

Review

Projection and synaptic connectivity of trigeminal mesencephalic nucleus neurons controlling jaw reflexes

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Abstract: Neurons in the trigeminal mesencephalic nucleus (Vmes) receive deep sensation (proprioception) from jaw-closing muscle spindles and periodontal ligaments and project primarily to the jaw-closing motoneuron pool (jaw-closing nucleus) of the trigeminal motor nucleus and to the supratrigeminal nucleus. Numerous articles have described the morphology and physiology of the central projections of Vmes afferents originating from the muscle spindles and periodontal ligaments. However, no report has provided a detailed description of projection and synaptic connectivity, especially of single afferents, and their functional implications. In this review, we reanalyze data obtained by single intra-axonal recording and labeling of functionally identified Vmes muscle spindle afferents and periodontal ligament afferents and by electron microscopic observation of their projection features and synaptic organization of boutons, to compare the data for the jaw-closing nucleus and supratrigeminal nucleus. Our analysis shows that each Vmes afferent type has characteristic projection pattern and synaptic feature that may be important in jaw-reflex control.

Keywords: jaw movement; trigeminal motor nucleus; supratrigeminal nucleus; muscle spindle; periodontal ligament; proprioception.

Introduction

The trigeminal mesencephalic nucleus (Vmes) contains primary sensory neurons that receive deep sensation (proprioception) from jaw-closing (JC) muscle spindles (MS) and periodontal ligaments (PL) of the upper and lower teeth, and project primarily to the dorsolateral division (JC motoneuron pool; termed JC nucleus) of the trigeminal motor nucleus (Vmo) and to the supratrigeminal nucleus (Vsup) (1-7). In humans, direct projections of Vmes MS afferents and Vmes PL afferents to JC motoneurons are involved in the jaw-jerk reflex (8) and the periodontal-masseteric reflex (9,10), respectively. Lorente de Nó was the first to identify the Vsup and describe it as an interneuron (premotoneuron) pool in the trigeminal reflex arc (11). The Vsup contains neurons that can be activated during jaw movement or pressure stimulation of teeth (12-14). Although the Vsup was believed to contain a large number of premotoneurons inhibitory to JC motoneurons (15,16), later studies (17-22) revealed that it contains a large number of excitatory neurons and a smaller number of inhibitory neurons, both of which function as premotoneurons not only to JC motoneurons but also to jaw-opening motoneurons in the Vmo. Thus, it is highly likely that indirect (disynaptic) projections from Vmes afferents to JC and jaw-opening motoneurons

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Table 1 Average number (range) [proportion (%) to the total number of boutons in jaw-closing (JC) nucleus and supratrigeminal nucleus (Vsup)] of axonal boutons of single afferents arising from neurons in the trigeminal mesencephalic nucleus (Vmes)

Vmes afferent types	in JC nucleus	in Vsup
Muscle spindle afferent		
group Ia	595 (302-1,400) [86%]	98 (0-283) [14%]
group II	244 (0-707) [41%]	355 (24-744) [59%]
Periodontal afferent		
SA type	29 (0-95) [11%]	245 (26-690) [89%]
FA type	13 (0-51) [4%]	291 (130-571) [96%]
M (motor) type	51 (30-95) [24%]	163 (26-228) [76%]
S (sensory) type	0 [0%]	344 (130-690) [100%]

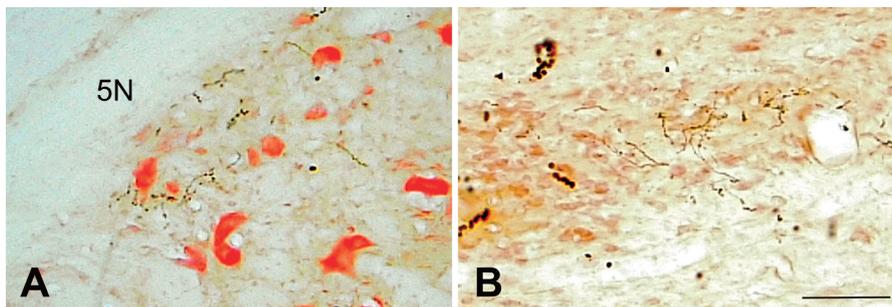


Fig. 1 Photomicrographs showing axonal fibers with boutons in the jaw-closing motoneuron pool (jaw-closing nucleus) in the trigeminal motor nucleus (A) and in the supratrigeminal nucleus (B). Axonal fibers and boutons are given off from one group Ia afferent (A) and one group II afferent (B) innervating the muscle spindle of the masseter muscle (a jaw-closing muscle); both are intra-axonally labeled with horseradish peroxidase. 5N: trigeminal motor nerve. Scale bar = 100 μ m.

through the Vsup are crucial in controlling jaw movements.

