Caterpillar Climbing: Robust, Tension-Based Omni-Directional Locomotion

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Abstract
Animals that must transition from horizontal to inclined or vertical surfaces typically change their locomotion strategy to compensate for the relative shift in gravitational forces. The species that have been studied have stiff articulated skeletons that allow them to redistribute ground reaction forces (GRFs) to control traction. Most also change their stepping patterns to maintain stability as they climb. In contrast, caterpillars, most of which are highly scansionial, soft-bodied, and lack rigid support or joints, can move with the same general kinematics in all orientations. In this study, we measure the GRFs exerted by the abdominal prolegs of Manduca sexta (Linnaeus) during locomotion. We show that, despite the orthogonal shift in gravitational forces, caterpillars use the same tension-based environmental skeleton strategy to crawl horizontally and to climb vertically. Furthermore, the transition from horizontal to vertical surfaces does not seem to require a change in gait; instead gravitational loading is used to help maintain a stance-phase body tension against which the muscles can pull the body upwards.

Key words: climbing, ground reaction force, caterpillar

Terrestrial locomotion is often challenging in natural environments due to unpredictable traction and obstacles interfering with smooth limb trajectories. Most animals maneuver in such environments by continuously adjusting limb movements on a cycle-by-cycle basis and by exploiting the passive dynamics of their limbs and body (Dickinson et al. 2000). To cope with a wide range of speeds, most animals also adopt different gaits: changes in the rate and patterning of limb movements that help to match mechanical demands and maximize muscle and skeletal performance.

These strategies work well for horizontal crawling, walking, and running in which the gravitational forces are perpendicular to the direction of travel, and the body mass helps to provide traction through frictional interactions. Even small inclines pose no major mechanical limits for most legged locomotion. However, when faced with a steeply sloping surface or a vertical wall, most animals must adopt a different tactic to climb effectively; bipeds use their forelimbs, fast quadrupeds such as cats use distinctive climbing kinematics. Some animals (e.g., gekkos, Gekko gekko, Linnaeus, 1758 [Squamata: Gekkonidae] and Eublepharis macularius Blyth, 1854 [Squamata, Eublepharidae] and cockroaches Blaberus discoïdalis Audivet-Serville, 1839 [Blattodea, Blaberidae]) are remarkable in being able to employ similar kinematics to move across level ground, climb straight up, or even to run upside down (Zaaf et al. 2001, Goldman et al. 2006). Although the movements are similar in each orientation, the substrate reaction forces are quite different and depend on the gripping and release mechanisms of the feet.

These substrate forces (also called ground reaction forces, GRFs) are important for understanding locomotive strategies by individual animals and across different taxa (Alexander and Jayes 1980, Full and Tu 1990, Alexander 1992). For example, a parameter in the Fourier series (the shape factor) can be used to describe the changing profile of bipedal GRFs between walking and running (Alexander 1992). One can also describe gait transitions in terms of energy using the Froude number (Alexander 1976).

However, all current mechanical descriptions of gait transitions between horizontal locomotion and climbing have been based on animals with articulated skeletons, so it is not known how soft animals make these transitions. This is of interest for several important reasons. First, some of the most prevalent and ecologically important climbing animals are soft-bodied without a stiff skeleton such as caterpillars (Thomas 2005). Although caterpillars can use the same kinematics for vertical climbing and horizontal crawling (van Griethuysen and Trimmer 2009), these animals are soft and mostly keep their body in tension (Lin and Trimmer 2010a,b) so it is not clear whether force transmission also remains identical in different orientations. Second, there is a growing need to understand the mechanisms by which soft animals control their movements in different contexts; these strategies can be exploited for the development of novel moving devices and control systems (Trimmer 2008, Laschi et al. 2009, Lin et al. 2011, Saunders et al. 2011, Umedachi et al. 2016).

Caterpillars are particularly useful for carrying out these studies because they crawl and climb using discrete bilaterally synchronized
contact points on the thorax (the small articulated thoracic legs) and abdomen (the large soft pouch-like prolegs). Each proleg grips the surface using an array of cuticular hooks called crochets. This grip does not require direct muscular activity but is similar to a grappling hook that catches on surface asperities and by indentation into a softer substrate. Grip is released by contracting a muscle inside the proleg to collapse and retract the crochet array (Mukherjee et al. 2018).

