

Climbing, falling, and jamming during ant locomotion in confined environments

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Locomotion emerges from effective interactions of an individual with its environment. Principles of biological terrestrial locomotion have been discovered on unconfined vertical and horizontal substrates. However, a diversity of organisms construct, inhabit, and move within confined spaces. Such animals are faced with locomotor challenges including limited limb range of motion, crowding, and visual sensory deprivation. Little is known about how these organisms accomplish their locomotor tasks, and such environments challenge human-made devices. To gain insight into how animals move within confined spaces, we study the locomotion of the fire ant *Solenopsis invicta*, which constructs subterranean tunnel networks (nests). Laboratory experiments reveal that ants construct tunnels with diameter, D , comparable to body length, $L = 3.5 \pm 0.5$ mm. Ants can move rapidly (> 9 bodylengths per s) within these environments; their tunnels allow for effective limb, body, and antennae interaction with walls, which facilitate rapid slip-recovery during ascending and descending climbs. To examine the limits of slip-recovery in artificial tunnels, we perform perturbations consisting of rapid downward accelerations of the tunnels, which induce falls. Below a critical tunnel diameter, $D_c = 1.31 \pm 0.02 L$, falls are always arrested through rapid interaction of appendages and antennae with tunnel walls to jam the falls. D_c is comparable to the size of incipient nest tunnels ($D = 1.06 \pm 0.23 L$), supporting our hypothesis that fire ants construct environments that simplify their control task when moving through the nest, likely without need for rapid nervous system intervention.

animal locomotion | extended phenotype | locomotion control | social insect | stability

Terrestrial animals and increasingly robots must move in diverse and complex environments, including running across flat landscapes (1), swimming in sand (2), climbing rough or smooth vertical surfaces (3), and squirming through cracks (4). The bulk of discoveries of locomotor behaviors and control strategies have been made by challenging animals in the laboratory in simplified environments that are typically featureless, flat, and unconfined (5). Such simplifications have allowed discovery of general principles in locomotor modes of walking, running, and climbing (6–9). Recent studies have generated appreciation for the importance of mechanical interactions with the environment, and through biological experiment (10) and robot modeling (11, 12) have demonstrated that stable and robust movement can emerge as a result of appropriately tuned dynamics of limb–ground interaction (13, 14). For example, rapid perturbations to locomotion may be corrected by so-called “preflexes” (15) in which mechanical design of the limb and appropriate kinematics enable rapid recovery from perturbation (6, 8, 10). However, typical substrates that legged locomotors contend with differ in orientation, can deform in response to foot/body contact (1, 11), and are rough on multiple size scales (16, 17); little is known about how organisms effectively use limb/body–substrate interactions in such environments. Practically, we expect that discovery of such principles can lead to advances of robotic devices that must operate in complex conditions; such devices often suffer performance loss in natural environments (11).

In particular, the role of confinement is relatively unexplored in locomotor performance and behavior. Many subterranean-dwelling organisms live and move within confined spaces in their environments (18, 19). The morphology (20, 21), energetic costs (22–25), and genetic basis (26, 27) for creating subterranean burrows and nests, which are examples of the “extended phenotype” (28), have been studied across a diversity of organisms. However, the constraints on locomotion of individuals and groups inhabiting these environments are largely unexplored (29). Rapid locomotion within the confines of a subterranean nest is essential for inhabitants to escape or respond to predators (18, 30), evacuate during flooding (31), or transport resources and information effectively (30). However, lack of vision (18, 19, 32), limited limb mobility (18), and excessive crowding among individuals (33) would seemingly challenge efforts at rapid locomotion within confined environments. Thus, we seek to understand how such environments influence the mobility and stability of animals moving within them.

Ants are excellent organisms with which to study confined locomotion. Many ant species construct large underground nests through the excavation of soil (34). Nest shape and size—in addition to ant shape and size—varies widely across species but typically consists of vertical tunnels that connect larger chambers used for food storage and brood rearing (21, 34). A majority of an ant colony worker’s life is spent below the surface within the nest—tending to brood or performing routine nest maintenance—and only near the end of life do worker ants forage above surface (34–37). The evolutionary pressure of subterranean life has led to several adaptations among ants such as partial or complete loss of vision in some species (38, 39) and long-range acoustic (40–42) and chemical communication systems (38, 43, 44). However, almost nothing is known about how ants move through their confined nest environments.

We hypothesize that ants have developed strategies and adaptations for rapid movement within nests, particularly during crucial times such as nest reconstruction or evacuation. A species that frequently must contend with such events is the red imported fire ant (*Solenopsis invicta*). Fire ants originate from the Pantanal wetlands in South America, which are subject to seasonal rains and flooding (37). Fire ant colonies construct large and relatively complex subterranean nests (37) that can be up to 2 m deep and contain greater than 50 m in length of tunnels (45). As an invasive species in the Southern United States, fire ants have demonstrated proficiency at constructing nests within a wide range of soil conditions (37). Construction of such large nests demands the ability to move repeatedly and stably within the nest confines while transporting soil.

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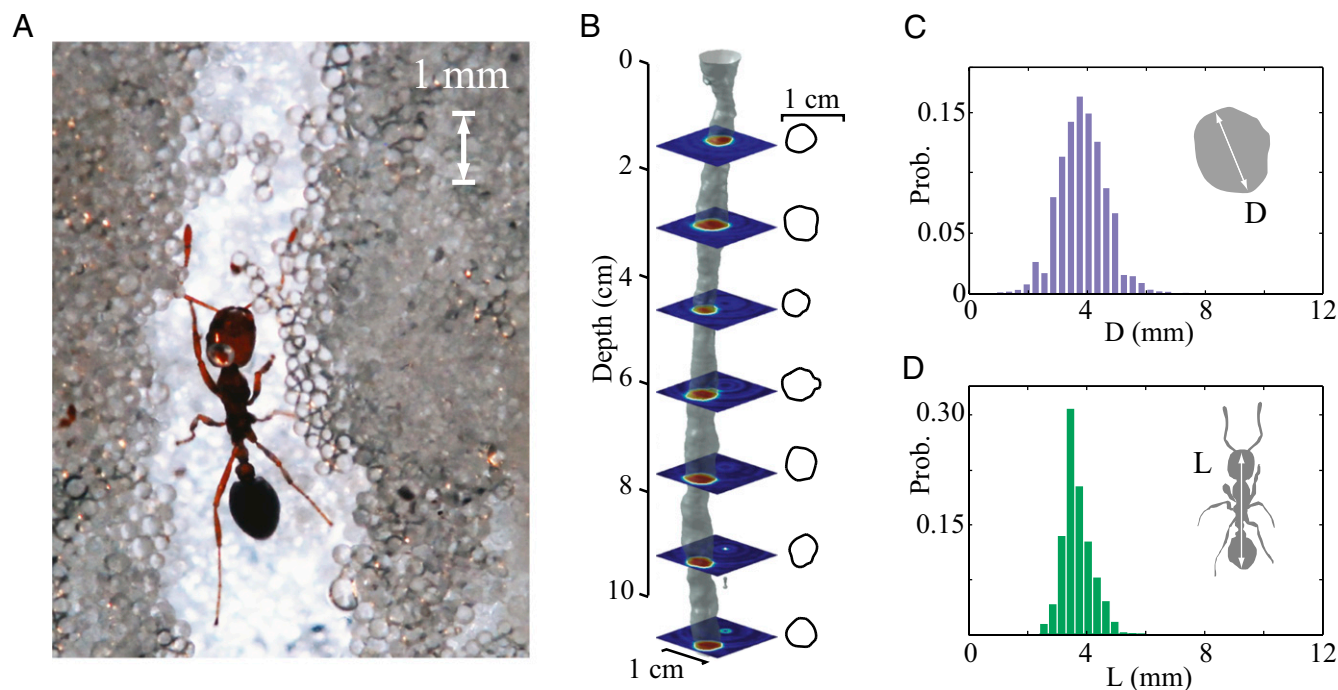


