The role of body undulation in centipede locomotion in a geometric mechanics perspective

[redacted]

I. Background

A. Chilopoda

Centipedes, class Chilopoda, have wide distribution over all continents except Antarctica [4]. Their habitats include leaf litter, soil, stones, forests, desert, caves, and the littoral zone [9]. The class Chilopoda can further devide into two subclasses, Anamorpha and Epimorpha [3]. In the subclass Anamorpha, the young centipedes (after hatching) do not possess the same number of legs as adult centipedes, All adult Anamorphic centipedes have 15 pairs of legs [4]. The subclass Anamorpha includes two orders: Scutigeromorpha and Lithobiomorpha. On the other hand, in the subclass Epimorpha, all centipedes on hatch have the full number of legs as adult centipdes. The number of leg pairs in subclass Epimorpha vary from 21 to 181. The subclass Epimorpha includes two orders: Scolopendromorpha and Geophilomorpha.

Note that there is a Chilopoda order, Craterostigmomorpha, considered as the intermediate stage of the switch from an anamorphic developmental mode to an epimorphic one in the course of centipede phylogeny. Centipedes in this order have some features of both subclasses. Due to the lack of data, the models in this paper does not include Craterostigmomorpha.

The centipedes in subclass Anamorpha have the characteristic direct wave locomotion pattern. That is, the leg wave of anamorphic centipedes propengate from tail to head [7]. The body undulation in anamorphic centipedes are rare. Body undulation in Anamorpha is only observed in Lithobiomorpha at high speed. Furthermore, the body undulations in Lithobiomorpha at high speed have limited amplitude and are believed to be passive[9].

Anamorphic centipedes have successful locomotive performance on solid substrate. Their speed can be as large as 19 body length per second. However, anamorphic centipedes have poor performance during swimming motion.

The centipedes in subclass Epimorpha have the characteristic retrograde wave locomotion pattern. That is, the leg wave of epimorphic centipedes propengate from head to tail [7]. The body undulation are common in anamorphic centipedes[9]. Besides, Anderson et al. [2] recorded EMG of body segments during epimorphic centipedes locomotion; the analysis of epimorphic centipedes body segments EMG indicates that the body undulation is active in epimorphic centipedes locomotion, partially to assist locomotion.

Epimorphic centipedes have great locomotive performance on solid substrate and in water (swimming), partially because their body undulation. This locomotive feature allow epimorphic centipedes to live in habitats where they often need to immerse during monsoonal floods [1]

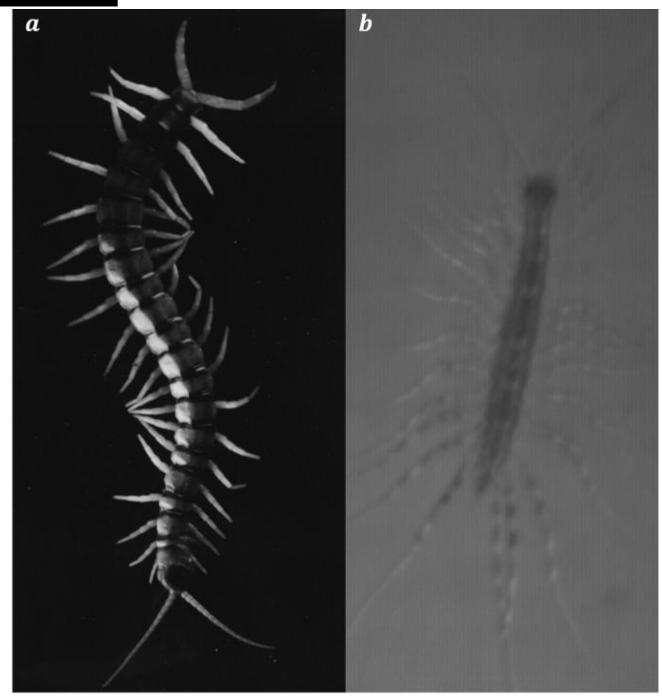


Figure 1. a. image of an epimorphic centipede (by the courtesy of Prof. Robert Full). b. image of an anamorphic centipede

B. Centipede locomotion

Centipede locomotion has been extensively studied in previous work [7, 11, 6, 9, 2]. In previous work, dynamic models were built to predict the locomotion behavior of centipedes. The complex equations of dynamic motion can often be less intuitive and difficult to visualize.

