Legged locomotion in lattices: centipede locomotion in obstacle-rich environments

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1 Abstract

Centipedes locomote through complex obstacle-rich environments by coordinating traveling body and limb-stepping waves. However, little is known about how terradynamic interactions influence their gaits. Here, we challenged *Scolopendra polymorpha* to negotiate model heterogeneous terrains - hexagonal and square lattices (1 to 2 cm distance between posts). Despite the abundant obstacles present in these lattices, the centipedes maintained rapid motion, traveling at 0.79 ± 0.39 body lengths per second regardless of lattice spacing. We posit that their performance remained relatively unchanged across lattices due to both passive and active gait adaptations of the limbs and body. We discover three key behaviors that we hypothesize are critical to their performance: streamlining, stretching, and twisting. Each of these behaviors serve to mitigate drag and/or generate thrust in these obstacle-rich scenarios. We quantify under what conditions each behavior was observed and show initial robophysical modeling to explore whether these gait adaptations are passive or active. This biological study demonstrates that multilegged locomotion is feasible within obstacle-rich environments given certain adaptations and behaviors to reduce the effect of limb collisions. Further, it provides insights for improving robotic morphologies for similar scenarios, suggesting that limbless designs are not singular solutions for locomotion in confined spaces.

2 Introduction

Principles of aerodynamics and hydrodynamics have helped facilitate biomechanical explanations of locomotion strategies used by flying[1] and swimming[2] organisms. Despite the ubiquity of dry, cluttered habitats in the biological world, the development of a corresponding set of principles for *terradynamics*[3] is still in its infancy. This reflects the complex nature of terradynamic environments, which often feature heterogeneous, complex, non-linear body-environment interactions, and a wide diversity of materials. Identifying principles of terradynamics relies in part on cataloging and describing the diverse locomotor strategies employed in these settings. The body plans and gaits of terradynamic locomotors display considerable variation – from limbless organisms like snakes, to bipeds, quadrupeds, hexapods, and myriapods, like centipedes – which reflects the richness and complexity of terradynamic interactions. Understanding how these different locomotors interact with their environments and how they adjust their gait can present insights into how these locomotors developed and how to build robotic systems to emulate their performance.

Centipedes present an interesting case study for terradynamic locomotion as they inhabit various complex environments (Figure 1) and exhibit limb-driven locomotor modes, with and without body undulation.[4,5] These animals locomote by propagating traveling waves of limb flexion (limb-stepping pattern).[4,5] These waves are classified by the direction of propagation. Limb aggregates traveling in the direction of motion (from rear to front during forward motion) are termed "direct". Conversely, propagation of limb aggregates opposite to the direction of motion (front to rear during forward motion) is called "retrograde".[6] Manton[5] classified various orders of centipedes based on whether they exhibited retrograde (Scolopendromorpha, Geophilomorpha, and Craterostigmorpha) or direct (Scutigeromorpha and Lithobiomorpha) limb-stepping patterns. Manton noted that centipedes with direct limb-stepping patterns were unable to exhibit body undulation[5] whereas those with retrograde limb-stepping patterns demonstrated an increase in body wave amplitude with increased forward speed[7].[5] Recent work has shown that different centipede species are not restricted to a single locomotive strategy, but can modify their gait based on their environment.[8–10] In particular, centipede locomotion in confined, obstacle-rich settings (Figure 1D) is not well understood. Such scenarios have been thought to drive the development of limblessness in lizards[11] and so, it is conceivable that centipedes would leverage this streamlined morphology and body-driven locomotion in similar conditions. Such work can provide insights into locomotion strategies in confined terradynamic environments and inform robot design and control for similar settings.

In this work, we present the first study of multi-legged locomotion in lattices, a model heterogeneous environment, typically used to study limbless systems.[12–18] We challenged *Scolopendra polymorpha*, a species known to exhibit retrograde limb-stepping patterns, to navigate arrays of rigid posts. We hypothesized that, at higher obstacle densities, the centipedes would undulate their body reminiscent of limbless organisms (e.g., snakes) to push off the obstacles, forsaking the use of their legs (i.e., body-dominated gait) due to leg collisions and drag induced by their sprawled posture. Instead, the centipedes adopted various strategies to continue using limb-dominant gaits (no evidence of lateral body undulation for propulsion) and in rare cases, exhibited a form peristaltic body-driven locomotion. We describe these various behaviors and propose possible mechanisms by which they occur. Lastly, we discuss potential insights these tests offer for the interplay between body and limb locomotion in complex environments and possible implications for multilegged robot design and control within similar terradynamic conditions.