Fig. 1. Fire ants create and move through subterranean tunnels (Photo credit: Laura Danielle Wagner). (A) Image shows fire ant worker climbing within an ant-constructed tunnel against a clear glass pane. (B) X-ray CT scan reconstruction of a fire ant tunnel segment. (C) Probability distribution of tunnel cross-sectional diameter, D . In A–C, the substrate consists of wetted 250 micron approximately spherical glass particles. (D) Probability distribution of ant body length, L (measured from head to gaster), in laboratory climbing experiments.

In this article we seek to identify principles of locomotion within confined environments that challenge animals with a different set of locomotive constraints than in above-ground study. We investigate the effects of subterranean confinement (tunnel diameter) on the mobility and stability of the fire ant (*S. invicta*). We show that climbing in confined environments is a robust mode of high-speed locomotion, in which slips, falls, and frequent collisions with the environment do not necessarily prevent high-speed ascent and descent. We also demonstrate an unusual stabilizing response of fire ants when dislodged from the tunnel wall—the use of antennae as limb-like appendages to arrest and jam falls. Overall, we find that stable locomotion within subterranean environments is a function of the local tunnel morphology within which the organisms move. We hypothesize that the principle of off-loading locomotor control to the environment can be used by animals in confined environments and can inspire the next generation of mobile robots.

Results and Discussion

Shape and Form of Excavated Fire Ant Tunnels. To examine the interaction of fire ants with the tunnels that they constructed, we first measured the size and shape of nest tunnels excavated by fire ant workers (body length $L = 0.35 \pm 0.05$, $n = 2,611$ measurements) in three-dimensions in a laboratory experiment using an X-ray computed tomography (CT) system (Fig. 1 and Fig. S1). We allowed isolated groups of fire ant workers to excavate tunnels within an 8 cm diameter, and 12 cm deep, cylindrical volume of laboratory soil (wet approximately spherical glass particles, see below) over the course of 20 h. The tunnels were roughly circular in cross-section (Fig. 1B, Fig. S2, and SI Text), and the effective cross-sectional diameter (SI Text) within the tunnels was $D = 3.7 \pm 0.8$ mm ($n = 2,262$ observations from 10 experiments).

To determine if the soil substrate had an effect on tunnel shape and size, we repeated this experiment using different substrate

combinations of particle diameter (50, 210, and 595 μm ; See [Table S1](#) for polydispersity) and soil moisture content (1%, 3%, 5%, 10%, 15%, 18%, and 20% by mass). We challenged worker groups from eight separate colonies to excavate tunnels in each substrate combination and collected 168 separate X-ray CT tunnel excavation observations ([Fig. S3](#)). We found a significant effect of both particle diameter ($F_{2,136} = 10.48$, $P < 0.0001$) and soil moisture content ($F_{6,136} = 5.38$, $P < 0.0001$) on excavated tunnel depth, indicating that substrate had a strong effect on digging proficiency. Soil moisture content had a nonlinear effect on tunnel depth. Tunnel depth was small at low soil moisture and rose to a maximum at intermediate soil moisture contents of 10–15%, above which tunnel depth decreased again at high soil moisture ([SI Text](#)).

Importantly, however, we found no significant effect of soil moisture ($F_{6,106} = 1.06$, $P = 0.39$), particle diameter ($F_{2,106} = 1.56$, $P = 0.21$), or the interaction of moisture and particle size ($F_{12,106} = 1.47$, $P = 0.15$) on the tunnel diameter (*SI Methods*). Moreover, tunnels constructed in the laboratory and observed in X-ray CT were similar in diameter to tunnels found in natural fire ant nest mounds (4.4 mm) (46), nest entranceways (3–4 mm) (45), and incipient nests (3.1 ± 0.1 mm) (47), although tunnels deeper within natural nests may be larger in size (6.0 ± 3.0 mm) (46). Our results demonstrate that during tunnel founding, fire ants show a relatively fixed behavioral program by building tunnels of approximately the same diameter in a variety of conditions. This suggests that the diameter of the tunnel could be important in fire ant locomotion.

Tunnel Size Effects on the Biomechanics of Confined Climbing. To investigate the biomechanics of locomotion within tunnels, we monitored fire ants climbing within ant-constructed tunnels within Quasi-2D arenas (Fig. 1*A* and [Movies S1–S3](#)) and smooth cylindrical glass tubes (Fig. 2*A* and *B*). We tracked the position of ascending and descending ants freely trafficking between

