

Dynamics of rapid vertical climbing in cockroaches reveals a template

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Summary

Rapid, vertically climbing cockroaches produced climbing dynamics similar to geckos, despite differences in attachment mechanism, ‘foot or toe’ morphology and leg number. Given the common pattern in such diverse species, we propose the first template for the dynamics of rapid, legged climbing analogous to the spring-loaded, inverted pendulum used to characterize level running in a diversity of pedestrians. We measured single leg wall reaction forces and center of mass dynamics in death-head cockroaches *Blaberus discoidalis*, as they ascended a three-axis force plate oriented vertically and coated with glass beads to aid attachment. Cockroaches used an alternating tripod gait during climbs at $19.5 \pm 4.2 \text{ cm s}^{-1}$, approximately 5 body lengths s^{-1} . Single-leg force patterns differed significantly from level running. During vertical

climbing, all legs generated forces to pull the animal up the plate. Front and middle legs pulled laterally toward the midline. Front legs pulled the head toward the wall, while hind legs pushed the abdomen away. These single-leg force patterns summed to generate dynamics of the whole animal in the frontal plane such that the center of mass cyclically accelerated up the wall in synchrony with cyclical side-to-side motion that resulted from alternating net lateral pulling forces. The general force patterns used by cockroaches and geckos have provided biological inspiration for the design of a climbing robot named RiSE (Robots in Scansorial Environments).

Key words: locomotion, dynamics, climbing, leg function, mechanical stability, cockroach, *Blaberus discoidalis*.

Introduction

To begin the construction of a simple dynamic model or template for rapid vertical climbing, one of nature’s most spectacular climbers, the gecko, was selected (Autumn et al., 2006). Autumn et al. reasoned that any template for rapid vertical climbing must meet at least three physical challenges. First, climbers must generate effective, cyclical fore–aft wall reaction forces to maintain constant average speed climbing, while minimizing decelerating forces. Second, climbers must develop effective wall reaction forces that facilitate rapid engagement and disengagement of an attachment mechanism. Third, climbers must stabilize their body axis. Geckos met these challenges with major alterations in the force production of each leg compared to running on the level, but with only minor changes in kinematics. Because geckos are among the most adept climbers, their climbing dynamics could be specific to their unique adaptations. Perhaps diverse solutions to the dynamics of rapid climbing exist, depending on attachment mechanism, foot morphology and/or leg number. Alternatively, physical constraints on vertical locomotion could result in common dynamics represented by a simple model. To test these hypotheses, we compared geckos with rapidly climbing insects that attach by claws alone on a single ‘toe’ while using six legs.

Effect of attachment mechanism

Rapidly climbing geckos produce no substantial decelerating leg forces impeding vertical motion, nor do they generate sizeable attachment or detachment normal forces upon foot contact and removal (Autumn et al., 2006). These dynamics may be a unique result of their specialized attachment and detachment mechanisms. Geckos can use hairs or setae to adhere to smooth surfaces by van der Waals forces (Autumn et al., 2000; Autumn et al., 2002; Dellit, 1934; Ruibal and Ernst, 1965; Russell, 1975). Setae can be preloaded and positioned for attachment by toe uncurling, potentially decoupling attachment from climbing force generation. Toe peeling may put an individual seta in an orientation or at a critical angle that facilitates its release and concentrates the detachment force on only a small subset of all attached setae at any instant (Autumn et al., 2000; Russell, 1975). A diversity of attachment mechanisms must be examined to determine if the gecko’s unique specializations lead to distinctive leg wall reaction forces during rapid climbing.

Insects possess a remarkably diverse array of attachment mechanisms that include hooks or claws, suckers, glue and friction (Gorb et al., 2002). Their design appears related to different functional loads and loading regimes (Betz, 1996; Betz, 2002; Federle et al., 2001; Gorb, 2001; Nachtigall, 1974;

Scherge and Gorb, 2001; Stork, 1980). These diverse mechanisms could require larger attachment or detachment forces, a specific orientation for loading or unloading, and differing times for attachment or detachment. Certainly, each of these differences could directly affect the leg wall reaction forces generated during vertical climbing, making the pattern in insects quite different from that measured for geckos.

Effect of toe number and orientation

Rapidly climbing geckos may avoid decelerating fore–aft forces and large lateral gripping forces due to the freedom afforded by toe and foot placement (Autumn et al., 2006). Toes developing force by using setae (Autumn and Peattie, 2002; Russell, 2002) or claws (Vanhooydonck et al., 2005; Zani, 2000) do so only in a particular direction. Shear reaction forces pulling the gecko upward operate along the toe's axis as the toe is pulled or loaded at its base. Multiple toes differing in orientation appear to ensure that effective fore–aft acceleratory forces are developed in most foot orientations and with surfaces that differ in attachment capability. Moreover, loads can be distributed among the toes, thereby reducing the risk of catastrophic failure of leg-force development should one or two toes not attach.

Animals with only single 'toes' or attachment structures, such as insects, may differ in the orientation and magnitude of their climbing foot force vectors when compared to those measured in geckos with multiple toes. Many insects possess a single toe or tarsus with pretarsal claws, tarsal setae and/or attachment pads to climb on both smooth and rough surfaces (Betz, 2002; Gorb et al., 2002). A single attachment structure as opposed to multiple structures projecting radially may be more likely to develop leg wall reaction forces in directions other than the direction of motion. Hind legs thrusting in a direction opposite to that which loads tarsal claws could increase the probability of generating decelerating fore–aft forces. Middle legs with attachment structures oriented perpendicular to the direction of motion might be expected to produce larger lateral forces. A single attachment structure also increases the likelihood that the structure will require larger displacements across the surface until effective attachment is attained. Alternatively, dual pretarsal claws orientated at different angles, flexible tarsi and multiple compliant adhesive pads (e.g. arolia, pulvilli, euplantulae and claw pads) may work in synergy to mitigate the constraints imposed by a single attachment structure.

Effect of leg number

Six-legged climbers, such as insects, appear to have an advantage over four-legged vertical runners like geckos when

