Journal of the Arkansas Academy of Science

Volume 34 Article 6

1980

Activation of Long Descending Propriospinal Neurons in Cat Spinal Cord

Robert J. Adams
University of Arkansas for Medical Sciences

Robert D. Skinner
University of Arkansas for Medical Sciences

Ronald S. Remmel
University of Arkansas for Medical Sciences

ACTIVATION OF LONG DESCENDING PROPRIOSPINAL NEURONS IN CAT SPINAL CORD*

ROBERT J. ADAMS[1], ROBERT D. SKINNER[1] and RONALD S. REMMEL[2]
Department of Anatomy[1] and Department of
Physiology and Biophysics[2]
University of Arkansas for Medical Sciences
Little Rock, Arkansas 72205

ABSTRACT

Isolated mammalian spinal cord has been shown capable of generating locomotor activity. Propriospinal systems assumed to coordinate fore- and hindlimb activity are poorly understood. This study characterizes the long descending propriospinal (LDP) neurons in terms of the location of the somas and their peripheral inputs by direct neuronal recording. Anatomical studies using axonal retrograde transport of horseradish peroxidase from the lumbar to the cervical spinal cord as a tracer first described these neurons. Two hundred and thirty-one LDP neurons were identified in electrophysiological experiments. Of these, 123 responded to natural stimulation, and about 50% of the others were activated only by electrical stimulation. The majority of cells were located in laminae VII and VIII in agreement with anatomical data. The most effective stimuli were mechanical stimulation of skin, deep pressure to subcutaneous tissues, and paw joint movement. Bot excitatory and inhibitory responses were observed.

INTRODUCTION

The mammalian spinal cord isolated from the brain can generate the basic rhythm of locomotion (Sherrington, 1910; Brown, 1911; Grillner, 1975). A cat which has its spinal cord severed at the level of the first cervical vertebra can walk when its paws touch a moving treadmill, provided its weight is supported and it is chemically stimulated with the drug Clonidine® . The walking rhythm is quite normal, and there is good coordination between the fore- and hindlimbs. The neurons which possibly coordinate the fore- and hindlimbs are the subject of this report. One neuron which could subserve this function is the type illustrated at the top of Fig. 1. Its cell body lies in the cervical enlargement of the spinal cord, and its axon descends to the lumbosacral enlargement. Because it is entirely within the spinal cord, it is called a propriospinal neuron—a long descending propriospinal (LDP) neuron in this case.

The location of the cell bodies of the LDP neurons was recently determined in cat and monkey by injecting a tracer substance (horseradish peroxidase) into the lumbosacral enlargement. The tracer substance was picked up by the terminals of LDP neurons and transported back to the cell bodies in the cervical enlargement. They are found mainly in the medial part of the ventral horn of the spinal gray, but a few are in the dorsal horn (Skinner et al., 1979).

It is known that stimulation of afferents in a forelimb can elicit reflexes in the hindlimbs (Sherrington and Laslett, 1903). The route by which this occurs is depicted at the top of Fig. 1. Afferent nerve fibers from the forelimb entering the cervical enlargement activate short-axoned neurons called interneurons (IN), which in turn, activate the LDP neurons. The reflex is completed in the lumbosacral enlargement by LDP neurons activating other interneurons which finally activate motor neurons having axons that go to muscles which cause them to contract.

Our interest is in the types of sensory stimuli which, when applied to the forelimb, bring about activation of LDP neurons. In this study the types of effective stimuli, the region of the body which could be effectively stimulated (receptive field), and responses to electrical stimulation of peripheral nerves were investigated while recording the action potentials of single LDP neurons.

*Supported by USPHS Grants RR-05350 and NS-10304

METHODS AND MATERIALS

In adult cats initially anesthetized with Ketamine® (15 mg/kg), the carotid arteries were tied and the trachea was cannulated. The spinal cord was severed at the C1 level. Blood pressure was maintained above 90 mm Hg (mean arterial pressure) with intravenous fluids, and other vital functions were supported. Animals were mounted with the cervical spinal cord exposed. Glass micropipette electrodes were inserted into spinal cord segments C5-T2 until they were near a LDP cell. LDP neurons were identified by electrically stimulating their axons at the upper end of the lumbosacral enlargement (S in Fig. 1); this caused an action potential in the axon which propagated to the cell body where it was observed. Photographs of the action potentials were made from an oscilloscope screen. The arrival of action potentials in afferent fibers of the spinal cord was monitored with a ball-tipped electrode near the dorsal root entry zone.