The GRFs generated by each proleg can be measured using a custom device with multiple sensors capable of recording both fore-aft (direction of locomotion) and normal (perpendicular to the substrate) forces simultaneously (Lin and Trimmer 2012). Forces produced by each thoracic leg cannot be measured directly, but crawling is dominated by the abdominal movements and continues even if the thoracic legs are removed. We have used this device to measure and compare the GRFs of caterpillars (Manduca sexta Linnaeus, 1763 [Lepidoptera, Sphingidae]) crawling upright on a horizontal substrate and climbing upwards on the same surface. The results show that although the weight loading is perpendicular in these orientations, the underlying pattern of propulsive forces in each body segment is the same in crawling and climbing. This result, together with the similar kinematics of crawling and climbing (van Griethuijsen and Trimmer 2009), confirms that, unlike cockroaches and geckos that change foot loading patterns for climbing, Manduca can use the same tension-based gait regardless of its orientation.

Materials and Methods

Animals

Second- to fifth-day fifth instar animals were taken from our colony of M. sexta (Linnaeus) raised on a 17:7 (L:D) h cycle at 27°C. Rearing was based on an established protocol (Bell and Joachim 1978).

Ground Reaction Force Studies

For all studies, second- to fifth-day fifth instar animals were taken from the colony, weighed, and placed into a large open container filled with a variety of wooden substrates on which they crawled and climbed spontaneously (Lin and Trimmer 2010a). The most active animals were used for the force recordings. To simplify the discussion of GRFs, we use the prefix f to designate fore-aft GRFs (in the direction of travel; positive values are propulsive and negative values represent drag) and the prefix n to designate normal forces (perpendicular to the substrate). The additional prefix H is used for forces measured during horizontal crawling and the prefix V is used for forces measured during vertical (upward) climbing.

For studies of thrust and drag during horizontal crawling (fH-GRF), animals weighing between 1.43 and 2.96 g were placed on a beam with a single embedded fore-aft force transducer (Model 60–2995, Harvard Apparatus, Holliston, MA). Animals (n = 7) were observed while crawling along this beam, and the timing of each proleg contact with the sensor was manually noted into the force data file. Because the proleg movements are bilaterally symmetrical, GRFs for each body segment result from the combined right and left proleg contacts. Signals were recorded at 100 Hz, processed using a low pass filter at 30 Hz, and extracted from this data by assigning continuous deviations from zero force to each contact. Thirty traces were collected for each proleg pair. Prolegs are named according to their corresponding body segments (abdominal segments three through six, designated A3–A6, and the terminal prolegs, designated TP, on the most posterior segment). Recordings of GRFs normal to the direction of travel during horizontal crawling (nH-GRFs) were made by allowing animals (n = 4, weight between 1.6 and 2.5 g) to crawl along an array of cantilever beams and strain gauges configured to be sensitive in a single direction (Lin and Trimmer 2010a).

For studies of vertical climbing, a custom-built Manduca force beam array capable of measuring both fore-aft (fV-GRF) and normal forces (nV-GRF) was mounted to a camera tripod so that its orientation could be easily adjusted using bubble levels to ensure a perfect vertical orientation. The animals (n = 6), weighing between 1.67 and 2.82 g, were placed on the beam, and forces during the climb were recorded at 100 Hz synchronized with a simultaneous video recording of the leg contacts on the array (Lin and Trimmer 2010a). Signals were processed using a robust lowess smooth function (lowess; MatLab 2010b, The MathWorks, Inc. Natick, MA, USA) with a window size of 30 per recording duration. Drift was generally linear and could be compensated using averages covering one second at the beginning and end of the recording. For two sets of data, drift was clearly nonlinear and was corrected by subtracting a strongly filtered signal (lowess, using a window of 1000 per recording duration) from the original signal. The GRFs for each pair of prolegs were identified from simultaneously recorded video data and normalized to percent of animal bodyweight and percent step length in the y and x directions, respectively.

The relative timing of GRFs at each contact point along the body was measured on the multibeam sensor array. Multiple crawl cycles were recorded for each animal to capture all overlapping events. Cycles of contiguous GRFs could also be assembled by combining data from anterior segments as Manduca crawled onto the array with GRFs from the posterior segments as Manduca crawled off the array. All traces were then normalized with the start of one TP touchdown to the next TP touchdown representing a full step cycle.

