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Organization of the spinal trigeminal nucleus in Star-Nosed Moles

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Abstract

Somatosensory inputs from the face project to multiple regions of the trigeminal nuclear complex in the brainstem. In mice and rats three subdivisions contain visible representations of the mystacial vibrissae: the principal sensory nucleus, the spinal trigeminal subnucleus interpolaris and subnucleus caudalis. These regions are considered important for touch with high spatial acuity, active touch, and pain and temperature sensation, respectively. Like mice and rats, the star-nosed mole (*Condylura cristata*) is a somatosensory specialist. Given the visible star pattern in preparations of the star-nosed mole cortex and the principal sensory nucleus, we hypothesized there were star patterns in the spinal trigeminal nucleus subnuclei interpolaris and caudalis. In sections processed for cytochrome oxidase we found star-like segmentation consisting of lightly stained septa separating darkly stained patches in subnucleus interpolaris (juvenile tissue) and subnucleus caudalis (juvenile and adult tissue). Subnucleus caudalis represented the face in a three-dimensional map with the most anterior part of the face represented more rostrally than posterior parts of the face. Multi-unit electrophysiological mapping was used to map the ipsilateral face. Ray-specific receptive fields in adults matched the CO-segmentation. The mean areas of multiunit receptive fields in subnucleus interpolaris and caudalis were larger than previously mapped receptive fields in the mole's principal sensory nucleus. The proportion of tissue devoted to each ray's representation differed between subnucleus interpolaris and the principal sensory nucleus. Our finding that different trigeminal brainstem maps can exaggerate different parts of the face could provide new insights for the roles of these different somatosensory stations.

Keywords

somatosensory; barrelettes; evolution; interpolaris; caudalis; RRID: nif-0000-23420

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Introduction

The trigeminal sensory complex in the brainstem is the first relay in the central nervous system for facial somatosensation. Upon entering the brainstem, sensory neurons branch to send inputs to four different somatosensory regions (Diamond et al., 2008; Bosman et al., 2011). This anatomical segregation suggests facilitation of parallel processing and raises the possibility that these regions are specialized for different submodalities of somatosensation.

The main trigeminal somatosensory nuclei in the brainstem are the principal sensory nucleus (PrV) and the spinal trigeminal nucleus (STN). The STN is divided into three subnuclei, subnuclei oralis (SpVo), interpolaris (SpVi) and caudalis (SpVc) (Fig. 1) (Olszewski, 1950). The PrV is found most rostrally, followed caudally by the SpVo, SpVi, and SpVc. The SpVi is further divided into a rostral and caudal component (Phelan and Falls, 1989). Primary somatosensory axons from the face project to both the STN and PrV. Thick axons, which are presumably from mechanoreceptor afferents, project to the PrV and to all subnuclei in the STN, whereas thin axons that are presumably nociceptive and/or thermoceptive project only to the STN (Ramon y Cajal, 1896; Gerard, 1923; Anstrom, 1953; Jacquin et al., 1986a; Jacquin et al., 1986b). Four parallel somatosensory pathways arise from the four trigeminal somatosensory (sub)nuclei suggesting that each pathway channels information for different facets of touch (Henderson, 1995; Diamond et al., 2008). The PrV is thought to be important for mediating discriminative touch (with high spatial acuity), the SpVi for accounting for sensation from movement initiated by the animal, and the SpVc for pain and temperature sensation (Diamond et al., 2008). The role of SpVo is more elusive but is thought to be involved in oral and perioral reflexes and nociception (Nash et al., 2009; Devoize et al., 2010). The functions of the PrV and each subnuclei of the STN have primarily been studied in the context of whisking behavior in rodents.

Rats and mice are useful for studying trigeminal somatosensation because their mystacial vibrissae have large, anatomically visible representations, with each facial whisker follicle visible as a distinct unit. In the brainstem, thalamus, and cortex, the arrays of patches representing mystacial vibrissae are known respectively as barrelettes (visible in PrV, caudal SpVi, and SpVc) (Belford and Killackey, 1979; Erzurumlu et al., 2010), barreloids (visible in the ventral posterior medial nucleus of the thalamus) (Van Der Loos, 1976), and barrels (visible in the primary somatosensory cortex) (Woolsey and Van der Loos, 1970).

The star-nosed mole (*Condylura cristata*) has sensitive, finger-like nasal appendages that are used for exploring their environment (Fig. 1 A-C). They have reduced eyes and instead rely primarily on the tactile star to explore the underground wetland areas of their habitat (Hamilton, 1931). The star consists of 22 fleshy rays (Fig. 1A-C) completely covered with a mosaic of touch receptors known as Eimer's organs. Externally, these receptors appear as 40-50 μ m diameter domes. Internally, they each house a Merkel cell-neurite complex, a laminated corpuscle, and two classes of free nerve endings (Catania, 1996; Marasco et al., 2006). Up to 28,000 Eimer's organs cover the star surface (Catania and Kaas, 1997). The small, closely packed Eimer's organs suggest that the star is a somatosensory surface optimized for high resolution touch and behavioral tests demonstrate that by rapidly repeating sequences of touching, withdrawing, and reorienting motions, moles can locate

and quickly eat prey items that are as small as 1 mm² (Catania and Kaas, 1997). Star-nosed moles preferentially use ray 11, their “somatosensory fovea,” for this task (Catania and Kaas, 1997).