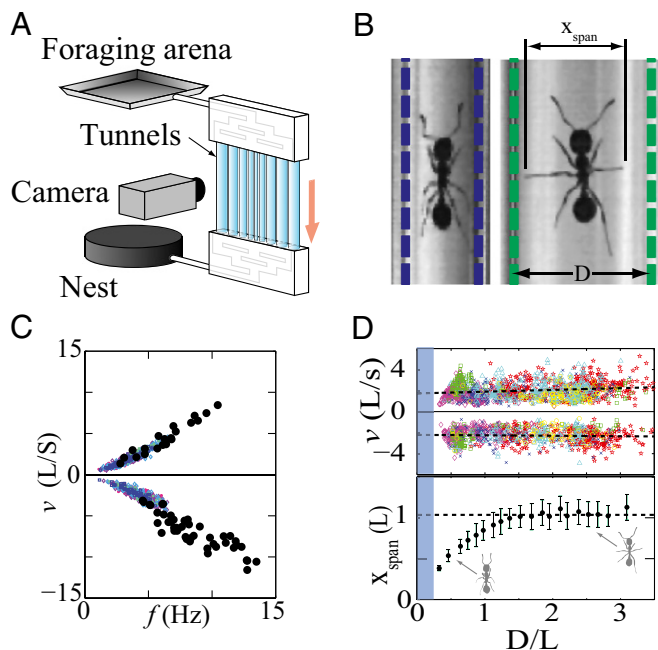


Fig. 2. Climbing posture and antennae use in glass tunnels. (A) Schematic of climbing biomechanics experiment. (B) Posture of ascending ant in a 2 mm diameter tunnel (Left; $D = 0.60 L$) and in a 6 mm diameter tunnel (Right; $D = 1.36 L$). Right image shows posture variable, x_{span} , measured in experiment. (C) Stride frequency and speed relationship for glass tunnels (colored points) and ant-created tunnels (filled black circles). (D, Upper) Speed versus D/L . Color indicates colony. Dashed lines are linear fits described in the text. Blue box indicates the minimum predicted tunnel diameter in which an ant could fit. (D, Lower) Lateral limb span (mean \pm SD) as a function of normalized tunnel diameter. Dashed line indicates constant limb span of $x_{span} = 1.04 \pm 0.14 L$ independent of tunnel diameter.

a foraging arena and nest through glass tubes of diameters, $D = 1.0$ – 9.0 mm (in increments of 1 mm). We will refer to these glass tubes as “glass tunnels.”

We found that ants rapidly ascended ($2.0 \pm 0.8 L s^{-1}$, $n = 1,621$ ants) and descended ($2.3 \pm 0.7 L s^{-1}$, $n = 990$ ants) in the glass tunnels (Figs. S4 and S5). The kinematic relationship between stride frequency and speed (Fig. 2C) was fit by the function $v = ax^2 + bx$ for both the ascending ($a = 0.039 \pm 0.003 L s$; $b = 0.41 \pm 0.01 L$) and descending ($a = -0.018 \pm 0.005 L s$; $b = -0.49 \pm 0.02 L$) climbs (Figs. S6 and S7). The speed–frequency relationship of ascent did not significantly differ among the ant-constructed tunnels and the glass tunnels of diameters, $D = 0.3$ – 0.4 mm (comparable to that of the self-constructed tunnels; $F_{2,361} = 1.8150$, $P = 0.1643$). We did, however, find a small but significant difference in functional form of the speed–frequency relationship during descent ($F_{2,252} = 113.9$, $P < 0.001$). To test maximal performance within ant-constructed tunnels, we induced an alarm response among the colony by exhaling into the tunnel entrance. Within ant-constructed tunnels, ants rapidly descended ($6.9 \pm 2.1 L s^{-1}$; $n = 21$) and ascended ($4.1 \pm 1.8 L s^{-1}$; $n = 45$) at speeds greater than observed in the glass tunnels and surprisingly were able to move at speeds greater than $9 L s^{-1}$ within the confined, simulated nest environment.

Tunnel diameter had a weak but significant effect on ascending speed (Fig. 2D, Upper), as a function of D/L [$v = m(D/L) + b$; F test for nonzero slope, $F_{1,1619} = 63.132$, $P < 0.001$; $m = 0.17 \pm 0.04 L^2 \cdot D^{-1} \cdot s^{-1}$, $b = 1.73 \pm 0.07 L s^{-1}$]. During descent in tunnels, D/L did not have a significant effect on speed (F test for nonzero slope, $F_{1,988} = 2.740$, $P = 0.10$). We thus hypothesized that the minimum tunnel diameter through which an ant can move is

slightly larger than the animal’s head width. Fire ant head width is $0.24 \pm 0.01 L$ (48), and this sets the lower limit of the range of observable D/L values (shaded blue box Fig. 2D). Both ascending and descending speeds near this lower limit ($D/L < 0.5$) sharply decreased (Fig. 2D, Upper), suggesting that only in the case of extreme confinement would we observe a strong effect of tunnel diameter on ascending or descending velocity. Overall, this suggests that ants move at a near constant upward and downward speed, over a wide range of tunnel sizes, while freely trafficking within the nest.

Tunnel diameter had a significant influence on climbing posture (Fig. 2D, Lower). Ants exhibited one of two stereotyped climbing postures: (i) within glass tunnels of $D > L$, ants adopted a sprawled posture in which midlimbs were extended laterally away from the body (Fig. 2B, Right), and (ii) within glass tunnels of $D < L$, midlimbs were bent and pointed posteriorly (Fig. 2B, Left). We determined the critical tunnel diameter at which this postural transition occurred by fitting

the function $x_{span} = \begin{cases} k(\frac{D}{L}) & \text{for } D < D_c \\ c & \text{for } D > D_c \end{cases}$. We determined that

in glass tunnels of diameter above $D_c = 1.03 \pm 0.01 L$ the lateral limb span, x_{span} , was independent of tunnel size ($R^2 < 0.001$) with mean value of x_{span} , determined from fit parameter $c = 1.04 \pm 0.14 L$ (Fig. 2D). In glass tunnels of diameter less than D_c , limb posture was altered by tunnel confinement and x_{span} subsequently decreased (Fig. 2D). For comparison with ant-created tunnels, excavated tunnel diameter was $D = 1.06 \pm 0.23 L$. Thus, ants modify their limb position depending on tunnel size, but maintain approximately the same rate of ascent and descent. Furthermore ants climbing within tunnels they construct are capable of using their spread-limb posture, which may have implications for locomotor stability.