To determine the contribution of both single leg pairs and the abdomen as a whole to the overall step cycle, data were averaged using MatLab 2010b (Mathworks). The data were normalized by dividing the observed force by the total animal weight and then using a spline function to fit each trace to consecutive windows of 100 data points (each representing 1/100th of a step). The average percentage of bodyweight supported by each contact point during each step was calculated by summing all positive values and all negative values separately.

Comparing f-GRFs During Crawling and Climbing

If Manduca uses the same strategy to crawl and climb, it is expected that the fV-GRFs will have the same profile as those seen during horizontal crawling but with additional forces created by the animal’s weight. To test this prediction, the mean values for the nH-GRFs in each proleg were subtracted from the corresponding segmental fV-GRFs and the results (|fV-nH|-GRF) compared with the empirical fH-GRF data.

Behavioral Observations

To investigate the role of thoracic legs during climbing, the movements of healthy third-day fifth instar animals climbing on a hanging soft suture were recorded using color digital video. We cold-sedated the caterpillar and bonded its thoracic legs together using cyanoacrylate glue (Gorilla, Cincinnati, OH). The animal was allowed to recover for 3 h and then placed onto a rigid vertical substrate to check the crawling behavior.

To test the effect of removing the central complex (the part of the brain implicated in behavioral gait transitions; Bender et al. 2010), some animals were debrained by removing their brain with forceps through a hole drilled into the head capsule (Dominick and Truman 2018).
1986a) using modifications to minimize the loss of hemolymph (Trimmer and Issberner 2007). Animals were anesthetized on ice and placed in a custom-built clamp that isolated the head above a test tube, while allowing the body to hang down into an ice-water bath. A small hole was drilled into the front of the frons, and the brain was excised using forceps. Surgical injuries were sealed with Gorilla brand cyanoacrylate glue. Animals were allowed to recover overnight and their behavior was observed ~15 h postoperatively. Each debrained animal was then dissected posthumously to ensure that the brain had been removed.

Results

Proleg-Specific GRFs

GRFs from individual prolegs on successive crawling cycles were highly variable with standard deviations almost equal in size to the average values. However, the time-dependent profile of these forces was slightly different for each body segment, and the differences were consistent throughout trials in the same orientation.

As would be expected, the \( nH \)-GRFs for each body segment were always positive (Fig. 1). In all of the mid-body proleg segments, these forces peaked during the initial loading and peaked again shortly before unloading. \( nH \)-GRFs for the TPs generally consisted of a monophasic force profile with gradually increasing and decreasing loads. In contrast, the \( nV \)-GRFs were largely negative in segments A3 through A5 and switched from negative to positive during the stance phase in segments A6 and TP. Presumably these profiles represent a pitch-back torque.

During horizontal crawling, the \( fH \)-GRF profiles were characteristic for each proleg segment. The anterior segments A3 and A4 consisted primarily of positive forces with small negative (drag) forces at the onset and end of the stance phase. The posterior body segments A6 and TP were largely negative forces keeping the body in tension as previously described (Lin and Trimmer 2010a). In contrast, during upward climbing the \( fV \)-GRFs were much larger and generally positive only rarely exerting drag force (Fig. 2). These forces represent those required for locomotion and the additional loading due to gravitational pull. Interestingly, in both horizontal and vertical directions, the fore-aft GRFs on segment A5 are relatively low.

Because crawling is quasi-static, the total force contributed by all the contact points is constant and the contribution of any particular pair of prolegs will depend on the duration of the proleg stance relative to the overall crawl cycle. It was found that the duration of proleg stance in each of the body segments was linearly related to the duration of the crawl cycle (Fig. 3, Table 1). It was therefore possible to calculate the relative force contributions of each proleg segment in multiple crawls and from multiple animals by combining force data scaled to stance duration.

During horizontal crawling the proportion of thrust generated by each proleg was segment specific; greater thrust was contributed by A3 and A4, and less thrust or greater drag from A5, A6, and the TP (Fig. 4A). Although the average drag forces in segment A5 were relatively small, because they were consistent over most of the stance phase, they contribute substantially to the maintenance of tension in the body. During vertical climbing, the anterior and posterior abdominal segments support the majority of the body weight and the prolegs in segment A5 contribute relatively little axial force (Fig. 4B).

