Water surface swimming dynamics in lightweight centipedes

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Study of the locomotion of a centipede (L. forficatus) at the air-water interface reveals that it does not predominantly use its 14 leg pairs to locomote; unlike most swimmers which propagate head-to-tail body bending waves, this species propels via tail-to-head waves. Its low mass and body-fluid contact yield locomotion dynamics in which fluid wave drag forces dominate inertia. Microorganism-inspired wave drag resistive force theory captures swimming performance of the macroscale animal, motivating a control hypothesis for the animals’ self-propulsion body and limb kinematics.

Locomotion at the water surface is a common behavior across scales [1]. Research on surface swimmers has focused on animals using limb-surface interactions for propulsion (e.g., arthropods [2,7], lizards [8,9]). Inspired by the diverse water-running strategies, researchers have developed cm-scale robots that model limb-surface interactions comparable to their biological counterparts [2,10-12]. Yet, locomotion at the interface is not solely achieved via limb-surface interactions. Various animals (e.g., waterlily leaf beetle larva, salamanders, geckos) locomote at the water surface using primarily body-surface interactions [3,13,14]. However, these studies have been limited to animals possessing two to four leg pairs; the swimming dynamics of many-legged animals are less studied. Particularly, centipedes possess many limbs and inhabit diverse environments. Studies on centipedes have explored limb and body dynamics [15-21] on solid surfaces. Studies of centipedes on fluids [22] have been limited to subsurface dynamics.

Arthropods with few limbs support their body at the interface for propulsion. In contrast, multi-legged systems potentially rely on continuous contact due to their multi-segmented, elongated bodies. Animals relying on body-surface interactions for locomotion experience forces on their body that depend on the physical properties of the environment, the body orientation, and the instantaneous velocity. To model swimming in bulk fluids, Resistive Force Theory (RFT) is used due to its efficacious approximations of complex hydrodynamics in the presence of moving boundaries [23,24]. Specifically, RFT integrates the experienced thrust and drag on infinitesimal body segments of slender objects, assuming each hydrodynamic field is decoupled from other elements. Previous work used RFT to model locomotion in highly damped regimes, where viscous or frictional forces dominate over inertial forces [25,26], and thus the integral of stresses is equal to zero. Further, hydrodynamic RFT has been extended to the locomotion of slender bodies with rigid components perpendicular to each element (i.e., microorganisms with hispid flagella [28,29]).

Body dynamics in centipede surface self-propulsion.

We performed the first study of a water swimming centipede using the environment generalist Lithobius forficatus (mass 0.12 ± 0.03 g, length = 2.3±0.3 cm, 16 segments, and 14 leg pairs, N = 8, n = 32 trials). Experiments consisted of placing the centipedes on a water-filled tank (128x48.5x32 cm, 4 cm deep, 25-26°C) and recording their kinematics using a high speed camera (AOS, S-motion) positioned over the tank (Figure 2). When
placed on the water surface, centipedes used body undulation for propulsion (Figure 1A, SI Movie 1). Surprisingly, the direction of propagation of the body wave was the same as the direction of motion (direct, Figure 1B-C,F).

The propagation of direct body waves was unexpected: other macroscopic swimming undulators (e.g., snakes, eels, amphibious centipedes) propagate waves against the direction of motion (retrograde). Further, centipedes in the order Lithobiomorpha are thought unable to generate body undulation; in general, centipede gaits and body dynamics are thought fixed. However, as observed in recent studies, centipedes can exhibit distinct behaviors upon external perturbations.

Unlike in amphibious centipedes which fold limbs to the body when swimming, L. forficatus did not change limb dynamics during aquatic locomotion. Instead, the limbs exhibited a direct stepping pattern, and oscillated using a maximum limb amplitude ($\theta_{\text{max}}$) of 34.2±7.5°. However, without body undulation, displacement was negligible (SI Movie 1). Using direct body waves, the centipedes achieved speeds of 0.22±0.03 body lengths per gait cycle (BL/cyc), with a maximum amplitude of 3.9±1.5 cm$^{-1}$ and a spatial frequency of 1.3±0.23. In addition, we digitized the body midlines and performed principal component analysis (PCA) on the body curvature ($\kappa$) to generate a low-dimensional representation of body shapes. Two principal components (PCs) captured 75.9% of the variance and were well fit by a sine and a cosine, corresponding to a traveling wave of curvature (Figure 1G-H).

