

# Somatotopic Organization of Perioral Musculature Innervation within the Pig Facial Motor Nucleus

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## Key Words

Somatotopy · Innervation · Facial nucleus · Perioral muscles · Orbicularis oris · Buccinator · Mammals

## Abstract

The orbicularis oris and buccinator muscles of mammals form an important subset of the facial musculature, the perioral muscles. In many taxa, these muscles form a robust muscular hydrostat capable of highly manipulative fine motor movements, likely accompanied by a specialized pattern of innervation. We conducted a retrograde nerve-tracing study of cranial nerve (CN) VII in pigs (*Sus scrofa*) to: (1) map the motor neuron pool distributions of the superior and inferior orbicularis oris, and the buccinator, to test the hypothesis that perioral muscle motor neuron pools exhibit a somatotopic organization within the facial motor nucleus; and (2) test the hypothesis that portions of the superior orbicularis oris (SOO) motor neuron pool also exhibit a somatotopic organization, reflecting a potential compartmentalization of function of the rostral, middle, and caudal segments of this muscle. Cresyl violet histological staining showed that the pig facial motor nucleus was comprised of 7 well-defined subnuclei. Neuroanatomical tracers injected into these perioral muscles transported to the motor neuron

pools of the lateral 4 of the 7 subnuclei of the facial motor nucleus. The motor neuron pools of the perioral muscles were generally segregated from motoneurons innervating other facial muscles of the rostrum. However, motor neuron pools were not confined to single nuclei but instead spanned across 3–4 subnuclei. Perioral muscle motor neuron pools overlapped but were organized somatotopically. Motor neuron pools of portions of the SOO overlapped greatly with each other but exhibited a crude somatotopy within the SOO motor neuron pool. The large and somatotopically organized SOO motor neuron pool in pigs suggests that the upper lip might be more richly innervated than the other perioral muscles and functionally divided.

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## Introduction

The lips and cheeks of mammals are comprised primarily of the orbicularis oris and buccinator muscles, respectively, and are a significant subset of the facial muscle complex. These perioral muscles are important for food acquisition, food transport, mastication, vocalization, speech production, as well as facial expression in some taxa. Neuroanatomical tract-tracing studies have

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demonstrated that motor neuron pools of mammalian facial muscles exhibit a somatotopic organization within the facial motor nucleus [e.g., Van Gehuchten, 1906; Yagita, 1910; Papez, 1927; Vrra-Jensen, 1942; Szentágothai, 1948; Courville, 1966; Dom et al., 1973; Martin and Lodge, 1977; Provis, 1977; Radpour, 1977; Kume et al., 1978; Radpour and Gacek, 1980; Ashwell, 1982; Dom, 1982; Watson et al., 1982; Hinrichsen and Watson, 1984; Komiyama et al., 1984; Friauf and Herbert, 1985; Uemura-Suma et al., 1986; Baisden et al., 1987; Satoda et al., 1987, 1988; Klein et al., 1990; Welt and Abbs, 1990; Tsai et al., 1993; Horta-Júnior et al., 2004]. Although a generalized somatotopic organization of the facial nucleus has been identified for most species investigated, many important species-specific differences exist [e.g., Satoda et al., 1987; Welt and Abbs, 1990; Tsai et al., 1993]. Facial subnuclear organization, such as number of subnuclei, consistency of subnuclear boundaries, and size and distribution of motor neuron pools varies, reflecting differences in functional importance. For example, the pinnae of the Egyptian Rousette bat [*Rousettus aegyptiacus*; Friauf and Herbert, 1985], dog [*Canis familiaris*; Vrra-Jensen, 1942; Courville, 1966], and cat [*Felis domestica*; Courville, 1966; Kume et al., 1978; Populin and Yin, 1995] are mobile and integral for localizing sound. Such mobility of the pinnae is an important component of the sensory ecology of these taxa [Schaefer et al., 1971; Siegmund and Santibañez-H, 1981, 1982]. Similarly, the motor neuron pools innervating the musculature of the pinnae in these taxa are concomitantly large and well represented relative to the motor neuron pools of other facial muscles, and relative to musculature of other taxa in which pinnae are not mobile. In addition, taxa that possess well-developed and mobile vibrissae also exhibit an expanded representation in their lateral facial motor nuclei [Huber, 1930a, b; Ashwell, 1982; Watson et al., 1982; Komiyama et al., 1984; Klein and Rhoades, 1985; Semba and Egger, 1986]. Similar specializations have been well documented for sensory systems; such neural compartmentalization is presumed to enhance the processing of sensory information [e.g., Woolsey and Van der Loos, 1970; Welker, 1971; Woolsey et al., 1975; Van der Loos, 1976; Johnson, 1990; Pokay, 1991; Catania and Kaas, 1995, 1997].

Despite the large literature on the mammalian facial motor nucleus, surprisingly less is known regarding the motor neuron pool distribution of individual perioral muscles within the facial motor nucleus. Neuroanatomical tract-tracing studies of facial muscles have either not included perioral muscles as part of their investigation, have grouped them within facial muscles, or have referred

to them as a generalized bucco-labial group. This is unfortunate because of the potential functional importance of the orbicular oris and buccinator for food acquisition and transport. The few studies that have included perioral muscles as a whole group demonstrate that their motor neuron pools reside in the lateral portion of the facial motor nucleus [Radbours, 1977; Kume et al., 1978; Uemura-Suma et al., 1986; Welt and Abbs, 1990; Horta-Júnior et al., 2004]. The method of food acquisition varies among mammals. Perioral and associated facial muscles are evolutionarily labile structures that can be modified by natural selection for specialized food acquisition and transport [Huber, 1930a, b; Herring, 1972]. Often the lips and cheeks of herbivores are elaborated in form [Getty, 1975; Hofmann, 1989; Frey and Hofmann, 1996, 1997; Clifford and Witmer, 2004] and exhibit a prehensile function; such structures can be subjected to extreme modification, as demonstrated by elephants [Boas and Paulli, 1908], sirenians [Marshall et al., 1998a, b, 2003], and tapirs [Witmer et al., 1999]. However, the patterns of facial muscle innervation in large herbivores remain largely unexplored. In contrast to herbivores, carnivores generally have small, simple lips and cheeks that are not prehensile. This is especially true for cats [Reighard and Jennings, 1935], which are obligate carnivores and possess specializations for a carnivorous life [Eisenberg, 1981, p. 127]. The size and organization of the portion of the facial motor nucleus that innervates these perioral muscles reflect their behavioral use and functional importance [Huber, 1930a, b; Radpour, 1977; Kume et al., 1978; Uemura-Suma et al., 1986]. Perioral muscles are also interesting in that they lack bony origins and insertions, and their fibers intermingle with each other. Therefore, perioral muscles are considered to form a muscular hydrostatic organ [Kier and Smith, 1985]. Movement is highly varied and complex relative to the more constrained movement of lever-based musculature. Electromyographic studies of human perioral muscles demonstrated that during contraction, their muscle fibers act in combinations involving both constrictors and dilators [Cacou et al., 1996], supporting the hypothesis that perioral muscles function as a muscular hydrostat.