If the mechanism of climbing is mechanically equivalent to horizontal crawling, the fore-aft climbing force profiles should match those of horizontal crawling once the gravitational contribution has been accounted for. To make this comparison, we subtracted the \( nH \)-GRFs from the

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**Fig. 1.** Normalized normal GRF traces (\( n \)-GRFs) for each pair of prolegs from *Manduca sexta* crawling and climbing. Each lower (red) line is the mean force during vertical climbs; upper (blue) lines represent horizontal crawling. Error bars represent standard error of the mean and are drawn at intervals of 10% from 5% crawl to 95% crawl. Each mean trace is derived from 30 traces gathered from six animals climbing vertically and seven animals moving horizontally.

**Fig. 2.** Normalized axial GRF traces (\( f \)-GRFs) for each pair of prolegs from *Manduca sexta* crawling and climbing. Each upper (red) line is the mean force during vertical climbs; lower (blue) lines represent horizontal crawling. Error bars represent standard error of the mean and are drawn at intervals of 10% from 5% crawl to 95% crawl. Each mean trace is derived from 30 traces gathered from six animals climbing vertically and seven animals moving horizontally.
removed or bonded to one another (Lin and Trimmer 2010a); are still able to crawl horizontally after the thoracic legs have been removed or bonded to one another (Lin and Trimmer 2010a); however, it is possible that body weight presses the thorax against the substrate to generate enough friction to maintain normal crawling.

To explore the role and necessity of the thoracic legs in normal climbing, they were bonded together so that they could not actively grip the substrate. Manduca could still climb both a stiff substrate and a flexible string, with an apparently normal wave of motion. However, careful observation showed that the bonded legs were pushed against the substrate to produce friction without gripping. When the thoracic legs were completely removed, there was no longer sufficient friction to crawl normally. Instead the crawl cycle changed so that only one or two legs were in swing simultaneously and the swing phase was very short (Fig. 7). Although this motion has not been analyzed in detail, it is clear that the effective wavelength of the crawl cycle was substantially shortened. The anterior prolegs (especially A3) stayed in contact during most abdominal movements to provide the anterior anchor point. This climbing is slower and more precarious.

Table 1. Each value is the coefficient of determination for a simple linear regression using duration of proleg stance and total crawl cycle duration for each abdominal proleg during vertical or horizontal crawls as shown in Fig. 3.

|       | A3 | A4 | A5 | A6 | TP |
|-------|----|----|----|----|----|
| Horizontal | 0.89 | 0.89 | 0.90 | 0.87 | 0.60 |
| Vertical  | 0.99 | 0.99 | 0.99 | 0.99 | 0.78 |

N = 25 for each regression.

Discussion

A General Strategy for Caterpillar Crawling

Recent work on M. sexta locomotion demonstrates that during horizontal crawling, the caterpillar keeps its body in tension and transmits forces through the substrate to the rest of its body. This has been described as an environmental skeleton (Lin and Trimmer 2010a,b). The present study examined a larger dataset of horizontal crawling and vertical climbing. The data show that while each pair of prolegs has a distinct average substrate reaction force profile, there is a large variability in both the magnitude and time course of forces within each body segment (Figs. 1 and 2). This is in contrast to rigid bodied animals of similar or larger weights, where GRFs are highly reproducible and largely speed dependent (Zaaf et al. 2001, Goldman et al. 2006). The variation in Manduca GRFs presumably arises from the highly coupled and nonlinear nature of force distribution in a soft, fluid-filled body. The effects of muscular contractions and other movements are transmitted through soft tissues with significant damping and delays that are not necessarily phase locked to the current crawl cycle. In a dynamic system, this often means that each cycle of movement may have residual effects on subsequent step sequences. Caterpillars are unlikely to be affected by residual dynamics because their locomotion is quasi-static, the inertial forces are small, and the stepping motion can stop and restart at any point in the crawl cycle without obvious consequences (Trimmer and Issberner 2007).

While individual segment GRF data are variable, general trends have been found by averaging traces. The normal GRFs in the mid-body proleg segments peaked during the initial loading and peaked again shortly before unloading (Figs. 2 and 4). Presumably this represents the progressive shift in body weight as the wave of movement progresses forward. These peaks may also include components due to a shift in the center of mass as the gut pushes forward, phase locked to the movements of the TPs (Simon et al. 2010b).

