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The Modulation of Presynaptic Inhibition in Single Muscle Primary Afferents during Fictive Locomotion in the Cat

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The aim of this study is to understand the functional organization of presynaptic inhibition in muscle primary afferents during locomotion. Primary afferent depolarization (PAD) associated with presynaptic inhibition was recorded intra-axonally in identified afferents from various hindlimb muscles in L6-L7 spinal segments during fictive locomotion in the decerebrate cat. PADs were evoked by the stimulation of peripheral muscle nerves and were averaged in the different epochs of the fictive step cycle. Fifty-three trials recorded from 39 muscle axons (37 from group I and two from group II) were retained for analysis. The results showed that there was a significant phase-dependent modulation of PAD amplitude ($p < 0.05$) in a majority of muscle afferents (30 of 39, 77%). However, not all stimulated nerves led to significantly modulated PADs in a given axon (36 of 53 trials, 68%). We also observed that the pattern of

modulation (phase for maximum and minimum PAD amplitude and the depth of modulation) varied with each recorded afferent, as well as with each stimulated nerve. We further evaluated the effect of PAD modulation on the phasic transmission of the monosynaptic reflex (MSR) and found that PADs decreased the MSR amplitude in all phases of the fictive step cycle, independent of the PAD pattern in individual group I fibers. We conclude that (1) PAD modulation patterns of all group I fibers contacting motoneurons led to an overall reduction in monosynaptic transmission, and (2) individual PAD patterns could participate in the control of transmission in specific reflex pathways during locomotion.

Key words: primary afferent depolarization (PAD); presynaptic inhibition; muscle group I fibers; fictive locomotion; spinal cord; motor control

Although the central pattern generator (CPG) (Grillner, 1981) in mammalian spinal cord is able to produce complex locomotor patterns in the absence of sensory input, sensory feedback in general, and proprioceptive input in particular, is needed for adaptive modifications of the step cycle (Roussignol, 1996). For instance, proprioceptive input from muscles is used to adjust the timing and amplitude of muscle contractions during the different phases of the step cycle (Pearson and Duysens, 1976; Conway et al., 1987; Gossard et al., 1994a; McCrea et al., 1995; Hiebert et al., 1996). To be meaningful, the efficacy of proprioceptive feedback must be physically controlled to induce adaptive responses in the proper phase of the locomotor cycle. Peripheral (e.g., gamma innervation of muscle spindles), as well as central, mechanisms participate in the phasic modulation of transmission in proprioceptive pathways.

One powerful central mechanism by which the CPG could control sensory feedback is presynaptic inhibition of primary afferent terminals. Indeed, there are GABAergic interneuronal networks in the spinal cord capable of decreasing transmitter release by evoking a primary afferent depolarization (PAD) through axoaxonic contacts (Eccles, 1961; Schmidt, 1971; Nicoll

and Alger, 1979). Presynaptic inhibition has been proposed often to explain changes in the amplitude of the monosynaptic reflex (MSR) during walking in humans (Stein and Capaday, 1988; Yang and Whelan, 1993). Moreover, when PADs reach firing threshold, the evoked discharges are antidromically propagated in primary afferent axons and may collide with incoming volleys and even change the excitability of peripheral sensory receptors (Tonnes, 1939; Lindblom, 1958; Loewenstein, 1959; Ito, 1968; Bevenegat et al., 1997). For example, rhythmic bursts of antidromic discharges can be found in a majority of cut dorsal rootlets of decerebrate cats walking on a treadmill (Beloszerova and Roussignol, 1994, 1995). The phasic timing of such discharges suggests that the underlying PADs are strongly influenced by the CPG. It is thus important to know more about the role of PAD pathways in the control of locomotion. There are, however, few studies focused on the transmission in PAD pathways during locomotion in mammals. Duenas et al. (1990) evoked antidromic discharges in dorsal rootlets belonging to the triceps surae muscles by stimulating cutaneous nerves during stepping in thalamic cats and found that maximal discharges occurred during the extensor phase of the step cycle. Similarly, previous intracellular studies of PADs in cutaneous afferents during fictive locomotion showed that the amplitude of the evoked PAD was maximal during the extensor phase (Gossard and Roussignol, 1990; Gossard et al., 1990). To our knowledge, there is yet no study investigating directly the changes in PAD amplitude in individual muscle afferents during locomotion. We thus used intra-axonal recordings to study PADs in single primary afferents from hindlimb muscles of the decerebrate cat during fictive locomotion. We also evaluated directly, and for the first time, the effect of PADs on the MSR amplitude during fictive locomotion.

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