Distributed mechanical feedback in arthropods and robots simplifies control of rapid running on challenging terrain

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Abstract
Terrestrial arthropods negotiate demanding terrain more effectively than any search-and-rescue robot. Slow, precise stepping using distributed neural feedback is one strategy for dealing with challenging terrain. Alternatively, arthropods could simplify control on demanding surfaces by rapid running that uses kinetic energy to bridge gaps between footholds. We demonstrate that this is achieved using distributed *mechanical* feedback, resulting from passive contacts along legs positioned by pre-programmed trajectories favorable to their attachment mechanisms. We used wire-mesh experimental surfaces to determine how a decrease in foothold probability affects speed and stability. Spiders and insects attained high running speeds on simulated terrain with 90% of the surface contact area removed. Cockroaches maintained high speeds even with their tarsi ablated, by generating horizontally oriented leg trajectories. Spiders with more vertically directed leg placement used leg spines, which resulted in more effective distributed contact by interlocking with asperities during leg extension, but collapsing during flexion, preventing entanglement. Ghost crabs, which naturally lack leg spines, showed increased mobility on wire mesh after the addition of artificial, collapsible spines. A bioinspired robot, RHex, was redesigned to maximize effective distributed leg contact, by changing leg orientation and adding directional spines. These changes improved RHex's agility on challenging surfaces without adding sensors or changing the control system.

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1. Introduction

When animals, such as spiders and cockroaches, scurry through their natural environment, debris can decrease the probability of a foothold, provide diverse asperities for contact and flow like a fluid causing the animal to slip. Effective mobility over varied terrestrial substrates in the natural world that differ in geometry, compliance and tendency to flow must require a feedback component. Thus, control strategies of legged locomotion in nature cannot be determined without regard to an animal's environment.

Distributed neural feedback that allows precise stepping is one biological solution to locomotion on complex surfaces. Active sensing in animals originates from an enormous number and rich variety of motion, contact, length and stress sensors. These sensors provide information for precise

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ordering of motor activity, the regulation of phase transitions and the reinforcement of motorneuron activity [1–4]. Legged arthropods are particularly effective in traversing terrain at slow speeds using distributed neural feedback [5, 6]. Local control of each leg, and possibly every joint, results in a secure-foothold and quasi-static stability [7, 8]. Given a limited number of coordination 'rules' among joints and legs [9–13], combined with sufficient descending input [14], arthropods can negotiate obstacles, ditches, gaps and uneven surfaces, as well as travel up and along inclines by slow, deliberate stepping [15–20].

As an alternative to precise stepping, animals can attempt to move rapidly through a complex environment. High-speed locomotion can be advantageous on irregular terrain because kinetic energy allows the organism to bridge gaps in footholds that slow-moving systems find impassible [21–25]. Rapid running, however, is a high bandwidth behavior. Delay in neural communication channels reduces synchronization gains, so that an animal's nervous system tends to operate in a decentralized, feedforward manner where coordination is achieved primarily through mechanical coupling and stability through preflexes [26]. It has been shown empirically [22, 27] and in simulation [28] that this *mechanical feedback* can play an important role in simplifying the control of dynamic locomotion, acting to stabilize locomotion through passive mechanisms alone. We take the term '*feedback*' to mean the use of *state information* to impose *additional inputs* that stabilize or improve an otherwise unstable or insufficiently well-performing dynamical process. By mechanical feedback we refer to passively compliant legs that *transduce perturbations away from the steady-state body posture during a stride*, to achieve a *net application of forces over time and space that tends to stabilize the body's steady-state orbit*. Low order models or templates of passive, dynamic running, such as the spring-loaded inverted pendulum [29–31] and the lateral leg spring [32, 33], show these self-stabilizing properties [34, 35]. When models are perturbed, mechanical feedback resulting in momentum trading allows recovery with minimal neural sensing. The problem is that these neurally feedforward templates are tuned for effective mechanical feedback with a particular structured environment. These templates use a single point contact, but represent the abstracted system behavior of diverse species that differ greatly in leg number and foot design.

While template models that demonstrate stability through mechanical feedback use single point contact, arthropods have an impressive array of attachment mechanisms on their feet that can increase a leg's probability of surface contact. Mechanisms include hooks or claws, suckers, glue and friction [36]. Distal tarsal claws have been shown to increase performance on rough, inclined surfaces [37–39] and during inverted locomotion [40]. Mechanisms in some orientations can require feedback from the nervous system to engage [39], whereas others operate by passive mechanical feedback to respond to specific mechanical events. For instance, the adhesive pad (arolium) in Asian weaver ants is deployed passively when legs are pulled naturally toward the body and claws fail to interlock. Regulation of pads use and surface attachment involves purely mechanical control inherent in the arrangement of the claw flexor system [41, 42]. Passive mechanical contact may not be restricted to feet alone. Roth and Willis [37] suggest that spines along the leg can increase traction on rough, inclined surfaces. Leg trajectory and configuration may also be adapted to the environment. The curved pointed dactyls of sideways running crabs attached to legs cycling in the sagittal plane allow rapid running in sand. Cockroaches using legs with broad feet or tarsi that operate more in the frontal or horizontal plane appear adapted to environments that possess a lower probability of surface contact.

We propose that the control of locomotion on challenging terrain can be simplified during rapid running using *distributed mechanical feedback*. We demonstrate that animals are effective at traversing challenging terrain at high speeds by distributing the mechanical feedback over limbs moving in appropriate trajectories with components that generate passive responses to leg–surface contact events. Distribution of the mechanical feedback creates effective coupling with environments, and results from the synergistic operation of leg trajectory, leg configuration and attachment mechanism. The control algorithms are in effect embedded in the form of animal itself: control results from the properties of their parts, their morphology and their passive interaction with the environment [21].

