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Yamadori, T

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A STUDY OF THE MOTOR NEURON POOL OF THE SUPERIOR RECTUS MUSCLE IN ALBINO RATS BY RETROGRADE FLUORESCENT DOUBLE LABELING TECHNIQUE

HANIE A. RAHMAN AND TAKASHI YAMADORI

First Division, Department of Anatomy
Kobe University School of Medicine

INDEXING WORDS

superior rectus; oculomotor nucleus; rat; fluorescent tracers; double labeling

SYNOPSIS

Recent investigations revealed the localized distribution of the motoneuron subgroups within the mammalian oculomotor nucleus. In this study, we examined the motor neuron pool of the superior rectus muscle (SR) in 12 albino rats by injecting the retrograde fluorescent tracers Fluoro-Gold (FG) into one SR and DiI into the contralateral SR. We also examined the topographic and functional correlation between the neurons controlling the muscles of the upward gaze, i.e., SR and the inferior oblique muscle (IO) in another 5 albino rats by means of the same tracers. Our results demonstrated that: 1) the average total number of the neurons in the motor neuron pool of SR was 322.7±40.1; 2) topographically, about 94.65% of the motoneurons controlling SR were located in the contralateral side, while the remaining 5.35% lay ipsilaterally; 3) all the IO motoneurons were present on the same side of the muscle they innervate; 4) the motoneurons of SR and IO did not form separate subnuclei, but were intermingling with each other; 5) functionally, about 94.59%, 4.26% and 1.15% of the total motoneurons in the SR subnucleus of either oculomotor nucleus were projecting contralaterally, ipsilaterally and bilaterally, respectively; 6) although the distribution of the perikarya was not homogeneous, the bilaterally projecting (i.e., to both SR) cells were disposed centrally, and their double labeling indicated that their axons innervate the bilateral SR via axonal bifurcation and / or collateral branching; and 7) the motoneurons of SR and IO were functionally segregated from each other as no bilaterally projecting neurons (i.e., to SR and IO) were found.

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INTRODUCTION

The localization of the motoneuron groups controlling the extraocular muscles has been studied by clinical [7, 14], neuroanatomical [1, 5, 9-11, 16, 19, 21-23, 32, 34, 35] and electrophysiological [3, 6, 8, 17, 20, 27, 31] methods in the cat [1,6, 8, 18, 20, 27, 31, 32], rat [10, 11, 14, 21, 22], kitten [9], monkey [3, 5, 16, 23, 34, 35], baboon [17], dog [31], rabbit [1, 5], and man [7,14]. It has been agreed upon that there is localized representation of motoneurons subgroups within the oculomotor nucleus. The superior rectus (SR) motoneuron pool is located mainly on the contralateral side of the rat oculomotor nucleus, with few neurons dispersed on the ipsilateral side [10, 11, 21]. Fluorescent tracers alone [16, 18, 22] or combined with horseradish peroxidase [10] were used to examine the topographic localization of the superior rectus motoneurons in relation to the other oculomotor subnuclei controlling the other muscles. Employing the double labeling technique to investigate the common innervation of SR and inferior oblique muscle (IO) in rats [10] and cats [18], it was found that the motoneurons of these vertical yoke muscles are projecting only to their respective muscles, and no bilaterally projecting neurons were detected at all, i.e., functionally segregated within the oculomotor nucleus. In this paper, we demonstrate - using the retrograde fluorescent neuronal tracers Fluoro-Gold [26] and DiI [12, 15, 33] - the topographic distribution and the projection pattern of the neurons innervating the superior rectus muscle in the albino rat. In addition, we proved the existence of few neurons that supply the bilateral SR via collateral branching and / or axonal bifurcation. Finally, we confirmed the functional segregation of the SR and IO motoneurons within the oculomotor nucleus.

MATERIALS AND METHODS

Surgery

Seventeen adult Wistar albino rats of both sexes, weighing between 200 and 400 grams were used. They were anesthetized by injecting 10% chloral hydrate intraperitoneally (350 mg/kg). The extraocular muscles were exposed on both sides by incising and retracting the eyelids, incising the conjunctiva, and extracting the soft tissue of the orbit. The aqueous humor was aspirated to partially collapse the eyeball and facilitate the surgery. Except for SR, the extraocular muscles were excised and their nerve stumps were cauterized in 12 rats. Then, the retrograde fluorescent tracers were injected slowly into SR via a glass micropipet (tip diameter 50-100 μm) connected to a 10 μl Hamilton syringe. The injection was always done near the insertion of the muscle. Fluoro-gold (FG; Fluorochrome, Englewood, CO) dissolved into distilled water at concentration of 4% was injected into one superior

superior rectus muscle, while the contralateral SR was injected with the lipophilic carbocyanine dye 1,1` - dioctadecyl 3,3,3`,3` - tetramethylindo-carbocyanine perchlorate (DiI; Molecular Probes, Eugene, OR) dissolved in dimethylformamide (Sigma) at concentration of 15%. Initially, the volume injected was about 3 μl, but was reduced later to 1 μl to avoid spread of the tracer to the surrounding structures. Also, a cotton wool pad was inserted under the injected muscle to absorb any escaping tracer solution.