Figure 1: **Natural environments.** *S. polymorpha* locomote across various terrains such as (A) leaf litter (image credit: Marshal Hedin), (B) rocks (image credit: Sven Ouille), (C) plants (image credit: Richard N Horne), and (D) holes and burrows (image credit: Margarethe Brummermann).

3 Methods and Materials

3.1 Animals

All centipedes were wild caught. *Scolopendra polymorpha* were caught in Del Rio Val Verde County, TX, USA. Nine *S. polymorpha* centipedes were used in experiments, with a mean body length of 8.6 ± 1.0 cm and mean body width of 0.8 ± 0.1 cm. *S. polymorpha* had 19 body segments with 19 joints and leg pairs. Centipedes were housed separately in plastic containers on a 12h:12h light:dark photoperiod at room temperature (20–22°C). Centipedes were provided a source of water and were fed mealworms weekly.

3.2 Lattice environments

Experiments were conducted in 10 different environments consisting of cylindrical wooden dowels (diameter = 0.25 cm) configured in either square or hexagonal lattice spacing on a lasercut sheet of acrylic with the protective layer still attached. The area of each terrain was consistent (11.20 cm x 11.20 cm) while the spacing between dowels (s) was varied for testing at 1 cm, 1.25 cm, 1.5 cm, 1.75 cm, and 2 cm spacing for both configurations. Lattices were placed on a slightly raised platform (2.4 cm) within a glass tank (length = 51 cm, width =

27 cm, height = 32 cm) for each experiment.

3.3 Kinematic recordings

Experiments were recorded using a high-speed camera (AOS, S-motion) positioned directly over the lattice environments capturing kinematics from a top-down view. Videos were recorded at a resolution of 1280×700 pixels and a frame rate of 738 frames per second. Each trial consisted of a singular centipede navigating a lattice without external stimulus. We began a trial when the entire body was within the lattice and ended it once the head exited. For each lattice type and spacing, 5 to 12 trials were conducted where the centipede was completely within the terrain area for at least 0.2 seconds (150 frames).

3.4 Calculation methods

We tracked the point on the head where both antenna meet for the first and last frames of the trial and divide that distance by the total trial duration (and centipede body length BL) to get the average Euclidean speeds (in units of body lengths per second, BL/sec) of the centipedes when in the lattice. It should be noted that this is not the path speed and is more a "as the crow flies" speed, meaning it serves as a lower bound for the centipede speeds in the lattices. We use this metric due to the frequent head oscillations observed during tests, with no characteristic period that falls within the trial duration. We calculate the rate of head collisions by manually counting the number of collisions per run and dividing by the duration of that trial. We classified a head collision as a post coming into contact with any point on the rounded part of the centipede's head. We classified whether a trial was twisted or not twisted by whether any legs were pointing towards the camera during the run for at least 0.1 seconds. To account for the various centipedes used, we normalized speeds by body length (BL) and lattice dimensions by body width (BW). Additionally, since the centipedes typically followed channels in the lattice (denoted by c in Figure 2 B and C), we plotted their behaviors as a function of the normalized channel width (c/BW).

4 Results and Discussion

4.1 Performance across lattices

The centipedes navigated the various lattices, provided the channel width was more than 1 BW (Figure 3). If smaller than 1 BW, the centipedes would instead walk on top of the lattices. They maintained approximately the same Euclidean speed of 0.79 ± 0.39 BL/sec across all lattices (Figure 4A), comparable to the average speed seen in the high rugosity terrains (0.77 ± 0.51 BL/sec).[8] Additionally, many of the trials fell within the range of velocities seen in open space (within the black dashed lines in Figure 4A).