The present study tests the hypothesis that distributed mechanical feedback simplifies the control of animal– and robot–surface interactions. Natural substrates, such as leaf litter, shrubbery and soil, are too complex to allow discovery of how animals scramble over terrain dynamically. To begin investigation, surfaces whose parameters can be systematically varied are required. To challenge their motor control system, we choose to focus first on foothold probability as it affects speed and stability. We used wire mesh to simulate terrain that has 90% of its surface area removed. We selected three of nature's fastest arthropods to study the differences in their leg trajectory, leg configuration, attachment mechanism and native substrate. Spiders (*Hololena adnexa*) with feet terminating in claws swing their hairy legs more in the sagittal plane. Cockroaches (*Periplaneta americana*) possessing broad feet with claws swing their spiny legs more in the frontal or horizontal plane. Both species operate in complex terrain with sparse foothold probabilities. Third, we selected sideways running ghost crabs (*Ocypode quadrata*) that use pointed feet lacking claws or leg spines as they swing their legs more in the sagittal plane. In nature, ghost crabs run on sand, a high probability of contact surface. We verified our results in a physical model, a rapid running, six-legged robot named RHex [43]. We altered leg configuration and attachment mechanism, but not its electronic control strategy. The biologically inspired leg design that incorporated mechanically responsive contacts allowed the robot to negotiate an otherwise impassible surface.

2. Materials and methods

### 2.1. Spider locomotion on control and wire-mesh surfaces

Hololena adnexa specimens were collected from the UC Berkeley campus and housed in snap-cap vials. To test locomotor ability on sparse foothold substrates, we used wire mesh that maintained the relevant properties of their preferred web substrate, the juniper plant (movie 1, available at stacks.iop.org/BB/2/9). We chose wire mesh with gap sizes comparable to one-half body length (square wire-mesh opening length 2.8 mm; figure 1(B)) and with mesh size comparable to foot size (diameter of mesh element = 0.21 mm; mean tarsal diameter of the spider = 0.26 mm). Runs on square meshes (1.4 mm)^2 and (2.8 mm)^2 and control surfaces took place in a corral 10 cm long × 2.6 cm wide. Spiders were video recorded using two or three synchronized cameras (Redlake Imaging MotionScopes and Kodak Ektapro) recording at 500 frames s^{-1} (movie 2, available at stacks.iop.org/BB/2/9). Mean speeds were calculated using the wire mesh as a measurement grid. Foot contacts were mapped onto a flat grid representing the mesh surface and characterized by the leg region touching the surface, the leg pair and the location of the interactions on the grid (movie 3, available at stacks.iop.org/BB/2/9). These maps were used for contact distribution analysis, follow-the-leader calculations and tuning tests.

2.2. Follow-the-leader gait analysis

We examined footfall maps for spiders (253 steps) and cockroaches (133 steps) running on the mesh. A 'follow-the-leader' gait step was recorded if an animal's posterior legs (leg pairs II and III for the cockroach, and II, III and IV for the spiders) engaged the same wire-mesh segment (6.4 mm wide for cockroaches, 2.8 mm wide for spiders) as a previous step by any anterior ipsilateral leg. The footfall maps also empirically established that all types of cockroach and spider 'following steps' appeared in at least one run and thus were physically possible.

### 2.3. Cockroach locomotion on control and wire-mesh surfaces with and without tarsi

To determine the effect of leg trajectory and orientation, we tested an arthropod that swings its legs more in the horizontal plane. Cockroaches (*Periplaneta americana*; n = 8 individuals, mean length = 3.7 cm) were run on a 1.5 m long, 10 cm wide balsa wood track enclosed by optically clear Plexiglas. For mesh runs, a section of (6.4 mm)^2 square wire mesh (length 15 cm) was substituted for the balsa surface near the center of the track. Video recording and foot-placement analyses were performed as described in spiders. For ablations, the tarsi were removed using dissecting scissors (figure 1(E)). After recovery, animals were run across the same trackway on balsa and wire-mesh surfaces (movie 4, available at stacks.iop.org/BB/2/9). Each individual served as its own control.
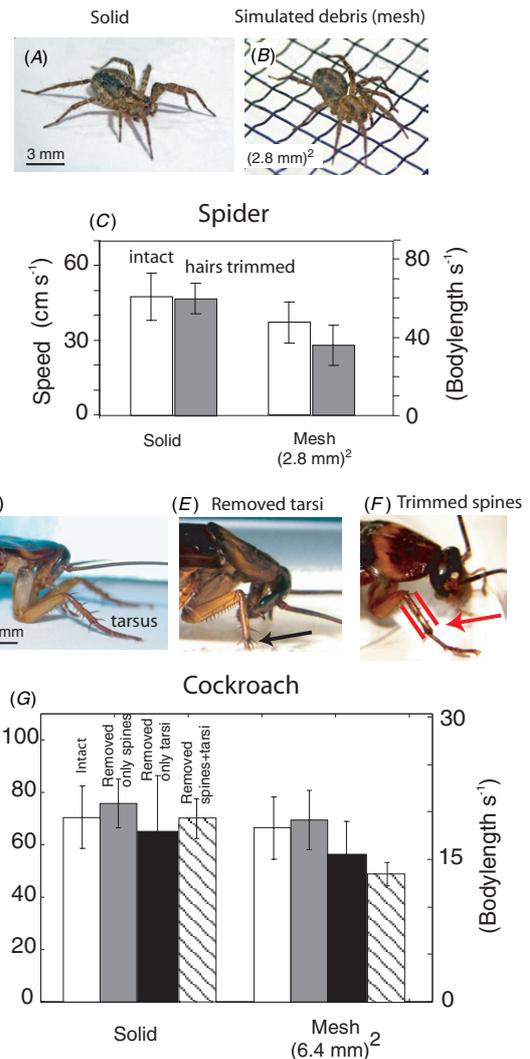
Figure 1. Speeds by arthropods on simulated terrain represented by wire mesh. (A) Spider (*Hololena adnexa, n* = 30, mean carapace plus abdomen length 6.7 ± 1.1 mm SD, mean mass 23.4 ± 11.2 mg SD) on control surface. (B) Spider on 2.8 mm × 2.8 mm wire-mesh surface. (C) Mean speed ± SD of spider on control and (2.8 mm)^2 mesh surfaces. Speed on wire mesh decreased by 22% from control (open bars; paired *t*-test; P = 0.03). Trimming hairs (macrosetae) from the ventral metatarsus (solid bars) did not affect speed on the control surface (P = 0.45), but decreased speed by 41% on the mesh relative to controls. (D) Cockroach (*Periplaneta americana*) on the control surface (n = 10, mean mass 0.92 ± 0.05 g SD). (E) Cockroach with terminal leg segments or tarsi on all legs ablated. Arrow shows location of tibial spines. (F) Cockroach with trimmed tibial spines on all legs. Red arrow and lines show location of trimming. (G) Cockroach performance on solid control and mesh surfaces intact (open bars), without tarsi (solid bars), without spines (gray bars) and without spines and tarsi (hatched bars). Cockroach only showed a statistically significant decrease in speed (mean decrease across n = 10 individuals of 30%) when both the tarsi and spines were removed on the mesh surface (paired *t*-test, P = 0.004 for tarsi plus spine ablations; P = 0.44 for spine ablation only).