Electrical stimulation of peripheral nerves was effected by single, constant current pulses of 0.1 msec duration delivered to the median, ulnar, or deep radial nerves through cuff wire electrodes. Natural stimulation consisted of hair movement, mechanical deformation of the skin, pressure to subcutaneous structures (deep pressure), and passive joint movement. Some of the stimuli were strong enough to be considered noxious.

RESULTS

Of 231 LDP neurons which were identified, 123 were activated by natural stimulation. Receptive fields of single LDP neurons for natural stimuli varied in size from one digit to the entirety of the forelimb; no receptive fields were found on the thorax, back, neck, or hindlimbs. Most receptive fields were found on the paws and upper arms, and almost one half of the responding neurons had more than one receptive field. Some had receptive fields on both forelimbs. Deep pressure proved to be the most frequently effective stimulus, followed by mechanical-cutaneous, and joint movement. About half of those not activated by natural stimuli were, however, activated by electrical stimulation of peripheral nerves.

Joint Movement: For 25 neurons the adequate stimulus was joint movement, mostly extension of the interphalangeal joints. Movement of the elbow joint was seldom effective. Unfortunately, the shoulder joint could not be adequately tested. Figure 1A-C shows the

responses of one LDP neuron which was activated by extension of metacarpo-phalangeal (MP) joints. In A, extension of the MP joints of the ipsilateral (same side) forelimb excited this neuron (bar denotes duration of extension). In B, extension of the MP joints of the contralateral (opposite) forelimb inhibited the firing of the cell evoked by extension of the ipsilateral MP joints. In C, the receptive fields for this cell are shown.

Deep Pressure: A common finding was that deep pressure applied to the belly or distal tendon of the triceps brachii muscle activated LDP neurons. Almost half of all receptive fields (51 neurons) were of this modality of stimulus.

Mechanical-Cutaneous: In this category, a few cells were activated by hair movement, while others required weak mechanical deformation of the skin (<5 gm), but some responded only to strong stimuli (5-40 gm). Forty-five neurons responded to this type of input.

Multimodal: Thirty-two neurons had receptive fields for two or more different modalities of stimuli.

Inhibition: A total of 24 inhibitory receptive fields were observed, in all cases, by a diminished response to an ongoing excitatory stimulus. An example of this is shown in Fig. 1A-C. Some LDP neurons had combinations of receptive fields such as excitatory areas on one upper arm and inhibitory fields on the paw of the opposite limb.

Electrical Stimulation: The purpose of nerve stimulation was to determine the degree of convergence from various forelimb areas onto single LDP neurons, and to determine the latency of activation. Of 105 cells tested, 68 were activated, 46 of these by stimulation of three nerves. No consistent differences were noted in the response characteristics of LDP neurons to deep radial (a pure muscular nerve) compared to median and ulnar (mixed cutaneous and muscular nerves). The mean latency (the time from the arrival of action potentials in afferent fibers at the spinal cord to the action potential in the LDP cell) was 6.6 ± 3.8 msec ($n = 68$), which suggests that one or more interneurons intervened. The latency of only one cell was short enough to suggest a monosynaptic connection (no intervening interneuron).

DISCUSSION

The principal findings of this study are: (1) several types of LDP neurons according to modality of stimulus to which they responded, (2) complex interactions of excitation and inhibition from different receptive fields of LDP neurons, and (3) convergence of input as from different receptive fields or peripheral nerves upon LDP neurons.

It is proposed that those LDP cells with mechanical cutaneous input might be involved in long spinal reflexes elicited by stimulation of the skin. Others, in particular those responsive to either joint movement or deep pressure, may function in relation to movements of the forelimbs. For example, the large group of cells activated by deep pressure to the triceps muscle might be active either during passive muscle stretch or during contraction. In either case, they could provide information as to the functional state of the limb during motor activity, such as locomotion.

Greater understanding of spinal mechanisms involved in motor activity and locomotion may lead to improved therapy for humans with spinal injury or disease.

LITERATURE CITED

BROWN, T. G. 1911. The intrinsic factors in the act of progression in the mammal. Proc. Roy. Soc. (Lond.), Ser. B. 84:308-319.

GRILLNER, S. 1975. Locomotion in vertebrates: central mechanisms and reflex interaction. Physiol. Rev. 55:247-304.

SHERRINGTON, C. S. 1910. Flexion reflex of the limb, crossed extension reflex, and reflex stepping and standing. J. Physiol. (Lond.) 40:28-121.

