The pinna of the cat differentially filters acoustic signals depending upon the location of the sound source. Signals delivered on the acoustic axis, which is the position in the free field where an acoustic signal produces maximal sound pressure level, are amplified and those delivered off the acoustic axis are attenuated (Wiener et al., 1966; Phillips et al., 1982; Calford and Pettigrew, 1984; Musicant et al., 1990; Rice et al., 1992). Unlike the pinnae of primates or humans, which are relatively immobile, the pinnae of the cat move extensively, allowing the animal to selectively amplify or attenuate auditory signals from different locations in space. Little is known about such movements and their functional significance, but roles in sound localization (Siegmund and Santibañez-H, 1981, 1982) and in the identification of novel auditory stimuli (Henkel and Edwards, 1978) have been suggested.

There are 22 muscles associated with each pinna of the cat (Crouch, 1969). Sixteen of them participate directly or indirectly in pinna movements, and the other six change its shape (Fig. 1). The motoneuron pools that innervate these muscles are found in the medial portions of the facial nucleus (FN; Papez, 1927; Courville, 1966; Henkel and Edwards, 1978; Kume et al., 1978; Vidal et al., 1988).

Prior anatomical studies of the FN of the cat, using degeneration techniques (Courville, 1966) and horseradish peroxidase (HRP) injections into muscle groups (Kume et al., 1978), examined the relationship between the different branches of the facial nerve and the subdivisions of the nucleus. With the exception of an abstract on the innervation to pinna muscles of the cat (Zook et al., 1981), the organization of motoneuron pools innervating any particular facial muscle group has not been characterized in this species. Kume et al. (1978) attempted to inject free HRP into individual facial muscles in the cat, but difficulties due to spread of the labeling enzyme into neighboring tissue forced them to inject groups of muscles instead. Thus the location of motoneurons that innervate the muscles of the pinna of the cat has been mapped only to the resolution provided by individual branches of the facial nerve (Kume et al., 1978). This is not the case in other species. Detailed anatomical studies comparing the topographical organization of pinna motoneuron pools of the rat, which does not move its pinnae very much, and the bat, which has very mobile pinnae, suggest that structural features such as the number of motoneurons and the degree of organization of the motoneuron pools reflect the differences in pinna mobility between the two species (Friauf and Herbert, 1985). If pinna mobility and anatomical organization are correlated, then we would expect the cat’s mobile pinnae to
be related with a high degree of organization among pinna motoneuron pools in the FN.

In the present study we have characterized the topographical organization of pinna motoneuron pools in the FN of the cat by injecting individual muscles with the B subunit of cholera toxin conjugated to HRP (CTB-HRP). The results show that the 22 pinna motoneuron pools are organized in a manner consistent with the somatotopic organization of the entire FN shown in other species. Pools innervating muscles with similar actions overlap to different extents, but those innervating muscles with different actions overlap very little or not at all. Preliminary results have been presented elsewhere (Populin and Yin, 1992).

**MATERIALS AND METHODS**

**Animals and surgical procedures**

Data from 17 cats (2.0–6.0 kg) are presented in this paper. Anesthesia was induced with Ketamine/Acinvormazine (20 mg/kg; 0.2 mg/kg, i.m.) and maintained during surgery with i.v. injections of sodium pentobarbital. Preparations for surgery also included the administration of 66,000 units/kg of penicillin and 0.022 mg/kg of atropine sulfate.

Horseradish peroxidase conjugated with CTB (List Laboratories) reconstituted with distilled water to a concentration of 0.1% was injected into individual pinna muscles with a 10 μL microsyringe. Since early experiments showed that, with the exception of the M. intermedius scutulum, labeling occurred in the ipsilateral FN only, two muscles, one on each side, were injected in most experiments. To maximize the number of muscle fibers reached by the labeling enzyme, the CTB-HRP was delivered in a series of small injections (1–2 μL each), intended to cover the cross-section of the target muscle. The total volume of CTB-HRP injected into each muscle varied between 20–50 μL depending upon the size of the muscle.