To assess the perturbations the obstacles imposed on the centipedes, we calculated the head collision rate as a function of the normalized lattice parameters

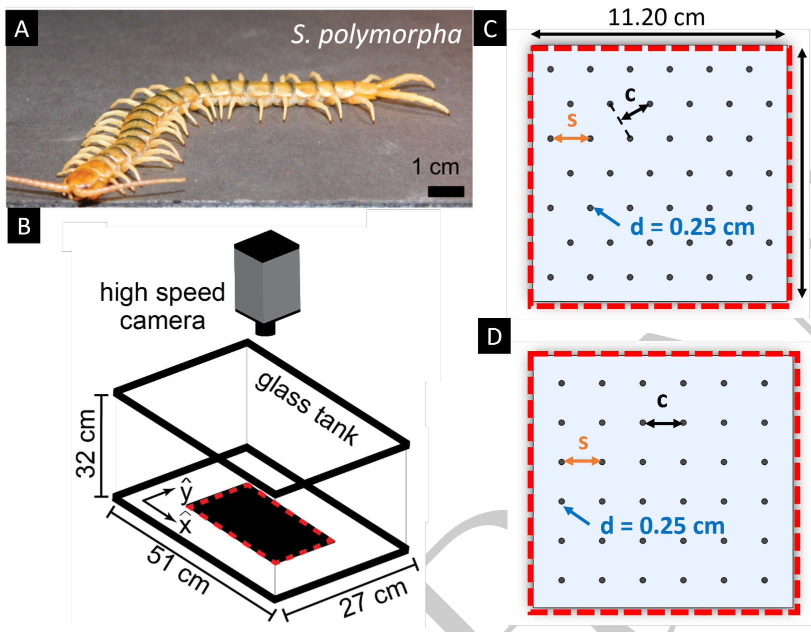

Figure 2: **Experimental Design.** (A) Photo of *Scolopendra polymorpha*. (B) Experimental setup. Trials were performed in a 51 x 27 x 32 cm glass tank with a high speed camera stationed above with the tested lattice located in the red dashed box. (C-D) Example hexagonal (C) and square (D) lattices with post diameter (d) and spacing (s) denoted, as well as the width of the channels (c) within the lattice.

(Figure 4B). We found that, regardless of lattice, the centipedes collided against posts at a rate of 2.4 ± 1.8 collisions/sec. However, the individual collision rates were correlated with their associated velocity (Figure 4C) with a Pearson coefficient of 0.56, p-value of 0.05, $R\hat{2}$ of 0.3, and slope of 3 collisions/BL traveled. This indicates that collisions occur more often as the centipedes move more quickly. Thus, centipedes do not achieve high speeds in the dense lattices by avoiding head-on collisions (Figure 4D). Instead, we observe the centipedes adopt various changes to their posture and gait. We hypothesize these changes mitigate drag from the increasing obstacle densities and collisions, enabling comparable performance across all lattices.

4.2 Posture and gait adaptations

When in the lattices, we observed three distinct behaviors: streamlining, stretching, and twisting. We hypothesize that each of these behaviors, were crucial to lattice traversal and the consistent locomotion performance.