The alteration of the midlimb posture in smaller tunnels suggests that a transition occurs in the direction of locomotor force production by the midlimb. In the sprawled posture, midlimb tarsi contact forces pull toward the body and the tarsal hooks and adhesive pads are likely engaged. In contrast, when the limb is in the compact posture, the limb pushes down and

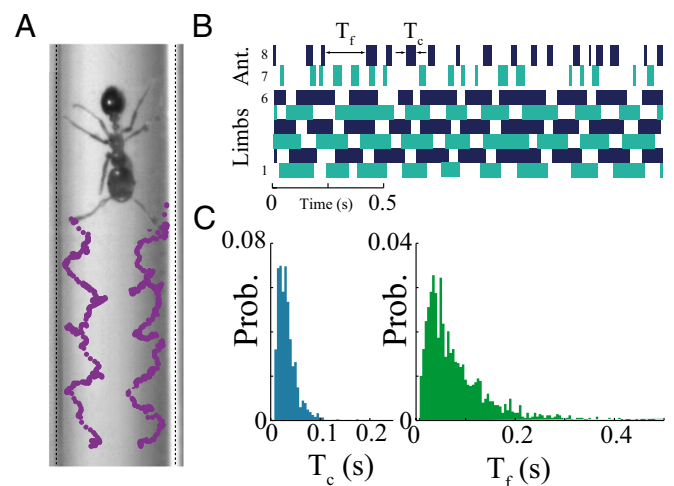


Fig. 3. Antennae use in confined locomotion. (A) Image of ant descending in a tunnel with tracked position of antennae tips shown in purple. $D = 3$ mm. (B) Stepping and antennae contact diagram for a vertical descent in a tunnel. Light and dark blue highlight limbs that form alternating tripods during locomotion: (1) right hind, (2) right mid, (3) right fore, (4) left fore, (5) left mid, (6) left hind. Right and left antennae are denoted by (7) and (8) respectively. Time of antennal contact, T_c , and time free, T_f , are highlighted. (C) Probability distribution for both T_c and T_f .

tarsi and adhesive footpads are robust to substantial perturbations, consistent with other measurements of the ant's adhesive strength (55–57). However, displacement from the tunnel surface did occur in 48% of experiments, and the outcome of perturbations was strongly influenced by the interaction of ant tunnel size.

We found that tunnel diameter, with respect to ant body length, had a significant effect on the probability to fall during a perturbation experiment, with smaller tunnels aiding in the ants' perturbation resistance (Fig. S12B). The probability to fall during a perturbation increased from 36% to 73% as D/L increased from 0.4 to 3.4; the increase occurred over a narrow range around D/L \approx 2.3. The resistance to perturbation in tunnels of D < 2.3 L was likely due to the ability of fire ants to robustly engage surfaces. When climbing vertical planar surfaces, animals have to contend with gravity, which, because the animal's center of mass is offset from the climbing surface, generates an overturning moment on the animal that must be overcome. In contrast, when climbing in small tunnels, ants may be able to minimize torque-induced gravity on the body by placing limbs laterally against walls and thus keeping the center of mass in the same vertical plane as limb contact points.

Ants perturbed from the tunnel wall either arrested their fall within a vertical distance Δy , or fell to the tunnel bottom (Fig. 5B and Movie S5). Arrest distance, Δy , increased with increasing tunnel diameter normalized by body length, D/L (Fig. S13). The upper envelope of Δy (dashed line in Fig. S13) increased linearly with a slope 67 ± 7 mm ($R^2 = 0.95$). This relationship can be understood through a kinematic argument: to arrest falls, ants extend limbs and antennae toward tunnel walls that are a further distance away within larger tunnels, and this results in longer fall distances in larger tunnels (SI Text).

The probability to arrest a fall, P_{arrest} , within a tunnel of size D/L decreased from 1 to 0 as D/L increased. We fit P_{arrest} to a logistic function, $P_{\text{arrest}} = 1/[1 + e^{\frac{\alpha}{L}(D - D_s)}]$ (Fig. 5B) and found the cutoff tunnel diameter, $D_s = 1.31 \pm 0.02$ L ($\alpha = -10.54 \pm 1.76$), at which arrest probability decreased to below 50% (see Fig. S5 and Table S2). Within ant-constructed tunnels (of mean diameter 1.06 L; Fig. 5B, Lower) we predict that 93% of falls will be arrested. This demonstrates that ants display a high degree of climbing stability within tunnels of comparable size to those they create (1.06 L); however, an increase in tunnel diameter by 50% reduced arrest probability to less than 5%.

We hypothesized that tunnel diameter would limit the ability to recover from falls through a “jam arrest” mechanism within tunnels. Thus, we expected that D_s was governed by morphological limitations of ant limb use. We measured the lateral limb span, x_{span} , for free-falling ants and found that ants extended limbs maximally to a width of $\max(x_{\text{span}}) = 1.33 \pm 0.22$ L independent of tunnel size when $D > 1.3$ L. This measurement is consistent with the typical midlimb span of fire ants 1.31 ± 0.09 L reported in the literature (SI Text and Fig. S15) (48) and suggests ants are extending limbs maximally to re-engage the tunnel wall while falling. In tunnels whose diameter exceeded the physical reach of the ants, $D > 1.3$ L, ants were unable to engage walls and the arrest probability decreased substantially (Movie S5).

We return to the digging experiments—in which groups of ants constructed tunnels—to understand how ant tunnel size relates to stability in confined spaces. The average diameter of tunnels created by ants across all excavation experiments was $D = 1.06 \pm 0.23$ L. Thus it seems reasonable to assume that fire ants construct tunnels that facilitate rapid locomotion through the enablement of slip recovery by antennae and limb jamming, without hindering limb kinematics. Many other factors are likely to influence equilibrium nest tunnel size. Traffic may be important in nest tunnel size determination as it is hypothesized that larger tunnels in the nest foraging network are due to higher traffic flow in these locations (46, 58). Further, food transportation

requirements, ventilation, protection from flooding, and protection from invasion by predators or other brood raiding colonies can also influence nest structure (34). We hypothesize that the shape and size of tunnels at any time reflects the important environmental and biological factors influencing the colony at that time (37, 47). However, during incipient nest construction, such as after a flood, we expect that high-speed locomotion and excavation are important to survival.

Conclusions

We have shown that fire ants are capable of moving rapidly within their nest through the use of multifunctional limbs and antennae, which effectively engage tunnel surfaces. We found that tunnel diameter had little effect on locomotion speed over a threefold range of tunnel diameters, although body posture and limb use differed in different-sized tunnels. We also discovered that fire ant antennae were effectively used as additional limbs during locomotion. Functionality of antennae as load-bearing, locomotor appendages was a surprising result, one which highlights the importance of studying locomotion within the context of the organism's natural environment. During locomotion, antennae were rapidly and repeatedly placed in contact with the tunnel surface for sensory feedback, however the antennae's multifunctional nature also implies that antennae may be the ant's first option to rapidly recover from missteps or slips. X-ray CT indicated that fire ants constructed tunnels of appropriate size to enable utilization of the slip recovery mechanisms we observed in laboratory climbing experiments.