In most experiments the head of the cat was positioned in a stereotaxic frame, and the microsyringe was held with a manipulator. In other experiments the position and orientation of the fibers of muscles such as those on the side of the head (e.g., M. adductor auris medius, M. antitragicus, and M. adductor auris inferior) required us to hand-hold the syringe. In general, to prevent wrinkling and tissue displacement, penetrations were made parallel rather than orthogonal to the orientation of the muscle fibers.

To minimize diffusion of the labeling enzyme into non-target tissue, all muscles were exposed and isolated prior to injection with the exception of the M. transversus aurculi and M. auricularis externus which were injected through the skin. The procedure normally included 1) identification and exposure of the target muscle, 2) removal or denervation of neighboring tissue (part of the M. platysma was removed to expose the M. depressor conchae and M. submentalis), and 3) sealing the area with silicon or vaseline. In addition, we selected CTB-HRP over free HRP because it is a more efficient marker (Trojanowski et al., 1982) that can be used at a much lower concentration (0.1% vs. 20–30%), which is thought to prevent diffusion (Welt and Abbs, 1990).

**Histology and data analysis**

After a survival period of 48–96 hours, cats were given a lethal dose of sodium pentobarbital intravenously (150 mg) and perfused intracardially with 1) saline and sodium heparin, 2) 1.0% paraformaldehyde and 2.5% glutaraldehyde in 0.1 M phosphate buffer at pH 7.4, and 3) 5% sucrose in 0.1 M phosphate buffer pH 7.4. The brainstem was removed and stored in 30% sucrose at 4°C for 24–48 hours. The portion of the brainstem containing the facial nucleus was frozen and cut in 70 µm sections in the coronal plane. All sections were processed with tetramethylbenzidine (Mesulam, 1978) and counterstained with cresyl violet.

Results are presented in the form of camera lucida drawings of coronal sections of the FN at approximately 25, 50, and 75% of its length (measured from the caudal pole of the nucleus) in which labeled cells from two adjacent sections are plotted (see Figs. 5–9), and in the form of photomicrographs of coronal (see Figs. 2–4) and parasagittal (see Fig. 10) sections of the FN. The boundaries of the FN were drawn around the outer edge of the cell bodies in the cresyl violet stained material. The different subdivisions of the FN were defined by areas without cell bodies. To facilitate the comparison between different muscles all drawings are shown on the right side of the brainstem; drawings corresponding to experiments performed on the left side are transposed.

**RESULTS**

**The facial nucleus and CTB-HRP labeling**

Figure 2 shows a series of coronal sections approximately evenly spaced through the FN and arranged from caudal to rostral. In the central two thirds of the structure four distinct subdivisions are distinguished: 1) intermediate (INT), 2) lateral (LAT), 3) ventromedial (VM), and 4) mediodorsal (MD) (Fig. 2B–E). Near the caudal and rostral poles the cross-sectional area of the nucleus is smaller, and the INT, LAT, and VM subdivisions gradually disappear (Fig. 2A,F).

**Motoneuron pools:**

**Topographical arrangement**

We have classified the muscles of the pinna into two major functional groups: those that 1) move the pinna directly or indirectly and 2) those that change its shape. We further subdivided the first group into four subgroups according to their principal action: muscles that pull the pinna a) dorsally, b) ventrally, c) caudally, and d) cranially. Data concerning the action, origin, and insertion points of each muscle were taken directly from Crouch (1969). In specifying the actions of muscles that act in two directions, the primary action is given first. Thus a muscle which pulls the pinna cranio-dorsally has a cranial action principally, whereas a muscle that pulls dorso-cranially has a dorsal action principally.

