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Review

Branched thalamic afferents: What are the messages that they relay to the cortex?

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ABSTRACT

Many of the axons that carry messages to the thalamus for relay to the cerebral cortex are branched in a pattern long known from Golgi preparations. They send one branch to the thalamus and the other to motor centers of the brainstem or spinal cord. Because the thalamic branches necessarily carry copies of the motor instructions their messages have the properties of efference copies. That is, they can be regarded as providing reliable information about impending instructions contributing to movements that will produce changes in inputs to receptors, thus allowing neural centers to compensate for these changes of input. We consider how a sensory pathway like the medial lemniscus, the spinothalamic tract or the optic tract can also be seen to act as a pathway for an efference copy. The direct connections that ascending and cortical inputs to the thalamus also establish to motor outputs create sensorimotor relationships that provide cortex with a model of activity in lower circuits and link the sensory and the motor sides of behavior more tightly than can be expected from motor outputs with a single, central origin. These transthalamic connectional patterns differ from classical models of separate neural pathways for carrying efference copies of actions generated at higher levels, and introduce some different functional possibilities.

Contents

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1. Introduction: early evidence from Golgi preparations

The patterns of axonal branching revealed by the Golgi method and described in significant detail by Cajal form the subject of this essay. They were early recognized as important. The Golgi method allowed investigators to trace axons for long distances, find branching points and often trace individual branches to several distinct end-stations, demonstrating functionally significant links. However, the full functional implications of these branching patterns could not be understood until the nature of axonal conduction was known. Cajal recognized that axonal conduction depended on neural impulses but his view of the conduction of impulses along the branches of an axon was based on a mistaken hydraulic model of the axon. He considered that, "At any point along an axon and its collaterals, the amount of energy associated with a particular input is proportional to the diameter of the process in question." (Ramon y Cajal, 1995, translation of Ramon y Cajal, 1911, p. 428). He argued that "the sum of the diameters of collaterals supplied by a dorsal root fiber (see Fig. 1) is far greater than the diameter of the terminal arborization *in the posterior column nuclei* arising from the same root fiber." (italics added). This led him to conclude that most of the information went to the collaterals, which mediated the fastest spinal reflexes. He wrote that "This is how the longest sensory fibers, which end in the dorsal column nuclei, relay that part of the activity giving rise to conscious sensations." (p 429). Although we can see that on the basis of contemporary knowledge the hydraulic model does not provide an accurate view of how the "conscious sensations" transmitted by the posterior column fibers relate to the spinal reflexes, we should not ignore Cajal's insight: that the branching pattern must represent some close relationship between the messages that are sent through the posterior column nuclei to the thalamus and cortex on the one hand and those that play a role in spinal reflexes, on the other. The role of branched axons in defining what exactly is happening in the brain during a sensory experience forms the subject of this essay. It is an important problem because essentially all of the axons that carry messages to the thalamus for relay to the cortex come from branched axons comparable to those illustrated by Cajal, with one branch supplying the thalamus or a relay to the thalamus and other branches supplying brainstem or spinal centers with connections to motor outputs (Guillery and Sherman, 2002; Guillery, 2003). The argument we present now is a tentative interpretation, based on the anatomy of the pathways and information about impulse conduction along branched axons. It raises a number of problems that currently have no answers in terms of clear experimental evidence about specific pathways and their demonstrable functions. Our aim is to point to many areas where more knowledge about the distribution and the functional organization of the motor branches is needed, and where the specific actions of thalamocortical axons on cortical circuits need to be defined.

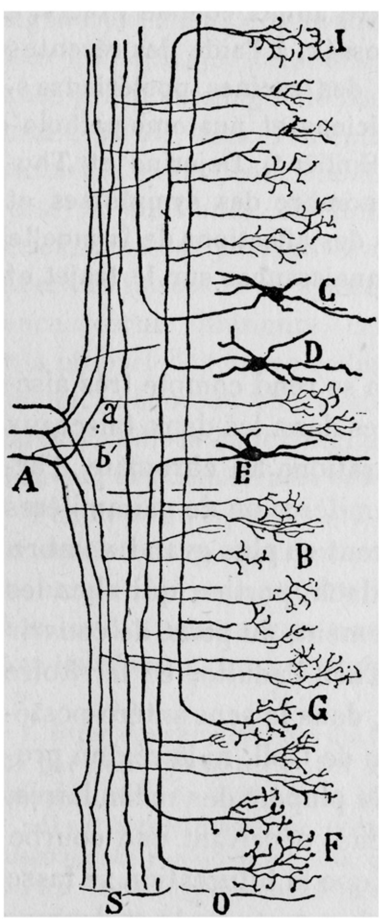

Fig. 1 – Drawing from Ramon y Cajal (1952, French translation) to show some of the branching patterns of incoming dorsal root axons that are entering the spinal cord at A and sending their ascending branches toward the posterior column nuclei at the top of the figure. They give off branches (e.g. a′, b′) that form dense terminal arbors in the region of the cord that contains cells (C,D,E) with further intraspinal connections.

2. Relating the ascending "sensory" axon to the innervation of spinal motor centers

Fig. 1 shows one of Cajal's drawings of the intraspinal branching patterns of the dorsal root inputs and Fig. 2 shows another of his drawings for the trigeminal nerve. In Fig. 1 the axons ascending towards the top of the figure on their way to the posterior column nuclei are shown with many spinal branches within the cord. Fig. 2 shows that nerve cells of the spinal nucleus of the trigeminal nerve (F) send axons towards the top of the figure on their way to the thalamus and also innervate two motor nuclei, the facial (D) and the hypoglossal (E) nuclei in the lower part of the figure, as well as the motor nucleus of the trigeminal nerve (C) in the upper part of the figure.

Fig. 3 shows Sherrington's (1906) representation of the spinal connections of the scratch reflex. This figure illustrates a complex reflex reaction that survives a low cervical transection, and perhaps for this reason the figure does not show the ascending branches of the dorsal root axons whose peripheral branches innervate the two hairs shown in the lower left part of the figure and whose ascending axons were cut in Sherrington's experiment. Cajal's evidence indicates that such an ascending branch must have been present as