Pigs (*Sus scrofa*) provide a good model for the investigation of perioral muscle innervation due to their long rostrum, anatomically interesting and well developed perioral muscles [Nickolai, 1953; Herring, 1972], and feeding behavior. The muscle fibers of both the superior orbicularis oris (SOO) and inferior orbicularis oris (IOO) intermingle with those of the buccinator (BUCC), and it is likely that the caudal portions of the SOO and IOO share sim-

ilar intraoral food transport functions with the BUCC. The rostral components of the SOO and IOO, however, function in food acquisition. Such division of muscle function is likely reflected in its innervation and motor neuron pool distribution.

The objectives of this investigation were to: (1) map the motor neuron pool distributions of the superior and inferior orbicularis oris, and the buccinator, to test the hypothesis that perioral muscle motor neuron pools exhibit a somatotopic organization; and (2) to test the hypothesis that portions of the superior orbicularis oris (SOO) motor neuron pool also exhibit a somatotopic organization, reflecting a potential compartmentalization of function of the rostral, middle, and caudal segments of this muscle.

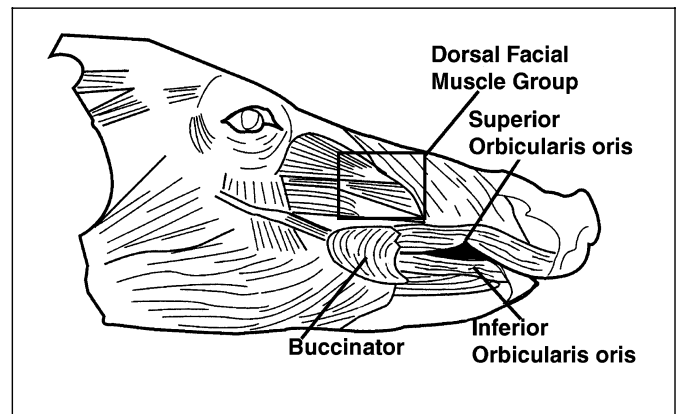
## Materials and Methods

### Subjects

A total of eight, 6–8 week-old pigs, weighing 9–15 kg, were used in this retrograde neuroanatomical tracing investigation. All procedures were approved by and performed under guidelines established by the University of Washington Institutional Animal Care and Use Committee.

### Injection of Neuroanatomical Tracers

Fluorescent retrograde neuroanatomical tracers were injected into the SOO, IOO, and BUCC of halothane anesthetized pigs using Hamilton syringes (figs. 1, 2). Adequate anesthesia depth was assured by frequent monitoring of pupil size and breathing rate. The method of neuroanatomical tracer injection was chosen due to its more precise representation of each muscle relative to nerve transection studies within the facial motor nucleus, and its relatively non-invasive nature [Hinrichsen and Watson, 1984; Welt and Abbs, 1990]. Neuroanatomical tracers injected into perioral muscles transported to the ipsilateral facial nucleus exclusively. Therefore, each subject was used in two separate neuroanatomical tracing experiments, thereby reducing the number of subjects needed ( $n = 16$  nuclei: 8 perioral, 6 SOO, and 2 non-injected controls; table 1). FluoroGold (FG; Fluorochrome, Inc.), FluoroRuby (FR), FluoroEmerald (FE; Molecular Probes, Inc.) and Fast Blue (FB; Sigma-Aldrich, Inc.) were used with varying success; one neuroanatomical tracer was used in each location over the course of the perioral muscle study (fig. 4). The SOO and IOO were each injected at 3 locations (rostral, middle, and caudal) along their length (fig. 2). The BUCC was injected at 5 locations throughout the muscle body (fig. 2). Each muscle was injected with a total of 100  $\mu$ l of a single fluorescent tracer (FG, FR, FE, or FB). All retrograde tracers were dissolved in 2% DMSO to facilitate tracer uptake. FluoroGold, FR, and FE were used in a 10% solution and FB was used in a 2.5% solution [Akintunde and Buxton, 1992]. Due to differences in transport of the four neuroanatomical tracers, labeled neurons were not quantified, only their distributions were mapped. On the right side of three pigs (283, 285, and 289) the rostrum facial muscles dorsal to the perioral muscles, here termed the Dorsal Facial Muscle Group (DFMG), were also