The afferents of Vmes neurons centrally give off many axonal boutons, all of which make synaptic contacts with their target neurons in the JC nucleus or Vsup (7,23), as described below. Therefore, to fully understand the functional significance of Vmes neurons in jaw movement control, it is essential to compare the distribution and synaptic features of axonal boutons arising from functionally identified Vmes afferents in the JC nucleus and Vsup. This review reanalyzes data for axonal boutons arising from functionally identified single Vmes afferents terminating in the JC nucleus and Vsup.

Bouton numbers in the JC nucleus and Vsup

Single Vmes MS afferents

The Vmes contains many neuronal cell bodies of two different Vmes afferents. In cats, the number of neuronal cell bodies is higher for MS afferents than for PL afferents (24). Intra-axonal recording and labeling techniques have been used extensively to describe

the detailed morphological features of electrophysiologically identified single Vmes afferents in the cat (2,6,7,23,25). Kishimoto et al. (7) and Yoshida et al. (25) classified single Vmes MS afferents innervating the masseter and temporal muscles as group Ia and group II afferents—on the basis of changes in their dynamic index after systemic administration of succinylcholine—and described the distribution and synaptic features of their axonal boutons. Kishimoto et al. (7) showed that single group Ia afferents give off many axonal boutons ($n = 595$ on average) in the JC nucleus (e.g., Fig. 1A) and far fewer boutons ($n = 98$) in the Vsup (Table 1). Interestingly, 30% of group Ia afferents do not terminate in the Vsup, although all group Ia afferents terminate in the JC nucleus. In contrast, single group II afferents issue a large number of axonal boutons ($n = 355$) in the Vsup (e.g., Fig. 1B) and a smaller number ($n = 244$) in the JC nucleus. It is particularly notable that 20% of group II afferents do not terminate in the JC nucleus, although all group II afferents terminate in the Vsup. Taken together, these data indicate that JC nucleus neurons receive much stronger projections from single group Ia afferents than

from single group II afferents, while the Vsup receives the contrasting input pattern. Group Ia afferents to the JC nucleus may control jaw-jerk reflexes phasically, while the group II afferents to the Vsup may control them tonically (8).

Single Vmes PL afferents

Shigenaga et al. used intra-axonal labeling techniques to describe the central projection features of electrophysiologically identified single Vmes PL afferents (2,26). Evidence regarding adaptation to stimulation applied to the peripheral receptive field indicates that PL afferents can be functionally classified as slowly adapting (SA) and fast adapting (FA). Single PL SA afferents give off an average of 245 axonal boutons in the Vsup and only 29 axonal boutons in the JC nucleus, while single PL FA afferents give off 291 axonal boutons in the Vsup and only 13 axonal boutons in the JC nucleus (Table 1) (2). Importantly, 43% of single Vmes PL SA afferents and 75% of FA afferents issue no axonal boutons in the JC nucleus, although all PL SA and FA afferents issue many axonal boutons in the Vsup. Taken together, these findings show that the JC nucleus receives much weaker projections and the Vsup receives stronger projections from both PL SA and PL FA afferents. The periodontal-masseteric reflex (9) may be induced by this direct, weak projection from PL FA afferents to the JC nucleus, whereas the tonic periodontal jaw muscle reflex (27) may be induced by indirect projection from PL SA afferents to the JC nucleus via their strong projection to the Vsup.

Vmes PL afferents labeled intra-axonally with a neuronal tracer can be morphologically classified as motor (M) and sensory (S) afferents (2,26). M-type single PL afferents have a stem axon that passes in the motor root of the trigeminal nerve, laterally adjacent to the caudal level of Vmo. S-type PL afferents have a stem axon that crosses the rostro-dorsomedial part of the trigeminal oral subnucleus, caudal to the Vmo. Importantly, both the M and S afferents include the FA and SA types described above. All M-type single PL afferents issue axonal boutons in the JC nucleus and Vsup (Table 1) (2). However, they issue a large number of axonal boutons ($n = 163$ on average) in the Vsup and a smaller number ($n = 51$) in the JC nucleus. In contrast, although all S-type single PL afferents issue axonal boutons ($n = 344$ on average) in the Vsup, no axonal boutons are issued in the JC nucleus. These findings suggest that the projection features of Vmes PL afferents to the JC nucleus or Vsup are strongly affected by the location of stem axons that issue axon collaterals.