2.4. Spider and cockroach hair and spine ablations

To test the contribution of the spider macrosetae to successful running on mesh, we collected additional spiders (n = 5) and ran them on control and (2.8 mm)^2 wire-mesh surfaces.

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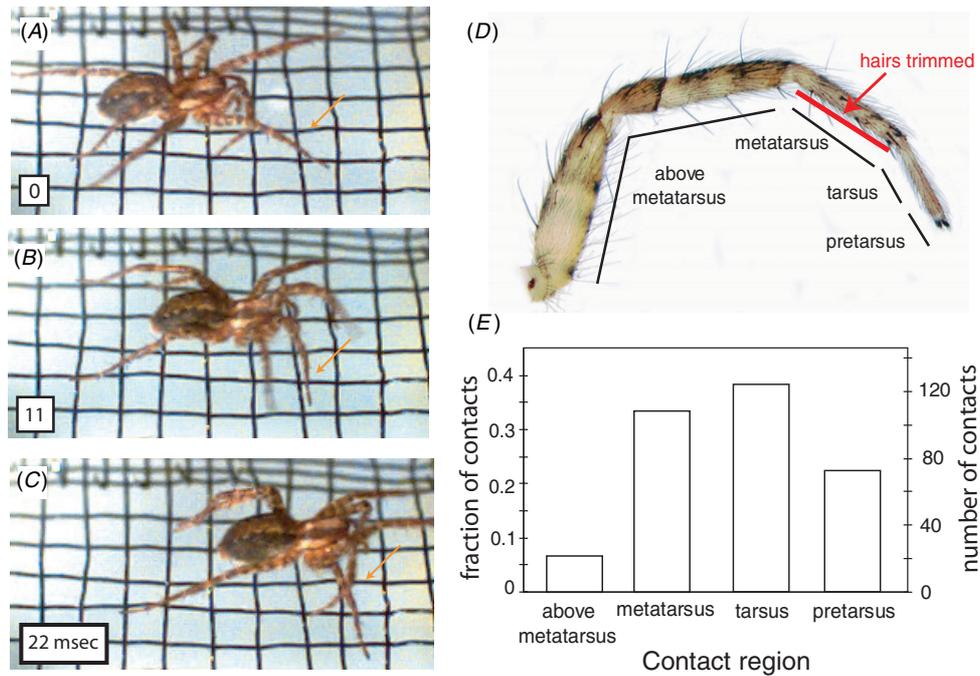
Figure 2. Spiders' distributed contact with wire mesh along leg. (*A–C*), High-speed video sequence of spider on $(2.8\ mm)^2$ mesh running at 30 body lengths per second showing contact of the metatarsus of leg two with wire mesh; see orange arrow. (*D*) Spider leg showing regions for which we measured contact events. Large hairs or macrosetae enhanced contact. Red bar shows the area where hairs were trimmed. (*E*) Histogram of distribution of spider leg segment contacts from all four leg pairs on $(2.8\ mm)^2$ wire mesh. Legs contacted wire-mesh elements on the tarsus and the metatarsus in over two-thirds of the trials (234 of 328 surface contacts), while the pretarsus, including the tarsal claw, contacted the wire mesh in only 22% of the trials (73 of 328 surface contacts). Pretarsus and tarsus were defined operationally as the distal half of the tarsal segment plus the tarsal claw, and the proximal half of the tarsus, respectively, as the distal half of the tarsus/claw combination normally makes contact on flat surfaces, but the proximal half does not.

Following these control runs, spiders were anesthetized and the macrosetae on the ventral side of the metatarsi on all legs (figure 2(*D*)) were shortened by 1/2 to 2/3 normal length with angled-blade microsurgical scissors, since this region made the most contacts with the mesh (see figure 2(*E*)). Following trimming and overnight recovery, the spiders were again run on both surfaces (4–6 runs per specimen per surface).