The ability for organisms to offload locomotion control to their environmental structures represents a new paradigm of locomotion control and a novel example of the integration of the organism's extended phenotype (the nest) for a locomotory purpose. We hypothesize that the construction of control surfaces suited to the locomotors' body size and limb kinematics reduces locomotion control requirements within subterranean environments and may be a general feature of robust control within organism-engineered substrates such as tunnels, trails, or burrows. A universal scaling of burrow cross-sectional area with body length (20)—sampled across a wide array of organisms varying by over six orders of magnitude by mass—provides evidence of the commonalities of locomotor constraints among subterranean animals. Thus, the robust locomotor control strategies for subterranean environments we have described for fire ants may apply to a diversity of subterranean animals. We also expect that our biological discoveries will provide inspiration for, and simplify control in, collective robotic devices that will have to move within confined environments such as search and rescue zones. We propose that future robot teams could enhance survival in harsh terrestrial and extraterrestrial environments through collective construction of appropriately engineered shelters and nests.

Methods

Digging Experiments. We used a custom X-ray CT system to observe tunnel excavation. Groups of 100–150 fire ant workers dug tunnels in 3.8 or 8.2 cm diameter chambers filled to a height of 12–15 cm with slightly polydisperse glass particles of diameter 50, 210, or 595 μ m (Jaygo Inc.; see Table S1 for particle size distribution). We varied water moisture content in the simulated soil between 1% and 20% measured by mass. From CT reconstructions we extracted the tunnel shape using the Chan–Vese active contours method (59). We measured the effective tunnel diameter, D , as the maximum of the distance transform of the tunnel cross-section (SI Text).

Climbing Experiments. Climbs in ant-constructed tunnels were observed in quasi-2D arenas, $27 \times 34 \times 0.3$ cm in size, filled with wetted granular material as described in ref. 60. Ants climbed between a nest and foraging arena through glass tunnels of diameter D 1–9 mm (in increments of 1.0 mm) and length 107.0 mm (Technical Glass). Movies of climbing ants were recorded at a frame rate of 200 and 400 Hz (AOS Technologies). To observe the falling response of ants within tunnels, we performed a perturbation experiment in

which a fixture holding the glass tunnels was mounted to a vertical, computer-controlled air piston. The air piston accelerated the tunnels from rest 5 mm downward over a time period of 0.15 s. Air piston activation was automated and triggered by ant movement, which in turn triggered the capture of high-speed video. All perturbed and unperturbed climbing experiments were performed while ants freely trafficked between the nest site and the foraging arena.

Statistics. In all experiments ant body length was measured from the base of the mandibles on the head to the tip of the gaster. Ant body length was

measured by selecting points in Matlab. Statistical tests were performed in Matlab and JMP (SAS Software). Analysis of variance was used for comparisons among treatments. In digging trials we treated colony and date as random factors in an analysis of variance. For comparing the statistical significance of nonlinear regression models to data, we used the method described in Motulsky (61). All results are reported as mean \pm SD.

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Supporting Information

Gravish et al. 10.1073/pnas.1302428110

SI Text

SI Methods

Ant Collection and Care. The *Solenopsis invicta* colonies were collected during the spring of 2012 from roadsides outside of Atlanta, GA. Nests were excavated and transported to the laboratory and ants were separated from the soil using the water drip method (1). Colonies were housed in open plastic bins in a temperature-controlled room with 12 h on, 12 h off lighting. Colonies were provided ad libitum water and insect larvae as food.

Digging Experiments. The digging arenas were placed on a rotating stage controlled by a stepper motor (Lin Engineering), which was located 76 cm from a 110 kVp, 3 mA X-ray source. An image intensifier was located 103 cm from the source and a Phantom v210 camera (Vision Research) was used to visualize the X-ray images. Samples images were taken at angular increments of 0.9°. We chose tunnels that were not adjacent to a wall (Fig. S1) and extracted the tunnel shape using the Chan–Vese active contours method (2). Tunnel properties were measured using the Matlab image morphology toolbox. We computed the distance transform of the tunnel shape using the Matlab command *bwdist* and considered the maximum value of the distance transform as the effective tunnel diameter.

Digging experiment 1. Groups of fire ant workers were challenged to dig tunnels in the laboratory. The 8.2 cm diameter cylindrical containers were filled to a depth of 12 cm with a dry granular material of particle size $250 \pm 50 \mu\text{m}$ (Jaygo Inc., Dragonite Soda Lime Glass beads, #5210). Arenas were first fully immersed in water to saturate the soil and then allowed to drain for 1 h. Wet soil is known to induce digging in natural fire ant nests (3). Workers were introduced into the arena and were allowed to dig for 24 h with a constant light source maintained above to stimulate digging. We evaluated the tunnel cross-section shape at various depths among 10 separate digging trials, each containing multiple tunnels, which resulted in 2,262 observations of tunnel diameter.

Digging experiment 2. In a second set of nest construction experiments, we varied soil moisture content and particle size. We used collections of glass beads of diameter 50, 210, or 595 μm (See Table S1 for polydispersity), which were mixed with water and prepared at moisture contents of 1%, 3%, 5%, 10%, 15%, and 20% (measured by mass). Table S1 summarizes particle size distribution. Digging substrate was placed in a 3.8-cm-diameter cylindrical digging arena filled to a height of 14.5 cm. A 1 cm diameter plastic tube inserted into the center of the surface constrained the workers to initiate digging away from walls. We generated uniform compaction of the moistened media by sieving the wetted granular material through a mesh grid with 1 mm grid spacing using VTS 500 single vibrator system. Groups of 100 workers were introduced into the digging arenas, and we evaluated tunnel shape in CT scans at 10, 15, and 20 h. Eight separate colonies were tested at each particle size and moisture content combination resulting in 185 excavation experiments. We measured tunnel depth and cross-sectional shape at a depth of half the tunnel depth. We tested for the effect of particle size, water content, and the interaction (particle size) \times (water content) using an analysis of variance in which colony and test date were treated as random effects.

Climbing Experiments. Arena experiments. Quasi-2D arenas, $27 \times 34 \times 0.3 \text{ cm}^3$ in size, were filled with the same wetted granular material as described in *Digging experiment 1* (above) and were

prepared to allow for ant visualization during locomotion (see ref. 4 for details). A group of 150 ants excavated in the simulated soil for 48 h. We observed tunnel locomotion using a macro-lens and a Phantom v210 camera, capturing video at 500 Hz. We encouraged high-speed ascent and descent through ant-created tunnels by triggering an alarm response among the workers in which we exhaled gently into the nest entrance at the top surface.

