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Research Highlight

Superior Cervical Ganglion: Axonal Passage and Inputs

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Axons of the rostral middle (MCG) and inferior (ICG) cervical ganglion were reported to bypass the superior cervical ganglion (SCG). However, the distribution of these neurons has not been determined. Meanwhile, it has been inconsistent with the distribution of the preganglionic neurons of the SCG. To examine the above issues, we recently injected wheat germ agglutinin-horseradish peroxidase (WGA-HRP) into the entire or partial (rostral or caudal) SCG of the rat (*Anatomical Record*, 301:1906-1916, 2018). By preparing complete whole-mounts of the sympathetic tissues and sections of the brainstem and spinal cord, we labeled neurons that are distributed evenly in the MCG (left: 258 > right: 121) ICG (left: 848, right: 681) and CST (up to 770). It is found specifically a novel cervical ganglion and termed it as the "pre-middle cervical ganglion" (pMCG) that is located rostral to the MSG and sends axons (left: 120 > right: 82) to bypass the SCG. In addition to the preganglionic neurons in the cervical (C1-C4) and thoracic (T1-T4) segments, we also labeled neurons (233) that extend dendrites into the vestibular nuclear complex and locate in the intermediate reticular nuclei (96%) and perifacial zone (4%) of the brainstem ranging from Bregma -10.0 to -11.0 mm, mainly in -10.80 mm. With tracer injection into the rostral or caudal SCG, we labeled neurons correspondingly in the brainstem, C1-C2 or T1-T2. These data indicated that many neurons in pMCG, MCG and ICG run rostrally within the CST to project to their peripheral targets rather than segmentally *via* the closest rami. For their close anatomical location, neurons in pMCG and MCG may have similar or complementary function. Numerous neurons in the CST and caudal cervical ganglia provide bypass axons *via* SCG may imply special function that is useful for electroceuticals. The newly identified preganglionic neurons located in the rostral brainstem may be involved in the vestibulo-autonomic interaction for their extending dendrites into the vestibular nuclear complex that has been known to form an interaction pathway with the vagal complex.

Key Words: Autonomic nervous system, sympathetic nervous system, preganglionic neurons; postganglionic neurons; paravertebral ganglia.

Introduction

Cervical sympathetic ganglia include the superior (SCG), middle (MCG), and inferior (ICG) cervical ganglion. The postganglionic neurons of the SCG innervate organs in the head and neck. In the rat, the MCG either fuses with the ICG to form the stellate ganglion or the ICG frequently fuses with the first and even caudally to the third thoracic ganglion to form the stellate ganglion (8). Furthermore, branches of the SCG connect to the 9th, 10th, 11th and 12th cranial nerves and the 1st, 2nd, 3rd and 4th cervical spinal nerves (8). Neurons in the SCG receive their preganglionic synaptic inputs from the cervical sympathetic trunk (CST) and the rostral SCG sends postganglionic axons *via* the internal carotid nerve while the caudal SCG *via* the external carotid nerve (2). The CST also contains postganglionic axons originating from the rostral MCG and ICG to exit the SCG *via* the external carotid nerve (3). The CST contains 84% preganglionic axons, 11% postganglionic axons of the SCG, MCG, and ICG, and 5% sensory fibers respectively (25). However, the distribution of these postganglionic neurons has not been determined.

The preganglionic neurons of the SCG are distributed in the medullary reticular formation of the lower brainstem (34) and the nucleus intermediolateralis (IML) of the spinal cord segments (9, 21, 22, 26). However, the distribution of these preganglionic