Central nervous system representations of the star have been investigated at the level of the somatosensory cortex (Catania and Kaas, 1995) and in PrV of the brainstem (Catania et al., 2011). In both areas a visible star pattern with individual representations of each nasal ray were found, similar to the barrels and barrelettes found for whiskers in mice and rats. The proportions of the cytochrome oxidase (CO) stained-segments in the star pattern are different in the cortex compared to PrV. For example, ray 11 has only 7% of the Eimer's organs on the star, yet accounts for 13% of the star representation in the PrV and 25% of the star representation in the primary somatosensory cortex (Catania and Kaas, 1997; Catania et al., 2011), which may be related to preferential use of ray 11 in fine discrimination tasks.

In the present study, we investigated whether the star representation was present in the SpVi and SpVc in a manner analogous to the barrelettes found in rats and mice. Using histological analyses and multi-unit electrophysiological mapping, we examined the organization and receptive field size of these subnuclei. We hypothesized that the different functional roles of the two areas might be represented anatomically in star representations that accentuated different regions of the star surface. To test this we measured the volume of the ray representations in SpVi and compared it to the ray representations in the PrV to see if the areas had same pattern of afferent magnification.

Methods

Animals

Eleven adult and six juvenile star-nosed moles were used in this study. The adults were used for electrophysiology and histology; the juveniles were used for only histology. The adult star-nosed moles were collected in Potter County, Pennsylvania (under permit # 112-2011). The juvenile star-nosed moles were obtained from the litters of wild-caught pregnant moles that gave birth and raised young while in laboratory housing. The juveniles used were 3.0, 10.5, 12.9, 13.8, 17.9 and 23.2 g (approximately postnatal days 0, 4, 5, 6, 9, and 15, respectively). Ages were estimated from similar anatomical stages in rodents and by tracking development from the time the juveniles were first observed in the nest. These were estimates because birth was not directly observed in the underground nest. The mass of the juveniles is reported when describing different juvenile cases. All procedures conformed to the National Institutes of Health standards concerning the use and welfare of experimental animals and were approved by the Vanderbilt University Animal Care and Use Committee (Animal Welfare Assurance Number A-3227-01).

Electrophysiology and receptive field mapping

Moles were initially anesthetized with 15% urethane (1.0 g/kg) and 10% ketamine (10 mg/kg). They were given supplemental injections to maintain a surgical plane of anesthesia as needed. The animal's head was fixed, and a craniotomy was made over one or both of the cerebellar hemispheres. The angle of the micromanipulator varied between experiments to

allow access to different areas of the brainstem. Recordings were made with low-impedance tungsten electrodes (1.0–1.5 M Ω at 1000 Hz) with a tip diameter of 1 μ m. Responses were amplified and monitored with a Powerlab 4/30 data acquisition unit using a speaker and a computer running LabChart software (ADInstruments). Electrode penetrations were made through the cerebellum into the brainstem nuclei. When responses to the face and star were obtained, receptive fields were defined using a fine wooden probe, and the extent of the receptive field for each recording site was drawn on a schematic of the mole's nose. Receptive fields were found exclusively on the ipsilateral face. Receptive fields were noted at 100 μ m intervals until responses were no longer obtained. After recording receptive fields, the electrode was returned to a site along that penetration, the receptive field was remapped, and the site was marked with a single electrolytic microlesion at 10 microamps for 5–10 seconds. For selected tracks a continuous lesion was made by withdrawing the electrode at 25 μ m/sec while the electrode was supplied with 10 microamps of current.

After recordings, moles were euthanized with an overdose of sodium pentobarbital (120 mg/kg) and transcardially perfused with phosphate buffered saline (PBS) (pH 7.3) followed by 4% paraformaldehyde. Rodents used for histology were euthanized using identical procedures.

Histochemistry

The brainstem was removed and cryoprotected overnight in 30% sucrose in PBS. The ventral surface of the brainstem was considered to be a horizontal plane. Brainstems were cut coronally at a thickness of 40 μ m. The sections were stained for Nissl substance with thionin, processed for cytochrome oxidase (Carroll and Wong-Riley, 1984) or myelin (Gallyas, 1979).

Sections were photographed with a Zeiss AxioCam HRc digital camera (Zeiss, Jena, Germany) mounted onto a Zeiss Axioskop microscope using Zeiss Axiovision 4.5 software (Carl Zeiss Microimaging, Thornwood, NY, USA). Images were imported into Adobe Photoshop CS5 and adjusted for optimal contrast and brightness but were otherwise unaltered.

Size of Receptive Fields

Lesions and electrode tracts were used to determine the location of each recording site and receptive field. Receptive field drawings were digitized and their areas were measured in ImageJ (Schneider et al., 2012). Additionally, the areas of receptive fields in PrV were measured from records from a previous study that used the same anesthesia protocol but for which receptive field size was recorded but not analyzed for area (Catania et al., 2011).

Reconstruction of star representations

The 3-dimensional organization of the subnuclei was investigated by volumetric reconstruction. Photomicrographs of serial sections were imported into *Reconstruct* software version 1.1.0 (Synapse Web Reconstruct, RRID:nif-0000-23420) (Fiala, 2005). Sections were aligned by matching anatomical landmarks and using the “rigid alignment” function.