Glass tunnel climbing experiments. We used a simulated nest environment to study ant climbing in smooth glass tunnels in which we could view the interaction of all limbs and antennae with the climbing substrate (Fig. 2). An enclosed, light-proof box that contained a wetted porous floor (plaster of paris) served as a nest, and housed 150–300 worker ants during the course of an experiment. The simulated nest was connected to a foraging arena through a series of nine glass vertical observation tunnels ranging in inner diameter from 1–9 mm in increments of 1 mm. Tunnels were 107 mm long, and we observed a 96 mm length of them. Tunnels were illuminated by LED lights for visualization with a high-speed camera. Ad libitum water and food were provided in the foraging arena, which encouraged worker traffic to and from the nest. A heat lamp was placed over the foraging arena to create a temperature gradient between the “above-surface” foraging arena and the “subterranean” simulated nest. The simulated nest and foraging arena setup encouraged ants to freely traffic within the tunnels and allowed us to observe tunnel climbing while performing a natural, unperturbed behavior.

Ant climbing posture was computed in Matlab in which we isolated the ant body from the stationary background using an active contours algorithm (2). We computed the vertically oriented bounding box of the ant profile with the horizontal dimension of this box representing x_{span} . Climbing ants could be found at any angular location along the tunnel wall, and thus we removed all runs in which ants were visualized from the lateral sides. Furthermore, in measuring horizontal limb span we only included ant postures in which the body axis measured from gaster to head deviated from the vertical by less than 10°. This resulted in 483,525 observations of climbing posture from all phases within the stride.

Glass tunnel perturbation experiments. To observe the falling response of ants within tunnels we performed a perturbation experiment. Glass tunnels were mounted to a vertical air piston maintained at 551 kPa and controlled through a computer. The piston’s motion stopped upon impact with the mounting plate, and vertical motion halted in less than 2.5 ms. We calculated that the final downward speed of the tunnels before impact was 0.66 m/s, which suggests that ants were subject to a mechanical perturbation of $\sim 27 \text{ g}$ upon stopping.

Activation of the air piston was controlled by a computer program that monitored motion in the upper portion of the tunnel region. When an ant was detected entering this region, a relay was activated that controlled a high-speed solenoid that engaged the air piston. Simultaneously a trigger signal was sent to a high-speed camera (AOS Technologies) that captured 2-s perturbation response videos at 1024×1280 , 400 frames per second and 500 μs exposure time. Analysis of perturbation experiments was performed using Matlab image analysis tools. Users determined fall distance, ant length, ant orientation, fall time, and fall code (successful arrest, no arrest, no fall) from the perturbation response videos. We observed 2,268 perturbation response experiments among worker ants from five of the six host colonies (B–F).

($t_{25} = -5.7862$, $P < 0.001$). Midlimb distance significantly decreased from 0.46 ± 0.04 L in the large treatment to 0.12 ± 0.04 L in the small treatment ($t_{25} = 22.55$, $P < 0.001$). Rear limb distance decreased from -0.53 ± 0.04 L in the large treatment to -0.32 ± 0.03 L in the small treatment ($t_{25} = -13.0435$, $P < 0.001$). Thus, all three limb pairs underwent a transition in kinematics between conditions of large tunnels, which allow for full limb mobility, to small tunnels, which constrain limb motion and require a postural alteration.

Evidence of Antennae Use During Falling. We observed that in perturbed and unperturbed falls, ants placed antennae against the tunnel wall and deflected or halted their center of mass motion about these antennae–tunnel contact points. Fig. S9 shows an unperturbed fall in which the antennae are spread toward the wall at the initiation of a fall. In this example, the ant fell a distance of approximately two body lengths and arrested the fall through a combination of antennae and limb contact with the tunnel wall. Following this fall, the ant continued descending within the tunnel and the tracked points after the fall show the use of antennae while climbing down. In Figs. S10 and S11, we show eight additional examples of antennae use during unperturbed head-first falls. Video of each fall is shown in [Movie S4](#).

Perturbation Experiment Statistics. We found that in 52% (1,092 falls out of 2,584 perturbations) of the perturbation experiments, ants were not displaced from the tunnel wall (Fig. S12A). Tunnel diameter, with respect to ant body length, had a significant effect on the probability to fall during a perturbation experiment, with smaller tunnels aiding in the ants' perturbation resistance (Fig. S12B). We fit the fall probability with a logistic function $p_{fall} = a + [b / (1 + e^{\frac{\alpha}{b}(D_f - D)})]$ ($a = 0.37 \pm 0.05$, $b = 0.36 \pm 0.09$, $\alpha = 12.69 \pm 17.95$, $D_f = 2.3 \pm 0.2$). The probability to fall during a perturbation doubled from 36% when $D < 2.3$ L to 73% when $D > 2.3$ L.

We measured the distance perturbed ants fell, Δy , within tunnels of different diameter (Fig. S13). We found that fall distance increased with increasing tunnel diameter. To gain insight into this relationship, we construct a simple model of fall arrest in tunnels. We assume that falling ants must extend their limbs to regain contact with the wall. We define the lateral limb distance from the body axis as l , and the distance the limb is from

the wall as $\Delta l = D - l$ (we assume the ant is in the center of the tunnel). An ant falling from rest under gravity will accelerate downward with a vertical position as a function of time given by $\Delta y = \frac{1}{2}gt^2$. We assume that the limbs are accelerated outwards from the body at a constant rate, a , which results in horizontal limb position $l = \frac{1}{2}at^2$. Eliminating t^2 from the two equations we obtain the relation $\Delta y = \frac{g}{a}l$, which can be put in terms of tunnel diameter as $\Delta y = \frac{g}{a}(D - \Delta l)$. Thus, we see that fall distance scales linearly with tunnel diameter and the upper envelope of arrest points is well approximated by a line.

Falling Posture and Lateral Limb Span. For each perturbation experiment, we measured the lateral distance, x_{span} , that falling ants extended limbs and antennae to in the horizontal plane as a function of time (Fig. S14). Ants perturbed from tunnel walls extend their limbs and antennae laterally away from their body to re-engage contact with the tunnel surface during a fall. To determine the maximum lateral limb and antennae span ants display when falling, we measured the maximum of x_{span} . We find that $\max(x_{span})$ was limited by tunnel diameter in tunnels $D < 1.3$ L and was fit by a linear equation, $\max(x_{span}) = aL$ ($a = 1.18 \pm 0.13$, $R^2 = 0.71$). In tunnels of $D > 1.3$ L, $\max(x_{span})$ was independent of tunnel size ($R^2 = 0.05$) with value $\max(x_{span}) = 1.33 \pm 0.22$ L. These measurements indicate the limits of limb–antennae extension when attempting to arrest falls. The value of maximum limb extension equal to 1.33 L suggests that in tunnels above 1.33 L in diameter, we should not observe jamming mode arrest and successful arrest of falls should decrease. This is supported by the logistic fit parameters of P_{arrest} in which the transition from successful arrest to unsuccessful arrest occurs at a critical tunnel size of 1.31 ± 0.2 L.