In this paper, we seek to build a simple kinematic model to study the locomotion behavior of centipedes. In previous work, our kinematic model have been applied to study the locomotion behavior of mud-skipper [10], snake [8], salamanders [12]. In this paper, we extended this kinematic framework to study centipede locomotion.

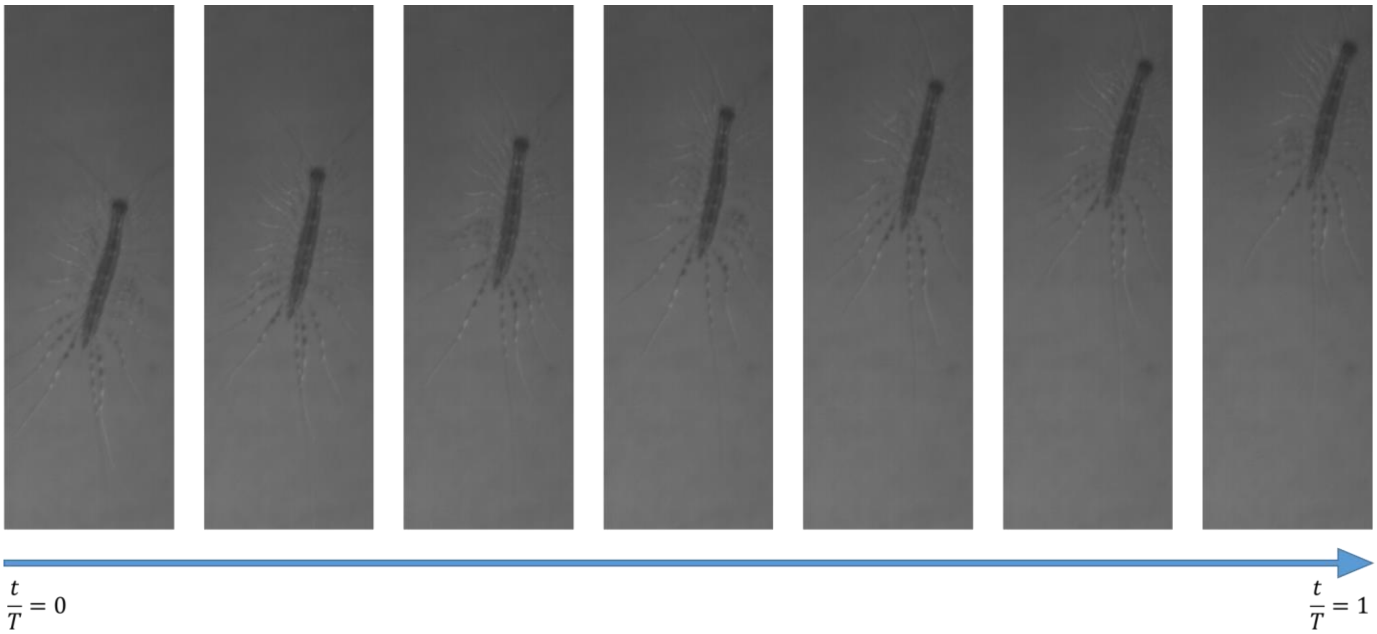


Figure 2. One period of an anamorphic centipede locomotion on glass arena

We first collect the animal locomotion videos of an anamorphic centipedes. We used high speed camera to record its motion on a glass arena. We then performed video analysis and tracked the its locomotion pattern. With morphological parameters, we built a model of anamorphic centipede locomotion. In our model, our prediction of speed agrees well with the animal speed.

Next, we seek to model the epimorphic centipede locomotion. Unlike anamorphic centipedes, epimorphic centipedes coordinate body undulation with leg movements to improve locomotion performance. By the courtesy of Prof. Robert Full, we obtained a video of a epimorphic centipede moving on trill mill. We performed video analysis and tracked the body undulation pattern and leg movement pattern. We observe that there is a mismatch in the body undulation spatial frequency and leg wave spatial frequency. We also observe a constant geometric phase offset of body undulation and leg movements.

In the model, we wish to predict the coordination of body undulation and leg movements. Specifically, we wish to optimize the optimal geometric phase offset, between body undulation and leg movement, that will lead to largest forward speed. We utilize geometric mechanics tool to run optimization. It turns out that the our theoretical predicted geometric phase agrees well with the observed animal data. The improper body undulation spatial frequency or improper geometric phase offset will lead to less forward displacement.

Finally, though there is less body undulation in anamorphic centipedes (direct leg wave), we test how body undulation can assist locomotion. Surprisingly, the proper body undulation coordinated with direct leg wave can lead to larger forward displacement than that with retrograde leg wave. It is interesting that the gaits never exist in biological systems turn out to have better locomotive performance.