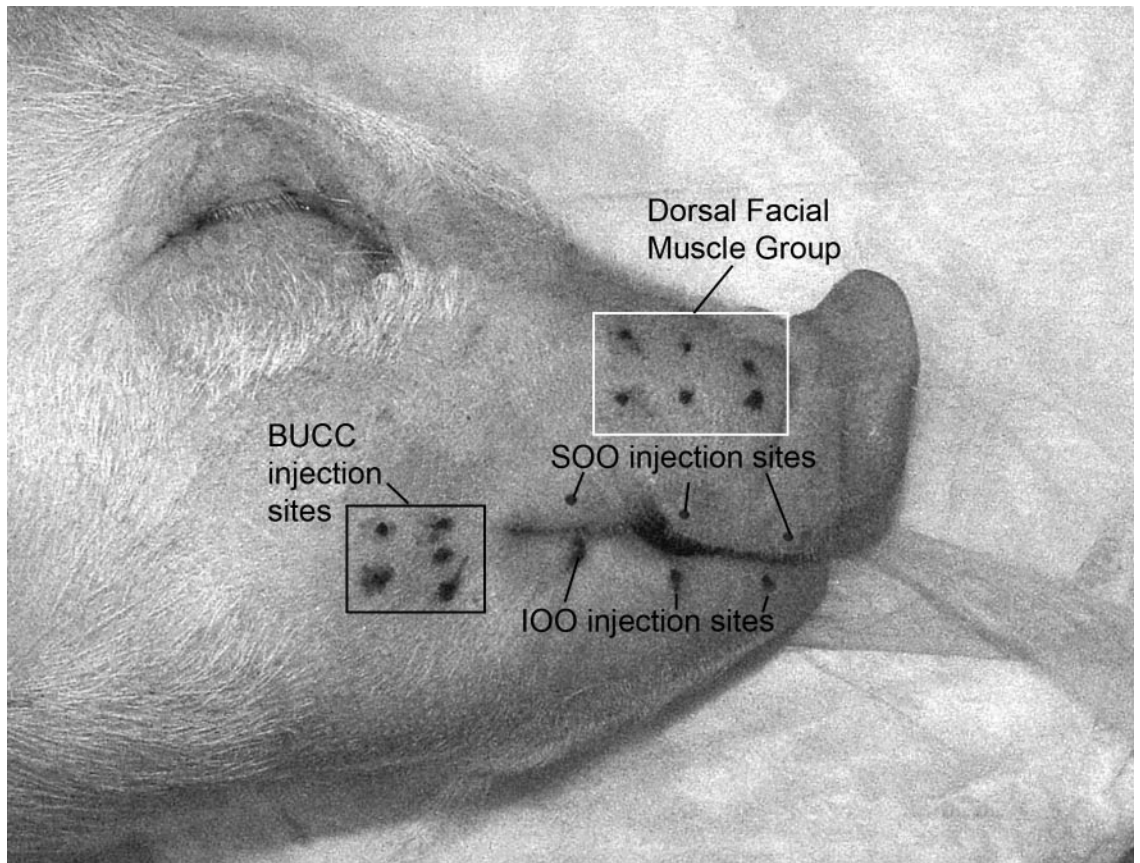
**Fig. 1.** Perioral and facial muscles of the pig rostrum [modified from Herring, 1972]. Note the rostroventral location of the perioral muscles relative to the DFMG. DFMG = nasolabialis, dilator naris, and depressor and levator rostri.

**Table 1.** Experimental design

Pig ID number	Sex	Muscles injected	
		left side	right side
267	M	Perioral (SOO, IOO, and BUCC)	Control (no injection)
268	M	Perioral	Control
282	F	SOO	SOO
283	F	Perioral	Perioral and DFMG
284	M	SOO	SOO
285	M	Perioral	Perioral and DFMG
289	M	SOO	Perioral and DFMG
290	M	SOO	Perioral

injected with fluorescent tracers. These muscles (nasolabialis, dilator naris, and depressor and levator rostri) were injected as a group in 6 locations (figs. 1, 2), with a total of 100  $\mu$ l, to map the location of their combined motor neuron pool distribution within the facial nucleus, and to determine the degree of overlap with those of the perioral muscles. In pigs 283 and 285, the SOO, IOO, and BUCC were injected on the left-side, whereas the SOO, IOO, BUCC, and DFMG were injected on the right-side which allowed direct within subject comparison of the motor neuron pool distribution of the DFMG to those of the perioral muscles. In pig 289, the right side SOO, IOO, BUCC, and DFMG were labeled; only the SOO was labeled on the left side. All combinations of neuroanatomical tracer injections are summarized in table 1.

To test the hypothesis that portions of the SOO might also exhibit a somatotopic organization the SOO was injected with 3 fluorescent tracers (FG, FR, and FE) bilaterally in 2 pigs and unilaterally in 2 pigs. Each tracer was injected in one of 3 locations (rostral, middle,



**Fig. 2.** Injection sites. The SOO and IOO were injected in 3 locations, rostral, middle, and caudal. The BUCC was injected in 5 locations throughout the muscle body. The DFMG was injected as a group in 6 locations.

and caudal). Each location received 50  $\mu$ l of a neuroanatomical tracer; each neuroanatomical tracer was used in each SOO location over the course of the study.

#### *Tissue Processing*

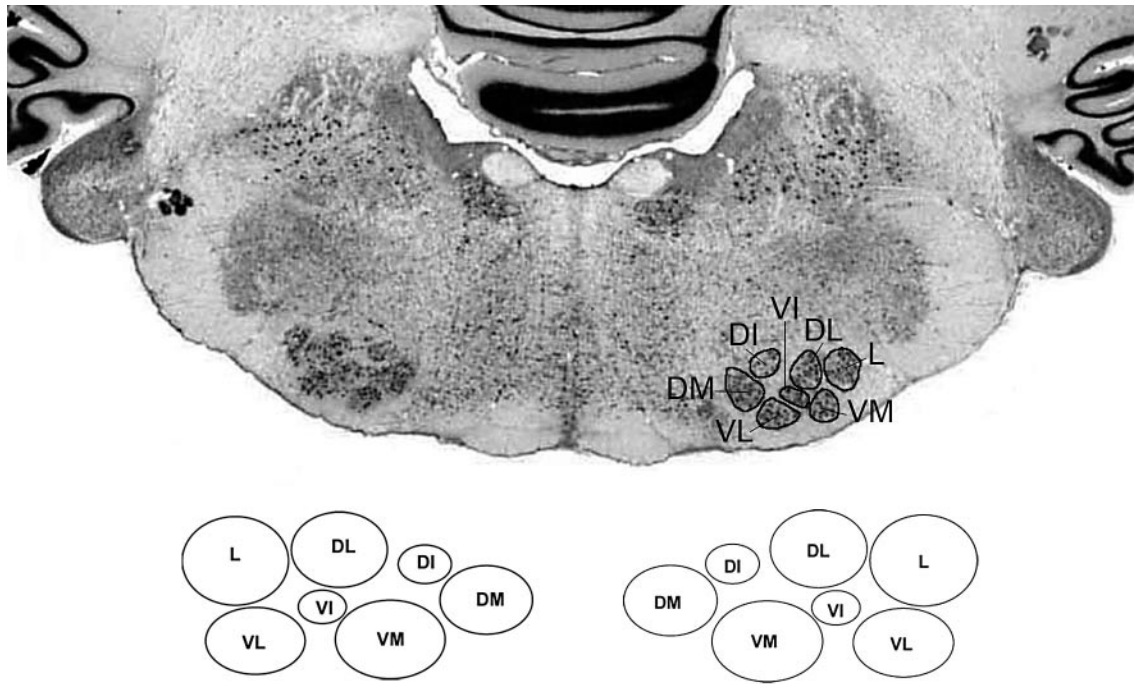
Pigs survived for 7 days, and then were sacrificed under halothane anesthesia by cardiac perfusion of 2–3 l of 0.9% buffered saline and heparin followed by 2–3 l of a buffered 4% paraformaldehyde. The long survival time was a necessity due to the long transportation distance from the perioral muscles to the brainstem in pigs. Brainstems were sectioned in the coronal plane at 40  $\mu$ m on a vibratome. Alternate sections were stained with cresyl violet for anatomical landmarks and subnuclear organization. Unstained sections were incubated for 15–45 min in a solution of 0.1% sodium borohydride to decrease background autofluorescence [Clancy and Cauller, 1998]. Incubation times of 40–45 min produced the best results for pig brainstem without marked tissue disruption. All slides were coverslipped with DPX medium (Fluka, Inc.) to decrease tracer bleaching. Images of thionin stained, coronally sectioned pig brainstem from the Wisconsin Comparative Brain Collection were used as a reference for anatomical landmarks and subnuclear organization [Welker et al., 1998].