Morphological Measurements of Fire Ants to Estimate Stability Limits for Tunnel Arrest. Using data from ref. 5, we estimated the maximum limb and antennae span fire ants were able to reach while falling (Fig. S15). We estimate the antennae span ($d_1 = 0.86 \pm 0.08$ L) as two times the total antennal length (scape length + club length). We estimate midlimb span, denoted simply as limb span ($d_2 = 1.31 \pm 0.09$ L), as two times the total leg length (femur + tibia + tarsi) of the midlimb. Lastly we estimate the full length along the head–gaster body axis ($d_3 = 1.85 \pm 0.09$ L) as the antennae length + head length + alitum length + hind limb length.

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5. Tschinkel WR (2011) The organization of foraging in the fire ant, *Solenopsis invicta*. *J Insect Sci* 11(26):11.



Fig. S1. Overview of the X-ray CT digging trials. (A) Digging arena consisted of a circular plastic, or aluminum container of diameters 8.2 or 3.8 cm, filled to a height of ~12–15 cm with a simulated soil of monodisperse 50, 210, or 595 μm diameter, wetted, glass beads. 8.2 cm diameter container shown in *left* and *right* images of (A). (B) A horizontal cross-section from X-ray CT reconstruction at a depth of 6.8 cm from the surface. Top and bottom arrow indicate two tunnels not adjacent to arena wall. Four other tunnels are present but against the tunnel wall. (C) Cross-section of the top (*Left*) and bottom (*Right*) tunnels from B with extracted tunnel shape from active contours method shown as green (*Left*) and purple (*Right*) lines.

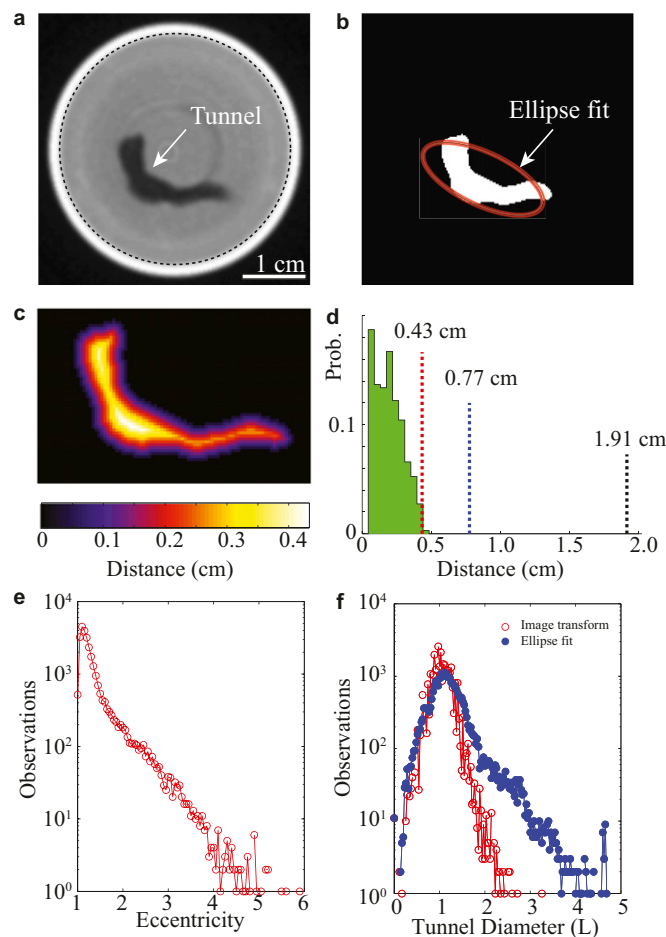


Fig. S2. Tunnel morphology analysis from X-ray CT data. (A) Tunneling experiment in a 3.8 cm outer diameter tube. Inner wall of digging arena shown as dashed line. An oblong-shaped tunnel is highlighted in the center of the arena. (B) Elliptical fit of tunnel shape. (C) Euclidean distance image metric of tunnel shape. Color represents minimum distance of each pixel location to tunnel wall. (D) Comparison of ellipse and image distance transform measures. Histogram of distance metric evaluated at all points in tunnel mask (green). Vertical dashed black line is major axis length from elliptical fit, dashed blue line is minor axis, and red line is maximum distance measured from distance transform. (E) Distribution of eccentricity defined as major axis divided by minor axis from fitted ellipse fits. (F) Distribution of tunnel diameter measured from distance transform and ellipse fit.

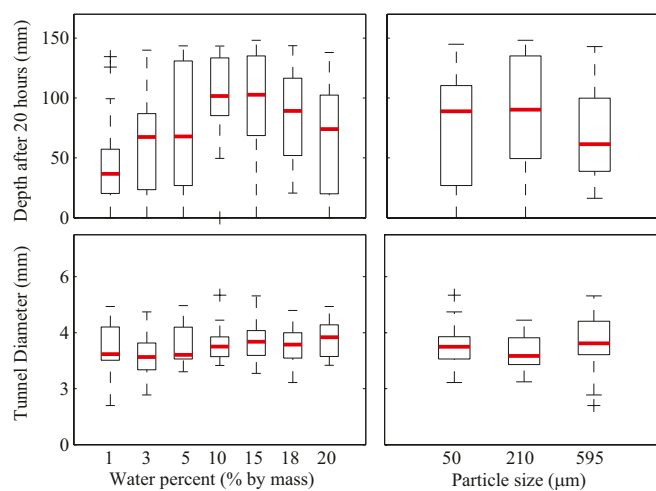
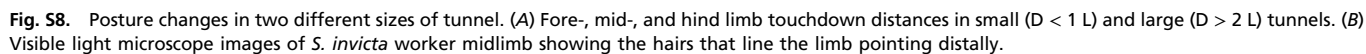
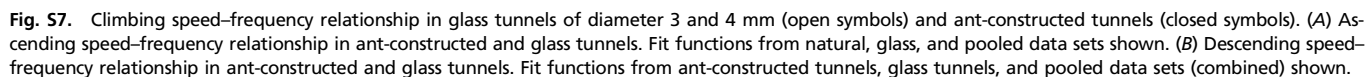
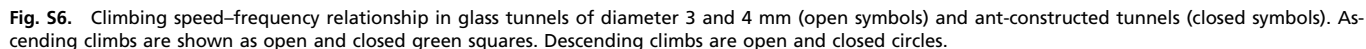