II. Method

A. Animal video

1) Anamorphic centipedes: Prof. Daniel Goldman obtained a house centipede (one of anamorphic centipedes). We used this house centipede and recorded their locomotion behavior on a glass arena. High speed camera (200fps) were unitized to record video (See Fig. 2). We manually tracked the motion pattern in the video and measured the morphology parameters. The parameters are listed in Table 1.

Parameter	Anamorphic centipede	Epimorphic centipedes
Number of legs	12	18
Leg spatial frequency f_β	0.15±0.04	−0.10±0.02
Body spatial frequency f_α	N/A	−0.06±0.04
Leg length (Pixels)	61±20	50±8
Leg Spacing (Pixels)	10.4±1.0	26.4±2.4
Leg Amplitude A_β (degree)	28±7	36±3
Body Amplitude A_α (degree)	0±0	15±4

Table I

TrackedParameters

2) Epimorphic centipedes: By the courtesy of Prof. Robert Full, we obtained a video of an epimorphic centipede

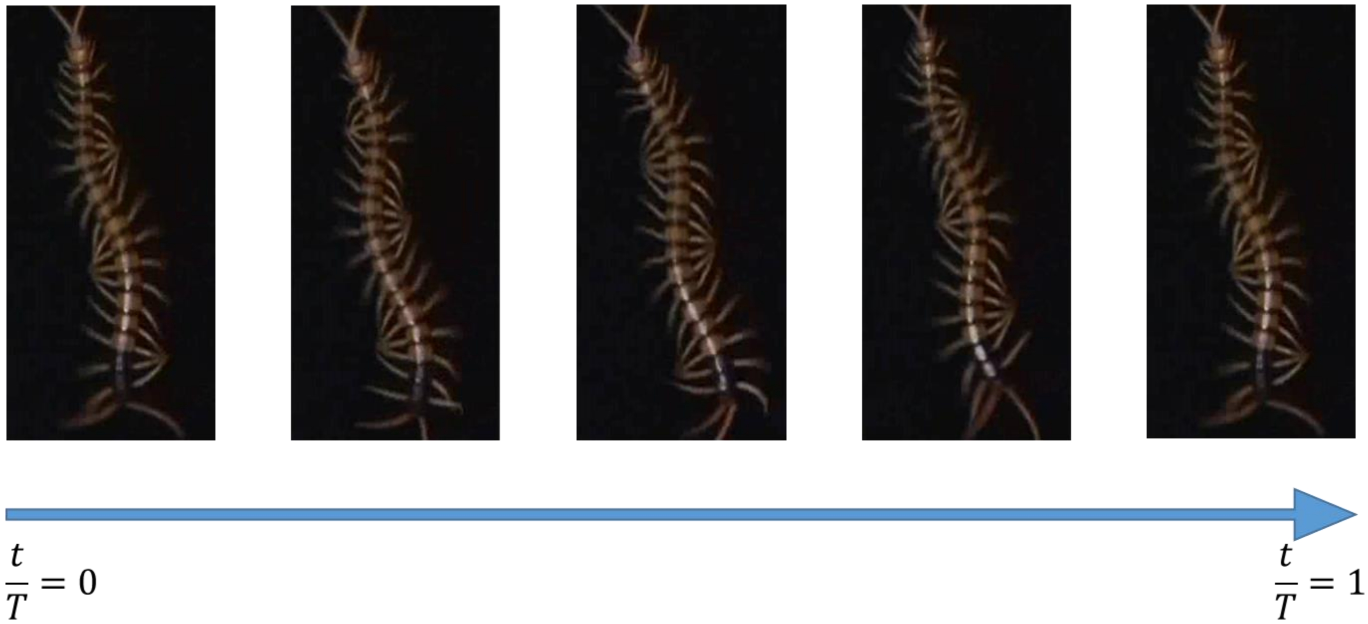


Figure 3. One period of an epimorphic centipede locomotion on trill mill

moving on trill mill. The snapshot of this video is shown in Fig. 3. Similar to anamorphic centipedes, we tracked the video and analyzed their morphology and motion parameters in Table 1. We manually tracked position of body segments and leg movements in each frame (see Fig. 8). We then fit a sinusoidal function to the obtained body segment position and leg joint angles. Then we can read the spatial frequency for both body undulation and leg movements. We can also read the geometric phase distribution along the gait.