The volume of each ray representation in SpVi was measured by tracing the pale septa that marked the boundary of each CO-segment. This was done in all sections in which the septa were present. A total of 6 complete representations were reconstructed from the 4 juvenile animals (body masses of 10.5g, 12.9g, 13.8g, 16.4g). In two animals, both sides of the brainstem had representations that were complete; in the other two animals, tears in the tissue precluded one side from being measured. The total volume of the ray representations was calculated using the following formula: volume = (area of each section) $\times$ (thickness of section) $\times$ (number of sections), which is consistent with similar studies (Ashwell et al., 2006; Catania et al., 2011).

Larger animals had larger SpVi's, but the proportions of the star did not systematically differ with animal size (none of the 11 linear regressions revealed a significant effect of the animal's mass on the proportion of the nucleus devoted to that ray). Therefore, the percentage of the star devoted to each ray, and not the absolute volume of the ray representation, was used for the remaining statistical analyses. All statistical analyses were done in SPSS version 21.

Results

Anatomy of Subnucleus Interpolaris

A star representation was observed in sections from caudal SpVi stained for CO in juvenile star-nosed moles (Fig. 1E). Lightly-stained septa divided the nucleus into 11 densely stained patches which together formed a characteristic star pattern similar to that observed in PrV, S1, and S2 of the star-nosed mole (Catania and Kaas, 1995; Catania et al., 2011). Densely stained barrelette-like patches were dorsal to the star representation (Fig. 1E, arrows). The star pattern was observed in animals that were approximately 4 to 9 days old (10.5 g to 17.9 g, respectively) but was not obvious in younger or older animals (3.0 g and 23.2 g, respectively). The 3.0 g animal (postnatal day 0) lacked septa in SpVi. The SpVi of the 23.2 g animal (approximately postnatal day 15) was similar to that of an adult star-nosed mole in lacking clear septa (Fig. 2A).

The topography of the representation of the star in SpVi was determined through multiunit electrophysiological recordings while stimulating the ipsilateral face and body. As the electrode was lowered ventrally through the nucleus, receptive fields systematically progressed from the forelimb (when the electrode was in the adjacent cuneate nucleus), to the mystacial vibrissae (when it was in the dorsal SpVi), to the more ventral rays (e.g., ray 11) followed by more dorsal rays (e.g., ray 1) (Fig. 2). This produced an inverted representation such that dorsal rays were represented ventrally in the nucleus, and the ventral rays were represented dorsally.

The volume of each ray representation was reconstructed from six juvenile samples processed for CO (Fig. 3). The star pattern was present at the caudal extent of SpVi with consecutive coronal sections revealing nearly identical segmentation patterns (Fig. 3A, B). The proportion of total SpVi volume devoted to each ray's representation was not equal (ANOVA, $F(10,55) = 59.744$, $p < 0.01$). Tukey's HSD test revealed that rays 1 and 11 had

volumes that were not significantly different from each other, but were larger than the volumes of any other ray (Fig. 3C).

Previous studies have reported the number of Eimer's organs on the star, the number of myelinated fibers dedicated to each ray, the volume of each ray representation in the PrV, and the area of the ray representation in S1 (Catania and Kaas, 1997; Catania et al., 2011). From that data we calculated the percent of neural tissue devoted to each ray at these various stations along the somatosensory pathway. This allowed us to compare the results in SpVi to previous work (Fig. 4). We then asked if the proportion of neural tissue devoted to each of the rays was equal at different stations. Rays that had a larger proportion of neural tissue in one station were overrepresented, and rays with a smaller proportion were underrepresented. These terms were used instead of magnification, as in cortical magnification, because that specific phenomenon is sometimes explained as a linear reflection of receptor density, which we are not suggesting here. It should be noted that, though the graph in figure 4 is organized to show the general progression from the periphery to the neocortex, the PrV and SpVi are parts of parallel somatosensory pathways.

The proportion of neural tissue devoted to each ray differed between stations in the somatosensory pathway. A two-factor ANOVA, with the factors of ray number and somatosensory station, showed a significant main effect for ray ($F(54,10) = 139.954$, $p < 0.01$) and an interaction effect for ray and somatosensory station ($F(54, 40) = 36.445$, $p < 0.01$). The ray effect reflected that the sizes of the ray representations are not identical. The interaction effect showed that the proportion of neural tissue devoted to each ray is different at each level of the somatosensory pathway. One-factor ANOVAs of each of the rays revealed that all rays had a significant area effect ($p < 0.01$ in all cases). Within each ray a Tukey's HSD test was used to determine how somatosensory station affected the percentage of neural tissue devoted to that ray. The effects can be summarized in that the majority of appendages, rays 2 through 9, were underrepresented in the central nervous system (i.e., S1, PrV, and SpVi) compared to the peripheral nervous system (i.e., Eimer's organs and myelinated afferents from each ray). Three rays - rays 1, 10 and 11 - did not fit this pattern. Rays 10 and 11 had a pattern opposite to rays 2 through 9 in that they were overrepresented in the central nervous system compared to the periphery. Finally, ray 1 was unlike all the rest. Ray 1 had the greatest percentage of neural tissue in the SpVi, and in descending order of proportion compared to the rest of the star, PrV, Eimer's organs, myelinated fibers from the ray, and S1 area (Fig. 4). Thus, SpVi differed from all other stations analyzed in that ray 1 was most overrepresented there.