Motoneuron pools innervating the muscles of the pinna are found in the INT (two), the VM (one), and the MD.
Tragicus lateralis
Abductor Auris Brevis
cartilage and on the surface of the auricle; it pulls the external ear dorso-caudally. Injection of CTB-HRP in this muscle produces a column of tightly packed labeled motorneurons in the most medial areas of the MD subdivision of the FN.

The M. auricularis superior runs from the sagittal crest, cranial to the interparietal bone, to the auricular cartilage. Its action is to adduct the external ear. The motorneuron pool innervating this muscle is more diffuse and located more dorso-laterally than that innervating the M. levator auris longus.

The M. adductor auris medius pulls the concha dorso-caudally. The origin of this muscle is in the middle two thirds of the caudo-ventral edge of the scutiform cartilage, and its insertion point is along the medial surface of the tragus. Its motorneurons are found in the dorsal region of the MD subdivision, slightly lateral to its midline. Unlike the motorneuron pools innervating the two preceding muscles, these cells appear to be arranged in a sheet-like fashion.

The M. intermedius scutulorum runs between the scutiform cartilage on both ears and pulls the two ears dorsally. CTB-HRP injection into one side of this muscle produces a column of tightly packed labeled motorneurons in the dorso-lateral aspects of the MD subdivision, where they are topographically organized; a few motorneurons innervating the M. zygomaticus are also found in the most medial edge of the LAT subdivision. Pools that innervate muscles with similar actions tended to overlap while those that innervate muscles with different actions tended to be spatially distinct (Fig. 3). In Figure 3 we contrast the location of motorneurons innervating two adjacent muscle that have different primary actions: the M. adductor auris medius pulls the pinna dorsally while the M. adductor auris inferior pulls it cranially.

To give an indication of representative labeled cells, Figure 4 shows high-power views of labeled motorneurons following an injection of CTB-HRP into M. levator auris longus. Labeled cells exhibited a variety of shapes and tended to be clustered together (Figs. 3, 4D).

Muscles that move the pinna

Muscles that pull the pinna dorsally. The motorneuron pools that innervate this group of muscles are located in the dorsal two thirds of the MD subdivision of the FN (Fig. 5).

The M. levator auris longus (caudal subdivision) is a large muscle that extends from the midline, dorsal to the atlas, and from the sagittal crest, and ends in the scutiform cartilage and on the surface of the auricle; it pulls the external ear dorso-caudally. Injection of CTB-HRP in this muscle produces a column of tightly packed labeled motorneurons in the most medial areas of the MD subdivision of the FN.

The M. auricularis superior runs from the sagittal crest, cranial to the interparietal bone, to the auricular cartilage. Its action is to adduct the external ear. The motorneuron pool innervating this muscle is more diffuse and located more dorso-laterally than that innervating the M. levator auris longus.

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The M. intermedius scutulorum runs between the scutiform cartilage on both ears and pulls the two ears dorsally. CTB-HRP injection into one side of this muscle produces a column of tightly packed labeled motorneurons in the dorso-lateral aspects of the MD subdivision.
Fig. 2. Cresyl violet stained coronal sections of the right facial nucleus at approximately 10, 27, 50, 63, 80, and 93% of its length (measured from the caudal pole). A, caudal pole; F, rostral pole. The four subdivisions of the nucleus are most clearly distinguished at the center (C): INT, intermediate; LAT, lateral; VM, ventro-medial; and MD, medio-dorsal. MSO, medial superior olive.
Muscles that pull the pinna ventrally. This group is composed of four muscles. Motoneuron pools innervating these muscles are located in the ventral half of the FN and in the lateral aspects of the MD subdivision (Fig. 6).

The M. zygomaticus major, which pulls the ear ventro-cranially, connects the angle of the mouth with the scutiform cartilage. Consistent with the location of other pinna muscles whose actions include a cranial component (see Fig. 8), the motoneuron pool of the M. zygomaticus major is located in the lateral aspect of the MD subdivision, overlapping considerably with those pools innervating the M. frontoscutularis, the M. adductor auris superior, and the M. intermedius scutulorum. A few motoneurons are also found in the medial edge of the LAT subdivision, giving the impression that the column winds from the MD to the LAT, and back to the MD subdivision as it runs rostro-caudally.

