Neuroscience Letters 675 (2018) 12–16

Contents lists available at ScienceDirect

Neuroscience Letters

journal homepage: www.elsevier.com/locate/neulet

Research article

Monkey extensor digitorum communis motoneuron pool: Proximal dendritic trees and small motoneurons☆

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ARTICLE INFO

Keywords:
Cervical gamma-motoneurons
Dendritic tree
Monkey

ABSTRACT

Transverse sections of the monkey cervical spinal cord from a previous study (Jenny and Inukai, 1983) were reanalyzed using Neurolucida to create a three-dimensional display of extensor digitorum communis (EDC) motoneurons and proximal dendrites that had been labeled with horse radish peroxidase (HRP).

The EDC motoneuron pool was located primarily in the C8 and T1 segments of the spinal cord. Small motoneurons (cell body areas less than 500 μm^2 and presumed to be gamma motoneurons) comprised about ten percent of the motoneurons and were located throughout the length of the motoneuron pool. Most small motoneurons were oblong in shape and had one or two major dendrites originating from the cell body in the transverse plane of section.

The majority of the HRP labeled dendritic trees were directed either superiorly, dorsal-medially to the mid zone area between the base of the dorsal horn and the upper portion of the ventral horn, or medially to the ventromedial gray matter. The longer HRP labeled dendrites usually continued in the same radial direction as when originating from the cell body. As such we considered the radial direction of the longer proximal HRP labeled dendrites to be a reasonable estimate of the radial direction of the more distal dendritic tree. Our data suggest that the motoneuron dendritic tree as seen in transverse section has direction-oriented dendrites that extend toward functional terminal regions.

1. Introduction

The segmental localization of motor columns innervating the primate forelimb muscles was originally described by Sherrington [2] in studies involving stimulation of individual ventral nerve roots. Topographical data of motoneurons in the primate cervical cord related to individual ventral roots were published by Sprague [3], and topographical data related to major peripheral nerves were published by Reed [4] and Chiken et al. [5]. The segmental and topographical organization of individual motor columns involved in the control of hand movement in the monkey was studied by the retrograde transport of HRP from selected muscles to motoneurons and reported by Jenny and Inukai [1].

In the present study, we re-examined transverse sections from one monkey (M7803) included in our original study to determine the distribution of small motoneurons (putative gamma motoneurons) relative to large alpha motoneurons. Our second goal was to characterize the proximal dendritic trees of motoneurons in the transverse plane. These issues were not addressed in our original report (Jenny and Inukai [1]). Information about the location, spinal distribution and properties of motoneuron pools has taken on new significance in relation to efforts to develop neuroprosthetic devices to bridge damaged sections of spinal cord in spinal cord injury and reconnect undamaged regions with higher centers through electrical stimulation (Moritz et al. [6]).

2. Materials and methods

All surgeries were performed according to the standards of the Guide for the Care and Use of Laboratory Animals, published by the United States Department of Health and Human Services and the National Institutes of Health. The protocol was approved by the Animal Care Committee at Washington University, St. Louis.

In brief, under appropriate anesthesia, the extensor digitorum communis (EDC) muscle of one rhesus macaque was exposed using an

☆ The original work was aided by United States Public Health Service Grants NS 05580, NS 05656, NS 04513, and NS 00470. Current work is supported by Northland Neurosurgery PC, Kansas City, MO and the Kathleen M. Osborn Endowment.

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[1] Note: The original work, Jenny and Inukai 1983, was done within the Department of Neurology and Neurological Surgery, Washington University School of Medicine, 1976–1980.

https://doi.org/10.1016/j.neulet.2018.03.051
Received 4 January 2018; Received in revised form 21 February 2018; Accepted 21 March 2018
Available online 22 March 2018
0304-3940/

operating microscope and injected with a concentrated solution of horse radish peroxidase (HRP). To prevent leakage of HRP from the EDC muscle from contaminating surrounding muscles, Silastic and cottonoid barriers were positioned between the EDC muscle and surrounding muscles; the surrounding area was frequently irrigated with normal saline for twelve hours. After 48 h of anesthesia the animal was heparinized and perfused through the heart with a saline, paraformaldehyde, and glutaraldehyde solution. The cervical spinal cord was processed according to Mesulam [7]. Please refer to Jenny and Inukai [1] for further detail about methods and control studies.

Serial transverse sections (50 μm^2) containing HRP (horseradish peroxidase) labeled EDC motoneurons of monkey M7803 were first retraced using a Leitz Wetzlar microscope and camera lucida (x600), and adjacent sections were compared to be certain that labeled neurons were counted only once. The neurons were then entered into Neurolucida using a Nikon E800 microscope (x600) for later 3-D reconstruction and analysis. The shape of each labeled cell body was also compared to original camera lucida tracings (Jenny and Inukai [1]) to assure the numbering of each motoneuron remained the same.