#### *Injection Sites*

After sacrifice, the entire perioral region (injected muscles and skin) was carefully dissected, histologically processed in paraffin, and sectioned longitudinally at 250–300  $\mu$ m. Whole mount sections were examined with an epifluorescent microscope to confirm the location and diffusion of neuroanatomical tracer through soft tissue. Neuroanatomical tracer spread was confined to each target muscle within 1–2 cm of the injection site; no spread to adjacent muscles was observed.

#### *Motor Neuron Pool Mapping*

Labeled neurons were located using a Nikon E400 epifluorescent microscope fitted with a digital image analysis system (Diagnostic Instruments, Inc.). All labeled neurons were viewed with multiple optical filters to determine if they were double-labeled. Locations of labeled neurons were mapped by hand onto images of cresyl violet stained sections of the facial motor nucleus using anatomical landmarks to characterize the boundaries of the motor neuron pool distributions. Because no rostrocaudal somatotopy was found, labeled neurons from each facial motor nucleus were collapsed rostrocaudally and mapped onto a single representative image to represent the boundaries of perioral muscle motor neuron pools.



**Fig. 3.** Facial nucleus organization. Representative thionin-stained section through the pig motor facial nucleus. Seven subnuclei are present, lateral (L), dorsolateral (DL), ventrolateral (VL), dorsointermediate (DI), ventrointermediate (VI), dorsomedial (DM), and ventromedial (VM). Polygons and labels define each subnucleus on the right side of the stained section. In addition, a labeled schematic is depicted below each facial motor nucleus. Images provided by the Comparative Mammalian Brain Collection [Welker et al., 1998].