The M. submentalis, like the M. zygomaticus major, is a long, wide, and very thin ribbon of muscle fibers which originates near the mid-ventral line and inserts into the pre-auricular aponeurosis. It pulls the external ear ventrally. The column of labeled motoneurons is found in the ventro-lateral aspects of the MD subdivision.

The M. tragicus lateralis pulls the external ear ventrally and rotates it outwardly. It originates on the caudal end of the mandible, and inserts on the caudal margin of the tragus and in the depression on the concha just caudal of the tragus. The motoneurons innervating this muscle are located in the ventral aspect of the MD subdivision.

The M. depressor conchae is also a long, wide, and very thin ribbon of fibers that originates on the ventral surface of the neck and inserts into the summit of the antitragus. It pulls the external ear ventrally. This is the only pinna muscle that is innervated by motoneurons located in the VM subdivision of the FN.

Muscles that pull the pinna caudally. This group is comprised of three muscles, innervated by motoneurons located medio-ventrally in the MD subdivision of the FN (Fig. 7).

The M. adductor auris brevis pulls the concha caudally. It is a small, thin, and narrow ribbon of fibers located immediately caudal to the M. adductor auris longus; it runs from the lambdoidal crest to the medial surface of the concha. Very few motoneurons are labeled after injecting 20 μl of CTB-HRP in multiple sites along the muscle; they are found scattered in a loose column in the ventral part of the MD subdivision.

The M. adductor auris inferior originates on the orbital ligament and ends on the tip of the M. antitragicus. This muscle pulls the ear cranio-dorsally and its motoneurons are located ventro-laterally in the MD subdivision.

The M. corrugator supercilii lateralis originates from the M. frontoscutularis and from the tendon lying just cranial of the external opening of the ear, and is inserted at the
Fig. 4. Cholera toxin B-horse radish peroxidase (CTB-HRP) labeled facial motoneurons after injections into the M. levator auris longus. Both the somas and dendritic processes are darkly stained. An extended survival time (96 hours) was used in this experiment.

caudo-lateral angle of the eye. This muscle acts upon the pinna indirectly, pulling it cranially. The motoneurons innervating this muscle are located in the INT subdivision.

The M. frontoauricularis originates along the upper eyelid and it is inserted in the auricular cartilage, along with the M. abductor auris superior at the cranio-medial angle. This muscle consists of scattered groups of fibers (a feature that makes its study particularly difficult) that pulls the ear cranially; it is also a weak adductor. Injection of CTB-HRP in several locations into this muscle labeled motoneurons in the INT subdivision only.

Muscles that change the shape of the pinna

This group is composed of six muscles, innervated by motoneurons that extend from the dorsal to the ventral edges of the MD subdivision and centered along its mediolateral axis (Fig. 9).

The M. auricularis externus begins on the eminentia conchae (distal to the insertion of the M. adductor auris longus) and ends on the concha. Its action is to flex the auricular cartilage. This muscle is innervated by tightly packed motoneurons located dorsally in the MD subdivision.

The M. transversus auriculi originates on the medial surface of the concha and inserts on the auricular cartilage. It flexes the scapha medially, enlarging the auditory opening. Injection of CTB-HRP into this muscle produces labeled motoneurons in the dorsal aspects of the MD subdivision.

The M. tragus medialis (cranial portion) flexes the concha. Its origin is on the ventral end of the tragus, and its insertion is in the cranial surface of the concha. Labeled motoneurons are found scattered in the ventral half of the MD subdivision. It was not possible to inject the caudal subdivision of this muscle.

