesion. We believe that coupled with appropriate body attitude control, these foot designs will mimic the actions of intact cockroaches on inclines that is lost in the CoCLs.

Currently, the body flexion joint is controlled remotely by the robot's driver. This is a complicated task. Guided by the observations described in this paper, we are working on designs that will allow body attitude to be controlled autonomously by the vehicle. To accomplish this goal, sensors on a head will detect objects, evaluate them and modify actions of the body flexion joint to maintain proper attitude.

These kinds of interactions between robotics and neuroethology, will benefit both the designs of the vehicles and our understanding of the animals that serve as their inspiration. Combined efforts will allow us to detect subtle but crucial control and mechanical properties in the animals and allow us to refine our robotic designs. In turn, evaluation of the mechanical improvements found in these newer designs assess how important these nuances are to locomotion in the animal.

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