To test the contribution of leg spines in cockroaches, we ran additional animals ($n = 4$) on the solid balsa and wire-mesh tracks under three treatments: intact animals, tibial spines trimmed, tarsi removed after tibial spines trimmed. The animals were run 4–6 times for each treatment on each surface. Cockroaches were anesthetized on a carbon dioxide platform and all tibial spines from all legs were removed using a dissecting scissors. Clipping did not disturb the socket, but left a small nub ($\sim$0.4 mm; figure 1(*F*)). After the animals recovered, they were run on the two surfaces. Tarsal ablation was then performed and, after recovery, the animals were run again.

2.5. Ghost crab locomotion on control and wire-mesh surfaces with and without artificial spines

Ghost crabs (*Ocypode quadrata*) were collected on the Outer Banks of North Carolina and in Florida and maintained in the UC Berkeley Animal Facility. Each animal ($n = 5$ individuals, average carapace length 3.3 ± 0.5 cm, average limb diameter 0.47 ± 0.1 cm) was run on the wire mesh on average ten times to record foot interactions (see movie 5, available at stacks.iop.org/BB/2/9). Two artificial spines were stapled to a thin paper backing (see figure 4). The backing was bonded to the segment above the dactyl, the most distal leg segment (see figure 4), using cyanoacrylate adhesive. The spines' staples created a hard angular stop at 90° while allowing flexion toward the leg with angular spring constant of approximately 0.002 N m rad^{-1}. The trackway measured 50 cm wide × 150 cm long with a section of 1.27 cm gap size wire mesh 50 cm long in the center. Animals running from sand onto the mesh were video recorded as with spiders. We operationally defined a misstep of a leading limb as penetration of the mesh beyond the dactyl. For the trailing limbs, missteps were defined as failure to contact a wire-mesh element for push-off (see movie 5 available at stacks.iop.org/BB/2/9).

2.6. Robot locomotion over mesh with three leg types

RHex, the robot hexapod, was challenged to run across a metal square wire mesh with a hole size of 7.6 cm^2 and a wire diameter of 0.64 cm. RHex's limb consists of a spring element attached to a shank with a small piece of rubber tire tread at the end (figure 5(*B*)). The cross section of the 'toe' was 1/4 the size of the mesh hole. Thus when challenged to cross the mesh, RHex often slipped and failed to advance more than a body length. To enhance leg contact, we reversed the leg, increasing the potential contact area (figure 5(*C*), red
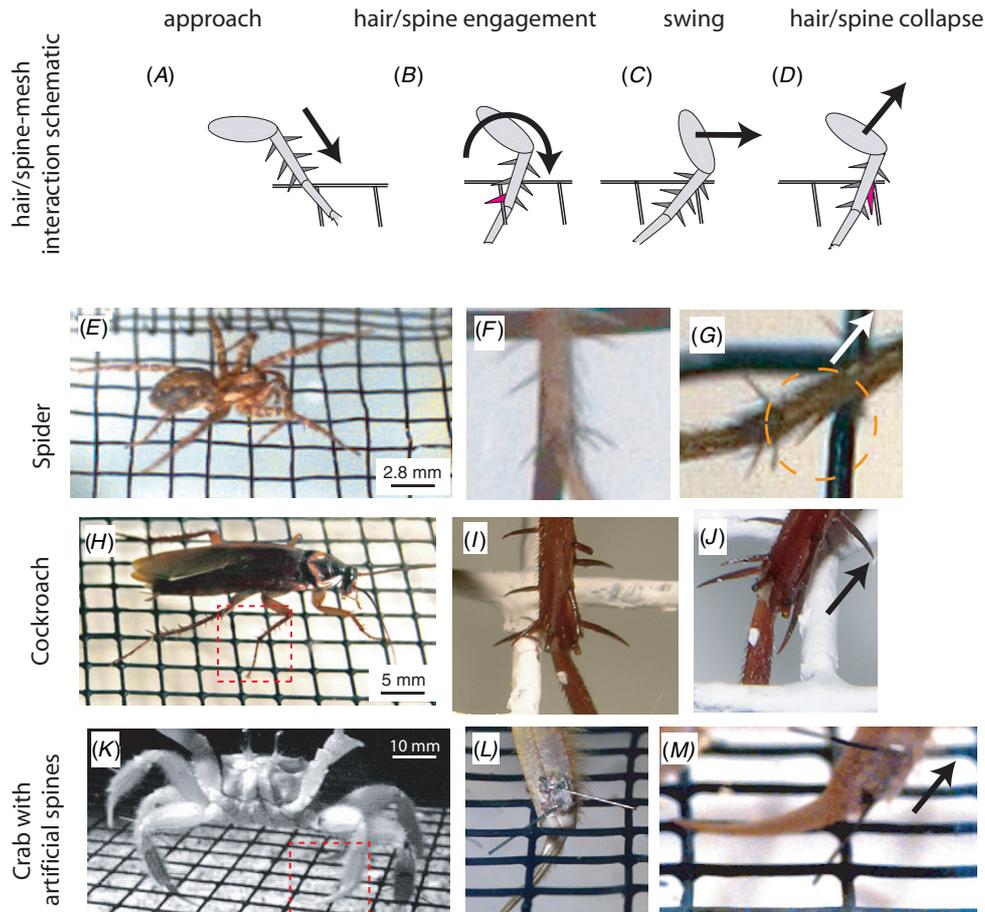
Figure 3. Natural and artificial spines increase distributed foot performance on simulated terrain. (*A–D*) Schematic of cuticular leg spines approaching the wire mesh (*A*), engaging for a more effective foothold (*B*), collapsing during the initiation of leg swing (*C–D*). (*E-G*) Video frames of a spider on the wire mesh (*E*). High speed video of cuticular leg spine engaging the wire mesh during stance phase (*F*) and collapsing during the swing phase (*G*; orange circle shows collapse and arrow the direction of leg movement). (*H–J*) Video frames of a cockroach on the wire mesh (H; red box shows leg in I, J). (*K–M*) Ghost crab successfully running on the wire-mesh surface using artificial spines attached to the segment above dactyl or foot (K). Without spines crabs misstepped frequently. Artificial leg spine engaging the wire mesh during the stance phase (L) and collapsing during the swing phase (M). Preliminary spine designs that did not collapse entangled with the wire mesh and impeded the beginning of leg swing.