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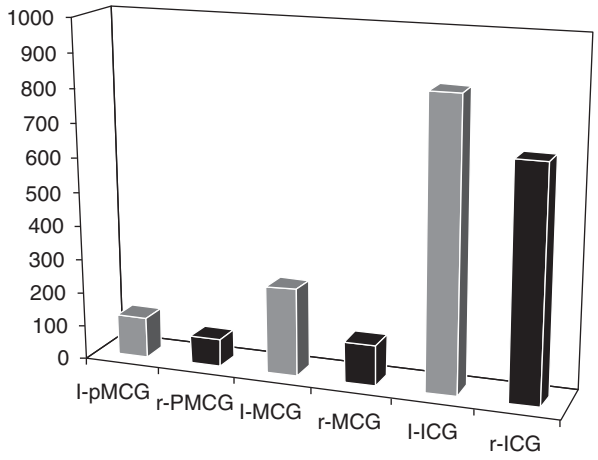

Fig. 1. Numbers of neurons labeled in the sympathetic ganglia (Modified with permission from Fig. 9 of Anatomical Record, 301: 1906-1916, 2018). After injecting WGA-HRP into the SCG (superior cervical ganglion), we found that the pMCG (pre- middle cervical ganglion) and MCG (middle cervical ganglion) have more neurons on the left side than the right side. The ICG (inferior cervical ganglion) has more neurons than the pMCG and MCG on both the left and right side.

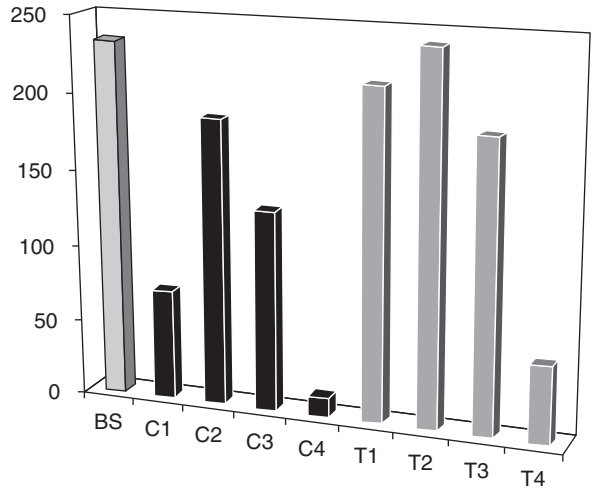

Fig. 2. Numbers of neurons labeled in the brainstem and spinal cord segments (Modified with permission from Fig. 10 of Anatomical Record, 301: 1906-1916, 2018). After injecting WGA-HRP into the SCG, we labeled neurons in the rostral brainstem and the spinal segments C1-C4 and T1-T4. BS: brainstem; SCG: superior cervical ganglion.

onic neurons has been reported inconsistently, ranging from C8 to T5 (10, 21, 22, 24), from C8 to T7 (9), and from T1 to T4 (25).

Axonal Passage and Inputs to SCG

Recently we injected neural tracer WGA-HRP (12, 30-33) into the entire (0.8 μl) or partial (rostral or caudal, 0.1-0.3 μl) SCG of male rats and prepared whole-mounts of the SCG, cervical sympathetic trunk, MCG, and ICG and systematic sections of the spinal cord and brainstem (27). We characterized the distribution of sympathetic preganglionic neurons that connect to the SCG and the postganglionic neurons that send axons rostrally and bypass the SCG to innervate their peripheral target tissues (27). For tracer leakage control, we injected the nodose ganglion or dripped the skeletal muscle surrounding the SCG with WGA-HRP and found no neurons being labeled in the CST and the caudal cervical ganglia (27).

After injecting WGA-HRP into the SCG, we labeled neurons and axons being distributed evenly in the CST (up to 770), MCG, ICG, brainstem, and spinal segments in C1-C4 and T1-T4 (Fig. 1 and Fig. 2). Consistently, a group of neurons on both sides of the very caudle end of the CST, almost just rostral to the MCG and ICG, were clustered in a ganglion-like bulge, which we termed it as the "pre-middle cervical ganglion" (pMCG) for its location (see Fig. 5 and Fig. 12 in our earlier report, Reference No. 27). As shown in Fig. 1, the left pMCG (120 ± 10) has significantly more neurons labeled than the right pMCG (82 ± 11) and Meanwhile, the left MCG (258 ± 34) has significantly more neurons labeled than the right MCG (121 ± 12). Whereas, numbers of neurons labeled in the left ICG (848 ± 94) and right ICG (681 ± 111) are not significantly different. The average total number of neurons labeled in the sympathetic ganglia is 2109 ± 172 and it is 1338 ± 148 in the brainstem and spinal cord. Overall, the numbers of neurons labeled in different brain locations (brainstem, cervical and thoracic segments) are significantly different.

