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Neuronal control of swimming behavior: Comparison of vertebrate and invertebrate model systems

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ABSTRACT

Swimming movements in the leech and lamprey are highly analogous, and lack homology. Thus, similarities in mechanisms must arise from convergent evolution rather than from common ancestry. Despite over 40 years of parallel investigations into this annelid and primitive vertebrate, a close comparison of the approaches and results of this research is lacking. The present review evaluates the neural mechanisms underlying swimming in these two animals and describes the many similarities that provide intriguing examples of convergent evolution. Specifically, we discuss swim initiation, maintenance and termination, isolated nervous system preparations, neural-circuitry, central oscillators, intersegmental coupling, phase lags, cycle periods and sensory feedback. Comparative studies between species highlight mechanisms that optimize behavior and allow us a broader understanding of nervous system function.

Contents

Abbreviations: BPE, bursts per episode—one measure of swim episode duration; CPG, central pattern generator; EAA, excitatory amino acid; DLM, dorsolateral mesencephalon; DLR, diencephalic locomotor region; DP, dorsal posterior nerve—in the leech; H, T, head or tail refers to the head (rostral) or tail (caudal) brain in the leech; IN, interneuron—*lamprey INs*: EIN (excitatory interneuron), CCIN (contralaterally and caudally projecting interneuron), LIN (lateral interneuron); MN, motor neuron—*leech MNs*: DE (excitor of dorsal longitudinal muscle), DI (inhibitor of dorsal longitudinal muscle), VE (excitor of ventral longitudinal muscle), VI (inhibitor of ventral longitudinal muscle); M*X*, midbody ganglion *X*—refers to a particular midbody ganglion, numbering starts at the anterior end; MLR, mesencephalic locomotor region; MRRN, middle rhombencephalon reticular nuclei; PRRN, posterior rhombencephalon reticular nuclei; RCI, recurrent cyclic inhibition; RLR, rostrolateral rhombecephalon; RS, reticulospinal; SR-E, excitatory stretch receptor—in the lamprey; SR-I, inhibitory stretch receptor—in the lamprey; T, P and N, cells (touch, pressure and nociceptive cells) sensory cells in the leech; VMD, ventromedial diencephalon; VR, ventral root—in the lamprey; VSR, ventral stretch receptor—in the leech.

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1. Introduction

The central goal of neuroethologists is to understand the neural underpinnings of animal behavior. This broad research endeavor requires comparative research on a comprehensive set of animals and their behaviors (Pearson, 2004; Marder and Calabrese, 1996). Since most individual researchers focus on the behaviors of one species, the effort is necessarily a communal one. Reviews that directly compare results from studies on similar behaviors in different species are essential for drawing broad conclusions from these undertakings. Rhythmic behaviors are studied in a wide variety of species (Delcomyn, 1980; Marder and Calabrese, 1996); such behaviors occur in nearly all animals and the repetition inherent to the behavior permits detailed study of the mechanisms which underlie it. Swimming is one such rhythmic behavior. Similarities in swimming locomotion are seen across many species including the leech, crayfish, lamprey and tadpole (Skinner and Mulloney, 1998). Our review closely compares the neuronal mechanisms underlying the swimming undulations in two distantly related animals, leeches and lampreys, for the purpose of illustrating general principles important to the generation of locomotion (Fig. 1).

The neural circuits underlying swimming in the leech and lamprey are among the best understood systems that generate complex behaviors and they produce remarkably similar rhythmic swimming movements (Fig. 2). Leeches and lampreys had their last common ancestor over 560 million years ago (Kumar and Hedges, 1998). Their disparate evolutionary lineages since that common ancestor gave rise to unrelated CNS morphologies, yet the nervous systems of the two animals share many features. For these reasons, a comparison of swimming behaviors between the leech and lamprey is particularly apt.

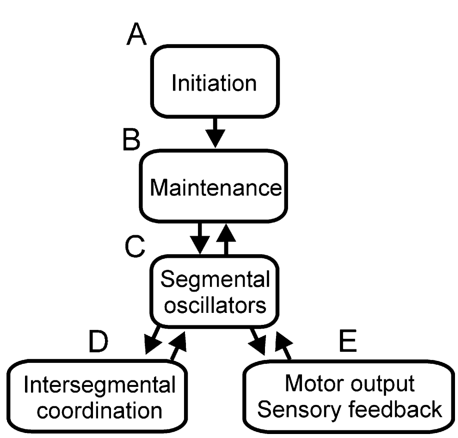

Fig. 1. Block diagram of leech and lamprey systems that control swimming. Arrows indicate the bidirectionality of all interactions but swim initiation.

Research on the nervous systems of the leech and lamprey has an extensive and rich history. Research on the neuronal substrates of leech behavior began in the 19th century with anatomic and embryologic observations, continued with behavioral and physiological studies in the first half of the 20th century, and now continues with numerous studies that also include development, pharmacology, evolution and ecology (Muller et al., 1981; Kristan et al., 2005; Siddall et al., 2007). Studies of the lamprey nervous system date back to at least 1840 and continue unabated (Rovainen, 1979; McClellan, 1987; Buchanan, 2001; Grillner, 2006; Dubuc et al., 2008). The lamprey holds a special position as "primitive" vertebrate; it shares many features with higher species, including humans, but is more tractable than other vertebrate systems. Neuroethological research in both animals is facilitated by their relatively simple nervous systems, comprised of relatively few, but often large neurons. The leech CNS comprises about 10^4 neurons, most of which are sufficiently large and distinct for identification as individual cells and delineation of circuit interactions. By comparison, the lamprey CNS is considerably more complex, comprising approximately 10^5 cells in the spinal cord alone; it is nevertheless amenable to cell-class identification and circuit mapping.

This review summarizes the parallel experimental approaches applied to swimming locomotion in leeches and lampreys and the findings from those studies. It is our hope that evaluation of these independent research programs will lead to a greater understanding of each species, as well as inform locomotion research in other animals. In particular, differences in results should highlight species-specific mechanisms and expand our understanding of which neural elements are essential and which are incidental for generating rhythmic movements.

We first address the establishment and justification of using isolated spinal cord and ventral nerve cord preparations, which are fundamental to the study of swimming. Comparisons of the mechanisms behind initiation, maintenance and termination of swimming follow. Finally, origins of rhythm generation, intersegmental coupling and sensory feedback are examined. This review focuses on the neurobiology of swimming behavior; although occasionally mentioned, details of studies on development, regeneration, swim mechanics, and modeling are not presented. Finally, only a fraction of the large amount of research on the neuromodulation of swimming is discussed in this review.