The M. antitragicus originates at the caudal border of the antitragus and inserts on the tragus. This muscle constricts the external auditory opening. In the coronal plane, labeled
Fig. 5. Innervation to muscles that pull the pinna dorsally, dorso-cranially, and dorso-caudally. This and the following four figures are camera lucida drawings of coronal sections of the facial nucleus at approximately 25, 50, and 75% of its length (left to right), showing the location of single labeled motoneurons (●) from two adjacent sections (each 70 μm thick), after injection of CTB-HRP into individual muscles of the indicated groups. The broken lines indicate boundaries that could not be clearly identified. For details on subdivisions see the legend of Figure 2 and the text. The scale bars, 1 mm, and the orientation is the same as in Figures 2 and 3.

The M. conchaeus externus constricts the concha. Both the origin and insertion points of this muscle are located in the concha. The origin is attached a short distance distal of the M. antitragicus, and the insertion is attached at a point caudo-dorsal of the origin. Motoneurons innervating this muscle are found in the ventral part of the MD subdivision, although at more rostral levels some cells are displaced to the center of the subdivision.

The M. helicis originates on the medial surface of the concha and ends on the auricular cartilage, along with the caudal fibers of the M. adductor auris superior. It draws the cranial margin of the auricle proximally. The cells that innervate this muscle are found in the ventral portion of the MD subdivision.

**Columnar organization**

The topographical organization of pinna motoneuron pools described in the previous section is generally well conserved along the rostro-caudal extent of the nucleus. Thus, when successive coronal sections are aligned, a columnar pattern of organization for individual motoneuron pools is usually evident. To illustrate the columnar...
volume varied from 20-50 µl, the number of labeled motoneurons varied from 7-322. In part this correlation is to be expected since larger muscles, with larger volumes, may be innervated by more motoneurons (Buchthal, 1960). Injections of five muscles (M. frontoauricularis, tragicus medialis, transversus auriculi, zygomaticus major, and submentalis) resulted in less than 20 labeled motoneurons; while six muscles (M. adductor auris superior, adductor auris medius, intermedius scutulorum, frontoscutularis, antitragicus, and rotator auris) resulted in more than 100 labeled motoneurons.

In contrast to the large variability resulting from injections into different muscles, there were very consistent results from replications of injections into the same muscle. The consistency was evaluated on a subset of nine muscles that were readily accessible for injection and resulted in many labeled motoneurons (M. abductor auris longus, organization along the rostro-caudal axis, we replicated injections of two muscles, the M. adductor auris medius and M. adductor auris inferior, whose motoneurons are seen in the coronal plane in Figure 3, but we cut the sections in the parasagittal plane (Fig. 10). Labeled cells are found in similar position along the dorso-ventral axis of the nucleus in both sets of figures. Columns formed by smaller numbers of labeled cells such as those innervating the M. abductor auris brevis and M. frontoauricularis (not shown) are less well defined.

**Variability in labeled motoneurons**

In spite of our efforts to use standardized procedures, there was considerable variability in the intensity and number of motoneurons labeled following injections into different muscles. This variability was only weakly correlated with the amount of CTB-HRP injected: while the

![Fig. 6. Innervation to muscles that pull the pinna ventrally and ventro-cranially.](image)
adductor auris inferior, adductor auris medius, adductor auris superior, auricularis superior, depressor conchae, intermedius scutulorum, levator auris longus, and transversus auriculii) as well as five muscles (M. frontoauricularis, submentalis, tragicus medialis, transversus auriculii, and zygomaticus major) that had very few labeled motoneurons following the initial injection. Without exception, the location of the labeled motoneuron pools and the number of labeled cells observed in the replications closely resembled those in the original experiments. For example the replications shown in Figures 3 and 10 resulted in 216 and 207 labeled motoneurons for M. adductor auris medius and 73 and 65 motoneurons for M. adductor auris inferior in the original and replication experiments, respectively. We were particularly concerned with the muscles that resulted in very low numbers of labeled motoneurons so that several replications were made of those injections. For example, we injected the M. frontoauricularis in four repeated experiments, in each case less than 20 cells were labeled. Similarly, in the other four muscles with few labeled motoneurons following the initial injection, we also obtained fewer than 20 labeled cells in the replication, all consistently located in the expected areas of the nucleus.