In the brainstem, multipolar neurons (233 ± 48, Fig. 2) and fibers were labeled in the sections ranging from Bregma -10.0 to -11.0 mm and mainly in the sections -10.80 mm rostral to the Bregma. Neurons were distributed in two different groups of nuclei, mainly (224 ± 48, 95.8%) in the intermediate reticular nuclei (IRt) and rarely (10 ± 1, 4.2%) in the perifacial zone, or P7 area. The dendritic fibers of the neurons labeled in the IRt congruently projected to the medial vestibular nuclei (see Fig. 6 in our earlier report, Reference No. 27).

In the cervical spinal cord, neurons were labeled in the segments of C1 (73 ± 7), C2 (188 ± 24), C3 (132 ± 19), and C4 (13 ± 4) as shown in Fig. 2. Neurons were distributed in the lamina IX of the

anterior gray horn. In the rostral C1, neurons were grouped together in the medial sub-area. Whereas, neurons in the caudal C1 and the C2-C4 were scattered in all of the three sub-areas of the lamina IX. Neurons in different sub-areas of the lamina IX were interwoven to each other with parallel dendrites.

In the thoracic spinal cord, neurons were labeled in the segments of T1 (216 ± 33), T2 (241 ± 42), T3 (190 ± 29), and T4 (52 ± 18) as shown in Fig. 2. Neurons were distributed within all of the four sympathetic autonomic subnuclei in the intermediate zone: mainly in the intermediolateral cell column (IML), partially in the nucleus intermediolateralis thoracolumbalis pars funicularis (ILf), and rarely in the nucleus intercalates spinalis (IC) and the nucleus intercalates pars paraependymatis (ICpe).

Preganglionic Neurons to Rostral/Caudal SCG

With WGA-HRP injection into the rostral SCG, we selectively labeled very few neurons in the intermediate reticular nuclei of the brainstem (about 20) and the medial area of the lamina IX of the cervical spinal cord (C1: ~20; C2: ~23) and labeled only two neurons in C3 in one case out of seven subjects. With WGA-HRP injection into the caudal SCG, we selectively labeled also very few neurons in the intermediolateral nucleus of the thoracic spinal cord (T1: about 20; T2: about 34) and labeled 12 neurons in T3 in one case out of seven subjects.

Methodological Consideration: Bypass Axons Absorb WGA-HRP

It has been demonstrated that the CST also includes postganglionic and sensory axons (3, 25). Furthermore, it is believed that WGA-HRP is a neural tracer to be selectively absorbed by the membrane of the somata in the nodose ganglion without concomitantly label the efferent axons (20). However, we demonstrated that WGA-HRP can be absorbed by the sympathetic preganglionic as well as bypass postganglionic efferent axons after being injected into the SCG (27).

It has been shown that volumes of 0.5 μl can spread solutions of 1.04 mm (15); thus, the labeling of the axonal passage and inputs of the SCG might be resulted from the leakage of the WGA-HRP. To prevent the false positive and false negative resulting from the tracer diffusion (6, 29, 30), we Injected or dripped WGA-HRP into the nodose ganglion or the muscles around the SCG and labeled no neurons in the pMCG, MCG and ICG (27). Actually, the SCG is a ganglion with a very long narrow shape and enveloped by connective tissue that can prevent the spread of the tracer solutions to the surrounding tissues such as the nodose ganglion. The long length of CST should be enough to rule out the possible labeling of the neurons *via* the diffusion of the neural tracer from the SCG to the MCG and ICG. Especially, larger volume (0.8-1.0 μl) of tracer injection into the SCG did not label any parasympathetic preganglionic neurons that project to the nodose ganglion. Furthermore, the smaller volume (0.1-0.3 μl) of tracer injection into one-site of the rostral or caudal SCG did selectively label neurons in the regions of rostral brainstem and cervical spinal cord or in the segments of the caudal thoracic spinal cord (27).