While in open space, the centipedes typically display a sprawled posture

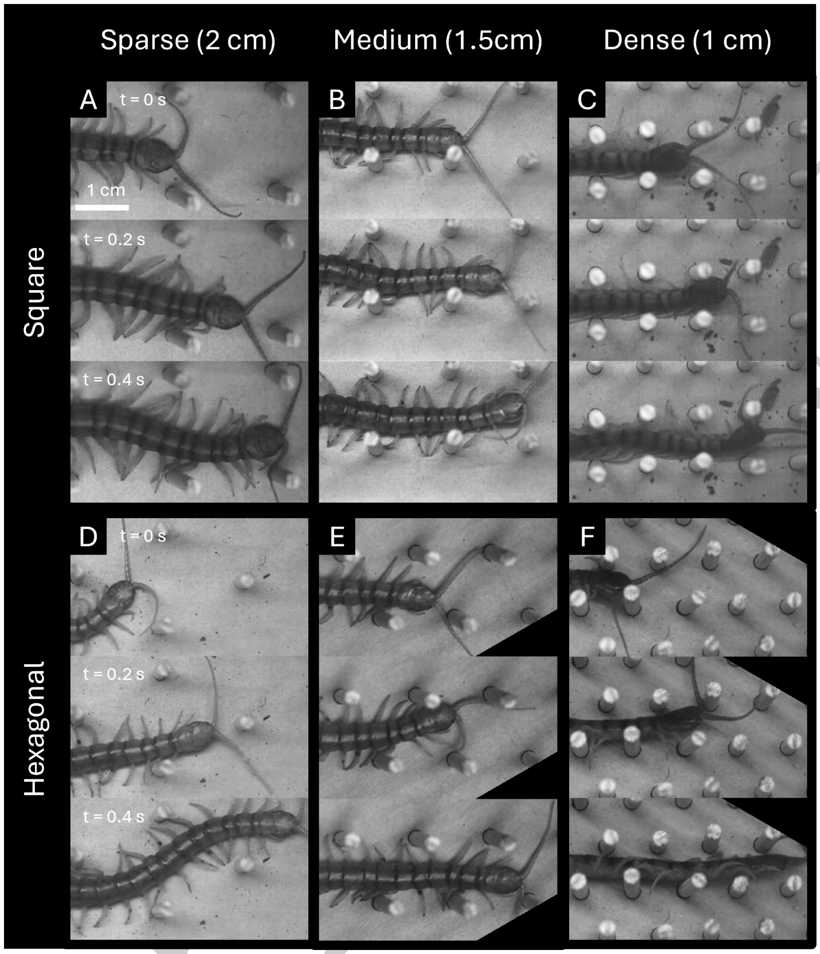

Figure 3: **Snapshots of centipedes in lattices.** Image sequences of centipedes running through some of the tested square (A-C) and hexagonal (D-F) lattices, with the two patterns separated with a black band and the post density increasing from left to right. Each snapshot is 0.2 sec after the one above it and the scale bar in the top left corresponds to all pictures.

where their limbs are close to perpendicular with the body when in their swing phase (Figure 5A). However, the centipedes adopted more terradynamically streamlined[19] postures in all tested lattices, as seen in Figure 5B). This behavior occurred within 0.2 seconds and consisted of half of the centipede's limbs folding against the body (Figure 5C). Notably, the limbs would remain folded against the body when not against an obstacle (highlighted in Figure 5B), suggesting it is an active response to the obstacles and repeated collisions. We hypothesize that this shift in posture serves to mitigate drag incurred by the limbs during