bar). Finally, we added spines based on those of the animals. Directly above the terminal piece of rubber, a unidirectional, collapsible steel spine element (figure 5(D)) was bonded to each side of the limb at a 70° angle. The robot started on a solid surface and accelerated to constant average velocity before entering the mesh. We recorded the distance RHex traveled on mesh before its legs penetrated the mesh, stopping forward movement.

3. Results and discussion

3.1. Negotiating terrain without precise stepping

To isolate one dimension from the many other dimensions of surface variability, we emulated the reduced percentage of available solid contact surface that spiders (*Hololena adnexa*) can encounter in nature (see movie 1 available at stacks.iop.org/BB/2/9) by using square wire mesh with gaps five to ten times the diameter of their feet or tarsi (figures 1(A), (B)). We compared speeds for the wire mesh to solid ground by video recording at 500 frames s^{-1} (movie 2, available at stacks.iop.org/BB/2/9). Despite removal of nearly 90% of the potential contact area, spiders ran over the wire mesh at 47±11 body lengths s^{-1} maintaining 78% of their mean speed on the solid control surface (figure 1(C)). This remarkable performance was not unique to spiders. The American cockroach, *Periplaneta americana,* ran at 19 ± 3.2 body lengths s^{-1} (70 ± 12 cm s^{-1}) without significantly decreasing their speed on the simulated terrain relative to the solid surface (paired *t*-test; one-tailed $P = 0.34$ figure 1(G)).

To explain their exceptional performance on sparse-foothold terrain, we tested the hypothesis that these arthropods adopt a 'follow-the-leader' gait where posterior feet use sensory information to follow or land on the successful foothold attained by anterior feet on the same side of the body [44]. Examination of footfall maps in the present study revealed that neither spiders nor cockroaches used a 'follow-the-leader' gait. Only 14% of spiders' leg contacts (37 of 257) and 11% of cockroach steps (15 of 133) could be characterized
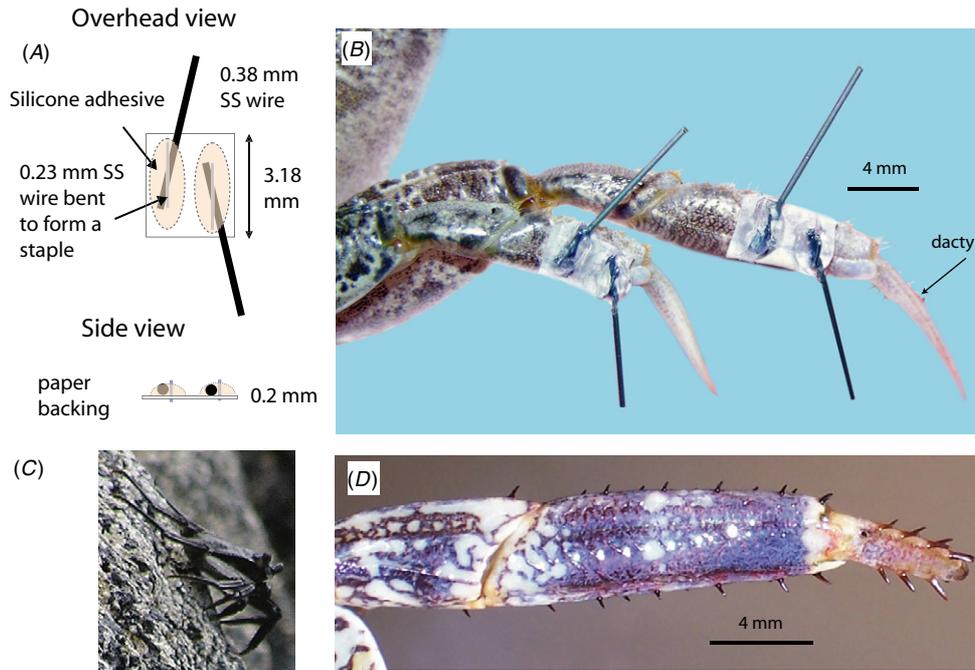
Figure 4. Artificial spines attached to the ghost crab *Ocypode quadrata,* and naturally spiny crabs of species *Grapsus tenuicrustatus*. A–D. (*A*) Schematic of prosthetic spine. (*B*) Artificial spines bonded to legs of ghost crab using cyanoacrylate adhesive and accelerant. For comparison to the naturally smooth-legged ghost crabs, we picture (*C*), a thin-shelled rock crab (*Grapsus tenuicrustatus*) climbing on the lava surface in Hawaii. (*D*) Spiny surface of *Grapsus* leg. The *Grapsus* spines have similar properties to the animal and artificial spines used elsewhere in this study.

as 'follow-the-leader' where posterior leg contacts were on the same section of wire mesh as an anterior leg with a successful foothold.