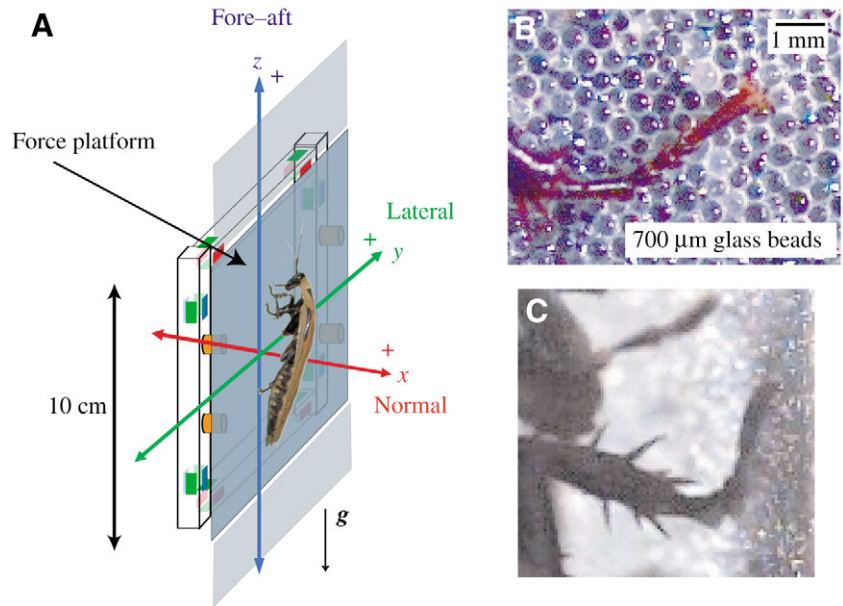


Fig. 1. The death-head cockroach *Blaberus discoidalis* climbs a force plate coated in 700 μm glass beads using claws and adhesive pads. (A) The fore–aft (blue), lateral (green) and normal (red) wall reaction forces are measured using a three-axis force platform. (B) Normal view of the middle right tarsus engaging the beaded surface. (C) Side view of front right tarsus engagement.

leg number is considered. With six legs, at least a stable tripod of support is present even during rapid running, whereas geckos and other lizards trot with only two legs on the vertical surface at one time (Autumn et al., 2006). Loss of attachment by a single leg in a hexapod appears less likely to result in catastrophic yaw to one side or pitch-back away from the surface compared to even sure-footed geckos.

Differences in leg force generation presumably depend on which legs of four- and six-legged vertical climbers are compared. Given the critical role of front legs in adhesion and searching for footholds, we might expect the least difference in the force pattern between front legs for different climbers. Ritzman et al. (Ritzman et al., 2004) contend strong convergent evolution for locomotion in insects and quadrupeds, particularly with respect to front leg orientation and its associated degrees of freedom. Cockroaches (Tryba and Ritzmann, 2000) and other many-legged arthropods typically use their front legs in a sensory role to reach forward (Durr, 2001). Hind legs might show similar force patterns in hexapods and quadrupeds because in both they appear oriented to generate thrusting forces (Ritzmann et al., 2004). However, the lateral undulation of climbers like geckos places the hind legs far forward at touchdown. Data on vertically running geckos do not support a greater role for the hind leg in producing fore–aft acceleratory force (Autumn et al., 2006). Mean acceleratory fore–aft forces are actually greater in the front leg. Finally, it is simply unclear whether middle legs of vertically running insects will generate forces more like the front legs or hind legs of quadrupedal climbers.

A single, general dynamic template for vertical climbers

appears improbable, given the potential differences in leg force production of animals that differ in attachment mechanism, foot and toe morphology, and leg number. Yet, a benchmark paper (Cruse, 1976) seems to suggest otherwise, at least for the slow, quasi-static walking of stick insects up vertical surfaces. The front and hind legs of stick insects produce wall reaction force patterns that are generally similar to those measured in rapidly climbing geckos (Autumn et al., 2006).

To test the generality of the dynamics measured in four-legged, back-undulating climbers that adhere by van der Waals forces (Autumn et al., 2006), we selected a six-legged, laterally rigid-body climber that adheres by claws. We chose the cockroach, *Blaberus discoidalis*, for several reasons. These cockroaches are the same body mass as the geckos previously measured. Both species are nimble, sprawled posture runners that can negotiate vertical substrates rapidly. Previous data collected on *Blaberus discoidalis* represent the most complete dynamics of any running invertebrate (Full and Tu, 1990; Full et al., 1991; Jindrich and Full, 1999; Kram et al., 1997; Ting et al., 1994). These dynamics for locomotion on the level are consistent with spring-mass templates that characterize diverse legged runners (Blickhan and Full, 1993; Schmitt and Holmes, 2000a; Schmitt et al., 2002; Seipel et al., 2004). Finally, detailed reports are available on *Blaberus discoidalis* climbing up a single vertical step and walking up inclines (Ritzmann et al., 2005; Watson et al., 2002a; Watson et al., 2002b).

The present study had three major objectives. First, we endeavored to collect the first data set on the dynamics of a rapid, vertically climbing insect. Second, we used a comparative approach to highlight the similarities and differences between the force patterns developed by the legs of vertically climbing cockroaches and geckos. Third, we searched for the first template of rapid vertical climbing – a low-dimensional, dynamic model that can serve as a target of control in climbing animals and robots.

Materials and methods

Animals

Blaberus discoidalis Servile (mass 2.9 ± 1.0 g, mean \pm s.d., $N=13$) were obtained from a commercial vendor (Carolina Biological Supply, Burlington, NC, USA). Cockroaches were housed in plastic containers with wood chip bedding and allowed to feed on dog chow *ad libitum*. The animals were maintained and trials conducted at temperatures between 26–30°C.

Climbing track

Cockroaches climbed a vertically oriented (90°), flat trackway (length 60 cm and width 8 cm) enclosed with Acrylic walls to confine their motion and allow visualization from the side. Unlike geckos whose claws and setae-covered toes allow them to adhere to most surfaces (Autumn et al., 2002), *Blaberus discoidalis* appear to rely on claws and to some extent non-adhesive frictional pads (Dai et al., 2002). To allow the

cockroaches to climb rapidly, we coated aluminum plates with a monolayer of 700 ± 100 μm (mean \pm s.d.) glass beads (Fig. 1). The beads (Jaygo Inc., Union, NJ, USA) were bonded to the surface using a mixture of acetone and Duco cement (ITW Devcon, Danvers, MA, USA). The mixture dried in a thin layer and left the surface with asperities for the claws and pads of the animals to engage (Dai et al., 2002). A three-axis force platform (Full and Tu, 1990) covered with the beaded aluminum plate (10×8 cm²) was placed in the middle of the track. The surface of the force platform was flush with the trackway. Animals started from the bottom of the trackway and were startled to climb up the track into a darkened box positioned 20 cm above the top of the force platform.

Force measurements

We recorded fore–aft, normal and lateral wall reaction forces as the animal crossed the miniature force platform (Fig. 1). The force platform consisted of four beams arranged as the sides of a rectangle (Full and Tu, 1990). The corners of the beams were instrumented with strain gages in three orthogonal directions. The average cross-talk between fore–aft, lateral and normal force measurements from the plate was less than 5% for all channels. The natural frequency of the plate was greater than 200 Hz in all channels, well above any single frequency of interest. To remove the oscillation frequency of the plate, the force data was fifth order Butterworth filtered at 180 Hz. We resolved forces greater than 0.5 mN in all directions.

We recorded front-leg forces as an animal moved onto the plate and hind-leg forces when the animal left the plate (Fig. 2A). To record middle-leg forces, we placed only the left half of the force plate in the trackway and placed a false plate coated with beads to the left of the force plate; we call this the half-plate configuration. Thus, we only measured the right middle legs of the cockroaches and assumed similar forces for the left middle legs. We recorded the whole body or integrated forces from all three legs of a tripod (Fig. 2B) when animals were fully on the plate (Fig. 2C). All measurements of single-leg and whole-body forces were taken during strides that attained a constant average velocity such that the magnitudes of fore–aft velocity at the beginning and end of a stride differed by less than 15%.