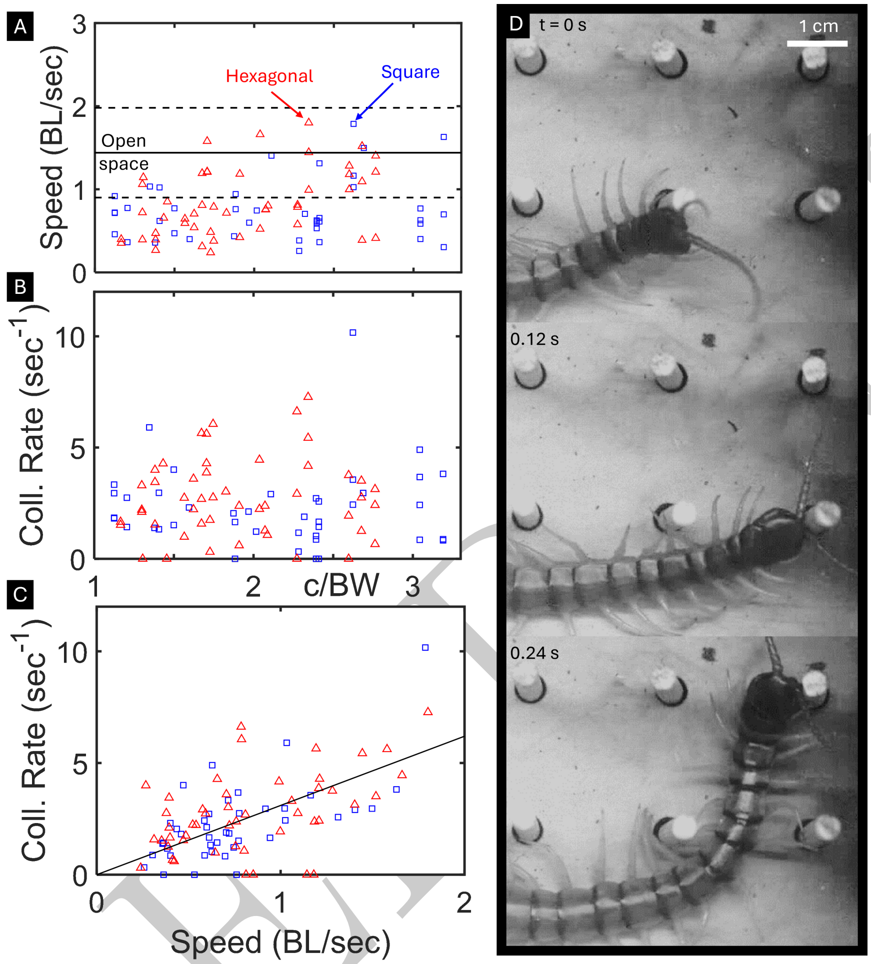

Figure 4: **Collisions and speeds.** (A) Overall velocity through the lattices in body lengths per second versus the normalized channel width. Black solid line corresponds to the average velocity of these centipedes in open space and dashed lines indicate the standard deviation. (B) Plot of the head collision rate of various trials versus the normalized lattice channel width. Instances of 0 collisions correspond to trials with no head impacts but several antenna collisions. (C) Plot of the head collision rate versus the velocity through the lattice. Least-squares regression line is indicated with the black solid line with a slope of 3 collisions per body length. Red triangles and blue squares in all plots correspond to hexagonal and square lattices, respectively. (D) Image sequence of centipede within 1.75 cm square lattice (2.6 c/BW) colliding into posts at a rate of 10 times per second.

forward motion by removing the collisions on one half of the body.

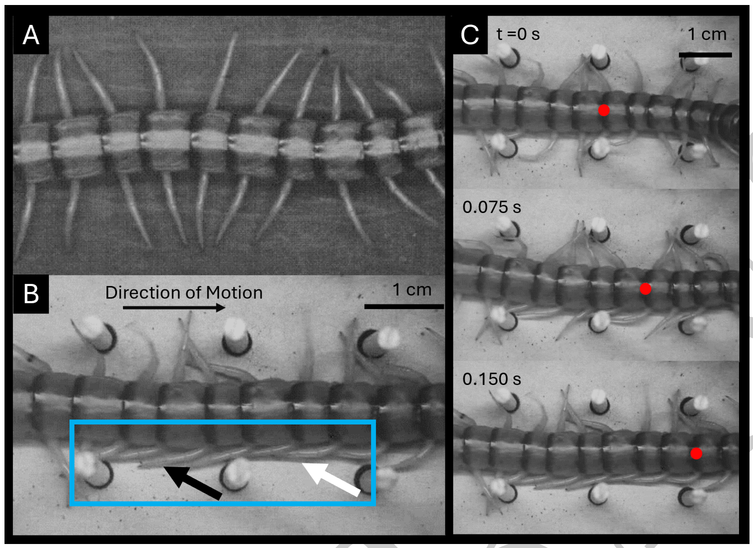

Figure 5: **Terradynamic streamlining.** (A) Centipede sprawled posture when in open space.[8] Note that all limbs are nearly perpendicular to the body. (B) Example of centipede posture within 1.75 cm square lattice (1.9 c/BW). Blue box highlights the observed terradynamic streamlining where limbs are near parallel to the body. Black and white arrows point out limbs that are tucked against the body even when not against an obstacle. Scale bar in upper right corresponds to panel (A) as well. (C) Image sequence across 0.15 sec of centipede transitioning from sprawled to streamlined posture (last image in sequence corresponds to (B)). Red dot indicates forward progression across the image sequence.

When navigating the intermediate lattices (around 1.5 to 2 c/BW), the centipedes oftentimes took paths that included consecutive large turns (45°or greater). In these cases or ones with a single turn of 90° (Figure 6A), we observed the centipede's head come to a complete stop immediately after the turn for at least 0.05 seconds. This coincided with either the legs in the "front" region (those past the turn) slipping significantly with little to no forward thrust or the "back" region continuing to move forward and compressing the overall body. Immediately after this event, the centipede "stretched" the front region forwards. In certain cases like the one in Figure 6A, this resulted in the centipede adopting an earthworm-like gait consisting of periodic stretching and contracting of its body segments similar to *S. polymorpha*[20] and Geophilomorpha[4] burrowing gaits. We calculate that during this motion (Figure 6B), the centipede compresses and extends its body by up to 10% (± 2mm)((Figure 6C) and this "compression wave" travels along the body with the rear section exhibiting a similar compression event nearly completely out-of-phase with the front section.