Anatomy of Subnucleus Caudalis

The SpVc is a laminated structure that resembles the dorsal horn of the spinal cord. We identified a series of lamina including a thin substantia marginalis along the lateral edge (consistent with Rexed lamina I), a thicker horseshoe shaped substantia gelatinosa (consistent with Rexed laminae II and III), and an innermost substantia magnocellularis (consistent with Rexed lamina VI) (nomenclature follows (Olszewski, 1950)). The layers of the SpVc can be delimited on the basis of cell distributions visible in a Nissl-stained preparation, with the thin substantia marginalis characterized by 2-3 rows of sparse large

neurons, the substantia gelatinosa being densely packed with small cells, and the substantia magnocellularis composed of both small and large neurons that are less densely packed (Olszewski, 1950). The substantia gelatinosa and substantia magnocellularis can also be distinguished by the denser network of fibers present in the magnocellular layer compared to the gelatinosa layer (Torvik, 1956) (Fig. 5 A-D).

The organization of SpVc varied along the rostral-caudal axis (Fig. 6). We found that measuring the rostral-caudal location of a section was best done in our study by designating the most rostral section in which caudalis was present (the SpVi/SpVc border) as our zero point.

Subnucleus caudalis in star-nosed moles had prominent septa that segmented the middle laminae of the nucleus into 11 regions, visible in CO-processed sections (Fig. 1F). Ray septa were observed consistently across adjacent sections, beginning approximately 400 μ m caudal to the SpVi/SpVc border and continuing caudally for approximately 300 μ m. The septa for ray 11 were consistently faint in CO stains.

Approximately 600 μ m caudal to the SpVi/SpVc border, a distinct area with barrelette-like patches was found in the medial and dorsal part of the nucleus (Fig. 6B). Based on comparisons between the sections stained for Nissl substance, myelin and CO these barrelette-like patches appeared to be located in the substantia magnocellularis. Further caudally the star pattern in the substantia gelatinosa layer diminished until it was no longer present at 700 μ m from the SpVi/SpVc border. Juvenile animals displayed the same pattern as adults but were scaled in the rostral-caudal axis to match the smaller brainstem (Fig. 6C).

In the dorsal/ventral plane, the orientation of the star representation was the same as that seen in SpVi such that ray 11 was represented dorsomedially, ray 1 was represented ventromedially, and the intervening rays were represented in sequence between those two. As the recording electrode was advanced ventrally through the nucleus, the receptive fields reliably shifted from more ventral rays (e.g., ray 11) to more dorsal rays (e.g., 1). Ray-responsive units were found in both the gelatinosa (Fig. 7A) and the magnocellularis division (Fig. 7B). The data suggest that receptive fields might be larger in the gelatinosa layer than in the magnocellular layer, but the sample size of recording locations definitively isolated to specific laminae precludes more strict assessment of this hypothesis. Some lesions appeared in locations rostral to the most distinct septa.

It was not possible to determine the rostral-caudal organization of the rays' representation in SpVc by comparing the location of lesions to the corresponding receptive fields on the star. However, lesions in areas of SpVc responsive to vibrissae were clearly caudal to the star representation (Fig. 6A).

Size of receptive fields

Neurons in the PrV had the smallest receptive fields of the nuclei tested (Fig. 8). There was no statistical difference between the size of the receptive field in neurons in the SpVi and SpVc.

The mean receptive field size for neurons in PrV was 0.69 mm^2 (SD = 0.45, $n = 68$), for the SpVi was 1.98 mm^2 (SD = 0.41, $n = 28$), and for the SpVc was 1.79 mm^2 (SD = 0.96, $n = 62$). The size of the receptive fields was different between PrV and SpVi or SpVc (Kruskal-Wallis $p < 0.01$), reflecting smaller receptive fields in PrV than in SpVi (T-test with equal variances not assumed, $t(31.3) = -6.26$, $p < 0.01$) or SpVc (T-test with equal variances not assumed, $t(82.8) = -8.16$, $p < 0.01$). If all receptive fields on ray 11, the fovea, are removed from the analysis the statistical significance of the results is unchanged.

Discussion

We identified representations of the star in the interpolaris (SpVi) and caudalis (SpVc) subnuclei of the spinal trigeminal nucleus of the star-nosed mole. Subnucleus oralis (SpVo) lacked CO-segments corresponding to the receptor arrays of star-nosed moles, consistent with the absence of barrelettes in this subnucleus in rats and mice. For SpVi and SpVc, segmentation was visible in coronal sections processed for CO and these segments were matched to the rays of the nose through multiunit electrophysiological recordings. The representation of the mole's face in SpVi was broadly similar to that found in rats and mice. The anatomy of SpVc suggests the anterior part of the face is represented in the rostral part of the nucleus, and the posterior part of the face is represented more caudally (Fig. 9 H, K).

In addition to mapping the nuclei, we measured the volume of the ray representations in SpVi. The relatively small ray 11 had a large representation in SpVi. A large representation for ray 11 has also been observed in the PrV and the somatosensory cortex (Catania and Kaas, 1997; Catania et al., 2011). However, SpVi differed from the other somatosensory stations in that ray 1 also had a disproportionately large representation. Lastly, we found that the mean areas of multiunit receptive fields in SpVi and SpVc were larger than in PrV.