Data acquisition

Signals from each force plate channel were amplified and collected by a 16-bit data acquisition system (National Instruments, Austin, TX, USA) on a computer (PowerMacintosh 9500) at sampling frequency of 10 kHz.

Kinematic analysis

We synchronized force recordings with high-speed video images recorded at 500 frames s⁻¹ from dorsal and sagittal views. We tracked circular reference markers placed on the dorsal surface of the animal to obtain two-dimensional kinematics in the frontal plane, including velocity of the estimated center of mass. To estimate foot position and

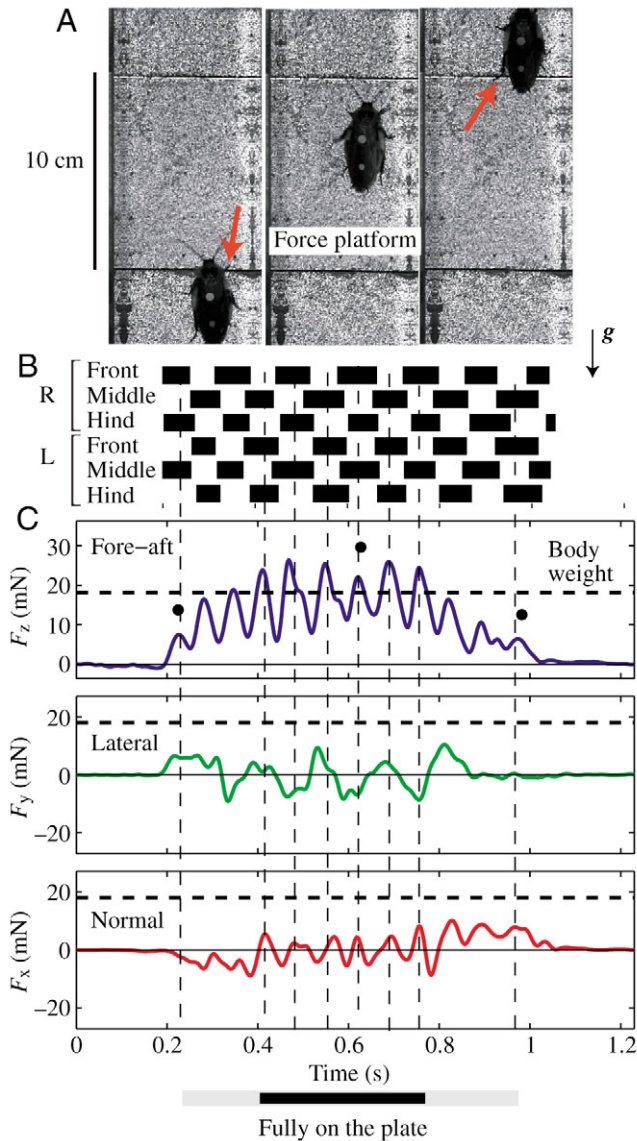


Fig. 2. Representative vertical climb of *B. discoidalis* up a force plate at average velocity 0.18 m s^{-1} . (A) Sequential video frames of the cockroach as it enters (left), is fully on (middle), and leaves (right) the force plate. Red arrows indicate single legs on the force plate. (B) Alternating tripod stepping pattern during the climb. Black bars represent stance period and white spaces the swing period. R, right side; L, left side. (C) Fore–aft (blue), lateral (green) and normal (red) wall reaction forces produced by the cockroach during a climb. Single-leg forces were measured as the cockroach entered (A, left) and exited the plate (A, right). The black circles correspond to the panels in A. Whole body (center of mass) wall reaction forces were measured while the cockroach was fully on the plate (middle) with at least three legs in contact (horizontal black bar below C). Horizontal broken lines represent average body weight.

touchdown timing, we tracked the end of the tarsus in the frontal plane and checked touchdown in the sagittal plane.

Velocity of the center of mass for template comparison

We calculated the average velocity of the animals from the

video recordings by digitizing the dorsal marker as they climbed the force platform. We selected force recordings for analysis if they contained one or more complete strides in which the sum of the increases and decreases in fore–aft velocity were within 15% of the average velocity of the animal. We only accepted trials for which the integration of the fore–aft force over a stride equalled body weight to within 5% as measured by a scale. We calculated the fore–aft velocity of the center of mass from integration of the fore–aft force recording minus body weight. We calculated the lateral velocity of the center of mass by integrating the lateral force recordings.

Statistics

We used a mathematics program (Matlab) for statistical analysis. We present all values here as means \pm s.d. unless otherwise noted.

Results

Kinematics

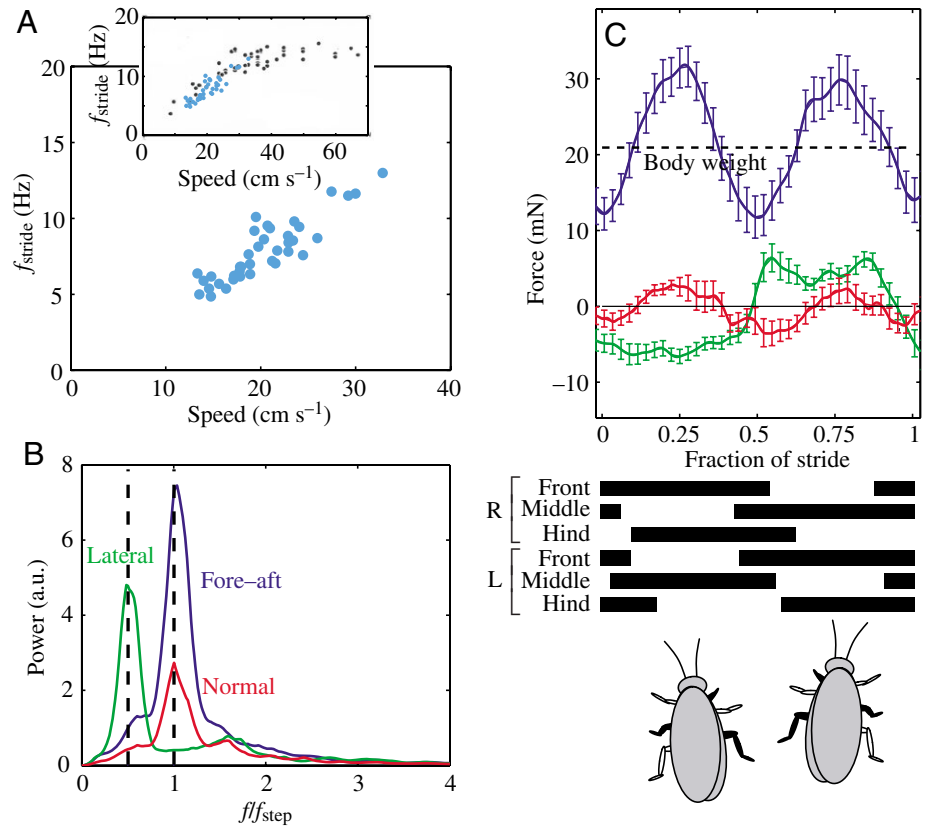
Cockroaches ascended the wall at fore–aft velocities between 0.10 and 0.35 m s^{-1} (average velocity $0.20 \pm 0.04 \text{ m s}^{-1}$). *B. discoidalis* used an alternating tripod gait similar to that found during level running. Three legs (front and hind legs on one side of the body and the middle contralateral leg) were on the wall while the other three were in the swing phase (Fig. 2B). Legs within a given tripod moved synchronously (average leg phase = 0.0 ± 0.05). Tripods were approximately in antiphase. The average normalized tripod phase relative to the opposing tripod equaled 0.51 ± 0.06 . There was no effect of speed on tripod phasing ($P = 0.82$).