FG and DiI were injected into one SR and the contralateral IO, respectively, in another 2 rats; and into one SR and the ipsilateral IO, respectively, in another 3 rats. After injection, the eyelids were sutured together, and the survival period ranged from 48 to 72 hours. Then, under deep anaesthesia with chloral hydrate, the rats were perfused transcardially with neutral saline solution (100 ml) for 5 minutes, then with 10% formol saline solution (600 ml, pH 7.4) for 30 minutes, and finally with 5% sucrose in the same fixative (300 ml) for 15 minutes.

Brain sectioning

The brain was dissected out of the skull, postfixed in 20% sucrose solution of the same fixative for 24 hours at 4^0 C, cut into serial sections (50 μm thick) in coronal (13 animals), sagittal (2 animals) and horizontal (2 animals) planes using a vibratome. The brain sections were mounted on glass slides, left to dry, and observed under a fluorescent microscope (Optiphot, Nikon, Japan) using filter system G (main excitation wavelength 546 nm) for visualizing DiI labeled cells, and filter system U (main excitation wavelength 420 nm) for visualizing FG labeled cells.

Quantitative analysis

All the labeled cells were photographed by double exposure technique, and their locations were plotted on camera lucida outline of the brain sections. We counted the number of the single and double labeled cells on both sides and estimated their percentages. The number of perikarya in each motor neuron pool was estimated as the sum of neurons labeled by the same tracer contralateral and ipsilateral to the side of its injection. Finally, the tests of statistical significance were applied to compare the results of both sides.

RESULTS

Morphology of the labeled cells

Observed with the U system, the FG labeled perikarya had a yellowish cytoplasm and whitish granules. Observed with the G system, the DiI labeled cells

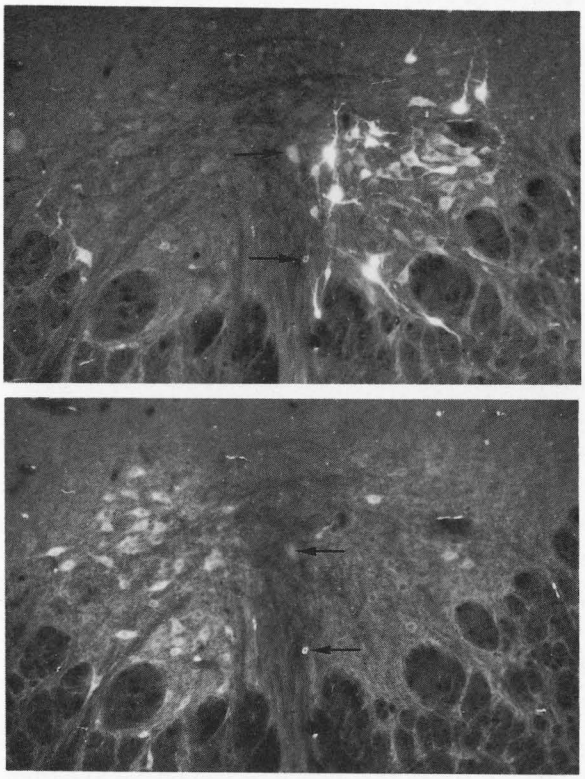

Figure 1. Photomicrographs of labeled motoneurons at the middle third of the SR subnucleus (experiment number 7; FG and DiI were injected into the right and left SR, respectively). The upper photograph demonstrates FG labeled neurons while DiI labeled perikarya are shown in the lower photograph. The arrows point to 2 double labeled cells. Note that more neurons are located dorsally than ventrally; the interneuronal spaces are wide; and the contralateral population is much larger than the ipsilateral group.