Surface waves. When the animals stopped undulating, “coasting” displacement was negligible (0.05 ± 0.02 BL), suggesting a dissipative locomotor regime analogous to the dynamics of microorganisms and sandswimmers. In such regimes, locomotors generate reaction forces to overcome viscous or frictional drag forces. In the centipede, no persistent flows were generated (SI Movie 1) and air resistance was negligible. However, we observed that the centipedes emitted waves during propulsion and thus posited that propulsion is dominated by surface wave drag, instead of viscous drag. Since little work has been done to study such a locomotor regime, we sought to measure the emerging surface waves to gain insight into the propulsion and dissipation mechanisms.

Surface waves generated by L. forficatus during swimming were reconstructed using a synthetic image (Figure 2A-B) Schlieren imaging (Fast Checkerboard Demodulation) (SI Movie 2, see Supplementary Information). Wave reconstruction resulting in measured wave height versus time revealed transient and periodic dynamics (Figure 2C-D). Transient motion of the wave heights occurred when the centipede’s shape changed from a straight to undulating body associated with changes in the gait (during startup, presumed to be from limb to body-dominated). Periodic motion of the wave heights occurred when the centipede constantly propagated body waves (Figure S2). Constant self-deformation for propulsion is characteristic of locomotion in non-inertial regimes such that coasting or gliding phases do not occur. In terrestrial and low Reynolds number regimes, dissipation is due to frictional and viscous forces. We hypothesize dissipation occurs in this centipede via the generation of fluid surface waves which carry energy away to the boundary. The transition from transient to periodic is characteristic of the shape changes in the animal and an increasing distance from the point where wave heights were measured. In the far field, we observe changes in the wave heights that correspond to a periodic phase and dissipation.

Drag measurements. RFT allows predictions of drag-based thrust in self-deforming locomotors. In non-inertial systems, the key insight is that the direction of motion and speed of an undulator are governed by the ratio of normal ($F_n$) to tangential ($F_t$) forces experienced by each presumed-independently translating element. When this drag anisotropy ($F_n/F_t$) exceeds unity for all elements, retrograde waves produce forward propulsion. RFT can be extended to objects with rigid components perpendicular to the object’s surface, as in hispid flagella in microorganisms. This flagellum’s morphology creates an effective $F_n/F_t < 1$ over the length of the flagellum, resulting in forward displacement using direct waves. We posit that because the flagella and the swimming centipede share similar morphology (i.e., extended components), comparable wave dynamics (i.e., direct waves), and op-
erate in non-inertial regimes, the centipedes experience an effective \( F_n / F_t < 1 \) and thus their locomotion can be modeled using RFT.

Since RFT requires inputs from drag forces and these had not been previously made at the air-water interface, we sought to obtain the appropriate force relations. Drag measurements were performed with an H-shaped resin printed segment (length = 12 mm, width and height = 2 mm, leg thickness = 0.5 mm) modeling the slender body with two leg pairs to obtain steady-state drag force (\( F \)). Drag was not previously made at the air-water interface, modeled using RFT.

As stated above, RFT assumes that forces along a deforming body are decoupled. Therefore, the swimmer can be divided into 14 independent segments. Further, in dissipation-dominated environments where inertial forces are negligible, the net force on a body is zero at every moment in time, giving

\[
F = \sum_{i=1}^{14} (F_n^{[i]} + F_t^{[i]}) = 0,
\]

increasing \( \beta_d \) for all \( v_d \) (Figure 4C-D). Although at \( \beta_d = 60^\circ \) \( F_n / F_t \) approached one, the centipedes exhibit attack angles (\( \beta_a \)) primarily from 0° to 45°. Further, \( F_n / F_t \) was insensitive to \( v_d \).

**FIG. 3. Water surface drag measurements.** (A) Experimental apparatus for drag measurements. Dashed square highlights model segment (inset). (B) Snapshot of surface waves generated by model segment dragged at the interface. Surface waves were not obtained from Schlieren reconstruction; a horizontal line background pattern was used to visualize surface waves [41]. (C) Drag force at \( v_d = 11.25 \text{ cm/s} \) for \( \beta_d = 0^\circ \) (light blue), 45° (medium blue), and 90° (dark blue) with five trials per condition. (D) Steady state force vs. \( v_d \) for \( \beta_d = 0^\circ, 45^\circ, \) and 90°.

