Decoding the Interplay Between Central and Peripheral Control for Versatile Locomotor Repertoire in Centipedes

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1 Introduction

Animals can generate versatile locomotor behaviors in response to the situation. For instance, they change gaits to increase locomotor speed [1] and use different locomotor patterns like walking and swimming to traverse different environmental media [2]. Such behavioral flexibility is realized through the coordinated motor outputs of the body parts. Extracting control principles underlying locomotor circuits contributes not only to neurobiological understanding but also to bio-inspired robotics aiming to establish the design methodology of locomotor intelligence.

Neurobiological studies have shown that locomotor movements are controlled by higher centers (brain) and lower locomotor circuits (ventral nerve cord in invertebrates) [3]. Higher centers select locomotor modes and adjust speed and direction, while lower circuits generate motor patterns via central pattern generators (CPGs). Peripheral sensory feedback adjusts these rhythms in response to environmental changes. Understanding the integration of higher centers, lower locomotor circuits, and sensory feedback is crucial, but their interaction remains largely unclear.

To address this issue, we use an amphibious centipede (*Scolopendra subspinipes mutilans*) as a model animal. This centipede exhibits versatile body coordination: it walks on land using leg movements, swims in water with body undulation, and combines both during fast walking [4, 5]. Its central nervous system, composed of the head and segmental ganglia, generates these movements. Since centipedes can walk without the head [6], the lower locomotor circuits are resilient. Due to their ability to endure neuronal lesions, these centipedes are suitable for studying interactions between higher centers and lower locomotor circuits in producing a versatile locomotor repertoire.

Although we have previously proposed neuromechanical models of centipedes that replicate slow and fast walking patterns [7–10] and transitions between walking and swimming [5], the influence of descending signals from higher centers on these behaviors remains unclear. In this study, we performed stepwise removal of the brain and subesophageal ganglion (SEG) in centipedes to identify the contributions of higher centers to locomotor control. In this presentation, we introduce new findings from behavioral experiments and our updated mathematical model, which reproduces versatile locomotor behaviors (transitions between slow walking, fast walking, and swimming) through simple descending control from higher centers interacting with lower locomotor circuits.

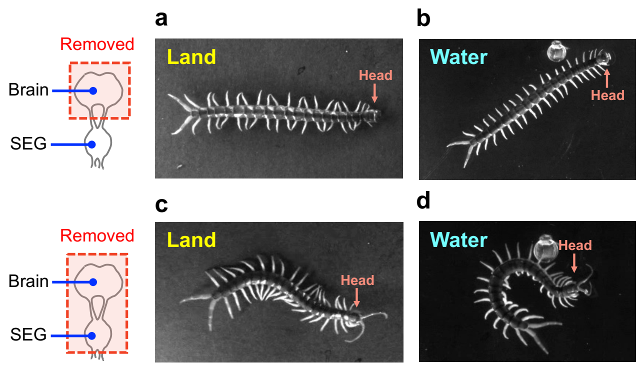

Figure 1: Snapshots of representative centipede behaviors in terrestrial and aquatic environments after surgical removal of: (a, b) the brain, and (c, d) both the brain and subesophageal ganglion (SEG).

2 Behavioral experiment

To understand the interaction between higher centers and lower locomotor circuits, we conducted behavioral experiments on centipedes after surgically removing their brain and SEG. The brainless centipedes exhibited coordinated walking on land with a straight body (Fig. 1a) and varied locomotor outcomes in water (Fig. 1b): body undulation and leg posture were decoupled and the propensity for rhythmic body undulation decreased. When both the brain and SEG were removed, the centipedes primarily showed fast walking on land (Fig. 1c) and, in water, exhibited rhythmic body undulation while holding their legs in an extended position (Fig. 1d). Thus, these behavioral changes suggest

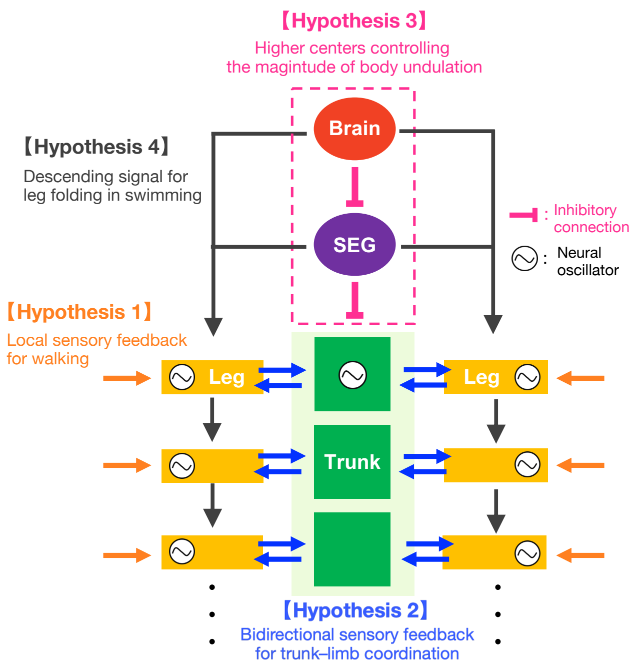

Figure 2: Overview of the hypothesized control circuits.