Other comparisons between types of single Vmes afferents

It is striking that a considerable population of single Vmes afferents (MS group II and PL SA- and FA-type afferents) does not project to the JC nucleus, while only a small population of single MS group I afferents does not project to the Vsup (Table 1). Only single MS group Ia afferents send a far larger number of boutons in the JC nucleus than in the Vsup. Among the six types of afferents, boutons arising from single MS group Ia afferents in the JC nucleus are most numerous. However, the other types of single afferents (MS group II afferents, PL SA- and FA-type afferents, and PL M- and S-type afferents) give off much larger numbers of boutons in the Vsup than in the JC nucleus. This suggests that Vsup neurons substantially contribute to jaw movement. Collectively, the number of boutons arising from single PL afferents in the JC nucleus is much lower than those from single MS afferents. This suggests that MS afferents, especially group Ia afferents, are most important in simple, quick (phasic) JC reflexes, while PL afferents are less important.

Synaptic features of boutons in the JC nucleus and Vsup

Electron microscopic studies showed that cat Vmes MS and PL afferent boutons synapsing on JC motoneurons and Vsup neurons are S-type boutons (23), which is consistent with the boutons of rat Vmes MS afferents on JC motoneurons (28,29). S-type boutons contain clear spherical vesicles and form an asymmetric contact with postsynaptic neurons. Many immunoelectron microscopic studies of the trigeminal (21,30-34) and spinal motor nucleus (35,36) showed that S-type boutons contain an excitatory transmitter, glutamate, and thus are likely to exert excitatory effects on their postsynaptic neurons. The boutons of MS afferents synapsing on the JC motoneurons express vesicular glutamate transporter 1 (37).

It is essential to examine the distribution and synaptic features of boutons arising from Vmes afferents that make synapses with dendrites of postsynaptic neurons, since these boutons affect the strength of excitatory effects, which are transsynaptically given to their postsynaptic dendrites and then conducted toward the soma (or axon hillock) (38). Thus, the distribution and synaptic features of boutons of Vmes afferents that are electrophysiologically identified and intra-axonally labeled have been examined in the JC nucleus and Vsup by light and electron microscopy.

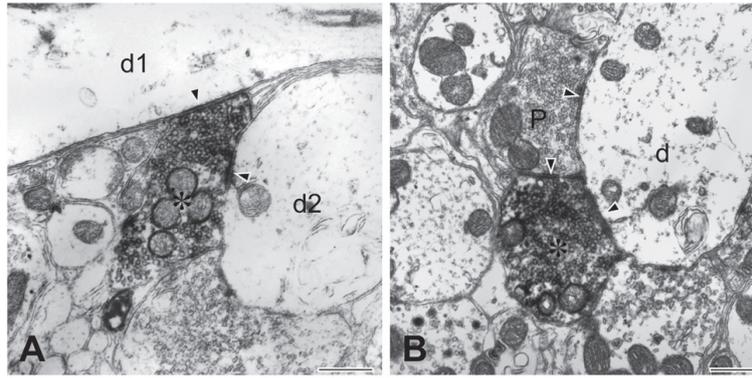


Fig. 2 Electron micrographs showing a horseradish peroxidase (HRP)-labeled group Ia muscle spindle afferent bouton (A) in the jaw-closing nucleus and a periodontal afferent bouton (B) in the supratrigeminal nucleus. A: An HRP-labeled masseter muscle afferent bouton (*) makes synaptic contact with two dendritic shafts (d1, d2). B: An HRP-labeled periodontal afferent bouton (*) is presynaptic to a dendrite (d) and receives an axoaxonic synapse from a P-ending (P) containing pleomorphic vesicles. Arrowheads indicate synaptic sites. Scale bar = 500 nm.