Stride frequency increased monotonically with increasing average fore–aft velocity ($f = 38.3v + 0.045$, $r^2 = 0.79$; $P < 0.001$; where stride frequency f is in Hz and velocity v is in m s^{-1}); Fig. 3A). Stance period (τ_{stance} , measured in s) decreased monotonically with increasing velocity in front legs ($\tau_{\text{stance}} = -0.40v + 0.17$; $r^2 = 0.5$; $P < 0.001$), middle legs ($\tau_{\text{stance}} = -0.47v + 0.17$; $r^2 = 0.2$; $P < 0.001$) and hind legs ($\tau_{\text{stance}} = -0.54v + 0.19$; $r^2 = 0.3$; $P < 0.001$). Swing period (τ_{swing} , measured in s) also decreased monotonically with increasing velocity for front legs ($\tau_{\text{swing}} = -0.19v + 0.08$; $r^2 = 0.3$; $P < 0.001$), middle legs ($\tau_{\text{swing}} = -0.17v + 0.07$; $r^2 = 0.1$; $P = 0.01$) and hind legs ($\tau_{\text{swing}} = -0.23v + 0.19$; $r^2 = 0.4$; $P < 0.001$). Duty factor depended on leg type (ANOVA, $P < 0.001$). The average duty factor for front legs was 0.68 ± 0.05 , for right middle leg 0.67 ± 0.07 , and for the hind legs 0.57 ± 0.07 . Front- and middle-leg duty factor did not depend on fore–aft velocity ($P = 0.96$ and 0.28 , respectively). Hind-leg duty factor displayed a weak dependence on velocity, decreasing by approximately 20% across the range of velocities (duty factor = $-0.55v + 0.68$, $r^2 = 0.1$; $P = 0.02$).

Cockroach center of mass wall reaction forces

The wall reaction forces on the center of mass of the animal showed strong periodic oscillations (Fig. 2C, Fig. 3C). The net fore–aft force oscillated around body weight at the average stepping frequency, f_{step} (Fig. 3B,C). Alternate tripod stances

Fig. 3. Frequency and phase of wall reaction forces during climbing. (A) Stride frequency increased with increasing average fore–aft velocity (blue circles). Inset: the relationship of stride frequency with speed was similar to the relation found in level ground running (black circles). Level data taken from Full and Tu (Full and Tu, 1990). (B) Power spectra of integrated forces (arbitrary units) while the animal was on the plate averaged over trials from different individuals. Fore–aft and normal forces oscillated at step frequency (average step frequency $f_{\text{step}}=17.7\pm 3.7$ Hz) while lateral force oscillated at half stepping frequency ($f_{\text{stance}}=7.8\pm 1.9$ Hz), the stride frequency. (C) Integrated forces from all legs during a single constant average velocity stride (two steps) in fore–aft (blue), lateral (green) and normal (red) direction. The data are normalized to the stride period. Error bars on plot represent ± 1 s.e.m. Standard deviations are approximately four times in magnitude (see Results section for a discussion). Black broken line represents average body weight ($N=7$ individuals). The stepping pattern for a single representative trial is shown below. The schematics of the cockroach indicate the approximate leg configurations at mid-stance. Legs colored black indicate feet that are in contact with the wall.



generated lateral forces that oscillated around zero force at one half the stepping frequency ($f_{\text{step}}/2$) or simply the stride frequency (f_{stride}). Normal forces oscillated around zero at f_{step} . The average center of mass (COM) wall reaction force pattern measured in the three orthogonal directions for a single stride (two steps) selected for constant cycle averaged velocity is shown in Fig. 3C. While the shape of the COM force traces during a stride was independent of speed, the magnitudes of the peak and minimum forces depended upon speed (regressions given below).

Fore–aft forces

During a stride, the fore–aft ground reaction force displayed two maxima corresponding to the stance phases of two tripod steps (blue curve, Fig. 3C). Peak fore–aft acceleratory forces were 1.7 ± 0.3 times the average body weight. The peak forces occurred at normalized phase in the stride cycle (fraction of the stride cycle) of 0.25 ± 0.07 and 0.78 ± 0.08 . Maximum peak fore–aft force increased with increasing velocity ($F_{\text{peak}}=4.3v+0.88$; $r^2=0.53$; $P<0.001$, where F_{peak} is normalized by body weight and v is in m s⁻¹). The minimum of the fore–aft force occurred in the overlap in the stances of the two tripods. This minimum was attained at a phase in the stride of 0.49 ± 0.08 . Minimum fore–aft forces averaged 0.26 ± 0.3 times the average body weight. Minimum fore–aft force decreased with increasing velocity ($F_{\text{min}}=-5.4v+1.4$; $r^2=0.46$; $P<0.001$

where F_{min} is normalized by body weight). Negative fore–aft reaction forces were observed in 7% of all steps recorded. Such forces occurred only at speeds above the average climbing speed (0.2 m s⁻¹) and equaled approximately 20% body weight.

Lateral forces

The COM lateral wall reaction forces alternated direction (green curve, Fig. 3C) during a stride. During each step the animal cyclically pulled itself laterally toward the middle leg in contact with the wall. The peak lateral forces remained large for the duration of a step and decreased to zero at mid-stance (phase= 0.48 ± 0.08). The peak magnitudes of positive and negative lateral forces increased with increasing velocity ($|F_{\text{peak}}|=3.7v-0.1$; $r^2=0.5$; $P<0.001$, where F_{peak} is normalized by body weight).