**FIG. 4. Force decomposition and drag anisotropy for surface wave drag.** (A) \( F_n \), (B) \( F_t \), and (C) \( F_n / F_t \) vs. \( \beta_d \) for varying \( v_d \). Inset in (A) shows top view of the model centipede segment moving at \( \beta_d \) with constant \( v_d \). Solid gray area in (C) shows probability distribution function (PDF) of the attack angle (\( \beta_a \)) measured in the centipedes. \( \beta_a \) is defined as the angle between a local tangent angle and the average direction of motion (inset). (D) \( F_n / F_t \) vs. \( v_d \) for varying \( \beta_d \). Black horizontal dashed lines correspond to \( F_n / F_t = 1 \).
where $F_n^i$ and $F_t^i$ are normal and tangential force on $i$-th element, respectively. We calculate BL/cyc as a function of mean relative curvature ($\kappa_m \lambda_s$, Figure 5). We hypothesize the animals preferentially use direct body waves, requiring no modulation of the limb-stepping pattern for propulsion. However, other centipede species modulate their body [22] and limb [19][21] dynamics upon external perturbations. Thus, as observed in amphibious centipedes [22], we extended the predictions to the case where the centipede uses a retrograde body wave (the chirality of the PC projections, Figure 5) with folded limbs towards the body. For direct waves, we assume forces act on the limbs. For retrograde waves, we assume forces act on the body segments (Figure 5C(i)-(ii)). Further, we compared across experimentally resolved and different $F_n/F_t$ and limb posturing for both direct and retrograde waves in simulations. Direct waves with folded limbs and retrograde waves with extended limbs lead to backward motion, and thus were not included in the comparison (Figure S4).

For direct waves, we obtained good agreement using experimentally resolved forces ($F_n/F_t = 0.75$) between RFT predictions and the animal’s performance (BL/cyc = 0.22 ± 0.03, $\kappa_m/\lambda_s = 8.54 ± 1.76$) (Figure 5D). This suggests that, as hypothesized, $F_n/F_t \leq 1$ emerges due to the centipede’s morphology (i.e., extended limbs). If L. forficatus changed its body profile during swimming, it would achieve backward displacement using a direct body wave (Figure S4). Thus, while the limbs did not contribute to propulsion, they modulated the animal’s $F_n/F_t$. Further, for all $F_n/F_t$, RFT predicts increasing BL/cyc with increasing $\kappa_m/\lambda_s$, decreasing at approximately $\kappa_m/\lambda_s = 11$.

For theoretical retrograde waves with folded limbs, performance also increased with increasing $\kappa_m/\lambda_s$, decreasing at approximately $\kappa_m/\lambda_s = 10$. However, independent of $F_n/F_t$, a direct wave with extended limbs achieved greater or comparable performance. Thus, the centipedes use the behavior that guarantees a high swimming performance, potentially desirable when subject to perturbations (e.g., choppy waters [43]). Moreover, using direct body waves may simplify the animal’s neuromechanical control: forward motion using retrograde waves requires a change in both limb behavior and body wave propagation direction. In contrast, a direct limb-stepping pattern requires only the addition of direct body waves for propulsion.

While drag measurements were performed for the case without limb oscillation ($\theta_{max} = 0^\circ$), the centipedes oscillate their limbs with $\theta_{max} = 34.2 ± 7.5^\circ$. This affects at what $\kappa_m \lambda_s$ limb-limb (L-L) and limb-body (L-B) intersections occur (Figure 5D). When $\theta_{max} = 0^\circ$, L-L and L-B intersections occurred at $\kappa_m \lambda_s \geq 5.9$ and 11.3, respectively. In contrast, when $\theta_{max} = 34^\circ$, L-L and L-B intersections occurred at $\kappa_m \lambda_s \geq 8.7$ and 11.5, respectively. While limb oscillations may not contribute to propulsion, $\theta_{max} = 34^\circ$ facilitates greater body bends and reduces emergent collisions. We observed L-L intersections in the centipedes primarily occurring at the limb tip, but no L-B intersections were observed. We posit limb oscillations allow the animals to function at the limit of achievable body bends, without introducing L-B collisions.

Although an RFT framework has not been previously utilized for locomotion at the interface, recent work has demonstrated that the effectiveness of RFT depends on the medium’s governing partial differential equations (PDE) [44]. When PDEs are hyperbolic (e.g., granular media [29][32]), stresses are localized and can be attributed to the motion of specific body elements [44]. For elliptic PDEs (e.g., viscous fluids), segmental stresses depend on the entire boundary [43] and accurate modeling of locomotion requires more sophisticated approaches [45]. The fact that the RFT approach functions well in the centipede surface swimming is in accord with the hyperbolic equations that describe surface waves [46].