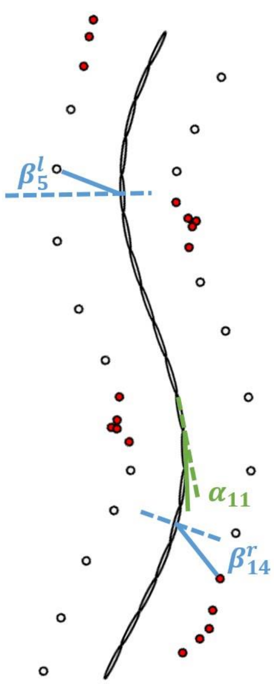


Figure 4. Shape variable in centipede model

B. Locomotion model

We built a simple kinematic locomotion model to study centipede locomotion. The shape variable of centipedes with n legs include the left leg joint angles $\boldsymbol{\beta^l} = [\beta_1^l\ \beta_2^l\ \ldots,\ \beta_n^l]^T$, left leg contact state $c^l = [c_1^l\ c_2^l\ \ldots,\ c_n^l]^T$, right leg joint angles $\boldsymbol{\beta^r} = [\beta_1^r\ \beta_2^r\ \ldots,\ \beta_n^r]^T$, right leg contact state $c^r = [c_1^r\ c_2^r\ \ldots,\ c_n^r]^T$, and body joint angles $\alpha = [\alpha_1\ \alpha_2\ \ldots,\ \alpha_{n-1}]^T$. The shape variables are labeled in Fig. 4. Note that contact state $c^{r,l}{}_i \in \{0\ 1\}$, such that 0 (open circle in Fig. 4) indicates in the air while 1 (red circle in Fig. 4) indicates on the ground. In simple kinematic model, we assume that the effect of inertia is negligible during centipede locomotion. With this assumption, the equation of motion reduces to:

$$\xi = A(c,r)\dot{r} \tag{1}$$

where $r = [\alpha,\ \beta^l,\ \beta^r]^T$ is the collection of joint angles, $c = [c^l,\ c^r]$ is the collection of leg contact state, $\xi = [\xi_x,\ \xi_y,\ \xi_\theta]$ is the body velocity; A is called local connection matrix, which maps the shape velocities to body velocities. In practice, A can often be numerically derived [12].

We further simplify the model, we assume that leg wave are traveling waves. That is,

$$\beta_i^r(\phi_1) = A_\beta \sin(f_\beta \times 2\pi \frac{i}{n} + \phi_1) \tag{2}$$

$$\beta_i^l(\phi_1) = A_\beta \sin(f_\beta \times 2\pi \frac{i}{n} + \phi_1 + \pi) \tag{3}$$

where φ_1 is the phase of leg movements, f_β is the spatial frequency of leg movements. $f_\beta > 0$ denote that the phase of hind leg is ahead of the phase of fore leg, the leg wave propagate from tail to head (direct wave); on the other hand, $f_\beta < 0$ denote that the phase of fore leg is ahead of the phase of hind leg, the leg wave propagate from head to tail (retrograde wave).

