POLARIZATION OF PRIMARY AFFERENT TERMINALS IN THE LUMBAR SPINAL CORD DURING FICTITIOUS LOCOMOTION

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Changes in electrical polarization of primary afferent terminals in the lumbosacral portion of the spinal cord were investigated during fictitious locomotion in immobilized decorticated and spinal cats. Fictitious locomotion was accompanied by stable hyperpolarization of the afferent terminals, against the background of which they were periodically depolarized in rhythm with efferent activity. These tonic and phasic changes were observed in terminals of all groups of afferent fibers tested: cutaneous and muscular (la and Ib). Periodic in-phase depolarization was carried out in different ipsilateral segments of the lumbosacral enlargement.

During fictitious galloping changes in depolarization of the primary efferents were in phase on different sides; during fictitious walking, these periodic changes were out of phase. On the basis of these results the physiological importance of changes in electrical polarization of primary afferent terminals of the spinal locomotor generator is discussed.

INTRODUCTION

It was shown previously [1] that fictitious locomotion of immobilized animals is accompanied by periodic changes in the dorsal root potential (DRP), which correlate definitely with discharges in motor nerves. Since real limb movement does not take place during fictitious locomotion and, consequently, the arrival of phasic afferent impulsion in the CNS is ruled out, it was concluded that periodic changes in primary afferent depolarization (PAD) are evoked by the spinal locomotor generator.

The character of changes in polarization of the central endings of different afferents in the lumbosacral portion of the spinal cord in the course of time during functioning of the locomotor generator is unknown. The investigation described below was devoted to its study. The kinetics of the change in polarization of primary afferent terminals during operation of the locomotor and scratch generators also was compared. As the results of a previous study [2] showed, during activity of the latter structure PAD contains tonic and phasic components: tonic depolarization develops in terminals of cutaneous afferents and fibers of groups la and Ib, and against its background phasic changes in depolarization of the terminals of cutaneous fibers and group Ib afferents take place in rhythm with generator function.

EXPERIMENTAL METHOD

Experiments were carried out on adult cats. The preparatory operation was performed under ether anesthesia. To record efferent activity, the nerves to m. extensor digitorum longus and m. tibialis anterior and to m. gastrocnemius were dissected in both hind limbs. Besides these nerves, n. saphenus, n. peroneus superficialis, and branches to m. posterior biceps and m. semitendinosus also were dissected in the ipsilateral hind limb. Laminectomy was performed in the lumbar segments. The animal was then decorticated, fixed in a stereotaxic frame, and immobilized with D-tubocurarine (1.0-1.5 mg/kg). Fictitious locomotion was induced by stimulation of one of the dorsal roots in segments L5-S or by stimulation of the dorsal columns in segments L1-L2. A short high-frequency series of stimuli (20-30 pulses with a frequency of 200-300 Hz) was applied for stimulation. Electrical activity in the peripheral nerves, DRP, and the dorsal cord potential were recorded by the usual method.

To test the level of polarization of primary afferent terminals during fictitious locomotion, Wall's method was used: this was described in detail previously [2]. During testing of the level of excitability of terminals of groups la and Ib by Wall's method on the side of recording of evoked antidromic re-
Fig. 1. Changes in dorsal root potential (DRP) and dorsal cord potential (DCP) during fictitious locomotion by decorticated cat. a) Fictitious locomotion evoked by stimulation of dorsal columns. Beginning of record corresponds to end of stimulation of dorsal funiculi. b) Changes in DRP during spontaneous fictitious locomotion. T. ant. and G) Recordings from nerves to m. tibialis anterior and m. gastrocnemius respectively. DRP recorded relative to steady current from filament of dorsal root in segment L6. Resting level indicated by zero on amplitude calibration marker. DRP records relative to steady current in segment L6 with time constant of 2.0 sec. Negative wave of potential represented by upward deflection in DRP and DCP. Time marker 1 sec.

Responses from the peripheral motor nerves, partial deafferentation of the lumbosacral portion of the spinal cord was carried out; the ventral roots of segments L4-S2 were divided and all connections with segments located more caudally were severed.

EXPERIMENTAL RESULTS

As already stated in the section "Experimental Method," fictitious locomotion occurred in response to stimulation of the dorsal roots or dorsal columns. Immediately after the negative wave of DCP evoked by this stimulation, the duration of which was not more than a few hundreds of milliseconds, a long positive (relative to the resting potential) wave was observed (Fig. 1a). The duration of this positive DCP was equal to that of fictitious locomotion and usually ranged from a few seconds to several tens of seconds, or sometimes even more. Against the background of this positive DCP periodic changes took place in it in the rhythm of efferent activity. The amplitude of tonic and phasic changes in DCP was closely connected with the intensity of fictitious locomotion, and the more intensive discharges in the motor nerves, usually with a higher following frequency, corresponded to the changes in DCP of higher amplitude. The temporal relations of the phasic DRP and efferent activity also depended on the intensity of fictitious locomotion. In the case of fictitious locomotion of high intensity the beginning of the "flexion" phase occurred at the end of the descending phase of the DRP (the peak and minimum denote the greatest and smallest values of negativity of the phasic change in DRP respectively). Beginning of the phase of "extension" coincided with the middle of the ascending phase of DRP, whereas maximal activity in the extensor nerve corresponded with its peak. With a decrease in the intensity of fictitious locomotion the beginning of the "extension" phase was shifted toward the peak of DRP, whereas the beginning of the "flexion" phase was shifted toward its minimum. With average and low intensity of fictitious locomotion the beginnings of the phases of "flexion" and "extension" coincided in time with the minimum and maximum of the DRP respectively. In cases when a short period of silence was observed between the end of the "extension" phase and the beginning of the "flexion" phase, throughout this period a more rapid diminution of DRP could be observed (Fig. 1a). The value of the peak of the phasic negative changes in DRP could be equal to that of the resting potential.

There are sufficient grounds for considering that all the above changes in DRP were due to activity of the spinal locomotor generator. The positive tonic component of DRP which was observed during spontaneous fictitious locomotion by the decorticated cats (Fig. 1b) was unconnected with stimulation of afferents and, consequently, it was central in origin. Fictitious locomotion could also be evoked by electrical stimulation of the dorsal funiculi in spinal animals for 1-2 min after spinalization. The changes in DRP observed under these circumstances were similar in character to those during evoked locomotion by decorticated cats.