**DISCUSSION**

**Methodological considerations**

The chief limitation of this study is the possibility that we have mis-estimated the number of motoneurons innervating individual muscles. Overestimates could result from spread of HRP from the injection site into neighboring muscles while underestimates could result from inadequate diffusion of CTB-HRP within the muscle. Clearly, reducing the spread of the labeling enzyme and maximizing the number of labeled motoneurons innervating each muscle are contradictory procedures. We feel it is more important that the labeled motoneurons resulting from a particular injection originate only from the injected muscle, and not neighboring muscles, than that all of the motoneurons innervating that muscle be labeled. Thus, in minimizing the possibility of overestimating, it is unlikely that all motoneurons of a given muscle were labeled.

There was considerable variability in the numbers of labeled cells following injections into different muscles, but repeated injections into the same muscle invariably led to similar numbers of labeled cells, which were located in the same part of the facial nucleus. If many, or few, labeled motoneurons were seen after injection of a particular muscle, then many, or few, respectively, were seen following a repeated injection.

**Topographical organization**

It has been established in a variety of species that pinna motoneuron pools are located in the medial areas of the FN (Papez, 1927; Courville, 1966; Martin and Lodge, 1977; Provis, 1977; Henkel and Edwards, 1978; Kume et al., 1978; Watson et al., 1982; Friauf and Herbert, 1985; Vidal et al., 1988). The topographical organization of these pools has been examined in detail in both rat and bat (Friauf and
The present results in the cat confirm the reports cited above concerning the location of pinna motoneuron pools within the FN, showing that this subgroup of facial motoneuron pools is arranged in a topographical fashion, which is consistent with the somatotopic organization of the entire nucleus in other species. In monkey (Welt and Abbs, 1990), possum (Provis, 1977), mouse (Komiyama et al., 1984), and rat (Watson et al., 1982; Semba and Egger, 1986), the rostro-caudal axis of the facial musculature is represented along the latero-medial axis of the FN, and the dorso-ventral axis is represented along the dorso-ventral axis of the nucleus.

Figure 11 is a composite picture of the cross section of the FN of the cat at approximately 50% of its length. Areas

Fig. 8. Innervation to muscles that pull the pinna cranially and cranio-dorsally.
Fig. 9. Innervation to muscles that change the shape of the pinna.
containing motoneurons that innervate muscles pulling in two directions (e.g., dorso-caudal) are plotted in two different figures. The organization of these panels is based on the action of the muscle groups which, in most cases, is consistent with their somatotopic arrangement. Figure 11A,B shows the location of motoneuron pools that innervate muscles with dorsal and ventral components in their direction of pulling; the former occupy approximately the dorsal two thirds, and the latter the ventral one half of the MD subdivision. An exception to this organization seems to be the innervation of the M. adductor auris inferior which pulls the pinna cranio-dorsally and is located in the ventral half of the MD subdivision. Based on the dorsal component in the line of pulling of this muscle, its motoneurons would be expected to be located more dorsally, but the orientation of its muscle fibers (see Fig. 1, lower left) indicate that such

Fig. 10. Cresyl violet stained parasagittal sections of the brainstem illustrating the rostro-caudal columnar organization of the motoneuron pools that innervate the (A) M. adductor auris medius and (B) M. adductor auris inferior. Data are from injections made on the left and right side of the same animal; the photomicrograph in B is shown reversed.
a component may be minimal. Thus it is consistent with all other cranially pulling muscles (Fig. 11D), whose motoneurons are located in the lateral portion of the MD subdivision. The motoneurons of the M. depressor conchae (a muscle that pulls the external ear ventrally) are located exclusively in the VM subdivision.