Anatomy of the Star

Initial patterning of the trigeminal nuclei was observed in the star-nosed mole as early as postnatal day 5. In 0-7 day-old moles the star appendages are folded back onto the snout (Fig. 1A) forming strips of sensory tissue parallel to the rostral-caudal body axis, with the tips of the rays most caudal on the animal and the bases most rostral. These strips are on the same rostral-caudal plane as whisker follicles. The rays become free at about one week of age (Catania, 2001), at which point the anatomy of the star is like that of an adult mole (Fig. 1 B). The mobile rays in adults can be in a plane perpendicular to the rostral-caudal body axis or swept forward so that the tips of the rays are more rostral than the bases.

Anatomy of Subnucleus Interpolaris

In the star-nosed mole, the glabrous skin of the nose dominates the map in caudal SpVi, and the mole's presumptive barrelettes are found in a small area dorsal to the star representation. As is the case for the barrelettes of rats and mice, the star pattern was only seen in the caudal part of SpVi. Different areas of the face are accentuated in moles and compared to rodents, so that in the mole the representation of the nose is large and the representation of the whiskers is small, but in mice and rats the reverse is true (Fig. 9 C-F). In moles, the large representation of the nose and the relatively small vibrissal representation are consistent

with the behavioral importance of the star and also with the large size of the star representation found in the neocortex and PrV (Catania and Kaas, 1995; Catania et al., 2011).

In moles the representation is inverted dorsoventrally so that the dorsal rays on the face are represented ventrally in the subnucleus, and the ventral receptors are represented dorsally in the subnucleus. The midline rays on the star are represented medially in the nucleus, and the lateral rays of the star are represented laterally in the nucleus.

The patterning along the medial-lateral axis of the nucleus is thus similar in rodents and star-nosed moles; in both animals the receptors nearest the midline are represented most medially, and those farther from the midline are represented more laterally. This interpretation is consistent for both juvenile moles, with the rays back, and adult moles with the rays detached. When the rays lay back on the snout, as when the brainstem patterning is first observed, then rays 1 and 11 are closer to the midline at the most anterior tip of the animal than the tips of lateral rays (eg., ray 5). This situation mimics the progression from high to low numbered whiskers in a mouse. When the rays are free from the snout in adults, the same progression would be from the midline rays toward the more lateral parts of the star. This overall topography is consistent with the clear map of the nose in primary somatosensory cortex in star-nosed moles and pigs (Catania and Kaas, 1995; Craner and Ray 1991). This organizational scheme is also consistent with that seen in the brainstem of other species including pigeons (Silver and Witkovsky, 1973), cats (Hayashi et al., 1984), and shrews (Catania et al., 2013).

Volume of ray representations in SpVi—The neural tissue devoted to each ray can be measured at many points from the periphery to the neocortex (Catania and Kaas, 1997; Catania et al., 2011). The anatomical parameters measured for the star to date include the number of Eimer's organs on each ray, the number of myelinated fibers innervating each ray, the volume of the ray representations in PrV, and the area of the ray representations in primary somatosensory cortex. This report adds the volume of ray representations in SpVi to that data set. The measurements in SpVi were limited to juvenile animals. The measurements were taken from animals at different developmental stages and the absolute volumes of the subnuclei increased with increasing age. As a result, data were analyzed as the percent of neural tissue devoted to each ray across the different cases.

In general, ray 11 monopolized an increasing percentage of the star representation at higher stations (Fig. 4). Ray 10 showed a more modest increase in proportional representation at higher stations, whereas the other rays showed a general decrease in proportional representation. The only exception to this trend was ray 1 in SpVi, which had a comparatively large representation.

The anatomical differences between the PrV and the SpVi is particularly interesting given that barrelettes in PrV and SpVi have similar relative sizes in rodents (Belford and Killackey, 1979; Ma, 1991). It is possible that the overrepresentation of rays 1 and 11 in SpVi, which are both medial in the nucleus, is due to a structural limitation in how areas can be mapped in medial SpVi. However, the fact that the most medial SpVi barrelettes in rats

and mice have the smallest cross-sectional area suggests this is not the case (Fig. 9C-D). The anatomical difference between the representations of the rays in the PrV and SpVi is consistent with specialization of these processing areas.

The PrV is usually considered the relay for touch with high-spatial acuity. It has been suggested that the SpVi maybe important in active, or generative, touch, (for review: Bosman et al., 2011; Diamond et al., 2008). If the SpVi has a special role in generative touch, then the large representations of rays 1 and 11 could be related to their special role in movement of the star. Ray 11 is the focus of ballistic reorienting movements of the star that reliably bring ray 11 into contact with a potential food item (Catania and Kaas, 1997). The movement of ray 1 is unique in that this ray often points forward while the rest of the star is flared back (Catania and Remple, 2004). Oriented this way, ray 1 is the first ray to contact a substrate. It is possible that the tactile information of first contact between ray 1 and a substrate could be useful in optimizing the force with which the rest of the star touches the ground. Given the speed of star movements, with 13 independent touches occurring within one second (Catania and Kaas, 1997), a sensorimotor loop mediating such optimization would need to be fast.