The contact state can then be inferred from the assumption

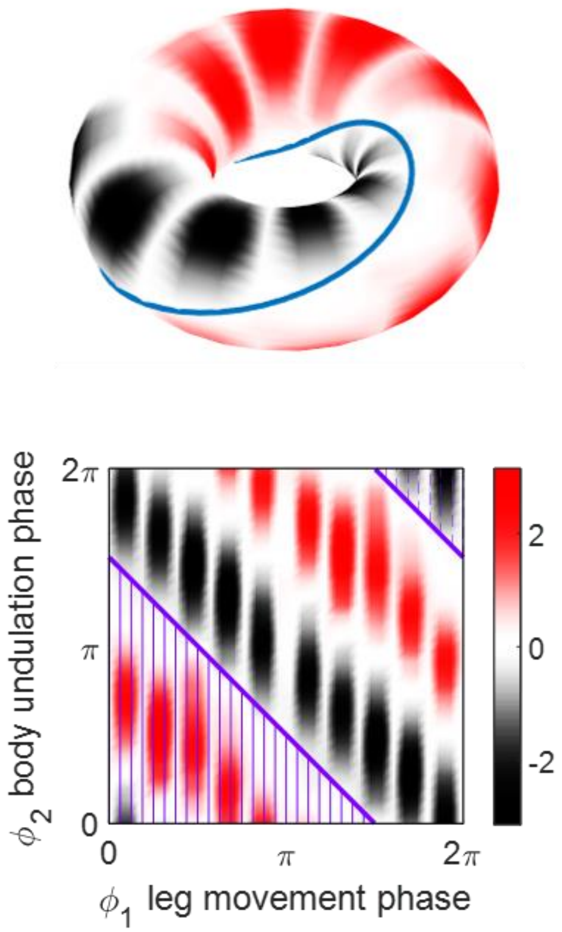


Figure 5. Height function on torus and its unfolded Euclidean space

state ($\frac{d\beta_i^{l,r}}{d\varphi_1}$ > 0); one leg is on the ground ($c_i^{l,r}$ (φ_1)=1) when it is in retrieving state ($\frac{d\beta_i^{l,r}}{d\varphi_1}$ < 0) that one leg is in the air ($c_i^{l,r}(\phi_1) = 0$) when it is in recover Similarly, the body joint angle also follows the travelling wave:

$$\alpha_i(\phi_2) = A_\alpha \sin(f_\alpha \times 2\pi \frac{i}{n-1} + \phi_2) \quad (4)$$

where φ_2 is the phase of body undulation, f_α is the spatial frequency of body undulation. Similar to leg movements, $f_\alpha > 0$ denotes tail to head body wave propagation while $f_\alpha < 0$ denotes head to tail body wave propagation. In this way, we can rewrite Eq. 1 as:

$$\xi = A(\varphi)\dot{\varphi} \quad (5)$$

where $\varphi = [\varphi_1\ \varphi_2]^T$ is the shape phase variable.

1) Geometric Mechanics: In Eq. 6, we formulate a two dimensional torus shape space, on which we can design gaits.

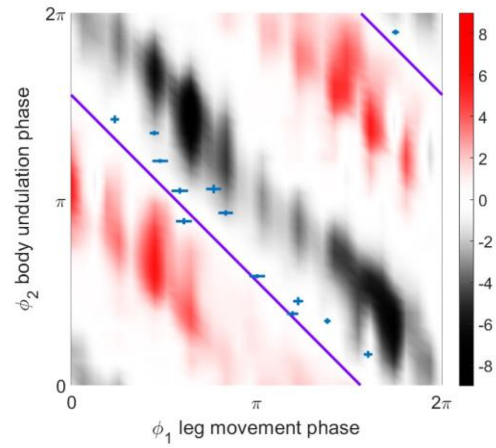
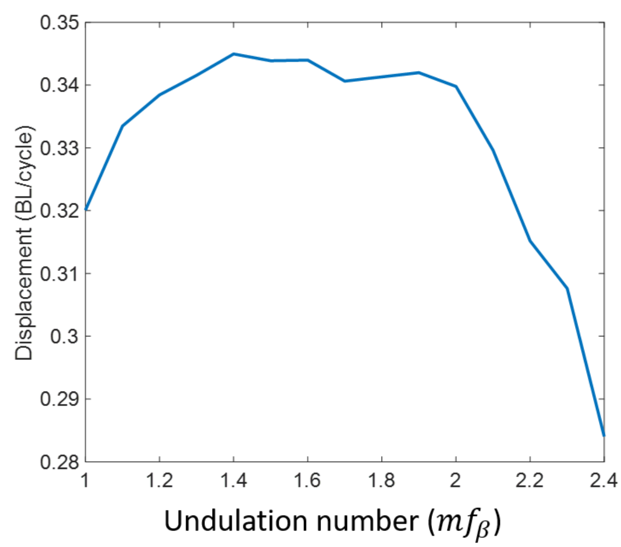


Figure 6. Tracked animal data VS theoretical prediction



Detail derivation of gait design on torus shape space can be found in [5].

We provide an example of geometric mechanics on torus shape space in Fig. 5. The gait path is illustrated as blue

Figure 7. Spatial frequency VS displacement

curves. The gait path that will enclose most volume (solid shadow) on lower corner and least volume (dashed shadow) on upper corner is predicted to be the gait with largest forward displacement.

III. Results

A. Anamorphic centipede model

To best our theory, we first ran simulation of anamorphic centipede locomotion model. Since there is no body undulation, the simulation is then straightforward. In simulation, the predicted displacement is 0.96 body length per cycle, in quantitative agreement with animal data (0.99 ± 0.02 body length per cycle).