Normal forces

During a stride, the normal wall reaction force (red curve, Fig. 3C) oscillated as the animal alternately pushed itself away and pulled itself toward the wall. The peak positive normal forces that pushed the animal away from the wall occurred at mid-stance (phase= 0.28 ± 0.12 , 0.78 ± 0.1). Peak positive normal force showed large fluctuations, but tended to increase with increasing velocity ($F_{\text{peak}}=1.5v+0.28$; $r^2=0.1$; $P=0.09$ where F_{peak} is normalized by body weight). The peak negative normal force that served to pull the animal back to the wall occurred

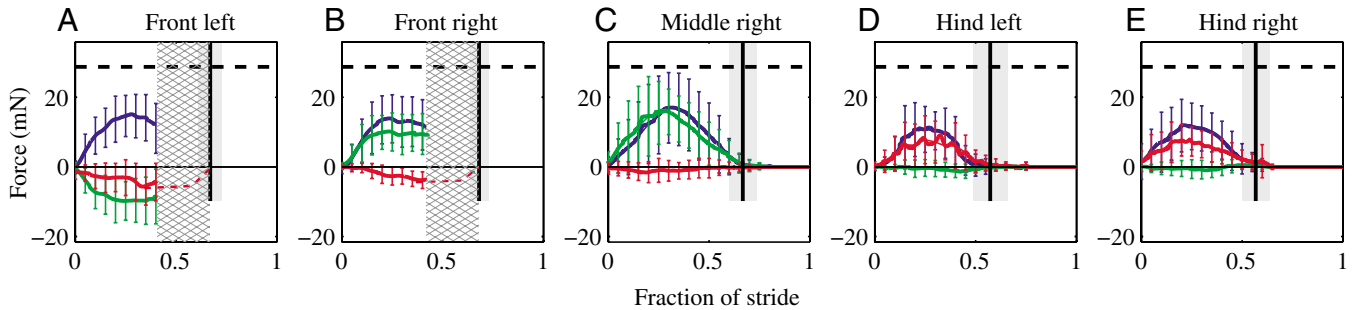


Fig. 4. (A–E) Fore–aft (blue), lateral (green) and normal (red) wall reaction forces developed by individual legs for one step during vertical climbing. Leg forces were averaged from $N=7$ individuals and normalized to stride period. Values are means \pm s.d. In each panel, the solid black vertical line shows the average, normalized stance period (gray bars indicate s.d.). The crosshatched region in A and B shows the overlap region of middle legs with front legs. Normal forces in this region were estimated from Fig. 3C. Black broken horizontal line represents average body weight.

at the overlap of the tripod stances (phase 0.49 ± 0.09). Peak negative normal force decreased with increasing velocity ($F_{\min} = -2.3v - 0.01$; $r^2 = 0.4$; $P < 0.001$, where F_{\min} is normalized by body weight).

Single leg wall reaction forces

Cockroaches produced stereotypical wall reaction force patterns with individual legs (Fig. 4). Measurement of single leg forces was restricted to periods when only a single leg was on the plate. Because stance duty factors for front and middle legs were approximately 0.70, we were unable to resolve single leg forces for front legs during the last third of the stance period (Fig. 4, hatched region). We used data from Fig. 3C to estimate the force in the overlap region. We could completely resolve the middle legs' forces because they were measured in the half-plate configuration of the force plate. The leg trajectories were such that the front legs' forces never appeared during middle-leg measurement. Because the duty factor for the hind leg was less than that of the front leg, there was a period during which whole-body forces (Fig. 3C) represented primarily front-leg normal force. The estimate of front-leg normal force in the region of overlap is shown by the broken red curves in Fig. 4A,B. Peak wall reaction forces are plotted in Fig. 5.

Fore–aft forces

All legs generated significant accelerating fore–aft forces equalling approximately $2/3$ average body weight (Fig. 5A). Peak wall forces were generated at the middle of a stance phase of a single tripod. There were no significant effects of leg on the magnitude of the peak forces (ANOVA, d.f.=4, $F=2.07$, $P=0.1$). The wall reaction forces for all legs were positive, although hind-leg steps generated small ($<20\%$ of body weight), negative deceleratory forces during the last third of the stance period in approximately 40% (22/55) of the steps.

Lateral forces

Lateral forces generated by the front and middle legs were larger in magnitude than in the hind legs (ANOVA on all leg forces, $P < 0.001$; Fig. 5B). Reaction forces of the front and middle legs were directed away from the midline, indicating

that animals pulled in toward the midline with these legs. Within a tripod, lateral force for the middle leg was significantly larger in magnitude ($P=0.002$) and opposite in sign to the lateral force generated by the front leg. Front- and middle-leg lateral forces peaked at mid-step. The hind-leg lateral forces were small, variable and not significantly different from zero ($P=0.4$; Fig. 4D,E; Fig. 5B).

Normal forces

Normal force magnitude depended upon leg type (ANOVA, $P < 0.001$). Normal wall reaction forces for front legs were always negative during a step, indicating that the animal pulled itself to the wall with the front leg (Fig. 5C). Normal forces for the hind legs were always positive and peaked at mid-step,

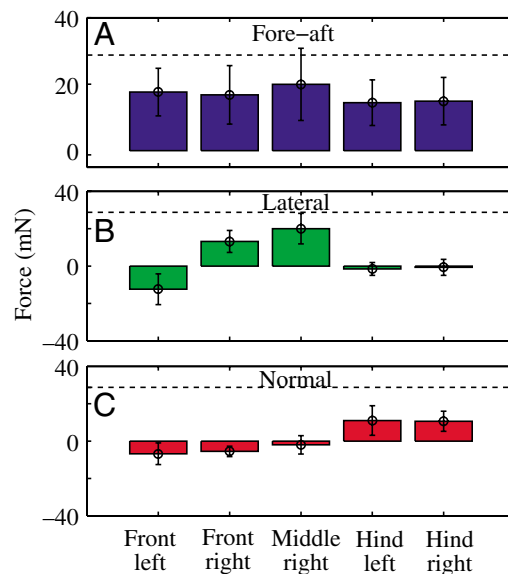


Fig. 5. Summary of peak single leg wall reaction forces in a cockroach during climbing averaged over different individuals ($N=13$). (A) Fore–aft forces. (B) Lateral forces. (C) Normal forces. The error bars represent s.d. The broken line in each panel represents average body weight (28.7 ± 11 mN). Forces for the middle left leg were not measured.

indicating that the animal pushed itself away from the wall with its hind legs. Hind-leg peak forces were approximately 1.8 times front-leg peak forces ($P < 0.001$). Normal forces for the middle legs were small but with non-zero negative peak values of approximately -1.8 mN ($P = 0.01$), indicating that the middle leg was also used to pull the animal toward the wall.

Discussion

During rapid vertical climbs, cockroaches displayed oscillatory center of mass dynamics that resulted from differential leg function. Climbing leg force patterns differed significantly from level running, whereas kinematics did not. The vertical climbing dynamics of cockroaches were remarkably similar to geckos, despite differences in attachment mechanisms, toe number and orientation, and leg number. Similar dynamics of the center of mass revealed the first template of rapid vertical climbing.

Climbing versus level running

Kinematics

Kinematic analysis alone was insufficient to explain the vertical climbing dynamics of cockroaches relative to running on the level (Fig. 3A). Watson et al. found that the dominant strategy used by *B. discoidalis* to climb over a single vertical step also required few changes from the leg kinematics used during horizontal running (Watson et al., 2002a). Zaaf et al. observed very few adjustments in gait characteristics when climbing and non-climbing geckos were required to move on a non-habitual substratum (Zaaf et al., 2001).