The brainstem tactile sensorimotor loop is an excitatory reflex arc in which deflection of a whisker can lead to a motor response with a short latency component of 5 to 10 ms (Nguyen and Kleinfeld, 2005)—fast enough to be involved in optimizing the force of a star touch. Nguyen and Kleinfeld, who studied this loop in rats, speculate that the trigeminal sensorimotor loop may be important for holding sensors against a surface and in controlling the force imparted on the sensors (2005). The same could be true in the star-nosed mole. This loop is likely mediated by direct projections from the trigeminal nuclei to the facial motor nucleus (Nguyen and Kleinfeld, 2005). Which subdivisions of the spinal trigeminal nucleus are involved is not known, but in rats both the SpVi and SpVc have direct projections to the facial nucleus (Hattox et al., 2002). It is possible that the large representations of ray 1 and 11 in SpVi are related to the trigeminal sensorimotor loop.

It is also possible that the representations of ray 1 and 11 SpVi are related to other aspects of star movement. It has been observed that during whisking in awake rats, inhibitory signals from the SpVi suppress neurons in the PrV (Furuta et al., 2008; Lee et al., 2008). This raises the possibility that movement-induced suppression by SpVi projections plays a role in selecting which of the inputs are relayed through the PrV and further along the lemniscal pathway. Actively touching materials with such a variety of physical properties likely places many further demands on the star-nosed mole somatosensory system. As part of a foraging excursion a star-nosed mole might burrow through mud, traverse rocks at the edge of the water, dive in, and then use its star to trap air bubbles as it locates invertebrates via underwater olfaction.

Regardless of SpVi's role in somatosensation, the difference in the star representation in the PrV and SpVi shows that the somatotopic maps in the PrV and the SpVi can develop to exaggerate different areas of the periphery, which suggests that the PrV and SpVi are anatomically specialized for different functions.

Anatomy of Caudalis

There is an inverted star representation in the rostral portion of subnucleus caudalis and a vibrissae representation in more caudal areas. The somatotopic organization of mole SpVc along the rostral-caudal axis is consistent with the organization of SpVc reported in other mammals, including humans (Dejerine, 1985; DaSilva et al., 2002), cats (Yokota and Nishikawa, 1980; Panneton and Burton, 1981; Shigenaga et al., 1986) and rats (Rustioni et al., 1971; Arvidsson, 1982; Jacquin et al., 1983). This organization of caudalis was nicknamed the onion-skin model in recognition of the way the concentric circles of innervation around the mouth mimic the anatomy of an onion (Dejerine, 1985). The representation of the star in SpVc is spread along the rostral-caudal axis such that no single 2-dimensional plane contains the whisker representation and all 11 rays. Instead, the map is contained within a 3-dimensional tube with the most anterior areas of the face represented in the most rostral part of the nucleus and more posterior elements of the face represented caudally in sequence. This is best demonstrated in this study by the star-responsive areas that are more rostral to whisker-responsive areas. Though we were unable to resolve shifts in receptive field locations on a single ray in the rostral-caudal axis for caudalis, we hypothesize that the base of each ray is represented rostrally within the nucleus, and the tip is represented more caudally. This organization is suggested by the progression from absent or faint septa rostrally in the nucleus to distinct septa more caudally. This pattern would be expected if the continuous sensory surface near the nostrils and the base of the rays was represented rostrally and the discontinuous surface at the tips of the rays was represented caudally.

It was difficult to resolve the receptive field shifts along a ray in this experiment because the microlesions we used to mark out rostral-caudal location were visible in at least 4 consecutive sections, which did not give us the resolution needed to map along the rostral-caudal axis. We did not attempt to reconstruct the volume of the ray representations in SpVc because we were not confident in the rostral boundary of the ray representations (the presumptive base representation). Thus, although the area of the representations of ray's 1 and 11 appear smallest in coronal cuts (Fig. 1F), additional studies will be required to investigate this question in detail.

SpVc is a laminated structure, consisting of three cell layers (Olszewski, 1950). The innermost layer, the magnocellular division, is the site of barrelettes in rodents (Ma, 1991). Other investigations have found that neurons in this layer can be induced to fire in anesthetized animals by lightly touching the face (Price et al., 1976; Hu et al., 1981; Amano et al., 1986). The middle layer, the substantia gelatinosa, does not have a visible whisker representation and is silent in many *in vivo* recordings that use gentle stimulation similar to the stimuli in this study (Price et al., 1976; Hu et al., 1981; Amano et al., 1986). Instead of processing light touch sensations, the substantia gelatinosa is thought to house interneurons that are critical to pain and temperature sensation (Davies and North, 2009).

Our results in the SpVc differ from work done in other animals in two ways. First, the star septa for the representation are in the substantia gelatinosa, not the substantia magnocellularis. The ray septa contain thick bundles of axons that course through the

substantia gelatinosa to the substantia magnocellularis. Such collaterals are seen in SpVc of rats and mice (Price et al., 1976; Ma, 1991) but the regular divisions of the substantia gelatinosa into segments that correspond to trigeminal anatomy is not previously reported. In rats a bundle of collateral axons tend to send their projections to just one barrelette-like cluster (Ma, 1991). Perhaps the 11 subdivisions observed in the star-nosed mole are the result of the afferents from the same ray grouping together. The absence of an obviously visible star pattern in the magnocellular layer of SpVc is noteworthy given the presence of the barrelette-like representation in that layer at more caudal levels. It is possible that a visible star representation would be found in the magnocellular layer by analyzing more cases, but that seems unlikely given the lack of any clear septa despite sectioning the nucleus at many angles and in many developmental stages.