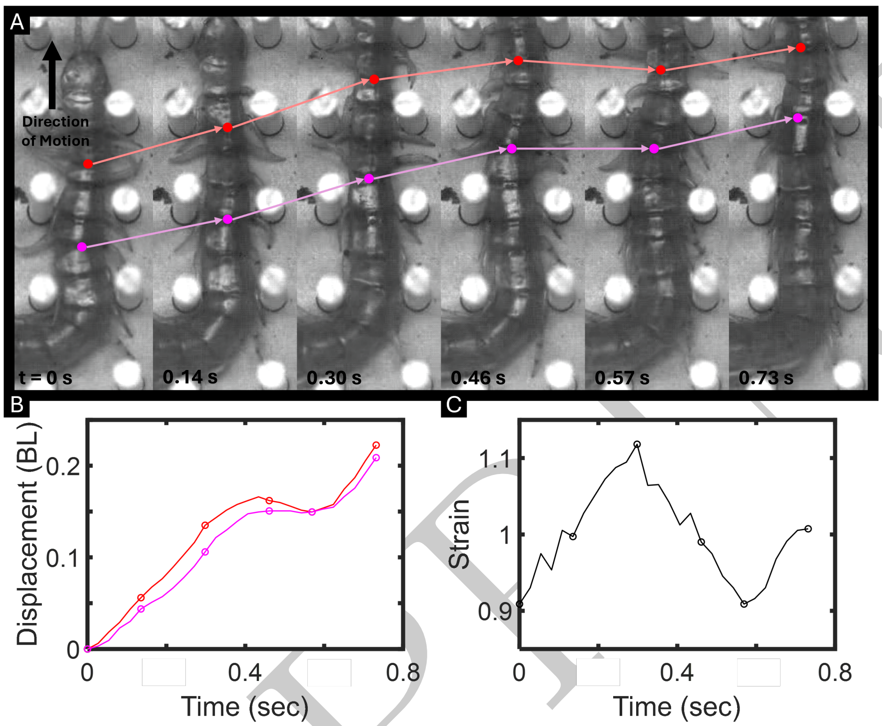

Figure 6: **Peristaltic-like motion.** (A) Image sequence of a centipede demonstrating peristaltic-like gait in 1 cm square lattice (1.6 c/BW) over 0.73 sec. Posts serve as scale bars in the images and time stamps are in the lower left corner for each image. Red and magenta dots are located at the center of a centipede plate and arrows visually indicate their displacement over this shown sequence. These dots are manually tracked every 0.027 sec and their displacement over time is shown in (B). Note that the entire body is moving forward as well. We take the difference in displacement between these two tracked points and divide by the average to get the strain vs time in (C).

However, it was rare (4 out of 89 trials) that the centipede would fully transition into this peristaltic-like gait within the lattice. Instead, would typically use this behavior as a mechanism to drag more limbs past the bend in the path. These front limbs then start their stepping motion while the back limbs shift into a streamlined posture. Additionally, we observed this stretching behavior occur more randomly when the centipedes reverse within the lattice or are exiting the lattice. In those instances, we see the centipede head retract or extend, respectively, without moving the back half of its body. In general, we hypothesize that this behavior allows the centipede to adopt complex paths and explore its environment without needing to use its limbs. Within these obstacle-rich environments, it enabled them to overcome areas with significant body drag and limited limb mobility.

Within the densest lattices (between 1 to 2 c/BW), the centipedes twisted their body and shift from ventral-substrate contact (legs on the ground) to lateral-substrate contact (legs on the posts) where they used the posts as propulsion (Figure 7A). This behavior is akin to that seen in snakes[12] where the backward slipping of their body bends is prevented by terrain heterogeneities and the resulting forces propel the snake forward. In the case of the centipedes, limb aggregates slip backwards until they made contact with a post. Once contact was made, we observed a postural shift in the centipede to locally twist its body, presumably to favor this new point of contact. It is worth noting that by twisting its body to perform lateral-substrate contact with one side of limbs, the other side's ability to perform limb strides was significantly impeded. By using the posts as footholds, the centipedes propel themselves forward in these dense environments despite only using half their legs for propulsion.