SHERRINGTON, C. S. and E. E. LASLETT. 1903. Observations on some spinal reflexes and the interconnection of spinal segments. J. Physiol. (Lond.) 29:58-96.

SKINNER, R. D., J. D. COULTER, R. J. ADAMS and R. S. REMMEL. 1979. Cells of origin of long descending propriospinal fibers connecting the spinal enlargements in cat and monkey determined by horseradish peroxidase and electrophysiological techniques. J. Comp. Neurol. 188:443-454.

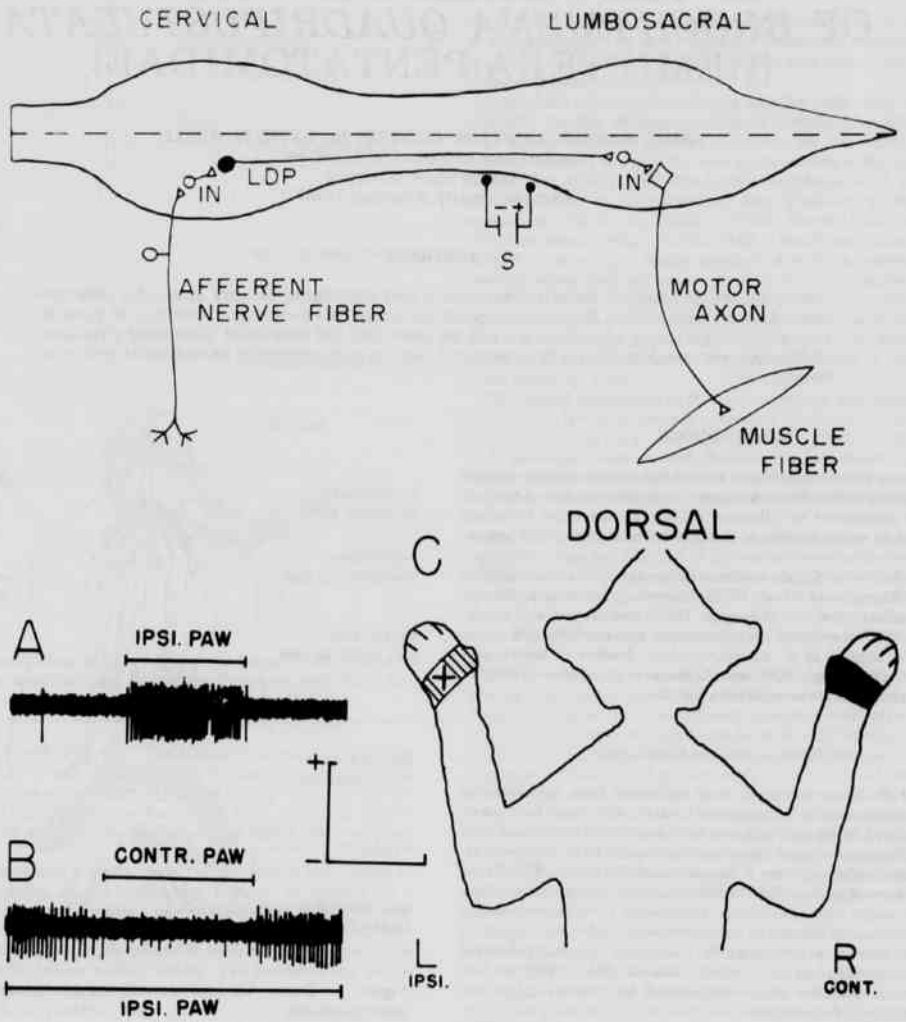

Figure 1. Top. Schematic drawing of isolated spinal cord and the reflex pathway from afferent fibers in the forelimb to motor neurons in the hindlimb. See text for explanation. IN = interneuron, LDP = long descending propriospinal neuron, S = electrical stimulator. In A-C are shown responses of an LDP neuron to extension of metacarpo-phalangeal (MP) joints. In A is shown the response of this cell to extension of the MP joints of the ipsilateral forelimb. Extension of the MP joints of the contralateral paw (B) could inhibit the firing of the cell evoked by extension of the ipsilateral MP joints. The receptive fields for this unit are shown in C. the plus sign (+) indicates an excitatory field and the negative sign (−) an inhibitory field. Another spike (smaller) was activated by extension of the contralateral MP joints. Horizontal bars indicate extension of the joints. Spikes were retouched. The calibration bars represent 0.4 sec and 1 mV.