The second distinctive finding was that light mechanical stimulation of the star was a sufficient stimulus for neuronal responses in the substantia gelatinosa. In other animals, such stimulation was usually not sufficient for activation in this layer (Price et al., 1976; Hu et al., 1981; Amano et al., 1986). Our findings in caudalis could reflect an adaptation of the mole as a light touch specialist and may relate to what has been seen as a de-emphasis of pain receptors in favor of touch receptors in the star (Gerhold et al., 2013).

Size of Receptive Fields

Star-nosed moles can use their stars to locate prey less than a millimeter in diameter (Catania and Kaas, 1997). Consistent with this ability, neurophysiological cortical recordings find receptive field sizes that average 0.71 mm^2 . These receptive fields of cortical neurons are among the smallest reported for representations of glabrous skin, including for the highest acuity areas of the primate hand (Sur et al., 1980; Pons et al., 1987; DiCarlo et al., 1998; Xerri et al., 1998; Vega-Bermudez and Johnson, 1999). Because these cortical responses must be transmitted from subcortical structures, we measured the sizes of multiunit receptive fields in SpVi and SpVc and compared these to receptive fields in PrV from a previous study. Although receptive field size can be affected by depth of anesthesia (Friedberg et al., 1999) the same procedure was used in all studies. We found that within the PrV receptive fields were 0.69 mm^2 , which is very similar to the size of receptive fields found in the cortex. In SpVi and SpVc the receptive fields were more than twice as large (though still extraordinarily small) (DiCarlo et al., 1998; Pons et al., 1987; Sur et al., 1980; Vega-Bermudez and Johnson, 1999; Xerri et al., 1998). This finding that the PrV had smaller receptive fields than the SpVi and SpVc is consistent with the PrV having a special role in high-acuity touch. It is also consistent with findings in rats that neurons in the PrV have receptive fields that encompass fewer whiskers than neurons in the SpVi (Timofeeva et al. 2004).

The segmentation of the SpVi and the SpVc is similar in many ways to the segmented organization observed for the whisker representation in rodent brainstem. The CO-segments that represent the nasal rays in moles are analogous to the barrelettes found in rodents and suggest that similar underlying developmental mechanisms are acting across diverse species and sensory systems to pattern the central nervous system. Despite these general similarities across species, the organization of star-nosed mole brainstem also reveals a number of

specializations that relate to the mole's particular sensory surface (the star) and behavior (tactile foveation). For example the different nasal rays are differentially proportioned (in contrast to rodent whiskers) at various stations and have differently sized receptive fields. These findings may ultimately provide further insights into the functions of the distinct trigeminal subnuclei and into how representations of important sensory surface develop at different CNS stations.

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Fig. 1.

The star and somatosensory brainstem of the star-nosed mole. **A:** A juvenile star-nosed mole, postnatal day 7, exhibiting nasal rays that have not yet detached from the snout. **B:** An adult star-nosed mole exhibits the mature morphology of the star. **C:** A diagram of half of a star with rays that are numbered following Catania and Kaas (1995) **D:** A representative horizontal section of the brainstem of a star-nosed mole processed for cytochrome oxidase (CO) with labeled subdivisions of the trigeminal nuclear complex. **E:** A representative coronal section processed for CO from a juvenile star-nosed mole (16.4 g) illustrating the star representation of the spinal trigeminal subnucleus interpolaris (SpVi). Black arrows point out barrette-like dark patches. **F:** A representative coronal section processed for cytochrome oxidase from an adult star-nosed mole illustrating the star representation in spinal trigeminal subnucleus caudalis (SpVc). Both micrographs display light septa separating 11 dark segments corresponding to each of the 11 rays. PrV = principal trigeminal nucleus, SpVo = spinal trigeminal nucleus oralis, D = dorsal, L = lateral. Scale bars= 1 mm

Fig. 2.

Electrophysiology of the spinal trigeminal subnucleus interpolaris (SpVi). **A:** A schematic of SpVi in an adult. The star representation is not visible in a cytochrome oxidase (CO)-stained adult SpVi. The pattern from a CO stained juvenile section is traced in dotted lines over the adult nucleus. **B:** Microlesions in vibrissae and star-responsive areas in SpVi. The shade of the arrows matches the receptive fields drawn in part C. The receptive field on the nose included both the whiskers and the hairy skin between the whiskers. Scale bar = 500 μ m. **C:** Left: The approximate locations of the lesions mapped onto the schematic of SpVi. Right: The locations of the receptive fields that correspond to the lesions in part B. Abbreviations: D = dorsal, L = lateral.

Fig. 3.

Reconstruction of the ray representations in the spinal trigeminal subnucleus interpolaris (SpVi). **A:** Consecutive coronal sections of SpVi processed for cytochrome oxidase from a 13.8 g juvenile mole. The number above each section is the distance in μm rostral to the SpVi/SpVc border, where the most rostral section with SpVc is set to zero. **B:** The 3-dimensional reconstruction of the ray representations in a variety of orientations and a key for the coloration of the reconstruction. **C:** Quantification of the volumes of the ray representations as measured by percent of star representation ((Volume of ray/volume of all rays) × 100). The representations of rays 1 and 11 were significantly larger than the other rays ($p < 0.01$). Error bars represent 95% confidence interval. **D:** A schematic of a horizontal section of the brainstem illustrating the extent of caudal SpVi from which sections in part B are depicted. Abbreviations: C = caudal, D = dorsal, L = lateral, M = medial, R = rostral, SpVc = Spinal trigeminal nucleus caudalis. Scale bars = 1 mm.