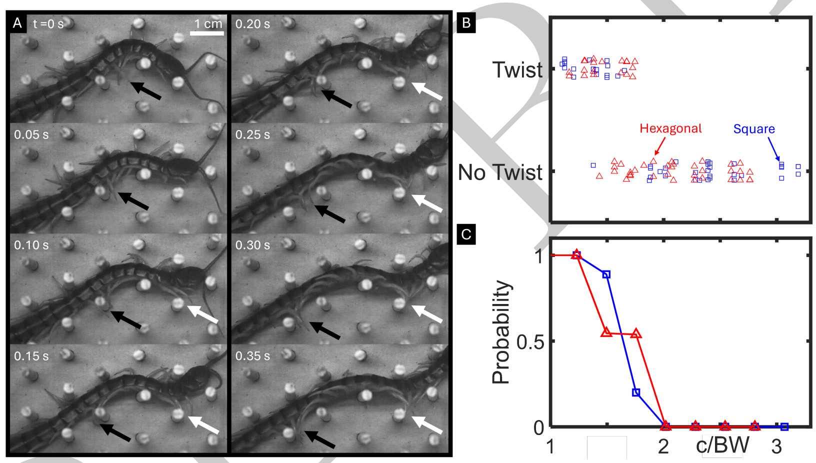

Figure 7: **Twisting behavior.** (A) Image sequence across 0.35 sec showcasing onset of body twisting and limb locomotion using posts when in 1.25 cm hexagonal lattice (1.9 c/BW). Black and white arrows indicate separate limb aggregates traveling along the body. Note that the white arrow remains stationary since that limb aggregate stays on that post. (B) Categorized plot of individual twisted and not twisted trials as a function of normalized lattice channel width. (C) Probability of twisting generated from the individual trials in (B) and plotted as a function of normalized channel width. The number of bins for the channel width is equal to the number of centipedes used across all trials.

Once in this twisted posture, the limb aggregates continued to travel along the body as in open space conditions rather than immediately settling on posts. Further, there were several instances where limbs would slip off a post or attempt to "walk on air" (Figure 7A black arrow). Based on this, we hypothesize that the centipede continues its normal gait pattern when twisted. Whether the onset of twisting is active or passive is unclear, however,the centipede's body locally shifted back to an untwisted posture when its limbs slipped off a post. This suggests that, if the twisting is an active response, it is only enacted for a short time before the legs reinforce this change in posture.

Classifying trials by "twist" or "no twist" revealed that transitions in body posture depend on normalized lattice width (Figure 7B,C). Further, these postural transitions always occurred in lattices less than 1.2 c/BW. However, between 1.2 and 2 c/BW, the centipedes exhibited both twisted and untwisted postures within different trials. These fluctuations are potentially due to the variety of paths chosen by the centipedes within the lattice. In cases where they took several turns, they were more likely to exhibit twisting around the bend than during forward motion. However, this does not capture all of the variability and thus, it remains unclear what drives the stochastic locomotor transition between twisted and untwisted postures between 1.2 and 2 body widths of spacing.

4.3 Robophysical model

To study the efficacy of the different behaviors noted above and whether they are active or passive, we developed a multilegged robophysical model (Figure 8A) to incorporate some of the various features observed in the centipedes. Specifically, this robot has a tunably compliant body that is inspired by direct compliant dynamics exhibited by bands of muscle activation observed in worms and snakes when in post arrays.[21,22] Further, similar bands of muscle activation are seen when these centipedes exhibit body undulations at high speeds.[23] By incorporating a tunably flexible body, we can study whether the stiffness has an effect on the types of paths taken by the centipede in the lattice. Additionally, it will enable us to explore whether body undulation with limbs could be helpful in lattices and what type of tradeoffs may occur.