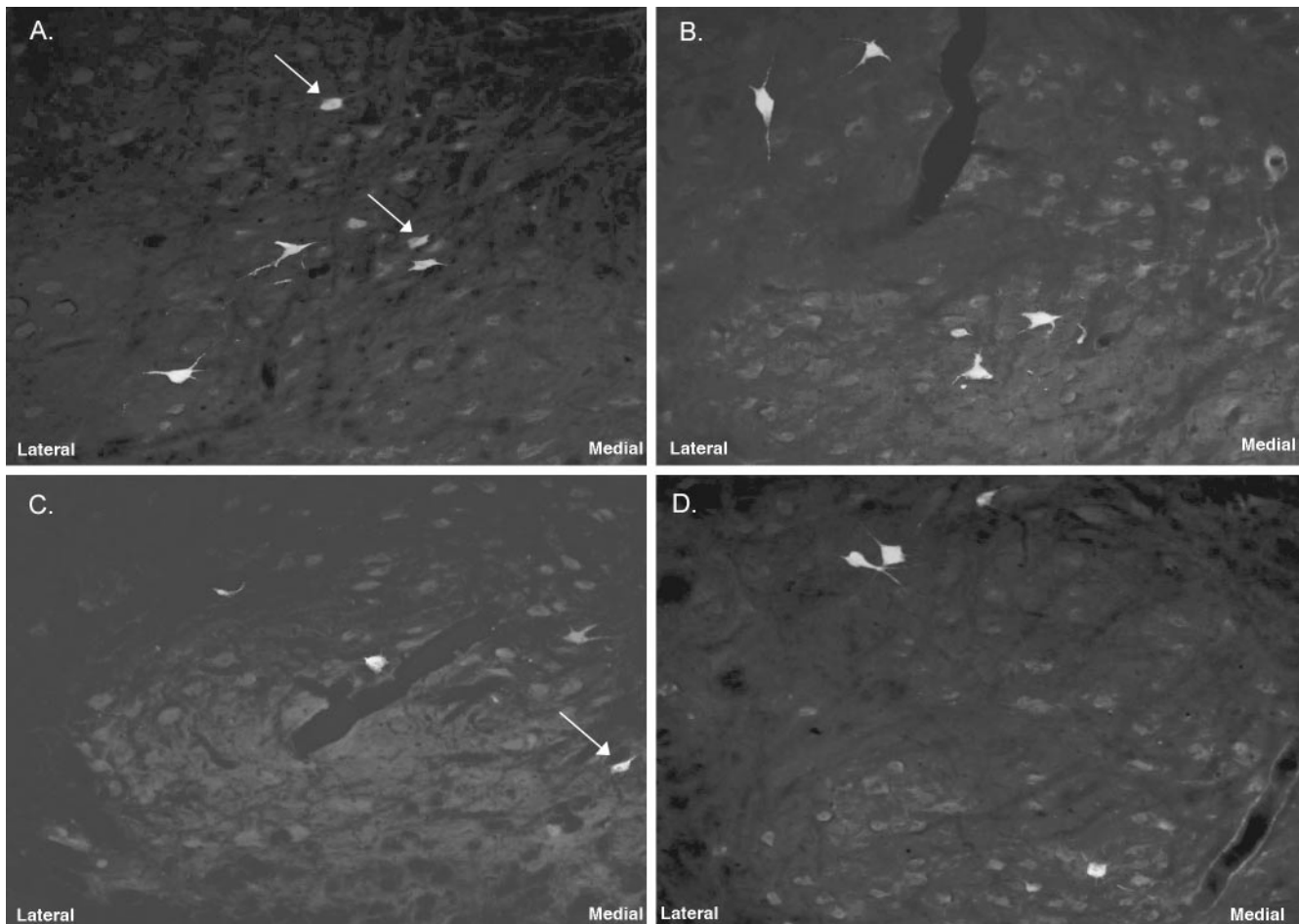
## Results

### *Pig Facial Motor Nucleus*

The pig facial nucleus was located in the ventrolateral pontine tegmentum, between the cranial and middle cerebellar peduncles, and was comprised of 7 discrete subnuclei (fig. 3). The facial nuclei were easily observed as a dense region of darkly stained large neurons organized into discrete subnuclei, each surrounded by cell sparse regions or small granular cells (fig. 3). Subnuclei were organized as rostrocaudal columns within the facial motor nucleus. These subnuclei were named according to their anatomical locations and following the nomenclature of other taxa described in the literature as follows: lateral (L), dorsolateral (DL), ventrolateral (VL), dorsointermediate (DI), ventrointermediate (VI), dorsomedial (DM), and ventromedial (VM). The pig facial motor nucleus is unusual among mammals for which data are available in that subnuclear boundaries are relatively distinct and well delineated throughout their rostrocaudal extent.

### *Pig Facial Nucleus Motor Neuron Pool Organization*

Labeling was never seen in uninjected contralateral control sites; neuroanatomical tracers transported to the ipsilateral facial nucleus only. Pools of motoneurons were labeled from each muscle injected. No multiple labeling of neurons occurred (fig. 4). Motor neuron pools innervating perioral muscles exhibited a somatotopic organization with the SOO motor neuron pool located dorsolaterally, the IOO ventrolaterally, and the BUCC intermediate and medial to the SOO and IOO, within the facial motor nucleus (figs. 5 and 7; table 2). Each motor neuron pool ran essentially the full length of the nucleus; no rostrocaudal somatotopy was observed. All motor neuron pools, particularly the SOO motor neuron pool, partially overlapped with each other, and were distributed over 3–4 subnuclei (figs. 5 and 7; table 2). Motor neuron pools were not confined to the cytoarchitectural boundaries of subnuclei. Neuroanatomical tracers injected into the SOO labeled neurons primarily in the L subnucleus, but also in the lateral portions of the DL and VI nuclei and the dorsal portion of the VL subnuclei. Neuroanatomical tracers