Fig. 4.

Percentage of tissue in the star pathway devoted to each ray, from the periphery to the cortex. The displayed measurements are the percentage of Eimer's organs on each ray (Catania and Kaas, 1997), the percentage of myelinated fibers devoted to each ray (Catania and Kaas, 1997), the percentage of PrV volume devoted to each ray representation (PrV; analyzed using coronal sections processed for cytochrome oxidase- CO) (Catania et al., 2011), the percentage of SpVi volume devoted to each ray representation (for the star pattern) (SpVi; analyzed using coronal sections processed for CO), and the percentage of primary somatosensory cortex devoted to each ray representation for the star pattern (analyzed using flattened cortex sections processed for CO)(Catania and Kaas, 1995). Within each ray grouping along the X-axis, the bars represent the more peripheral measurements on the left to the more central measurements to the right. Error bars represent 95% the confidence interval.

Fig. 5.

Laminae in the spinal trigeminal subnucleus caudalis (SpVc). **A:** A coronal section of the SpVc processed for cytochrome oxidase showing the septa dividing the nucleus into 11 darkly stained CO-segments. **B:** A coronal section stained for Nissl substance, showing the laminated structure of the SpVc. **C:** A coronal section stained for myelin and further illustrating laminar differentiation and fibers traversing the substantia gelatinosa (arrows). **D:** Schematic of the laminae and the septa marking the rays. Abbreviations: MG= substantia magnocellularis, MZ = substantia marginalis; SG= substantia gelatinosa; spV= spinal trigeminal tract. Scale bar = 500 μ m.

Fig. 6.

The transition from the star representation to the vibrissae representation in spinal trigeminal subnucleus caudalis (SpVc). **A:** Left column: Consecutive cytochrome oxidase (CO) processed sections in an adult. The number in the upper left of each photomicrograph is the distance caudal to the spinal trigeminal subnucleus interpolaris (SpVi)/SpVc border in μm . Sections 560-760 illustrate a lesion made along the entire electrode tract. Right column: Receptive fields on the skin on the face and the vibrissae that correspond with the lesion on the left. **B and C:** Left: Consecutive CO stained sections in SpVc in an adult and juvenile, respectively. Right: a schematic of the segmentation visible in the section with black lines representing ray septa and red circles representing barrelette-like CO-patches. **D:** Top: coloring scheme for schematics in B and C. Bottom: a schematic of a horizontal section of the brainstem, showing where along the rostrocaudal axis the sections in part A-C are located. Abbreviations: C = Caudal, D = dorsal, L = lateral. Scale bars for micrographs = 1 mm

Fig. 7. Microlesions in the spinal trigeminal nucleus caudalis (SpVc) and corresponding receptive fields. **A:** Sections with lesions in the substantia gelatinosa layer. **B:** Sections with lesions in the substantia magnocellularis layer. Abbreviations: D = dorsal, L = lateral Scale bar for micrographs = 500 μm.

Fig. 8.

Size of receptive fields in the principle sensory nucleus (PrV), spinal trigeminal subnucleus interpolaris (SpVi) and spinal trigeminal subnucleus caudalis (SpVc). **A:** Graph of the average size of the multiunit receptive fields recorded in the PrV, SpVi and SpVc in dark grey, grey and light grey, respectively. Receptive fields in PrV are smaller than in the other two areas ($p < 0.01$). Error bars represent 95% confidence interval. In PrV $n = 68$, in SpVi $n = 28$ In SpVc $n = 62$. **B:** Schematic of half of a star with the size of the receptive fields displayed to scale.. Scale bar = 1 mm

Fig. 9.

A comparison between peripheral sensory surfaces and corresponding brainstem representations (subnuclei interpolaris (SpVi) and caudalis (SpVc)) in rats and star-nosed moles. All sections in this figure are in the coronal plane and stained for cytochrome oxidase. **A:** A schematic of the mystacial vibrissae of a rat and **B:** A schematic of the star, mystacial, and mandibular vibrissae of a star-nosed mole. **C:** A section of SpVi from a juvenile rat. **D:** A schematic of C. **E:** A section of SpVi from a juvenile star-nosed mole. **F:** A schematic of E. **G** and **H:** Sections of the SpVc from a juvenile rat and star-nosed mole, respectively. In each pair the section on the right is more rostral in the nucleus than the section on the left, showing how the pattern changes along rostral-caudal axis. **I** and **J:** Spaced, schematized coronal sections of SpVc in rats and star-nosed moles illustrating the rostrocaudal organization of the nucleus. High-numbered whiskers in rats and the base of the rays in moles are more rostral in the nucleus. Lower-numbered whiskers in rats and all mystacial vibrissae in moles are more caudal. The rostrocaudal scale is the approximate distance caudal from obex, which was selected in this diagram to match the metrics in Arvidsson (1982). **I** is modified from in Arvidsson (1982) Fig. 6. The insert in **J** is a drawing of a horizontal section of the brainstem to give the approximate rostrocaudal location of the diagram.