Figure 11C,D depicts the location of motoneurons innervating muscles that pull the external ear caudally and...
INNERVATION OF PINNA MUSCLES OF THE CAT

cranially. Caudally pulling motoneurons are located medio-ventrally in the MD subdivision, and cranially pulling motoneurons are located laterally in the MD and INT subdivisions. Along the dorso-ventral axis of this lateral half of the MD subdivision, motoneurons that pull dorso-cranially (e.g., M. adductor auris medius) are located dorsal to those that pull crano-dorsally (M. adductor auris inferior). Another apparent inconsistent finding is that motoneurons that pull ventro-cranially (e.g., those innervating the M. zygomaticus major) are located more dorsally than those that innervate the M. adductor auris inferior, a muscle with a crano-dorsal line of pull. However, M. zygomaticus major is located more cranially than perhaps any other muscle associated with the pinna (Fig. 1). Thus, consistent with the general somatotopic scheme, its motoneurons are located laterally in the areas of the FN devoted to the pinna. Furthermore, a few M. zygomaticus major motoneurons are located in the medial edge of the LAT subdivision. Motoneurons of two cranially pulling muscles, the M. frontoauricularis and M. corrugator supercilii lateralis, are found in the INT subdivision; an observation that also fits within the general organizational scheme. Caudally pulling motoneurons are located medio-ventrally in the MD subdivision, with dorso-caudally pulling motoneurons located more dorsally (Fig. 11C).

Figure 11E illustrates the location of motoneuron pools innervating the six muscles that change the shape of the pinna, which are arranged in a dorso-ventrally oriented ribbon in the central region of the MD subdivision. Roughly, the dorsal one half of this area is occupied by motoneurons of muscles that flex the external auditory structures, and the lower one half is occupied by motoneurons of the muscles that constrict the concha and the external auditory opening. The topographical organization of these motoneuron pools is also consistent with the somatotopic arrangement of the musculature they innervate. That is, muscles with a flexing action are located in the most distal parts of the pinna, and the motoneurons that innervate them are located in the dorsal one half of the MD subdivision, while muscles that constrict the external auditory structures are located more ventrally, and so are their respective motoneurons.

Friauf and Herbert (1985) concluded that such organization was not found among pinna motoneuron pools in the FN of the rat or the bat, which is surprising for the bat since it moves its pinnae very extensively. We found, however, that the location of four of the five motoneuron pools studied by Friauf and Herbert (1985) in the bat is very similar to the location of motoneuron pools innervating homologous pinna muscles in the cat. The same comparison holds for only one motoneuron pool in the rat.

Rostrocaudally the FN seems to follow the columnar organization observed in a variety of other motor systems such as the larynx (Yoshida et al., 1983), the tongue (Sokolov and Deacon, 1992), the trigeminal motor nucleus (Jacquin et al., 1983), and the spinal cord (Burke et al., 1977; Brink et al., 1979; Larnicol et al., 1982; Swett et al., 1986; Miller, 1987).

Overall, motoneuron pools within individual groups overlap to different degrees. Those that innervate smaller muscles are not as tightly clustered as those that innervate larger muscles. However, there is little overlap among the five different muscle groups. To some extent these observations could have been favored by the design of our experiment, which minimizes the possibility of overestimating the number of labeled motoneurons. As discussed above, it is unlikely that all motoneurons innervating any given muscle are backfilled by our procedures. On the other hand, the consistency of results when the same muscle was injected repeatedly makes us believe that the overall pattern observed is genuine, though perhaps not to the quantitative extent seen in our experiment. We conclude, therefore, that the edges of the areas in Figure 11A-E, although arbitrary, are likely to reflect the segregation of these pools within the confines of the nucleus. This is consistent with the clear-cut topographic organization of pinna motoneuron pools in the FN of the bat (Friauf and Herbert, 1985).

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