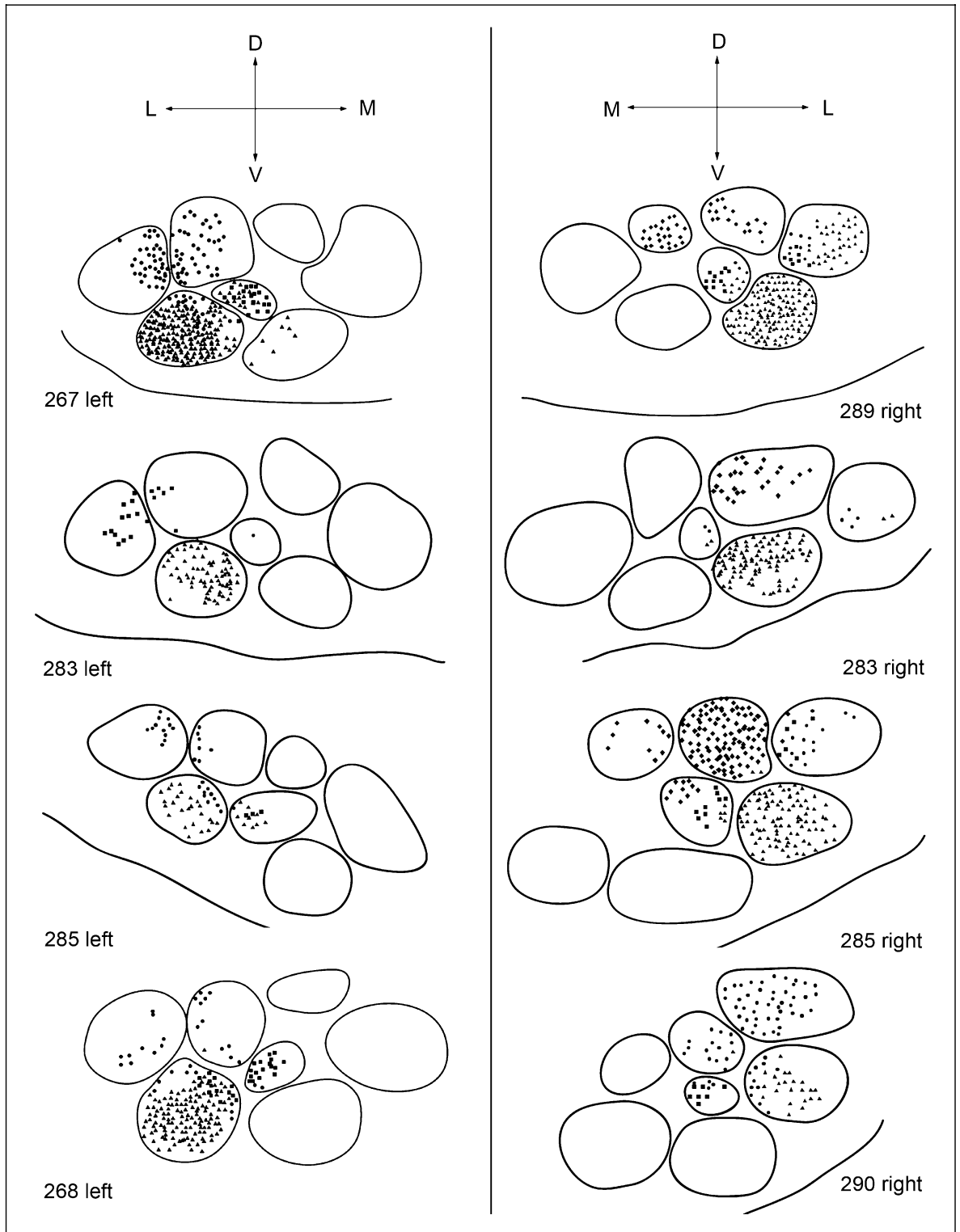


**Fig. 4.** Examples of neuroanatomical tracer retrograde transport to the pig facial motor nucleus neurons labeled with FluoroRuby, Fast Blue, and FluoroEmerald represent injections of neuroanatomical tracers into the SOO, IOO, and BUCC, respectively. **A** Neurons labeled with Fast Blue (indicated by arrows) and FluoroEmerald. **B** Neurons labeled with FluoroRuby and FluoroEmerald. **C** Neurons labeled with Fast Blue (indicated by arrow), FluoroEmerald, and FluoroRuby. **D** Neurons labeled with FluoroRuby and FluoroEmerald. Not all muscles are represented in a single section.

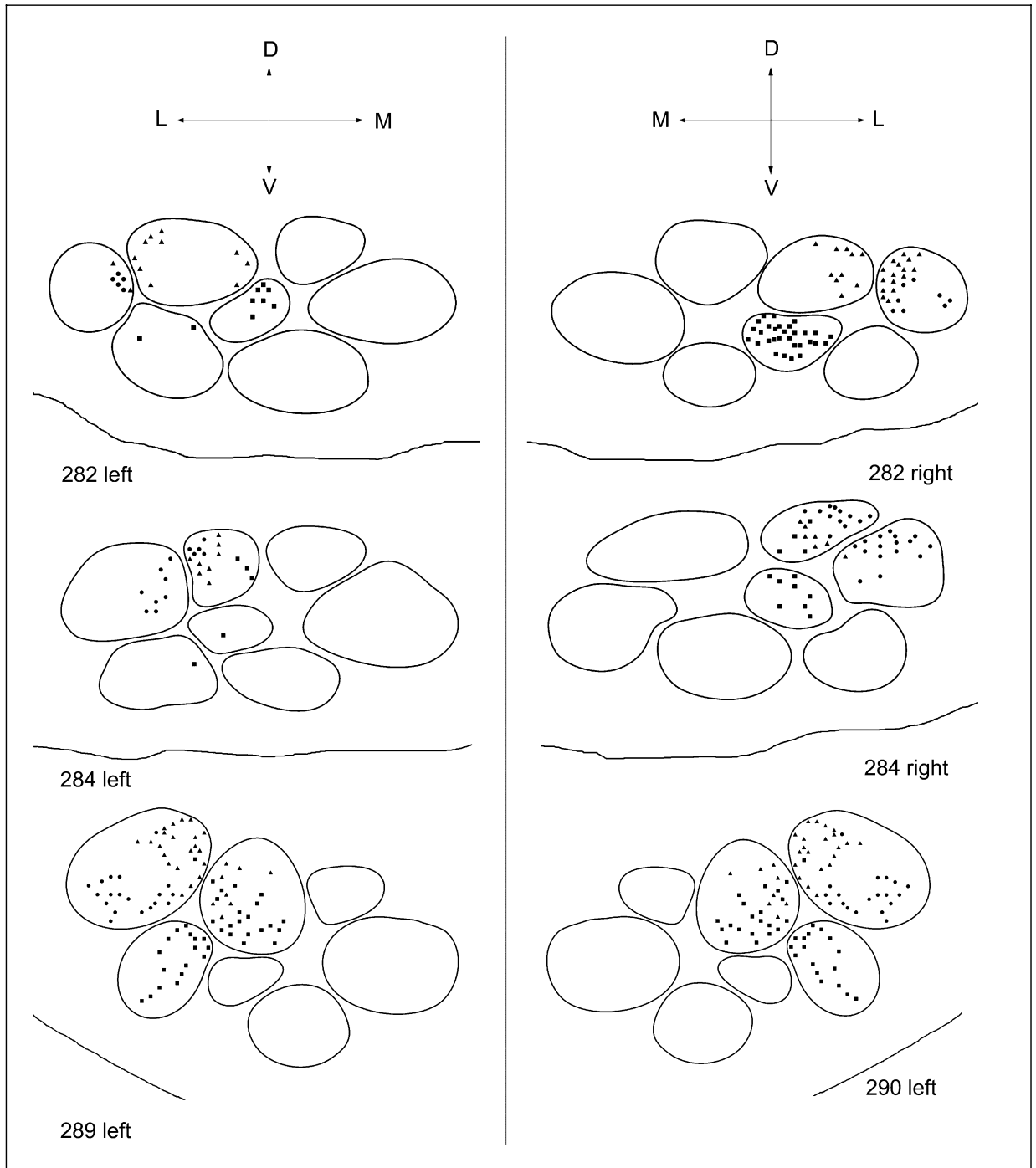
injected into the IOO labeled neurons primarily in the VL subnucleus, but also in the ventral L and DL subnuclei and the ventral portion of the DL subnuclei. Neuroanatomical tracers injected into the BUCC primarily labeled neurons in the VI subnucleus, but also in the medial portion of the VL and L subnuclei. Neuroanatomical tracers injected into the DFMG labeled motoneurons primarily within the DL subnucleus, but also in the medial portion of the L subnucleus and the lateral portion of the DI subnucleus. In pig 283, a few labeled DFMG neurons were also seen in the dorsal portion of the subnucleus VI (figs. 5 and 7).