Stride frequency for rapid vertical climbing in *B. discoidalis* showed the same increase with speed measured for level running (Fig. 3A). As on the level, stride length was independent of velocity over the range of speeds we measured during vertical climbs. American cockroaches *P. americana* also follow a similar stride frequency–speed function when running and climbing (Full and Tullis, 1990). By contrast, the general relationship between stride frequency, stride length and velocity for climbing lizards appears highly variable. *Hemidactylus garnoti* increased velocity by increasing stride length during rapid vertical climbing (Autumn et al., 2006), whereas both stride frequency and stride length increased as speed increased on the horizontal (Chen et al., 2006). Irschick et al. showed that two gecko species increase speed during climbing primarily by increasing stride frequency (Irschick et al., 2003). Zaaf et al. found that one species of climbing gecko modulates speed almost entirely by changing stride frequency, whereas a similarly sized terrestrial gecko changes speed primarily by changing stride length (Zaaf et al., 2001).

Cockroaches used an alternating tripod gait (Fig. 3C) with duty factors similar to that observed on the level. Duty factors for front and middle legs were approximately 0.67, with the hind-leg duty factor near 0.57. Duty factors for level running range from 0.53 to 0.56 (Kram et al., 1997). When similar speeds are compared, duty factors did not differ significantly

in American cockroaches running on the level, at 45° or vertically (Full and Tullis, 1990). If any trend exists in the present data, it supports the hypothesis that duty factor increases as load increases (Spirito and Mushrush, 1979). Stance duration was prolonged and the next swing phase was delayed when stick insects and cockroaches walked up slopes (Cruse, 1976; Delcomyn, 1985; Spirito and Mushrush, 1979; Tang and Macmillan, 1986). Duty factors in climbing locusts increased from 0.80 during slow level walking to 0.88 during vertical climbing (Duch and Pfluger, 1995).

Single leg force production

Force patterns developed by individual legs of rapidly climbing cockroaches differed markedly from those generated during running on the level (Full et al., 1991). During climbing, all legs generated accelerations in the fore–aft direction (Fig. 4, Fig. 5A). Cockroaches effectively contacted the surface and generated these forces in less than 1/20 of the time of a climbing stick insect (Cruse, 1976). Hind legs with their claws oriented in the direction opposite to the direction for attachment produced small deceleratory forces at the higher speeds, but even these legs generated forces that contributed significantly to thrusting the animal upward. Hind legs gained sufficient friction on the beaded surface by pivoting on their pliant pads (pulvilli) and attaching with claws aligned due to the lateral displacement of the tarsi resulting from the flexibility of the tarso-pretarsal joint (Gorb, 1996; Kendall, 1970). Front and middle legs relied on distal tarsal claws, shown to be effective on rough, inclined surfaces (Frazier et al., 1999; Larsen et al., 1997; Roth and Willis, 1952) and during inverted locomotion (Larsen et al., 1995). During level running, front legs only decelerated the center of mass in the fore–aft direction, hind legs produced fore–aft acceleration, and fore–aft middle-leg forces changed from deceleration to acceleration at mid-step (Full et al., 1991).

Lateral wall reaction forces were directed outwards during climbing as the cockroach pulled inward with all its legs, allowing interlocking with its claws (Fig. 4, Fig. 5B). Middle-leg lateral forces were the largest, while hind-leg lateral forces were near zero. Stick insects also pulled in with all their legs during climbing, but hind legs produced large lateral forces (Cruse, 1976). Lateral ground reaction forces in running cockroaches are opposite to the direction produced during climbing. Animals pushed outward as they bounced laterally from side to side (Full and Tu, 1990; Full et al., 1991; Schmitt and Holmes, 2000a; Schmitt and Holmes, 2000b).

Normal ground reaction forces during level running in animals are always directed away from the substrate in support of body weight (Full et al., 1991). During rapid climbing, front legs generated attachment forces that pulled the head toward the wall to counter pitchback while hind legs pushed the abdomen away from the wall (Fig. 4; Fig. 5C). Middle-leg normal forces were small. Beetles lean toward the slope tilt to increase stability (Frantsevich et al., 1998). Climbing stick insects pull their bodies toward the wall with both their front and middle legs (Cruse, 1976). Their hind legs initially pull toward the wall, but push away later in stance.

The substantially different force patterns observed between vertical and level locomotion will result in significant differences in muscle force production *and* work. These findings do not support the assumptions of scaling arguments predicting the metabolic cost of uphill locomotion (Taylor et al., 1972). Small animals use more metabolic energy per unit mass than large animals to run on a level surface. If the cost to lift one gram of mass one vertical meter is constant, small animals should require proportionally smaller increases in metabolic cost to run uphill. Data on climbing cockroaches reject this hypothesis by showing that the cockroach's metabolic cost of ascent greatly exceeds that predicted by a constant efficiency for vertical work (Full and Tullis, 1990). Present data on climbing leg force development confirm the hypothesis that increases in the rate or amount of force production may best explain the metabolic cost of climbing. Increases in the metabolic cost of uphill locomotion cannot be simply attributed to a constant efficiency of vertical work without examination of ground reaction forces (Lipp et al., 2005).

Comparison to rapid gecko climbing

Similarity in single leg force pattern

While the single-leg force patterns generated by the cockroach during climbing were qualitatively different than those generated during level running, they were qualitatively similar to the rapid climbing single-leg force patterns observed in the gecko *Hemidactylus garnoti* (Fig. 6) (see Autumn et al., 2006). Both animals effectively placed their feet during rapid climbs so that minimal fore–aft deceleration forces were generated by legs, thus reducing the power requirements necessary to ascend. Lateral wall reaction forces were directed away from the midline as animals pulled in. The middle legs of cockroaches functioned like the hind legs in geckos, while the hind legs in cockroaches generated near-zero lateral forces. Like the geckos, the cockroaches countered pitchback moments due to gravity by using the front-leg normal forces to pull the head toward the surface. Hind legs in both species push away from the surface. Middle legs in cockroaches generated small normal forces. It is striking that animals with differing attachment mechanisms, ‘toe’ morphology and leg number both change the direction of reaction forces in a similar way to accommodate changes in orientation.

Common center of mass dynamics

The single leg forces of rapidly climbing cockroaches and geckos sum to produce common center of mass dynamics in the frontal plane (Fig. 7). Three legs of the cockroach and two legs of the gecko sum to act as a single leg accelerating the center of mass upward cyclically. Integration of these force patterns results in common fore–aft velocity fluctuations of the center of mass (Fig. 7A,B). At the same time, these sets of legs pull the animals laterally. Cockroaches attained these lateral dynamics by the resultant force of the three legs of a tripod that pulled toward the side of the body on which the middle leg is in contact with the surface (Fig. 6A). In the geckos, the lateral pull of the front leg exceeds that of the hind leg (Autumn et al., 2006).