By compiling the GRFs in different body segments, it can be seen that during horizontal crawling the abdomen produces a net drag force. This suggests that tension is normally maintained between the thoracic leg contacts and the proleg bearing segments, and the compressive forces are largely carried by the substrate. The forward wave of movement is a progressive release of body axial tension. Further experiments are necessary to determine how the thoracic legs develop thrust.

On the Difference Between Horizontal and Vertical Crawling

Although caterpillars can change their stepping patterns (Metallo and Trimmer 2015), it is unclear whether such variations in gait are
necessary for climbing. A comparison of proleg stance and swing timing during vertical and horizontal crawling in a large number of individuals did not find any significant differences (van Griethuijsen and Trimmer 2009). Furthermore, the kinematics of crawling and climbing, both within and between individuals, is highly variable, which implies that a precise sequence of proleg movements is not necessary for normal locomotion. This study shows that the pattern of horizontal and vertical GRFs are very similar when differences in torque and gravity are taken into consideration. The calculated traces based on vertical fore-aft data and horizontal normal data are not distinguishable from measured horizontal fore-aft traces (Fig. 5). Although the force profiles in each body segment are similar, the average calculated \((f V - nH)\)-GRF is mostly higher than the observed \(fH\)-GRF. This is likely caused by the abdomen supporting a larger proportion of the body weight in vertical crawling because the internal body cavity is not segmented and the gut, which is free to move relative to the body wall (Simon et al. 2010b), can slide posteriorly.

After accounting for the addition of bodyweight in vertical crawling, the abdomen produces the same amount of net drag during horizontal and vertical locomotion. This supports the idea that the animal is maintaining the same tension between the thorax and abdomen in both crawling modes. Analysis of the average vertical crawl shows that little drag force is produced during vertical crawl cycles. Therefore, Manduca cannot be tensioning itself by exerting opposing forces on the substrate. Instead, it appears that a shift in

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**Table 2.** Results of debraining experiments

| Animal number | Ability to transition 90° (healthy) | Ability to transition 90° (sham surgery, 10 h postop) | Ability to transition 90° (debrained, 46 h postop) |
|---------------|-----------------------------------|--------------------------------|-----------------------------------|
| 1             | Yes                               | Yes                           | Yes                               |
| 2             | Yes                               | Yes                           | (Animal died during surgery)      |
| 3             | Yes                               | Yes                           | Yes                               |
| 4             | Yes                               | Yes                           | Yes                               |
| 5             | Yes                               | Yes                           | Yes                               |
| 6             | Yes                               | Yes                           | (Animal died during surgery)      |
| 7             | Yes                               | Yes                           | Yes                               |

All animals are second-day fifth instar, and those that survived were able to continue from a horizontal onto a vertical surface.
the direction of the weight is itself enough to provide the necessary tension for climbing. This interpretation is supported by observations of locomotion on different substrates. Although *Manduca* cannot crawl horizontally along highly flexible braids of string (Lin and Trimmer 2010a), it can climb them vertically without causing the string to loop and curl beneath. In this case, the bodyweight provides the necessary force to stretch the body tight; thus, a stiff substrate is not needed.

The largest observed difference in the crawls is in the normal forces. In horizontal crawling, the normal forces generally push the body toward the substrate, but for climbing caterpillars the anterior segments are often pulled away from the surface. This results from the pitch-back torque on the body typical for a long animal with its center of mass posterior to its anterior attachment points. This also implies that the body is stiff enough to allow transmission of bending torque when attached on a vertical surface. This effect is most pronounced.

Fig. 6. Debrained animal (46 h postop) transitioning from horizontal (not shown) to vertical orientation. Motion occurs in all three directions (forward, up, and to the right). Each frame represents +6 s.