**Conclusion.** We performed the first centipede loco-
motion experiments and RFT modeling at the air-water interface. Our study revealed that the animal operates in a regime in which inertia is dominated by fluid wave drag. The centipede locomotes using direct waves of a characteristic amplitude, due to its splayed limb posture and the functional forms of the wave dominated resistive forces. In addition to advancing understanding of neuromechanical control of myriapod locomotion [18–22], our work can lead to hydrodynamic capabilities of existing terradynamically capable multilegged robots [47, 48].

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SUPPLEMENTARY INFORMATION

Animals. Centipedes were wild caught from Cuyahoga County, Ohio. Each centipede was individually housed in a plastic container on a 12 hr:12 hr L:D photoperiod at room temperature (20-22°C). Centipedes were provided a source of water and fed mealworms biweekly.

FIG. S1. Raw data obtained from drag measurements. (A) Measured pixel intensity along the long axis of the laser spot. Blue curve corresponds to a fitted Gaussian. (B) Raw force measurement (black) obtained from drag experiments for βd = 60° at vd = 11.25 cm/s. Yellow and blue line correspond to forces along the normal and tangential direction of the model centipede segment, respectively.

Reflection based drag measurement apparatus. The drag apparatus consisted of a model segment, a laser, and a camera. The model centipede segment was attached to a thin beam (0.25 mm thick aluminum, McMaster-Carr, 9708K51). The laser was reflected off the thin beam and a camera (Basler, acA1300-200um) recorded the laser spot to obtain beam deflection. The centroid of the laser was obtained by finding the global maximum pixel intensity for each frame using a custom MATLAB code (Figure S1A). Steady state force was resolved from laser centroid displacement by calibrating the beam to objects of known mass (0.01 g, 0.05 g, and 0.1 g). Figure S1B shows example drag measurement obtained from apparatus for βd = 60° at vd = 11.25 cm/s.

FIG. S2. Surface wave heights during centipede swimming. Wave surface height over time for a selected region (white circle in Figure2C,D) at the (A) near and (B) far field. Single sided amplitude spectrum of surface wave heights at the (C) near and (D) far field.

Synthetic Schlieren imaging. Before starting the experiments, we captured a reference image of the background pattern (checkerboard) as seen through a still free surface with the high speed camera. During experiments, surface waves created by the swimming centipedes appeared as a distortion field ü applied to the checkerboard. We compared the spatial Fourier transform of the distorted checkerboard to that of the reference image to find how the carrier peaks were modulated. When the free surface curvature had focal length greater than the distance to the background pattern (i.e., the invertibility condition is met [36]) we filtered the modulated signal to extract ü(r,t), which is proportional to the gradient of the free surface height. Moisy and colleagues [36] quantify this invertibility condition as follows:

\[ h_p < h_{p,c} = \frac{\lambda^2}{4\pi^2\alpha \eta_0}, \]  

where \( h_p \) is the effective surface-pattern distance, \( h_{p,c} \) is the free surface focal length, \( \lambda \) is the wavelength, \( \alpha \) is the ratio of indices of refraction given by \( 1 - n_{air}/n_{fluid} \), and \( \eta_0 \) is the wave amplitude [36]. Further, We adapted the open-source code in [40] for use with our apparatus (Figure2A), incorporating both a scale factor to account for additional interfaces between the background pattern and the fluid free surface [36].

Quantitatively identifying where the invertibility condition fails requires knowledge of wave properties that are not known a priori and cannot be reliably obtained from
the reconstruction itself. However, we note that failed reconstruction surface height data typically is highly discontinuous, both with itself and with successfully reconstructed surface heights. We used this characteristic to estimate regions where the reconstruction failed per video frame with an autocorrelation method described by the following steps:

1. Perform a 2D spatially-moving variance with square kernel given by the 8-way nearest pixel neighbors.

2. Compare the moving variance to a threshold value. We obtained our threshold through trial-and-error but postulate that it is related to the effective distance between the free surface and background pattern.

3. Convert any pixels for which the variance exceeds the threshold to a mask.

4. Perform minor cleanup on the mask using morphological operations. The result is an estimate of all failed surface reconstructions in the frame.

FIG. S3. Force decomposition fits. Normalized (by \( F_t(\beta_d=0) \)) (A) \( F_n \) and (B) \( F_t \) as a function of \( \beta_d \) for varying \( v_d \). Solid black lines correspond to sine and cosine fits for \( F_n \) and \( F_t \), respectively.

FIG. S4. Surface wave RFT for varied limb posturing. RFT predictions of swimming performance for direct waves with folded limbs (gray line) and retrograde waves with extended limbs (black line).

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