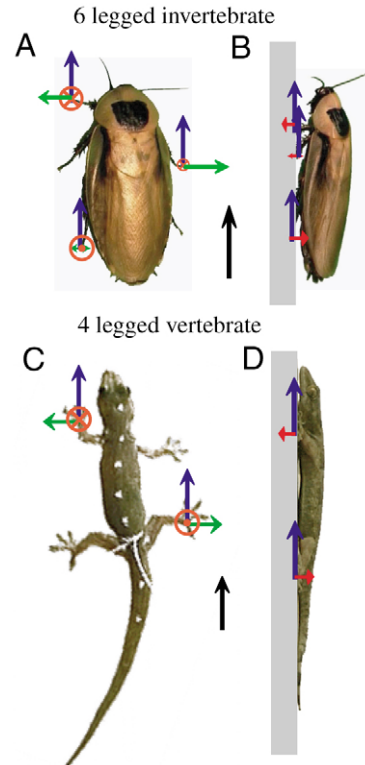


Fig. 6. Cockroaches (A,B) and geckos (C,D), with different leg number, morphology and adhesive mechanism, have similar single-leg wall reaction force patterns during climbing. Dorsal (A,C) and sagittal (B,D) views are shown. The arrows represent average peak wall reaction forces for single legs in fore–aft (blue), lateral (green) and normal (red) directions. All legs in both animals pull up the wall. Legs pull in toward the midline, except for the hind cockroach legs where lateral forces were near zero. Front legs pull the head toward the wall, while hind legs push the abdomen (below the COM) away from the wall. In the cockroach, the middle-leg normal forces were small. Black arrows indicate average body weight for the animals studied (≈ 30 mN for cockroaches, ≈ 20 mN for geckos). Arrows that represent limb reaction forces are scaled relative to the length of the black arrows. Gecko data are from Autumn et al. (2006).

Proposed template for rapid climbing

The similarity of the center of mass dynamics for two diverse species suggests the possibility of a unifying principle for rapid climbing (Fig. 7C). We propose that these climbing dynamics constitute the first template of rapid climbing. Templates are valuable because they solve Bernstein's ‘degrees of freedom’ problem (Bernstein, 1967) by representing in as few as possible degrees of freedom the task of translating the body's mass center (Full and Koditschek, 1999; Koditschek et al., 2004). Templates for running on the level continue to offer insight on passive dynamic stability, control and energetics. Diverse species that differ in leg number and posture run stably like sagittal- (Blickhan, 1989; Blickhan and Full, 1993; Cavagna et al., 1977; Farley et al., 1993; McMahon and Cheng, 1990) and horizontal-plane (Schmitt and Holmes, 2000a; Schmitt and Holmes, 2000b; Schmitt and Holmes, 2001) spring-mass systems, referred to

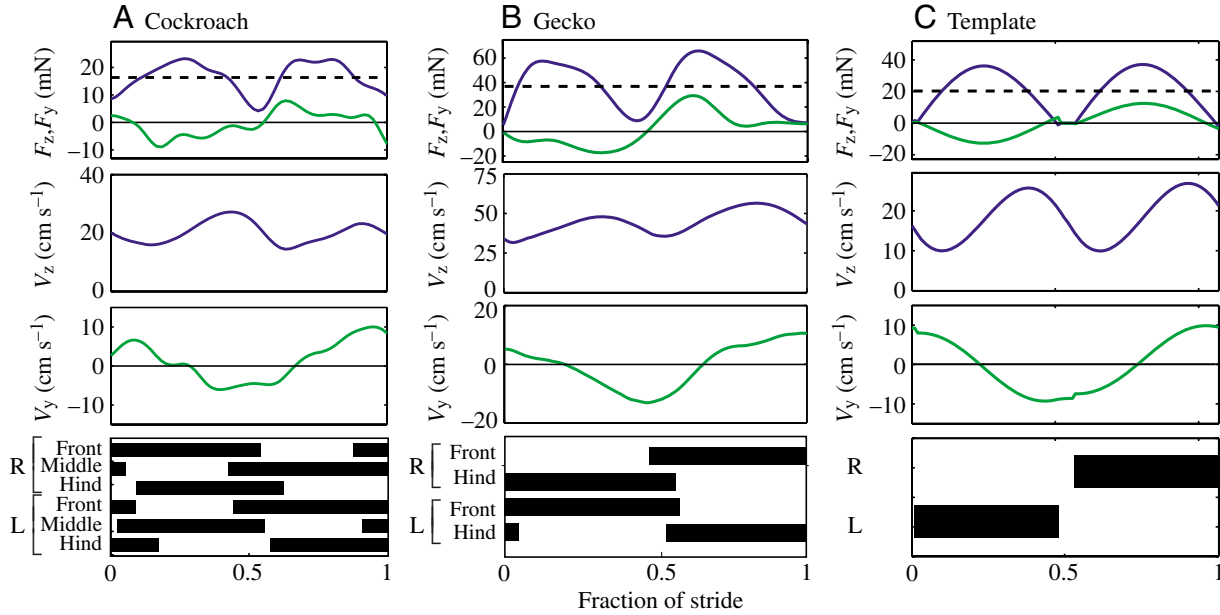


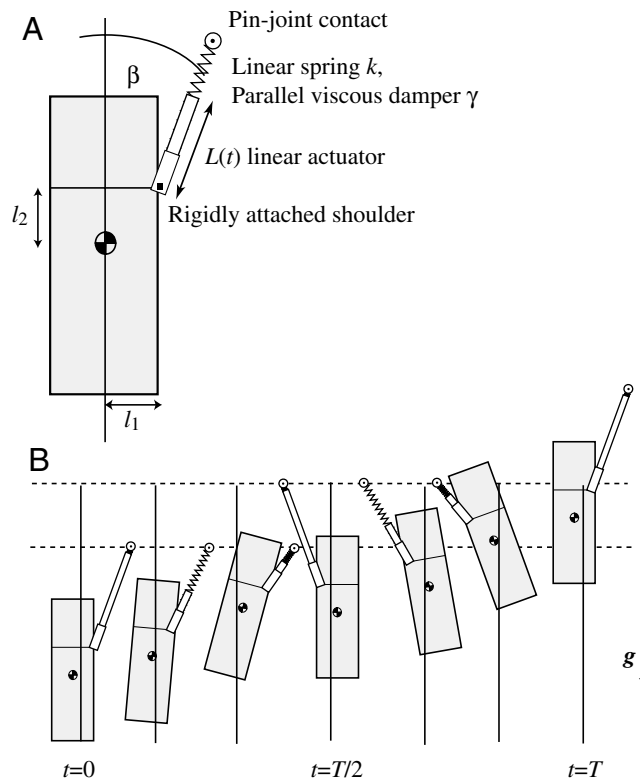
Fig. 7. Fore–aft (blue) and lateral (green) center of mass (COM) wall reaction forces, COM fore–aft and lateral instantaneous velocity for two steps (one stride) during climbing for (A) a cockroach, (B) a gecko and (C) the spring-mass model (template). Cockroaches and geckos show similar COM wall reaction forces and velocities. This pattern can be represented by the template described in Fig. 8. The fore–aft and lateral forces are in-phase and the lateral force is one-half the oscillation frequency of fore–aft force. The velocities are phase-delayed from the corresponding forces by approximately $\pi/2$. Climbing velocity for the cockroach is 20 cm s^{-1} , the gecko 49 cm s^{-1} , and the template 18 cm s^{-1} . Broken lines indicate body weight. The stepping patterns are shown below for a normalized stride. Black bars represent stance period and white spaces the swing period.

as the Spring-Loaded Inverted Pendulum (SLIP) and Lateral Leg Spring (LLS) models, respectively.