To further test the hypothesis that these arthropods might incorporate rapid neural feedback while running over sparse-foothold terrain, we determined if spiders adjusted their steps to attain optimal foot placement on the wire mesh. We examined all steps to establish a null hypothesis for a non-parametric test (Chi-square) to determine whether the second or final steps differed from random with respect to the overall probability of contacting a more distal, more proximal, or the same leg region. We compared the regions of the spider's leg contacting the wire mesh during their first step, second step and last step as they exited the mesh. The second and last steps were scored as: no change in contact location relative to the first step, more distal toward the clawed foot (pretarsus) or more proximal toward the body (tarsus or metatarsus). We did this for all legs of 30 trials. Chi-square analyses showed that neither first–second nor first–last step comparisons differed significantly from chance ($P = 0.27$, $P = 0.36$, respectively). Therefore, we could not show that rapidly running spiders used neural feedback to adjust their steps so that a specific location of the foot or a particular leg segment contacted the wire mesh.

3.2. Distributing contact along the leg and using collapsible spines

Spiders and cockroaches used a passive mechanical approach to negotiate the wire mesh that did not rely on contacting specialized feet. We discovered that these rapid running arthropods were extremely agile because they effectively

contacted the mesh at multiple points distributed along their legs (figure 2). Spiders contacted the wire-mesh elements more often with their more proximal leg segments (metatarsi and tarsi) than with their feet (pretarsi) that contain specialized claws for gripping (figures 2(*D*), (*E*) and movie 3, available at stacks.iop.org/BB/2/9). Cockroaches contacted leg segments above their terminal tarsal claw segment nearly 60% of the time (121 out of 205 contact events).

To test the hypothesis that legged arthropods use distributed leg contact when negotiating sparse-foothold terrain, we compared the speed of a cockroach running over solid and wire-mesh surfaces with and without their specialized feet (see removed tarsi; figure 1(*E*)). The tarsal claw on feet has been shown to actively engage at slow speeds on level substrates [44]. Surprisingly, removal of the tarsi resulted in no significant decrease in speed on the solid control surface or the mesh (paired *t*-test, $P = 0.36$ and $P = 0.29$, respectively; figure 1(*G*); see movie 4 available at stacks.iop.org/BB/2/9). Cockroaches with ablated tarsi showed no significant decrease in speed when they ran on the wire mesh relative to the solid control surface ($P = 0.42$). High-speed video recordings revealed that the more frontal or horizontal plane trajectories of the hind and middle legs increased the probability of effective leg contact.

In spiders, whose legs cycled more in the sagittal plane causing near vertical penetration of the mesh, spines increased the effectiveness of distributed leg contact. Trimming spines or macrosetae on just the ventral side of the metatarsi on all legs (figure 2(*D*)) significantly decreased speed on the mesh by 22% compared to controls on mesh with spines intact (paired *t*-test; $P = 0.006$; figure 1(*C*)). By contrast, removing the leg

RHex with prosthetic spines

RHex with C-shape legs
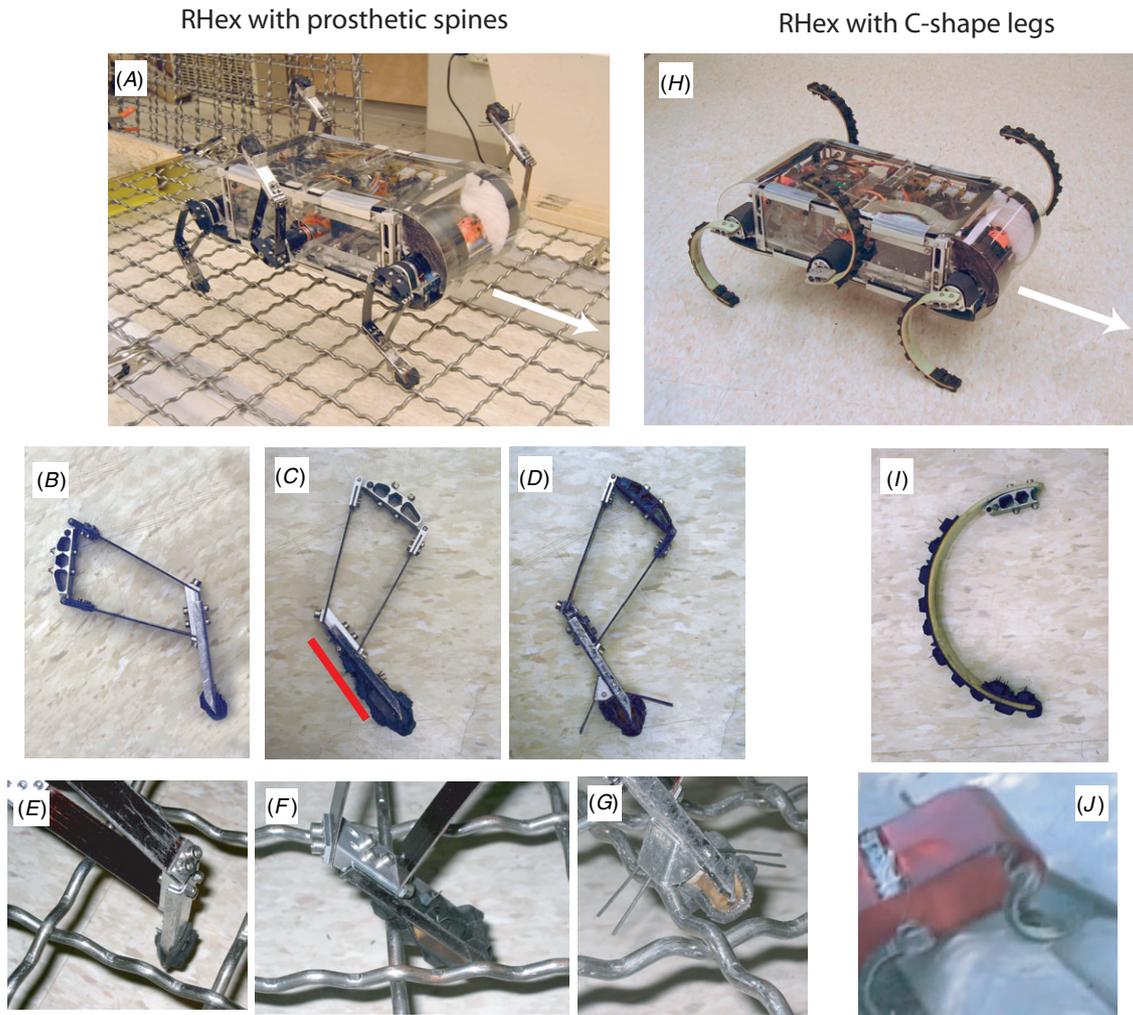
Figure 5. Legs of the robot hexapod, RHex. (*A–G*) RHex with four-bar legs and added spines on mesh of size 7.6×7.6 cm^2; white arrow shows direction of motion (*A*). Close-up of RHex's four-bar legs with small rubber feet and no broad area of contact (*B*), a broad area of contact shown by red bar (*C*) and a broad area of contact and collapsible spines projecting distally (*D*). Note position of legs in frames B, C and D represents positions of leg elements as attached to robot. Close up showing RHex's rubber-foot leg penetrating the mesh (*E*), contacting the broad contact area (*F*) and engaging spines of the leg with broad contact and collapsible spines (*G*). (*H–J*) RHex with half-circle legs (58); white arrow shows direction of motion (*H*). Half-circle leg of RHex with rubber tread to increase its effectiveness for distributed leg contact (*I*). RHex distributes leg contact by using half-circle leg to scale an obstacle (*J*). Maneuverability in debris was more successful when contact is frequently made above the foot tip.