Fig. S3. Tunnel morphology as a function of particle size (left column) and water percent (right column). Box plots of maximum tunnel depth after 20 h are plotted along the top row, and box plots of tunnel diameter are plotted along the bottom row. We find that particle diameter and water percent statistically affected tunnel depth, but did not statistically affect tunnel diameter.



a Fall 1

0.5 cm

b Fall 2

0.5 cm

c Fall 3

0.5 cm

d Fall 4

0.5 cm

8 of 13

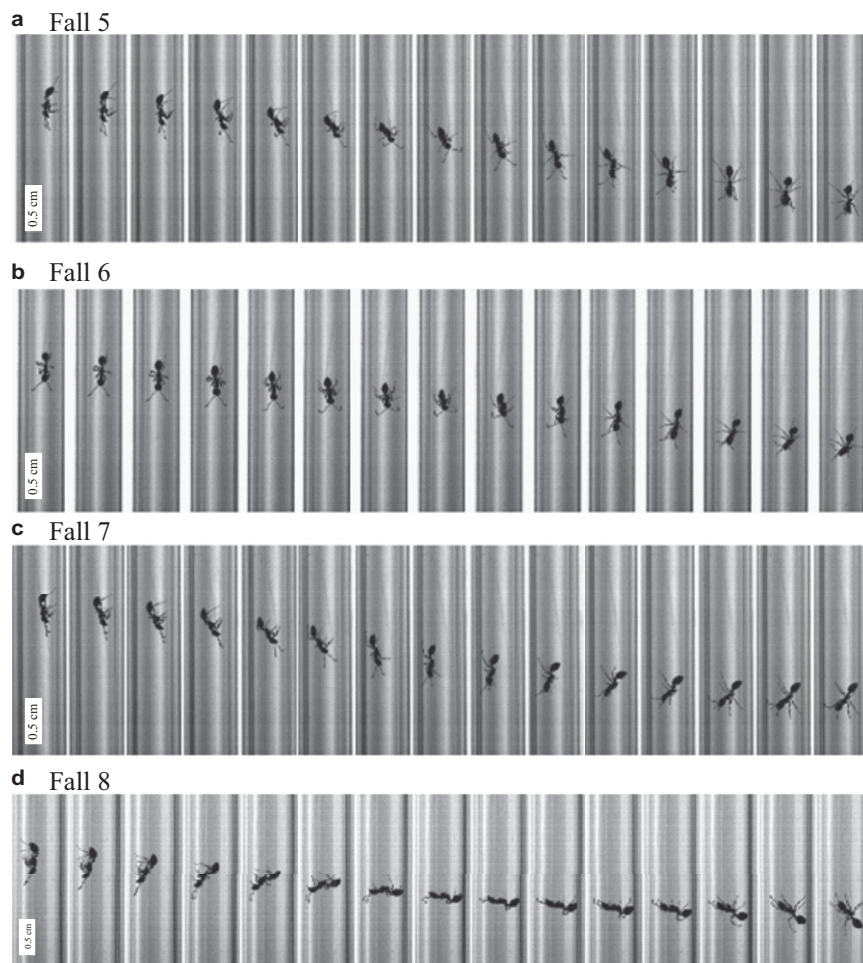


Fig. S11. Four unperturbed, head-first, fall arrest sequences in glass tunnels. All falls illustrate use of antennae during fall arrest. Images are separated by 5 ms time intervals. Tunnel size $D = 4$ mm (A), 4 mm (B), 4 mm (C), and 6 mm (D).

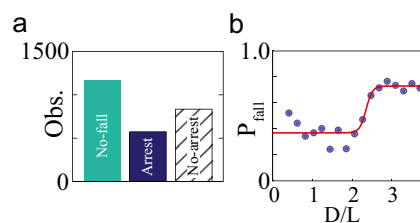


Fig. S12. Falling statistics. (A) Number of observations from perturbation experiments. (B) Probability to fall during a perturbation experiment as a function of D/L. Red line is logistic fit described in text.

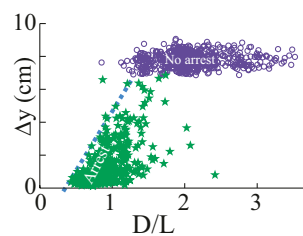
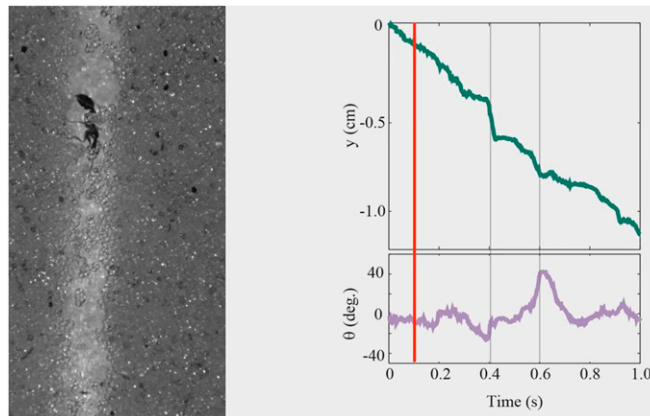


Fig. S13. Correlation between tunnel morphology D/L and fall distance. Fall distance, Δy , as a function of D/L. Purple circles indicate no arrest, while green stars indicate arrest.



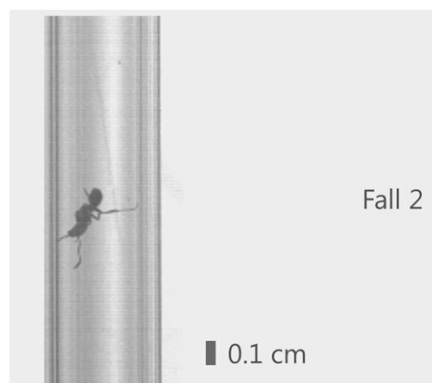
Movie S2. Rapid ascent in ant-constructed tunnel. The substrate consists of wetted 250 micron approximately spherical glass particles. During the middle of the climb, ant slips and falls backward but its motion is rapidly arrested.

[Movie S2](#)



Movie S3. Rapid descent of an ant in an ant-constructed tunnel subject to two slip arrests. The substrate consists of wetted 250 micron approximately spherical glass particles. Tracked body position and orientation are shown with video and correspond to Fig. 3.

[Movie S3](#)



Movie S4. Nine slip arrests observed in glass tunnels of diameter $D = 3\text{--}4$ mm. All falls are headfirst and antennae are used as seventh and eighth limbs to arrest fall.

[Movie S4](#)



Movie S5. Movie illustrating perturbation experiment and stable and unstable falls.

[Movie S5](#)