Decoding Motor Control Mechanisms Underlying Adaptive and Versatile Locomotion in Centipedes

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学位論文題目	Decoding Motor Control Mechanisms Underlying Adaptive and Versatile Locomotion in Centipedes（ムカデの適応的かつ多様なロコモーションに内在する運動制御メカニズムに関する研究）
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要約

Locomotion, such as walking, swimming, flying, and crawling, is one of the fascinating abilities of animals. They move around complex, unpredictable, and variable environments by coordinating the many degrees of freedom of their bodies. Notably, animals can adaptively change their body coordination, *i.e.*, locomotion patterns, in response to changes in the physical properties of environment and changes in locomotion speed. Therefore, animals must have ingenious mechanisms to generate adaptive and versatile locomotor movements in real-time, which may have been sophisticated through the long evolutionary process. To understand adaptive motor control mechanisms, it is important to capture the interplay between local pattern-generating circuits (*i.e.*, central pattern generator [CPG]), descending commands from higher centers (*e.g.*, the brain), and sensory feedback (Fig. 1). Biologists have investigated the structure and function of the nervous system using neurophysiological methods. Although the independent function of each element above has been clarified to some extent, the essential interplay between the three elements remains unclear. This is because the interactions between the three and each component are based on highly complex dynamics and it is difficult to understand using only analytical approaches.

To address this issue, the thesis employed a synthetic approach in which we built a mathematical model based on behavioral experiments and tested this model with physical simulation. Furthermore, this thesis focused on amphibious locomotion of centipedes. Centipedes exhibit different body–limb coordination during amphibious locomotion: It swims in water with a traveling wave of body undulation, whereas on land, it walks by propagating a wave of leg movement (Fig. 2). Thus, amphibious locomotion is achieved by drastically changing the coordination patterns of body movement in response to substrates, *i.e.*, land and

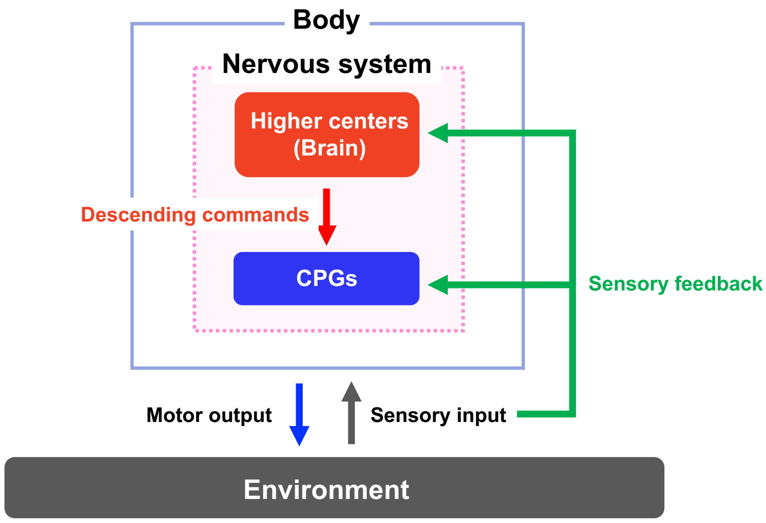

Fig. 1: Key elements of motor control in animal locomotion

water, physical properties of which are significantly different. Therefore, studying the behavioral switch in amphibious locomotion would reveal the interplay between the central pattern generators, descending commands from the higher centers, and sensory feedback. Centipedes are important model animals because their homogeneous and segmented body structure enables investigation of the role of local sensory feedback in switching motor coordination. Their unique body structure facilitates the visualization of kinematic changes in the body as the animal crosses between terrestrial and aquatic environments. In addition, lesion experiments in which the continuity of neural signals along the animal is altered are much easier to perform compared to performing these analyses in fish, tetrapods, and hexapods, all of whom have fewer limbs and less homogeneous structures.

The thesis mainly consists of two parts. First, we investigated the switching mechanism between walking and swimming in centipedes. In behavioral experiments, the transitions between terrestrial and aquatic environments were observed. The results suggested a role for mechano-sensory feedback based on ground contact. In addition, the locomotion of ventral nerve cord-transected centipedes suggested a role for descending control from the brain. Based on these findings, possible control mechanisms for flexible locomotor pattern switching between walking and swimming were modeled mathematically and validated in physical simulations.

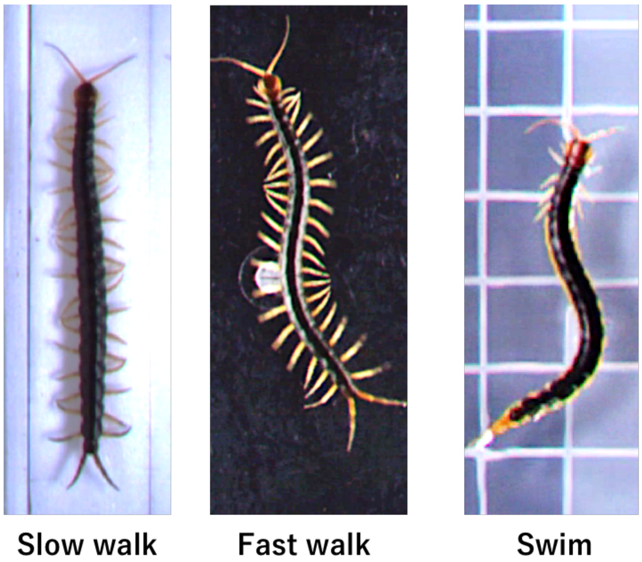

Fig. 2: Adaptive locomotion of centipedes

Next, we explored the possible control mechanisms to reproduce a larger behavioral repertoire in centipedes, especially focusing on fast walking which is the locomotion pattern combining leg motions and body undulation (Fig. 2). To investigate the control mechanisms underlying body undulation, we performed behavioral experiments on the locomotion of a centipede whose higher centers (*i.e.*, brain and subesophageal ganglion) were surgically removed in a stepwise manner. These results suggested that the body undulation during swimming and fast walking might be controlled by descending inputs from the higher centers. Based on this finding, we extended the model by combining the descending control for body undulation and sensory feedback between the body trunk and leg for adaptive body–limb coordination. Consequently, versatile locomotor patterns in centipedes including fast walking as well as transition between walking and swimming were reproduced in simulations.

In summary, the thesis succeeded in extracting the essential interplay between the local pattern generating circuits (central pattern generators), descending commands from higher centers, and sensory feedback with a simple mathematical model based on behavioral findings in amphibious centipedes. The significance of the proposed model is that it can reproduce the adaptive and versatile locomotion patterns in response to the environmental changes and changes in internal motivation during the speed-dependent gait transition. Thus, these results provide a foundation for understanding the principles of flexible motor control in animals and can help enhance the adaptability and versatility of robotic locomotion.