spines of cockroaches (figure 1(*F*)) decreased their speed only when their tarsi were also removed, thus supporting the notion that a more horizontal leg trajectory may increase effective distributed contact (figure 1(*G*)).

In both species, distally projecting spines were oriented at approximately a 70° angle with the long axis of the segment (figures 1(*D*), 2(*D*)). During experiments, spines that caught on the wire mesh provided greater purchase as the animal pivoted on the engaged spine (figures 3(*A–B*), (*E–F*), (*H–I*)). High stiffness of spines in the direction away from the leg segment was sufficient for even single spines to transmit large propulsive forces during high-speed locomotion. By contrast, spines and hairs collapsed easily when pushed toward the leg segment (figures 3(*D*), (*G*), (*J*)). This important asymmetry— a simple example of a mechanical component that responds passively to mechanical events—allows a leg to be pulled out from debris without the spines catching and impeding

leg return during swing. Cuticular spines in arthropods have been extensively studied in their role as mechanoreceptors transducing environmental contact and vibration stimuli [45–47]. Although cuticular spines may play a mechanical role in cockroach climbing [37] and cricket jumping [48], perhaps a better functional comparison is to a ratchet, like those seen in the alternately extensible and collapsible hind-leg 'paddles' of water beetles [49].

3.3. Adding passive spines increases performance on non-native surfaces

If distributed leg contact is primarily responsible for the increased performance on surfaces possessing a low probability of secure footholds, then we predict animals lacking advantageous leg trajectories, configurations and spines will run poorly on these surfaces. Alternatively, animals native to surfaces with a high probability of contact, such

as sand, may run capably on these non-native surfaces by altering their leg orientation and placement in response to neural feedback. We tested these hypotheses by selecting the world's fastest legged invertebrate, the sideways running ghost crab, *Ocypode quadrata* [50, 51]. Ghost crabs ran feebly over the wire mesh, misstepping on approximately half the limb placements (see movie 5 available at stacks.iop.org/BB/2/9). Because ghost crabs move their legs more in the sagittal plane, have a narrow pointy foot and lack stiff cuticular spines, leading legs penetrated the wire mesh well past their foot or dactyl in 30% of the steps. Trailing legs failed to contact the mesh sufficiently to generate any force in 20% of the steps. Twelve percent of the leading-leg missteps led to catastrophic failures where the animal's velocity decreased to zero, or where the crab awkwardly changed orientation.

If simple passive structures, such as spines, are all that is required to increase the effectiveness of a distributed leg contact, then addition of artificial spines to a species not adapted to sparse terrain should increase running performance. Alternatively, if major adjustments in motor output are necessary to reliably engage these new structures, then performance may remain poor. We added 'prosthetic' spines to the legs of ghost crabs and ran them over the same wire mesh (see figure 4). We bonded two distally projecting, artificial spines on each leg above the dactyl (figures 3(K), (L)). Ghost crabs with artificial spines ran smoothly across the wire mesh engaging the spines on 24% of leading-leg steps, comparable to the number of leading-leg missteps without the 'prosthetics' (see movie 6 available at stacks.iop.org/BB/2/9). Addition of artificial spines reduced the percentage of leading-leg missteps to just 1.5% and catastrophic failures from leading-leg steps to only 2%. During leg return or upswing, artificial spines collapsed avoiding entanglement (figure 3(M)). Spines that simply increased the contact area without collapsing failed to provide an effective, passive mechanical response and did not increase performance.