A specific model that generates the template dynamics of vertical climbing is shown in Fig. 8A and a schematic of its motion in Fig. 8B. The model consists of a rigid body that is pulled side-to-side through the action of a spring in series with a linear actuator. The rigid body has a moment of inertia of

$8 \times 10^{-7} \text{ kg m}^2$, the order of magnitude of cockroaches ($2 \times 10^{-7} \text{ kg m}^2$) (Schmitt et al., 2002). Unlike the level ground frontal plane LLS model (Schmitt and Holmes, 2000a; Schmitt

Fig. 8. A dynamic template for climbing. The two degrees of freedom model that generates the template climbing dynamics shown in Fig. 7C. (A) Schematic of the model. (B) Schematic of the motion of the model during two steps (one stride of period T). In the first step with the right leg, at touchdown ($t=0$) the right actuator is maximally extended, and the spring is un-extended with zero rest length. Touchdown is created by establishment of a rotationally free pin-joint with the wall. As the actuator length $L(t)$ decreases, the spring in the leg extends, the foot freely pivots about the point of contact and the center of mass (COM) is translated vertically and laterally. The cycle repeats for the left leg. The actuator changes length sinusoidally such that $L(t)=L_0[1+z\sin(2\pi ft)]$, where z is the fractional length change and $f=1/T$ is the stride frequency. The solid vertical line in each panel indicates the fixed lateral position about which the COM laterally oscillates. The angular excursion of the body relative to vertical is exaggerated for clarity. Actual angular excursion of the body relative to vertical is approximately $\pm 3^\circ$. The model was coded and integrated in the Working Model 2D (Design Simulation Technologies, Inc) simulation environment. The parameters used to generate Fig. 7C were body mass=2 g, body dimensions= $4 \text{ cm} \times 0.95 \text{ cm}$, $l_1=0.71 \text{ cm}$, $l_2=0.84 \text{ cm}$, $\beta=10^\circ$, $L_0=1.54 \text{ cm}$, $z=0.6$, $k=6 \text{ N m}^{-1}$, $\gamma=0.09 \text{ N s m}^{-1}$, $f=9 \text{ Hz}$. The attachment duty factor in the model is 0.46.



and Holmes, 2000b) and other passive brachiating models (Bertram et al., 1999), vertical climbing requires work against gravity. Therefore, the spring must be actuated at each step. A step (Fig. 8B) consists of fixing the most distal point of the leg to the wall with a rotationally free pin-joint at a set phase in the oscillation cycle. Decreasing the length of the actuator, fixed at angle β with respect to the body axis, extends the spring that at touchdown is at zero rest length. As the spring lengthens, it develops force that accelerates the body mass upward and laterally. The foot is then released at a set phase in the oscillation cycle and the pattern repeats on the other side of the body. The length $L(t)$ of the actuator changes such that $L(t)=L_0[1+z\sin(2\pi ft)]$, where z is the fractional change of the actuator around the rest length L_0 . The arm is rigidly fixed to the body displaced from the center of mass distances l_1 and l_2 . A small viscous damping term (dashpot) in parallel with the spring is needed to damp large lateral oscillations due to the swing of the pendulum. (The data in Fig. 7C are for parameters listed in the legend of Fig. 8.) Since the limb is sinusoidally actuated, the maximum fraction of the cycle that the leg can be attached to the wall is 50%. Rapid climbers like geckos use 50% duty factor by maintaining equal stance and swing durations [duty factor 0.5 ± 0.06 independent of limb (Autumn et al., 2006)]. The cockroaches maintain stance duty factor greater than 50% (0.67 for front and middle limbs) by decreasing swing duration. We plan to investigate the role of duty factor on climbing stability in the model through modulation of swing and stance periods.

The forces and resulting center of mass velocities generated by the model are shown in Fig. 7C and agree well with the pattern measured in cockroaches and the geckos. This pattern was found after systematic variation of k , γ , β and l_1 and l_2 to attain the representative magnitude and phasing of the forces, as well as the appropriate center of mass velocities.

We hypothesize that animals generate the template dynamics in Fig. 7 to passively control body oscillations. At first glance, it might seem that the template, and thus animals, could take advantage of the natural oscillation of the body as a pendulum by effectively swinging themselves up the wall. However, preliminary studies of the template indicate that this body pendulum motion is undesirable as typical oscillation frequencies are set by $(1/2\pi)\sqrt{g/l}$ (near 2 Hz for animals of length 1–5 cm like the cockroaches and geckos discussed in this study). Body oscillation frequency is far from the average stride frequency of the animals (i.e. 10 Hz). Because of this frequency mismatch, the template can swing wildly out of control for many oscillations when perturbed laterally, depending on sprawl angle, spring and damping coefficients. Preliminary stability studies of the model in Fig. 8 indicate that generation of lateral forces can produce rapid, passive stabilization of the climbing gait after a significant lateral perturbation. Our next step is to perform a stability analysis similar to that performed for the LLS model (Schmitt and Holmes, 2000b).

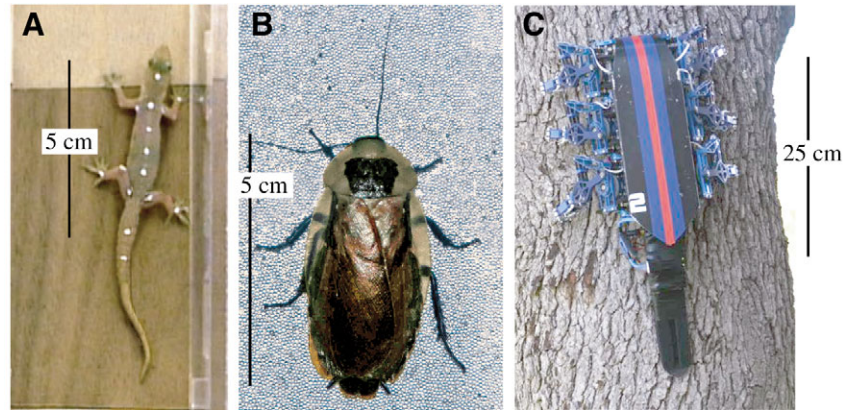


Fig. 9. Climbing gecko (A), cockroach (B) and robot (C). The biologically inspired climbing robot named RiSE (Robots in Scansorial Environment) is using the force generation concepts discovered for cockroaches and geckos (Autumn et al., 2005).

Advances in the biological understanding of vertical locomotion are directly benefiting scansorial robots just the way that biological principles of bouncing locomotion have been applied to the design of legged level terrain robots (Cham et al., 2002; Saranli et al., 2000). The present study on cockroaches and previous research on geckos (Autumn et al., 2006) have provided biological inspiration for the recently designed climbing robot named RiSE (Robots in Scansorial Environments; Fig. 9) (Autumn et al., 2005).

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