Fig. 7. Climbing by a second-day fifth instar *Manduca* with its thoracic legs removed. Successive frames show the stepping pattern in a single crawl cycle. Dots (red) indicate a proleg in stance and white arrows show prolegs in swing phase. *Manduca* is able to climb the rigid substrate using only the prolegs, but this gait does not resemble normal crawling. Each step is very short and without an anterior anchor point the anterior abdominal segments are compressed together.
in the more posterior anchor points (A6 and TP) where the intrinsic stiffness is sufficient to make the TP n-GRFs slightly positive. Despite this change in normal force distribution, there is no need for the animal to actively account for torque by changing its movements; grip by even one pair of prolegs is sufficient to support the entire body weight (Belanger et al. 2000). Caterpillars’ passive gripping system really enables them to employ a one-for-all locomotor strategy. This is largely confirmed by electromyographic recordings from the muscle responsible for crochet retraction during both upright and upside-down crawling. Although activity in this muscle is slightly phase-advanced (relative to the stepping movements) during upside-down crawling, there is no significant increase in the muscle stimulation frequency, despite the massive difference in crochet loading magnitude and direction (Mukherjee et al. 2018). We are currently testing the mechanisms of proleg grip to better understand how the material and mechanical properties of the proleg achieve this performance.

**How Robust Is the Crawling Motor Pattern?**

Because the nervous system and body have co-evolved as a behavioral system (Chiel and Beer 1997, Chiel et al. 2009), it is important to consider how both mechanical and neural components contribute to locomotion in changing environments. Soft animals are mechanically complex with many degrees of freedom and strongly nonlinear, time-dependent changes in the responses of the body tissues (Dorfmann et al. 2007, 2008; Lin et al. 2009). *Manduca* also has a relatively small nervous system that could limit the range and diversity of available motor programs. In previous work, the activity of motor neurons involved in *Manduca* locomotion has been monitored using electromyographic recordings of major body wall muscles. It was shown that during crawling there is substantial overlap in the activation of longitudinal muscles in successive segments. Furthermore, dorsal, ventral, and oblique muscles within a single body segment are usually co-activated (Simon et al. 2010a, Metallo et al. 2011). The main crawling motor program appears to be loosely coordinated, and this interpretation is supported by similarly variable bursts of abdominal motor activity during fictive crawling (Johnston and Levine 1996). It has been proposed that the antero- grade wave of movements is primarily coordinated by the carefully timed release of the crochets in successive segments (Simon et al. 2010a, Trimmer and Lin 2014).

Using a custom-built, flexible multi-electrode array (Metallo et al. 2011), it has been possible to record the electrical activity of a major longitudinal dorsal muscle (DIM) during horizontal crawling and vertical climbing (Metallo and Trimmer 2015). In both orientations, the burst of muscle activation in a single body segment is long lasting and occupies much of the overall crawl cycle. The intensity of DIM activation (i.e., the frequency of excitory junction potentials during a burst) is not increased during vertical climbing despite having to lift the body against gravity. Instead there is a shift in the timing of muscle activation such that DIM is more active toward the end of the segment swing phase during climbing. This delay is only seen in the activity of one of the two motoneurons innervating DIM, but it might explain how the environmental skeleton strategy can produce similar kinematics independently of orientation. One interpretation is that in horizontal crawling each segment actively pulls on the more posterior segments to develop tension before they release the substrate. During vertical climbing, the body is in a pre-tensioned state, so by delaying activation the more anterior body segments can pull the body forwards when the following segment is in swing phase. This would not necessarily change the kinematics but would instead accommodate for the change in crawling orientation (Metallo and Trimmer 2015). This hypothesis can be tested by recording GRFs and muscle activation patterns simultaneously in a climbing caterpillar, but such experiments are at present technically challenging.

Although the current article does not directly address the nature of motor control during locomotion, the experiments on debrained animals suggest that horizontal crawling and vertical climbing do not involve a central complex-mediated gait transition. Removal of the central complex prevents most insects from switching gaits or modes of locomotion, including turning (Graham 1979, Ridgel and Ritzmann 2005, Ritzmann et al. 2005). In the case of *Manduca*, removal of the entire supra-esophageal ganglion (i.e., debranching, which includes the central complex) is thought to have the same effect and leads to uninterrupted locomotion in prewandering larvae (Dominick and Truman 1986a,b). Debranching had no effect on the ability of *Manduca* to transition from horizontal to vertical surfaces. This result shows that the supra-esophageal ganglion is not required for normal locomotion in each orientation. It is possible that sensory feedback is sufficient to make any necessary changes to the motor program, although we have not ruled out a purely mechanical adaptation that makes caterpillar crawling so robust.

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