A key feature that we seek to test with this robophysical model is whether terradynamic streamlining could be replicated passively and what benefits it could offer over the previous mechanism for limb gliding seen in robots.[24–26] To that effect, we introduce a new directionally compliant "hip joint" (Figure 8A, inset). This joint allows a limb to fold against the body upon an externally applied force (for the duration the force was applied). Without this joint, the robophysical model struggled to make forward headway through the lattice despite the relatively wide lattice channel width (5 c/BW). With the hip joint, the model's limbs passed against the body during limb-post collisions (Figure 8B) which facilitated forward motion in the lattice. Additionally, this hip joint resulted in a behavior not seen in the biological experiments. After a limb unfolded, it hooked onto the obstacle it just passed and used that post as a source of propulsion. This obstacle-aided locomotion was never seen in the live centipedes while making ventral-substrate contact and was only observed when in the twisted posture. We suspect that this behavior may be caused by the difference in relative post diameters in the lattice. Thus, in future work, we seek to investigate this both biologically and robophysically by varying the diameter

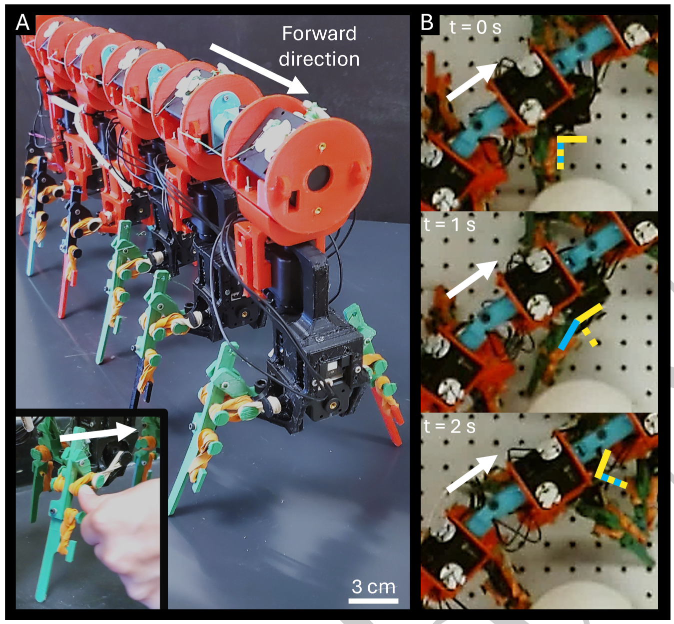

Figure 8: **Robophysical model for multilegged lattice locomotion.** (A) Robophysical model with directionally compliant hip joints and body. Inset showcases hip joint action. (B) Image sequence across 3 sec of the hip joint passively deforming on the robot during a lattice trial. White arrow indicates forward motion. Solid and dashed yellow lines correspond to the limb rotation angle and its perpendicular, respectively. Cyan line indicates motion of limb and hip joint as it collides with a lattice post, moving away from the dashed yellow line at t = 1 sec until returning at t = 2 sec.

of the posts in for both systems.

5 Conclusion

We performed, to the best of our knowledge, the first experiments of multi-legged locomotors in lattices, a model environment previously used to study limbless systems.[12–18] We explored whether *Scolopendra polymorpha* changed its gait in response to the obstacle-rich environments, and hypothesized that, since limbs in sprawl posture might lead to inhibitory collisions with posts and entanglement, increased obstacle density would induce a transition to limbless locomotion driven by body-post contact. We found that, instead of using primarily their bodies (similar to limbless undulators), the centipedes continued to use their limbs as their main source of propulsion and experienced little to no change in their net speed. This was despite various head collisions that would momentarily cause the centipedes to pause or redirect. The centipedes leveraged their versatile morphology to change their posture and gait during each trial such that the obstacles and collisions did not affect their speed. We make note of three distinct behaviors that we posit are crucial for the centipedes' success in the lattice: streamlining, stretching, and twisting. We hypothesize that these adaptations serve to mitigate drag in the lattice and allow for legged locomotion in these obstacle-rich environments to be not only feasible but robust and effective.

We developed a robophysical model to explore the individual effectiveness of each of these behaviors and whether each is active or passive. Preliminary work indicates that a passive directionally compliant hip joint can emulate simple terradynamic streamlining when hitting of an obstacle. Further, this joint augments a robophysical model to locomote across a lattice it could not otherwise fit within. This augmented robot displays emergent obstacle-aided locomotion after a streamlining event which we do not observe in the live centipedes. We propose to study this effect in future work both robophysically and biologically by varying post diameter for both systems.

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