**Table 2.** Motor neuron pools innervating perioral muscles

Muscles injected	Subnuclei labeled
SOO	L, DL, VL, and VI
IOO	VL, VI, and L
BUCC	VL, VI, and L
DFMG	DL, L, and DI

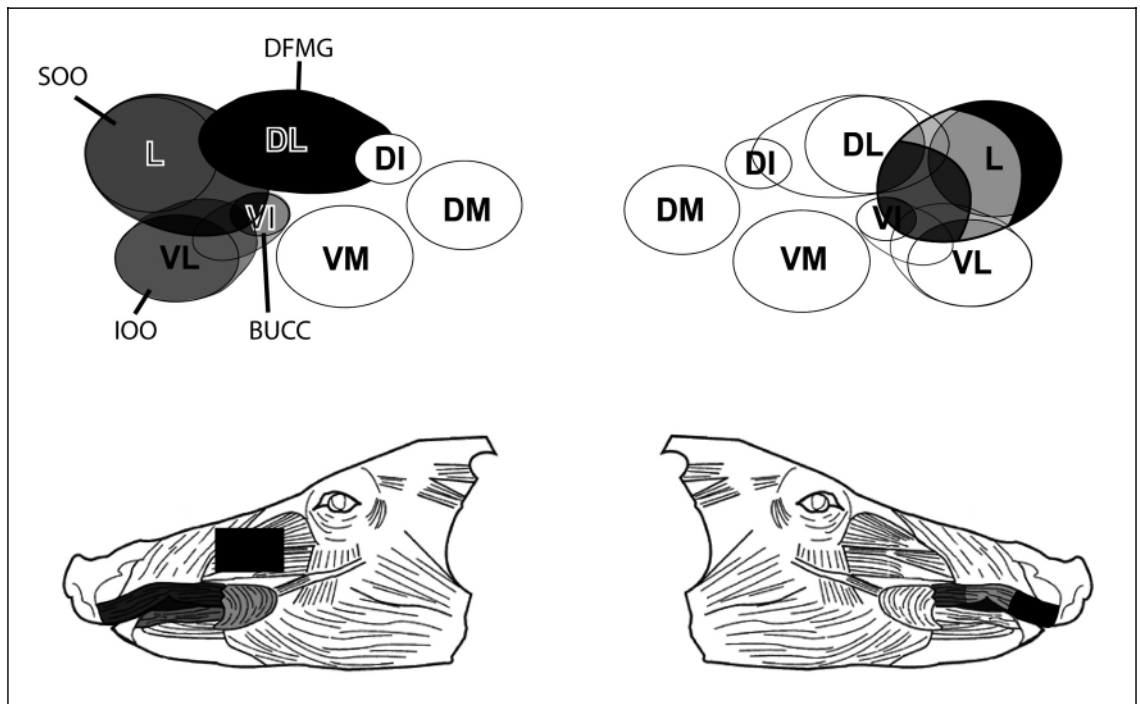


**Fig. 5.** Perioral muscle motor neuron pool distributions. Each facial motor nucleus from each subject (right or left); the boundaries of each subnucleus have been encircled by a polygon. The crossbars at the top of each column designate dorsal (D), ventral (V), medial (M), and lateral (L) orientation for each facial nucleus depicted below. Symbols designate motor neuron pools for each perioral muscle injected: SOO = ●, IOO = ▲, BUCC = ■, DFMG = ◆.



**Fig. 6.** SOO motor neuron pool distributions. Each facial motor nucleus from each subject; the boundaries of each subnucleus have been encircled by a polygon. The crossbars at the top of each column designate dorsal (D), ventral (V), medial (M), and lateral (L) orientation for each facial nucleus depicted below. Symbols designate motor neuron pools for each portion of the SOO injected: rostral = ●, middle = ▲, caudal = ■. The facial nucleus for pig 290 left has been reversed and placed in the right-side column for convenience.





**Fig. 7.** Summary of perioral and SOO motor neuron pool distributions within the pig facial motor nucleus. Top: The motor neuron pool distribution of each perioral muscle is mapped over the boundaries of the subnuclei of the facial motor nucleus (left) to depict the somatotopic organization. Similarly the motor neuron pool distribution of the rostral, middle, and caudal portions of the SOO are mapped over the boundaries of the lateral subnuclei of the facial motor nucleus (right) to depict its crude somatotopic organization. Bottom: Schematics of the location of facial muscle injections are arranged to correspond with the motor neuron pool somatotopic organization of the perioral muscles (left) and the SOO (right) within the facial motor nucleus.

**Table 3.** Motor neuron pools innervating the SOO

Portion of SOO injected	Subnuclei labeled
Rostral	L and DL
Middle	Medial portion of L and lateral portion of DL
Caudal	DL and VL

#### *SOO Nucleus Motor Neuron Pool Organization*

A more detailed study of the SOO motor neuron pool revealed a crude lateral-to-medial somatotopy, although not as clear as for the perioral muscles as a whole (figs. 6 and 7; table 3). Neuroanatomical tracers injected in the rostral SOO labeled motoneurons primarily in the L subnucleus, but also in the lateral portion of the DL subnucleus. Neuroanatomical tracers injected into the middle

SOO primarily labeled motoneurons in the medial portion of L subnucleus and the lateral portion of the DL subnucleus, and were usually medial to those neurons labeled by injections in the rostral SOO. Neuroanatomical tracers injected into the caudal SOO labeled motoneurons primarily in the DL and VL subnuclei, usually medial to those motoneurons labeled by injections in the middle SOO. These three subdivisions of the SOO motor neuron pool overlapped greatly (figs. 6 and 7). Each distinctly colored neuroanatomical tracer was injected into each portion (rostral, middle, and caudal) of the SOO to control for neuroanatomical tracer specific transport differences. No differences in rostrocaudal motor neuron pool distribution of the SOO were noted.