Table 2 Proportions (%) of boutons of Vmes afferents, according to the number of postsynaptic targets in the JC nucleus

Type of Vmes afferents	No. of postsynaptic targets			
	1	2	3	4 or more
Muscle spindle afferent				
group Ia	62%	19%	14%	5%
group II	60%	32%	4%	4%
Periodontal afferent	57%	28%	13%	3%

Table 3 Number of contacts synapsing with different postsynaptic targets per Vmes afferent bouton in the JC nucleus and Vsup

Type of Vmes afferent/Location of boutons	No. of contacts synapsing with				Total no. of contacts
	Soma	Proximal dendrite	Distal dendrite	P-ending	
Muscle spindle afferent					
group Ia afferent in JC nucleus	0.17	0.52	0.46	0.46	1.62
group II afferent in JC nucleus	0.13	0.29	0.72	0.42	1.56
in Vsup	–	0.02	1.28	0.72	2.02
Periodontal afferent					
in JC nucleus	–	0.07	1.55	0.42	2.04
in Vsup	0	0.01	1.21	0.87	2.09

Vmes MS afferents

In cat JC nucleus, approximately 80% to 90% of boutons of MS groups Ia and II afferents make synaptic contact with one or two postsynaptic elements (Fig. 2A, Table 2) (7,23). The distribution patterns of the MS afferent boutons in the JC nucleus—which are presynaptic to the soma, proximal dendrite, or distal dendrite and postsynaptic to axonal boutons (P-endings)—are similar in group Ia and II afferents (Table 3) (7). However, in the JC nucleus, boutons from group Ia afferents make synapses with proximal dendrites a little more frequently than do those from group II afferents. This difference suggests that group Ia afferents have a stronger excitatory effect to JC motoneurons than do group II afferents, as indicated

by bouton numbers in Table 1. P-endings are axonal boutons containing pleomorphic vesicles (a mixture of round, oval, and flattened vesicles) and are presynaptic to Vmes afferent boutons that make synapses with JC motoneurons. They are involved in presynaptic inhibition of Ia afferent input to motoneurons (39,40). Interestingly, 40%, 26%, and 26% of P-endings presynaptic to cat Vmes Ia afferent boutons—which make synaptic contact with JC motoneurons—are immunoreactive to both GABA and glycine, GABA alone, and glycine alone, respectively (41).

In the Vsup, a much larger number of MS afferent boutons make synaptic contacts with distal dendrites (Table 3). The proportion of MS afferent boutons that

receive a synapse from the P-ending is higher in the Vsup than in the JC nucleus.

Vmes PL afferents

In the cat JC nucleus, approximately 85% of Vmes PL afferent boutons make synaptic contacts with one or two postsynaptic elements, as is the case for MS afferents (Fig. 2B, Table 2) (23). Although the proportion of boutons that receive a synapse from P-endings in the JC nucleus is similar between PL afferents and group Ia or II afferents, the frequency of boutons making synapses with distal dendrites in the JC nucleus is much higher for PL afferents than for group Ia and II afferents (Table 3). This also suggests that PL afferents to JC motoneurons have a lower excitatory effect than do group Ia and II afferents, as indicated by bouton numbers in Table 1.

In the cat Vsup, no Vmes PL afferent boutons are presynaptic to the somata (Table 3) (31). The proportion of PL afferent boutons that makes synapses with distal dendrites is also higher than that with proximal dendrites (Table 3) (23). The proportion of boutons receiving synapses from P-endings in the PL afferents is much higher in the Vsup than in the JC nucleus (23). All P-endings presynaptic to PL afferent boutons in the cat Vsup are GABA-immunopositive (31).

Other comparisons between types of Vmes afferents

In the JC nucleus, group Ia of Vmes MS afferents has a larger number of boutons synapsing on proximal dendrites or soma, as compared with other types of Vmes afferents (Table 3) (23). This suggests that group Ia MS afferents have a stronger excitatory effect than group II afferents and PL afferents on JC motoneurons. For Vmes MS and PL afferents, boutons receive synapses from P-endings much more frequently in the Vsup than in the JC nucleus. This suggests that excitatory inputs from Vmes afferents to Vsup neurons are more frequently and precisely controlled (inhibited) by a presynaptic mechanism than those to target neurons in the JC nucleus.

This review clearly demonstrates that the distribution and synaptic features by which individual subtypes of Vmes MS and PL afferents issue axonal boutons are distinct in the JC nucleus and Vsup. The distinct projections and synaptic connectivity of the Vmes afferent subtypes in the JC nucleus and Vsup suggest that these subtypes have specific and important roles in the control of jaw reflexes.

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Conflicts of interest

None declared.

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