3.4. Effective bio-inspired robot legs

Lacking evidence of active neural feedback, we were encouraged that the effectiveness of passive, distributed leg contact in arthropods could be tested in a physical model, the robot hexapod, RHex. Careful empirical studies on RHex and other robots have led to appropriately shaped, compliant legs [52–55] that greatly improve speed and efficiency over rough level ground. RHex matches a rapid running insect's pattern of whole body dynamics and single leg forces [56], figure 5. Early versions of RHex showed remarkable passive self-stabilization and agility with minimal sensing of its legs, body or the environment [43]. RHex rotates its legs in a circular motion producing trajectories in the sagittal plane more comparable to the spiders and crabs we studied. Because we could hold RHex's electronic control strategy constant, we reasoned that changes in performance on sparse-foothold terrain would solely be due to differences in distributed mechanical feedback. Specifically, we hypothesized that a robot possessing legs with a broader, more horizontally oriented foot, as we observed in cockroaches would travel

a longer distance on mesh than would a robot with legs using more of a point contact like crabs. A robot using legs with both a broad contact area and collapsible spines like spiders should show fewer miss-steps (penetrations) and traverse a longer distance on mesh than a robot with legs lacking spines like crabs or spiders with trimmed hairs.

We ran RHex approximately 180 times over a wire mesh $(76.2 \text{ mm})^2$ using three different leg types. One leg had only a small rubber foot allowing little opportunity for distributed leg contact (figure 5(B)). A second leg was configured so that a broader area of contact was possible (figure 5(C)) and a third leg offered distributed contact and had collapsible spines (figure 5(D)). RHex ran over three-fold farther on the mesh before failure with legs that allowed broad distributed contact (103.3 cm ± 7.7 SE) than with legs possessing small rubber feet (31.7 cm ± 1.4 SE; $P < 0.001$; ANOVA; see movies 7 and 8, available at stacks.iop.org/BB/2/9). Robots using spiny legs with distributed contact attained greatest running distance before failure (113.3 cm ± 7.0 SE). We did not find a significantly longer distance to failure in robots using spiny legs relative to those using broad contact ($P = 0.15$), in part, because in several trials the robots ran the length of the entire track without failure. Video analysis revealed that the collapsible spines on RHex increased purchase with the mesh (figure 5(G)) just as they did with the wire mesh in the spider experiments (figures 1(C), 3(E)–(G)). Versions of RHex with considerable stability and maneuverability have been built using a C-shaped leg with a high-friction rubber tread along its posterior surface rather than at its tip [52] (figure 5(I)). It is clear from video of RHex using C-shaped legs that a significant part of its success results from using distributed leg contact so effectively when traversing challenging natural surfaces, such as rock fields and forest debris [52] (figures 5(H)–(J)).

4. Conclusion

Understanding control of terrestrial locomotion over substrates in the natural world has been challenging because substrates differ in geometry, compliance and tendency to flow. To meet this challenge, we began a systematic approach to varying terrain parameters by first altering the probability of foot contact. By taking advantage of the diversity in nature, we selected animals that differ in their solutions to negotiating challenging terrain. We discovered that animals use passive distributed mechanical feedback to create an effective coupling with environment that results from the synergistic operation of leg trajectory, leg configuration and attachment mechanism. Animals possessing feet with a broader contact area, a more horizontal leg swing and/or effective attachment mechanisms, such as collapsible spines, can rely less on neurally mediated precise stepping. We found no evidence that these multi-legged runners use neural feedback to follow a foreleg's secure foothold or to adjust the location of where their legs contact the substrate. By using the kinetic energy of rapid running to bridge gaps in footholds and distributing mechanical feedback over many legs and locations along the leg, animals can overcome the inherent delays of neural feedback as well the problem of noisy sensors, thereby simplifying control. Use of

a physical model, a legged robot, supported our contention because the hexapod was able to traverse low probability foothold terrain better with a broader leg contact area and collapsible spines, but without a single change to its electronic controller. Our discovery of distributed mechanical feedback provided biological inspiration to a robot that can now traverse terrain previously impassable.

More generally, understanding of the control strategies that legged runners use in nature suffers from the lack of a satisfactory model of the terrestrial environment. An understanding of leg–surface interaction thus appears to be as important to terrestrial locomotion as the interaction of fins with water for swimming and wings with air for flying. The challenges of modeling terrestrial environments may be greater than in characterizing fluids. While models of air/water interaction with solid matter are difficult to analyze, such models in principle exist as solutions to the Newtonian Navier–Stokes equations with moving boundary conditions. Equivalent models of interaction with complex, heterogeneous, multi-scale fluidizing terrain do not exist [57, 58] and this precludes detailed modeling of terrestrial legged locomotion [59]. The most detailed locomotion interaction studies have been in the field of terramechanics, in which empirical models are developed to account for the interaction of soil, muskeg and snow cover with track and wheeled vehicles [58]. However, models of substrates at the level of Navier–Stokes equations are rare. For example, no fundamental model of granular materials is available that describes behavior in the solid and fluid regimes [60] and models for the heterogeneous material like debris are typically concerned with large-scale flow [61]. Pioneering studies of regimes of granular materials behavior in gas, fluid, solid [60, 62–65] and mixed [66–68] regimes suggest a day when detailed contact models may be possible for more complex materials such as tree bark, forest debris and heterogeneous soils. Continuing advances in the analysis of simple spring–mass mathematical models for single point leg contact running give the promise of a more cogent underpinning for tuning reflex and preflex feedback controllers on smooth level ground [69], but new models are needed that focus on leg–surface coupling. The use of robots as physical models that meet actual environments to test hypotheses promises to accelerate our understanding of animal locomotion. Adopting robots as physical models for biology has a return benefit. A continued systematic study of the manner in which diverse animals combine distributed neural and mechanical feedback to negotiate the heterogeneous material distributed over substrates of widely varying geometry and material properties seems likely to provide biological inspiration for near-term gains in robot mobility over natural terrain.

Acknowledgments

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