that descending signals from the higher centers have a modulatory effect on the magnitude of body undulation during walking and swimming, and are necessary for leg folding in swimming.

3 Modeling

Based on the new findings from the behavioral experiments, we updated our hypotheses on the locomotor circuits in centipedes and constructed a mathematical model to simulate the hypothesized control mechanisms. Our latest hypotheses are summarized as follows (Fig. 2):

Hypothesis 1 The inter-limb coordination pattern for walking can be generated through a decentralized control system using mechano-sensory feedback based on the ground contact of the legs [7, 8].

Hypothesis 2 The coordinated pattern between the trunk and legs during fast walking can be established through bidirectional local sensory feedback between the trunk and legs [9].

Hypothesis 3 The SEG inhibits the rhythmic motion of body bending, and the brain initiates body bending during fast walking and swimming by inhibiting the activity of the SEG.

Hypothesis 4 The brain and SEG signals initiate and maintain leg folding for swimming and these signals are additive and propagate posteriorly.

We built a simple two-dimensional physical model of the centipede with 20 pairs of legs (Fig. 3). The body is modeled using a mass-spring-damper system, and each leg and trunk segment has one rotational degree of freedom for leg swinging and body bending. Our model assumes that the rhythmic motions of the leg and trunk are controlled according to the phase oscillators implemented in each actuator.

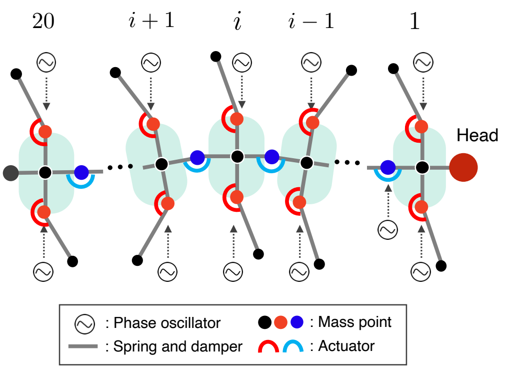

Figure 3: Schematic of the physical model of centipedes.

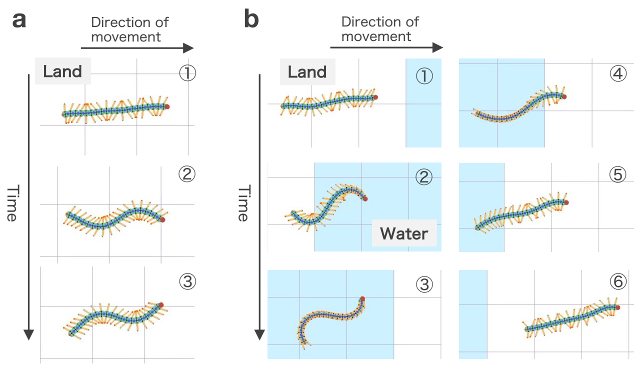

Figure 4: Snapshots of the simulation results: (a) spontaneous gait transition on land, (b) adaptive walk-swim transition in response to the environmental changes.

4 Simulation results

To validate the hypothesized control circuits, we performed simulation experiments using our model. First, we simulated gait transitions on land in response to body undulation. Specifically, the gain value and amplitude of the trunk actuators were increased by strengthening the descending signal from the brain. The trunk and leg coordination patterns spontaneously shifted from slow to fast walking (Fig. 4a), accompanied by changes in the phase difference in inter-limb coordination [4]. Next, we simulated locomotion across land and water. Increasing the descending signals for leg folding from the brain and SEG when the head was in water, and modulating the magnitude of body undulation based on the descending signal from the brain, enabled the simulated centipede to transition adaptively between walking and swimming (Fig. 4b), as observed in our previous study [5]. Thus, our model could replicate slow walking, fast walking, swimming, and transitions between them, possibly capturing the interplay between higher and lower locomotor circuits in centipedes.

Acknowledgements

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