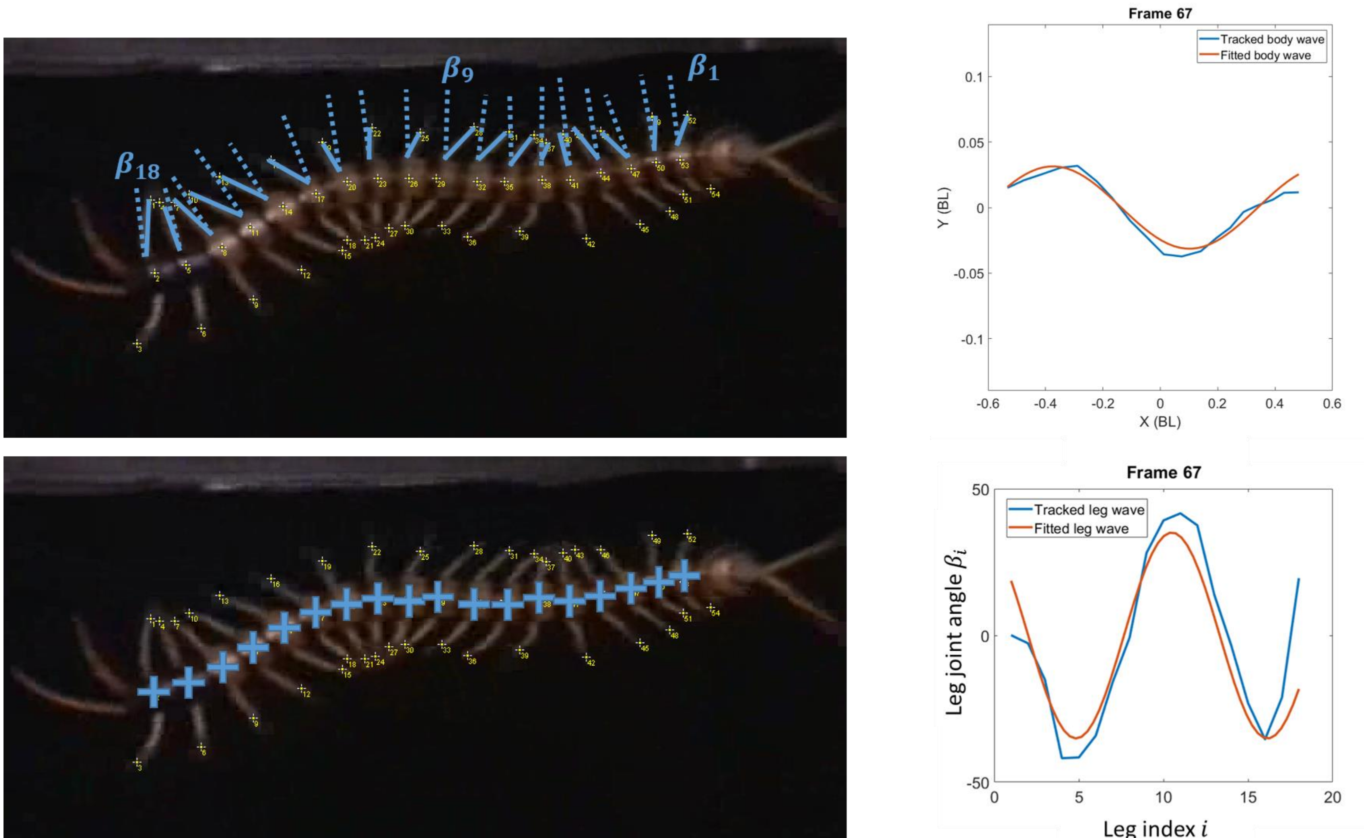


Figure 8. Tracked body position and leg joint angles

B. Epimorphic centipede model

1) Direct comparison: We compared the obtained optimal gait path and the tracked animal data in Fig. 6. Good agreement is observed.

2) Body wave spatial frequency: Next, we explore the effect of body wave frequencies. It is counter intuitive that the body wave spatial frequency is different from the leg wave spatial frequency. Thus, we sample a series of spatial frequency and test how spatial frequency can affect the displacement.

Specifically, for each body wave spatial frequency, we applied geometric mechanics to obtain the optimized geometric phase offset between body wave and leg wave. Next, we run simulation to find the corresponding displacement (see Fig. 7).

IV. Conclusion

In this paper, we build a simple kinematic model to study centipede locomotion. In our model, our theoretical prediction of geometric phase offset between body undulation and leg movements agrees with the tracked animal data. From animal video, we observed that there is a mismatch of spatial frequency of body undulation and leg movement. We studies the effect of spatial frequency on the displacement.

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