Indeed, the "preganglionic neurons" located in the brainstem and spinal cord send axons to form synapses on the neurons of the peripheral sympathetic ganglia such as the superior, pre-middle, middle, and inferior cervical ganglion. From our earlier tracing, we cannot determine whether all of the preganglionic neurons that we have labeled in the brainstem and spinal cord project only to the SCG (27). It is possible that other neurons located in the caudal ganglia also receive the synapses from the preganglionic neurons labeled in the brainstem and spinal cord (27).

Numbers of Axonal Passage and Inputs to SCG are Within Regular Range

After applying HRP to the cutting end of the CST just caudal to the SCG, Bowers and Zigmond (1981) labeled only about 300 neurons in the more rostral regions of the inferior and middle cervical ganglia. Using the more sensitive tracer WGA-HRP, we labeled significantly more postganglionic neurons (2109) distributed evenly in the caudal cervical ganglia and CST to send axons to bypass the SCG. Obviously, these sympathetic postganglionic neurons in the CST, pre-MCG, MCG and ICG do not project segmentally through the closest rami, but rather run rostrally within the CST and *via* the SCG or above to project to their peripheral targets.

In our earlier review (28), the rat SCG contains neurons ranging from 13000 to 39200 and the preganglionic neurons that project to the SCG ranging from 970 to 8610. Thus, the numbers of postganglionic neurons (2109) in three caudal sympathetic ganglia (pMCG, MCG, ICG) and preganglionic neurons (1338) in the brainstem and spinal cord we labeled are not a few and their special functions are to be explored.

Tracing Disparity for Spinal Projection to SCG

It has been shown that different tracing methods resulted in different spinal projections to the SCG in

the rat: 1) HRP and Fluoro-gold studies showed from C8 to T5 (10, 21, 22, 24); 2) cholera toxin subunit B showed from C8 to T7 (9); and 3) cholera toxin b-HRP showed from T1 to T4 (25). However, it has been consistently shown that the projections are ipsilateral to the application side of the neural tracer (9, 21, 22, 26).

Researchers have difficulties in defining the segmental boundary between the brainstem and the rostral C1 segment due to the lack of visible dorsal roots in animals which have been investigated (14). Thus, the difficulty in defining the spinal segments might justify the discrepancy of the above reports.

Pre-Middle Cervical Ganglion: Possible Function

We identified a small novel ganglion, i.e. the pre-middle cervical ganglion, and it is located at the caudal end of the CST. The left pMCG is either connected to the MCG or directly to the ICG and is larger than the right pMCG that is always connected only to the MCG. This neural lateralization in connection and distribution might present special functions in regulating the cardiovascular system, thus for the autonomic response that follows the flight-or-fight defensive behaviors. Besides, the pMCG might provide similar or complement functions of the ICG or MCG for their closeness. Further chemical and connection analysis of these bypass neurons should be useful for electroceutical therapy.

Innervations to the Heart

Anatomically, neurons in the periaqueductal gray matter modulate cardiovascular-related sympathetic outflow system to regulate the heart (7) and most of the sympathetic fibers that innervate the heart run through the ICG (11). The MCG and ICG provide almost 90% of the innervations to the heart; while the sympathetic chain provides the rest of innervations and the SCG provides only a few neurons (17).

