BILATERAL HINDLIMB MOVEMENT AND MOTOR PATTERNS EVOKED BY ELECTRICAL MICROSTIMULATION IN THE VENTROLATERAL FUNICULUS (VLF) OF THE TURTLE SPINAL CORD.

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Introduction

Low-spinal-tail-suited turtles display vigorous, asymmetric locomotor movements in right and left hindlimbs in response to unilateral electrical stimulations of sites in the dorsolateral funiculus (DLF) of the mid-body spinal cord, typically consisting of contralateral forward swimming (Hicks et al., 1977) and ipsilateral back paddling (Currie, unpublished). DLF stimulation in low-spinal-immobilized turtles has also been shown to evoke forward swimming in contralateral hindlimb muscles (Hicks and Currie 2000). In addition to being sufficient to activate forward swim motor patterns during electrical stimulation, these DLF tracts are also necessary for normal voluntary control of contralateral hindlimb swimming movements (Hicks and Currie, 2000). Spinal lesions in otherwise intact turtles showed that unilaterally damaging the DLF but not other areas of white matter in 45 µA, greatly reduced the amplitude of unilaterally but not bilaterally voluntary hindlimb forward swimming movements (Hicks and Currie, 2000).

These same lesion studies also implicated the contralateral pathways that couple the locomotor movements of the spinal cord and hindlimb to contralateral stimulation in the ventrolateral funiculus (VLF) of the mid-body spinal cord. In our current work, we electrically stimulate sites in the VLF of mid-body (tortoise D3) while recording hindlimb movement in low-spinal turtles with movement, and while recording fictive motor output as electromyograms (ENGs) from hindlimb muscle nerves in low-spinal-immobilized preparations. We find that in contrast to the strongly rhythmic locomotor movements and output patterns evoked by sustained, tonic DLF stimulation, sustained stimulus trains applied to sites in the VLF elicit mainly non-rhythmic hindlimb movements (tonic ipsilateral protraction and contralateral hip contraction) and ionic or weakly modulated discharge in the hip protractor (HP) and contralateral hip extensor (HE). Shorter trains of VLF pulses, applied in right-left alternation, drive alternating swim-like movements of both hindlimbs. These data are consistent with our hypothesis that longitudinal inter-segmental coupling effects are concentrated in the VLF and contribute to the activation and coordination of hindlimb movements during tonic stimulating.

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Methods

Electrical stimulation of the turtle spinal cord

Percutaneous electrical stimulation was applied to the VLF or DLF at the aboral cut end of mid-body spinal segment D3 (low-spinal preparations), using a pair of concentric metal microelectrodes (Rhodes Med.). Stimulation consisted of 50-Hz trains of 5-6 pulses with amplitudes of 50-60 µA in moving animals and 40-60 µA in fictive preparations.

Hindlimb kinematics in moving low-spinal animals

Low-spinal animals were held by a hand-clamp around the shell, just beneath the water surface in a clear tank. Digital videos were recorded from below the shell, just beneath the water surface. In a 45° view. Markers on the hindlimbs and ventral shell (plastron, see diagram) permitted us to monitor right and left side HP and HR movements as a function of time, using motion capture and analysis software (Biopac, 5.5 Bio Technologies).

Identity of hindlimb muscle nerves in fictive preparations

HP - innervates the hip protractor muscle, puboischiofemoralis internus pars anteriores

HR - innervates bilateral hip retractor/long limb muscles of the flexor thalamicis group

HR - innervates bilateral hip retractor/limb muscles of the flexor thalamicis group

Electrical stimulation of sites in the right and left DLF in the cut anterior end of the spinal cord in low-spinal turtles elicited rhythmic asymmetric locomotor movements in the hindlimbs, consisting typically of (1) contralateral forward swimming and (2) ipsilateral back-paddling. In the present work, ipsi back-paddle cycles were coupled 2:1 in control forward swim cycles. A. Slow sweep speed showing the bilateral limb responses to 6-sec stimulus trains applied to the right and left DLF. B. and C. Fast sweeps of two shaded responses in A. Vertical calibrations indicate 50-deg. for hip and 100-deg. for knee angles.

Electrical stimulation of sites in the right and left VLF in the cut anterior end of the spinal cord elicited (A) slow sweep speed showing the bilateral limb responses to 6-sec stimulus trains applied to the right and left DLF. B. and C. Fast sweeps of two shaded responses in A. Vertical calibrations indicate 50-deg. for hip and 100-deg. for knee angles.

Summary

1. Previous work (Lennard and Stotz 1977, Jurenka and Currie 2000; Samara and Currie 2008) and the present study showed that the DLF of the mid-body spinal cord contains command pathways that are both sufficient and necessary for the activation of normal rhythmic forward swimming movements in the hindlimbs.

2. A lesion study also indicated that the mid-body VLF lies between the limb-elongators, caudal longitudinal coordinating tracts that were required for forelimb-hindlimb phase-coupling during voluntary swimming (Samara and Currie, 2000).

3. In the present experiments, we showed that electrical stimulation within the VLF produced dramatically different hindlimb motor responses than DLF stimulation. In contrast to the strongly rhythmic DLF-evoked hindlimb movements and motor patterns, sustained VLF stimulation elicited a tonic pattern of spindled hip flexion (flexion) and contralateral leg extension.

4. These observations are consistent with our hypothesis that the VLF lacks command pathways that drive spinal locomotor CPGs, but does contain coordinating tracts that are critical for maintaining an out-of-phase hindlimb-frontlimb coupling.