## Discussion

Compared to other mammals for which data are available, the cytoarchitectural subnuclear boundaries of the pig facial motor nucleus were well defined throughout their rostrocaudal limit and the number of subnuclei (7) was relatively high. These data do not support the concept that the facial motor nuclei of all mammals possess incomplete cytoarchitectural boundaries of subnuclei [Welt and Abbs, 1990]. However, the functional importance of these boundaries is not known, especially in light of the fact that motor neuron pools of individual muscles cross these boundaries. Numerous subdivisions of the mammalian facial motor nucleus are common. However, there is much variation reported among different species and within species. For example, the number of subnuclei in cats is reported to be between 2 and 6 [Vraa-Jensen, 1942; Radpour, 1977], *Macaca* between 4 and 6 [Jenny and Saper, 1987; Satoda et al., 1987; Welt and Abbs, 1990], rats (*Rattus rattus*) from 4 [Papez, 1927; Friauf and Herbert, 1985] to 5 [Martin and Lodge, 1977; Watson et al., 1982; Semba and Egger, 1986]; mice (*Mus musculus*) 6 [Ashwell, 1982; Komiyama et al., 1984] and guinea pigs (*Cavia porcellus*) 4 or 6 [Papez, 1927; Uemura-Sumi et al., 1986].

In general, the motor neuron pools innervating all the facial muscles of the rostrum (DFMG) in pigs were relatively large, located in the lateral half of the facial nucleus, and were oriented as rostrocaudal columns of motoneurons. The perioral muscle motor neuron pools (SOO, IOO, and BUCC) were located lateral and ventral to those of the facial muscles of the rostrum (DFMG). The distribution of the perioral muscle motor neuron pools was somatotopic, lateral-to-medial in the coronal plane with the more rostral muscles located most laterally in the facial motor nucleus and the more caudal muscles oriented most medially in the facial motor nucleus. Each motor neuron pool was distributed over several subnuclei and the location was not confined to any cytoarchitectural boundaries of specific subnuclei. Furthermore, the motor neuron pools were not discrete; each partially overlapped with the others. The SOO motor neuron pool was the largest among those labeled. Its somatotopic organization was crude, but mimicked that of the perioral muscles as a whole. More rostral fibers in the muscle were represented more laterally in the SOO motor neuron pool, and more caudal fibers were represented more medially. The relatively large and somewhat somatotopically organized SOO motor neuron pools in pigs suggests that the upper lip might be more richly innervated than other perioral muscles and functionally divided.

The organization of the pig facial motor nucleus supports the premise that motor neuron pools within the mammalian facial motor nucleus are organized as overlapping rostrocaudal columns. This study is also consistent with the concept that motor neuron pool organization is related to differential developmental patterns of the facial muscles, as well as associated behavioral patterns [Papez, 1927; Huber, 1930a, b; Vraa-Jensen, 1942; Friauf and Herbert, 1985; Welt and Abbs, 1990]. In the case of pigs, which possess elaborated perioral musculature (for foraging and food transport), the motor neuron pools innervating these muscles are also concomitantly large.

Facial muscles differ among other skeletal muscles in their innervation patterns (e.g., the number of muscle fibers per motor unit), histochemical, and immunohistochemical properties [Feinstein et al., 1955; Happak et al., 1988; Freiling et al., 1990; Stal, 1994; Happak et al., 1997]. Furthermore, perioral muscles are unique among facial muscles in that the muscle belly is multiply innervated along its length by a complex anastomosis of CN VII branches [Katz and Catalano, 1987]. This innervation pattern is similar to other large complex muscles that possess functional compartmentalization, such as the pectoralis major [Stern et al., 1980], latissimus dorsi [Herring et al., 1993], masseter [Hannam et al., 1981; Herring et al., 1989; Hannam and McMillan, 1994; Weijs, et al., 1993; Weijs, 1996], and the temporalis [Wood, 1986]. These muscles are subdivided into functional compartments with partitions of sensory output and segmental pathways to the motor nuclei. The data presented in this study suggest that the SOO might exhibit similar neural compartmentalization.

The functional significance of somatotopy, overlapping motoneuron pools, and motoneuron pools overlapping several subnuclei within motor pathways is not clearly understood. Other complex compartmentalized muscles, such as the masseter [e.g., Weijs, 1996], exhibit similar overlap of populations of motoneurons (up to 50% in some instances) that innervate different compartments within a single muscle. Whether somatotopic organization of the facial motor nucleus, or motor subnuclei, is functionally significant or a result of development process not related to muscle activation awaits further investigations on the distribution of input to these motoneurons [Weijs, 1996]. The somatotopic organization of the pig facial motor nucleus differed from the somatotopic organization of the trigeminal motor nucleus for the rabbit and pig in that no rostrocaudal organization was found [Herring, 1992; Weijs, 1996]. The somatotopic organization of the pig facial motor nucleus differed from trigemi-

nal afferent organization within the principalis and oralis subnuclei in that a rostrocaudal or an inverted representation of orofacial structures was not found [Shigenaga et al., 1986a, b; Yoshida et al., 1994; Jacquin et al., 1993]. Facial nucleus motoneurons are driven by synaptic inputs from sources including primary motor cortex (M1). Thus, to some extent, somatotopy within the facial motor nucleus might reflect or be constrained by somatotopy within M1. Primary motor cortex was once thought to exhibit a detailed somatotopic organization [Penfield and Rasmussen, 1950; Woolsey et al., 1952]. However, recent work has demonstrated that the somatotopic pattern of M1 might not be so precise [see Schieber, 2001 for a review]. Instead, distributions of neurons that innervate adjacent muscles within M1 overlap with each other [Schieber, 2001]. Intracortical microstimulation (ICMS) mapping studies of M1 corticobular projections to the head and face does demonstrate a simple somatotopic organization, but also with overlapping territories [Huang et al., 1988]. This organization is similar to that observed in the pig facial motor nucleus [this study]. Because each motoneuron within the pig facial motor nucleus that innervates a perioral muscle receives direct corticobulbar input from the upper neurons in M1, it is reasonable to suspect that the organization of motoneurons within the facial motor nucleus would be influenced by the organization of upper neurons in M1.

In conclusion, the motoneuron pools of the SOO, IOO, and BUCC of the pigs are organized somatotopically, lateromedially, and dorsoventrally across the lateral 4 of 7 subnuclei of the facial motor nucleus. This segregation of perioral innervation could be an adaptation for manipulating food items while foraging. A detailed study of the SOO suggests a crude lateral-to-medial somatotopy that corresponds to the rostrocaudal orientation of this muscle. This somatotopic segregation of the SOO motoneuron pools suggests that pigs might possess functional compartmentalization of the SOO, and that pigs can be used as a model of specialized perioral muscle function.

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