2.1. Size determination

The perimeter of each neuron at the level of the nucleolus was traced into Neurolucida. Many neurons had large dendrites that originated from one portion of the cell and created a polar appearance. Determination of where the main portion of the cell body ended and the large dendrite began was arbitrarily determined to be where the periphery of the cell body lost its convex outer shape and changed into either a concave inward curve or became parallel to the other side of the proximal dendrite. The size of the motor neurons was then determined by using Neurolucida Explorer to calculate the cross-sectional area at the level of the nucleolus (Fig. 1).

2.2. Dendrites

Most dendrites were broadly based as they originated from the soma and had only minimal initial taper. Vacuolization artifact could be seen in many of the larger dendrites. Whenever possible dendrites were traced into the adjacent sections.

Vector analysis of each motoneuron and its primary, secondary, and tertiary dendrites in the transverse plane of section was done using the "quick angle measure" and "quick distance measure" features of Neurolucida. Adjacent digital sections were rotated slightly in Neurolucida to align the posterior median septum with a vertical grid line. The central canal was used as a common reference point between sections. A navigational orientation (360° being vertical) was selected for data analysis (Fig. 1). The three-dimensional position of each labeled motoneuron was determined by measuring its distance and angle from the center of the central canal and then combining those data with its Neurolucida rostro-caudal (Z axis) position. These data were entered into a Microsoft Excel Spreadsheet.

2.3. Axons

Axons had small axon hillocks that quickly tapered into thin structures that contained HRP reaction product (HRP-RP) grains in single or double file. Thereafter axons could be 3–4 HRP-RP grains wide. Axons usually had an irregular course and, unlike dendrites, could curve in a different direction after leaving the cell body. Shortly after leaving the cell body a halo effect (possible myelin sheath) could be seen around the axon. Vacuolization was never observed.

2.4. Small neurons

Neurons with areas smaller than 500 μm^2 were examined in more detail as putative gamma motoneurons (Fig. 1). The three-dimensional reconstruction of each small neuron was studied by tracing the perimeter of the neuron (x1000) at 1–2 μm intervals on the Z axis using Neurolucida contours (Fig. 2). Dendrites were entered using Neurolucida cell body at x600.

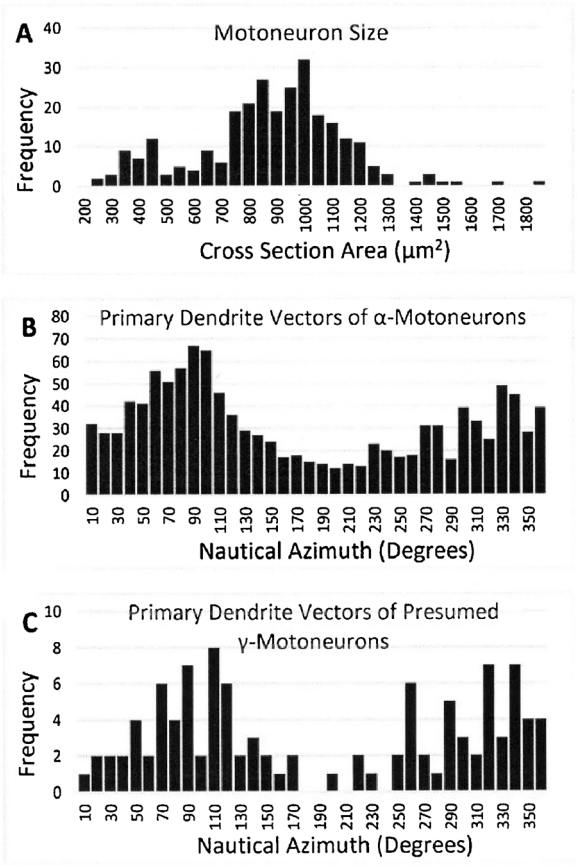

Fig. 1. A: Size distribution of motoneurons based on area (μm^2). B: Azimuth distribution (radial direction) of α-motoneuron primary dendrites. C: Azimuth distribution (radial direction) of presumed γ-motoneuron primary dendrites. A navigational orientation (clockwise with 360° being vertical) was selected for data for analysis.

3. Results

The extensor digitorum communis motor pool was located in the lateral aspects of the ventral horn at caudal C7, C8 and T1 segment levels of the spinal cord (Fig. 3). The motor pool numbered 277 neurons, four more than the original count in 1983.

3.1. Dendrites

Most of the proximal dendritic trees for both alpha and presumed gamma motoneurons were directed either superiorly, superior-medially to the mid zone area between the base of the dorsal horn and the upper portion of the ventral horn, or medially to the ventral-medial gray matter (Figs. 4 & 5). In our material the primary dendrites that arose from the cell body usually continued in a straight direction. The secondary dendrites usually branched off the primary dendrites at an angle; the primary dendrites usually continued on their original course. [Note: There appears to be differences among authors as to the naming of the dendritic tree stems and branches. As our material deals only with the proximal dendritic tree we have used the terms primary (stem) and secondary (first branch) dendrites. See Discussion].

Dendrite lengths ranged between 5 μm and 400 μm (median length 55 μm) before leaving the plane of section. Seventy-two percent of the