Lateralized Cardiac Control of the Inferior Cervical Ganglion

Neural control of the heart rate is achieved mainly by sympathetic and parasympathetic innervation of the sinoatrial node. It has been well established that the lateralized sympathetic innervations of the heart influences cardiac activity in an asymmetric manner (35). Innervations of the pacemaker sinoatrial node are mainly from the right ICG cardiac nerves and sparsely from the left ICG (13). In dogs, cardiac acceleration resulting from stimulation of the right ICG is several times higher than from the left ICG. In humans, heart rate decreases considerably following right ICG block, whereas the left ICG block fails to produce significant heart rate slowing (23). However, the myocardial contractility seems to be more efficiently controlled by the left sympathetic outflow. Left ventricular systolic pressure, a measure of contractile force, rises much more following left as opposed to right ICG stimulation (7).

Ectopic or Organized Neural Migration of the Pre-middle Cervical Ganglion?

Since the pMCG was consistently found in one single cluster rather than in scattered groups in all of the subjects examined, it is reasonably to treat them as an independent ganglion. However, the formation of the pMCG might be just a result from a developmental ectopic migration of the neurons that are presumably to be moved to the MCG or ICG. In this case, the roles of pMCG must be no difference to those of the MCG or ICG. Nevertheless, some special chemical(s) should be involved in the migration of the neurons of the pMCG and/ or even the CST during the developmental stages. Further examination on the genetic and chemical expression of these neurons will be useful to clarifyknow their involvement in the cardiac control mechanism.

Neurons in Cervical Sympathetic Trunk

It has been reported that the CST contains mainly preganglionic fibers. Bowers and Zigmond (3) reported that the CST also contains postganglionic axons originating from the rostral MCG and ICG to exit the SCG *via* the external carotid nerve. However, we showed numerous neurons are distributed evenly in the pMSC, MSC, and ICG and send axons along the CST to bypass the SCG in the rat (27). In the rabbit, almost 95% of the spinal preganglionic neurons project to the SCG by passing through the ICG and then sympathetic trunk (18). In the rat, the CST contains very few sensory fibers (4) and only 13 sensory neurons were labeled among the dorsal root ganglia from T1 to T6 of the cat in tracing the CST (16). Therefore, the CST is not a pure preganglionic trunk and any electrical measurement or electroceutical treatment in the CST must consider these postganglionic fibers and the little amount of sensory fibers. Although it is well known that the postganglionic neurons do not provide synapses to each other, it is to be determined whether axons from the pMCG, MCG or ICG have synaptic contact with neurons in the SCG to form a local circuit among these ganglia.

Preganglionic Neurons in IRT: Possible Function

After injecting the tracer into the SCG, We labeled preganglionic neurons distributed in the rostral brainstem (Bregma -10.0 to -11.0 mm), C1-C4, and T1-T4.

The preganglionic neurons we newly labeled in the rostral brainstem were mainly distributed in the intermediate reticular nuclei. It has been reported that neurons projecting to the SCG were distributed in the reticular nucleus of the lower part of the brainstem (Bregma -14.08 mm) and 90% of the labeled neurons were located in the ventral medullary reticular nuclei (34). Since the mark for the border of the most caudal brainstem and the beginning cervical spinal cord is not clear (14), the neurons we labeled in the section of C1 might be the ones labeled by Wiberg and Widenfalk (34) in the lower part of the brainstem.

Neurons in the rostral brainstem that project to the SCG should belong to the sympathetic preganglionic. Interestingly, the dendritic fibers of these neurons labeled in the IRt congruently project to the medial vestibular nuclei. Since the vestibular nuclear complex and the vagal complex form a vestibulo-autonomic interaction pathway (1, 19), these IRT preganglionc neurons in the rostral brainstem may function as the sympathetic limb to be involved in the vestibulo-autonomic interaction.

Summary

We identified neurons in the rostral brainstem also project to the SCG. Moreover, there are lots of neurons in the caudal cervical sympathetic trunk, the pMCG (newly found), MCG, and ICG evenly deliver bypass axons through the SCG with a lateralization pattern. These neurons might be involved in the regulation of the cardiovascular system and the vestibulo-autonomic interaction. Further exploration to these anatomical connections may be useful for the development of “electroceuticals”.

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Conflict of Interest

The authors have no conflicts of interest to report.

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