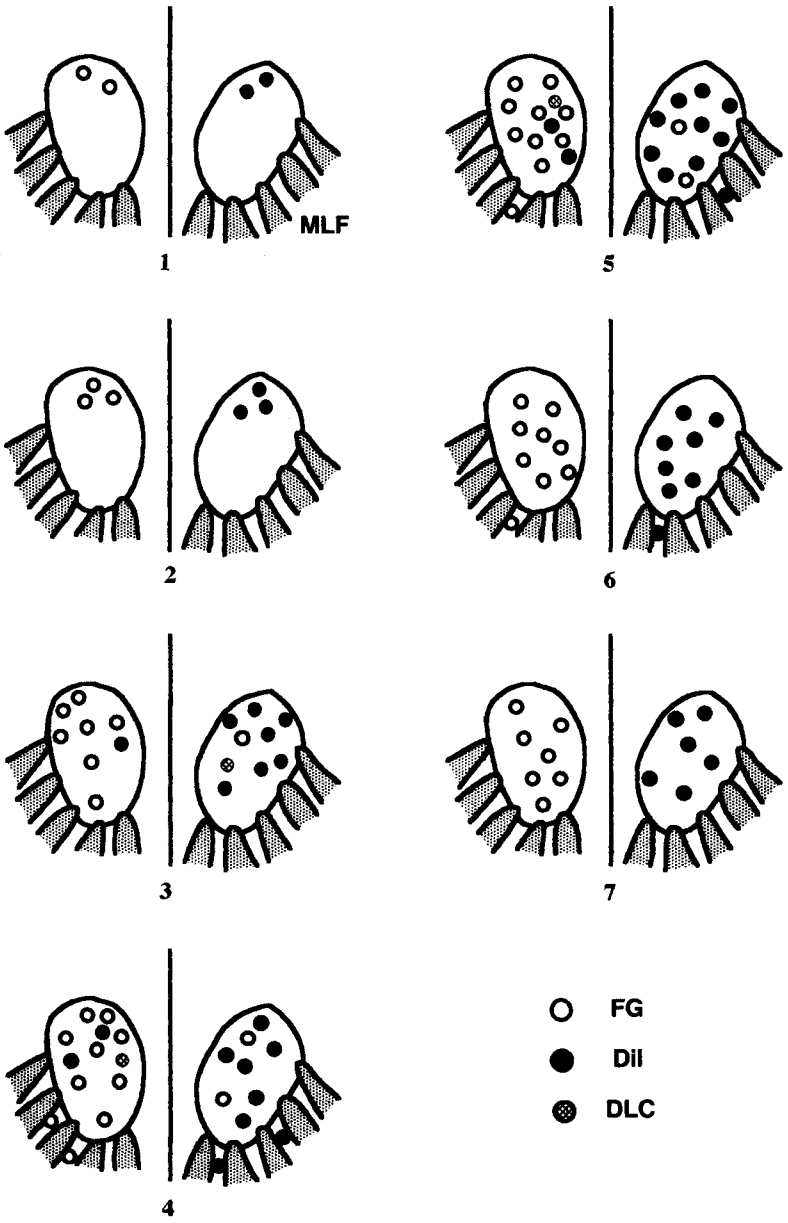

Figure 2. Camera lucida drawings showing the locations of the labeled motoneurons after injecting FG into the left SR, and DiI into the right SR (experiment number 8). Note that the double labeled motoneurons are present in the middle and caudal thirds of the SR subnucleus.

looked red with orange tint. The SR and IO motoneurons were multipolar and the tracer filled also the radiating dendrites. The majority were polygonal or oval in shape, while few smaller cells were spindle shaped (Fig. 1).

The density of labeling decreased as the volume of the injected tracer was reduced. Although Dil labeling was more persistent than FG, lightly labeled and heavily labeled motoneurons were seen with either tracer.

No morphological differences were observed between the ipsilateral and the contralateral populations of the SR motor neuron pool, as well as between the SR and IO motoneurons.

Topographic distribution of SR motoneurons

The SR motoneurons were seen bilaterally, and no labeled neurons were seen in the intervening zone. Also, there were no labeled cells in the trochlear or abducent nuclei.

1) The contralateral side:

Most of the SR motoneurons labeled with a specific retrograde tracer were located contralateral to the side of its injection. This neuronal group occupied an area of about 900 - 1100 μm (18 - 22 sections) in the rostrocaudal axis, 250 - 300 μm (5 - 6 sections) in the dorsoventral axis, and 300 - 400 μm (6 - 8 sections) in the mediolateral axis. In the rostral region, the motoneurons were disposed dorsally. In the middle region, the density of the neurons increased in the ventral area, but more neurons were present in the dorsal area, and some neurons intermingled with the fibers of the medial longitudinal fasciculus. In the caudal region, the motoneurons extended dorsoventrally in almost equal proportions, and few neurons were scattered among the fibers of the medial longitudinal fasciculus.

The double labeled cells were seen dispersed among the single labeled cells in the middle and caudal regions only (Fig. 2).

2) The ipsilateral side:

The labeled motoneurons territory was about half that of the contralateral side; corresponding to its middle two quarters (on the average from the 6th to the 15th section). Rostrocaudally, they extended along an area of approximately 400 - 500 μm. No labeled neurons were found among the fibers of the middle longitudinal fasciculus. The few double labeled multipolar cells were randomly dispersed among the single labeled cells along the entire rostrocaudal extent of this ipsilateral population. Their topographic locations did not match exactly with their counterparts on the contralateral side.

3) Topographic correlation with IO motoneurons :

The IO motoneurons were exclusively ipsilateral with very few cells in the median raphe. Their rostrocaudal extent was almost similar to that of the contralateral

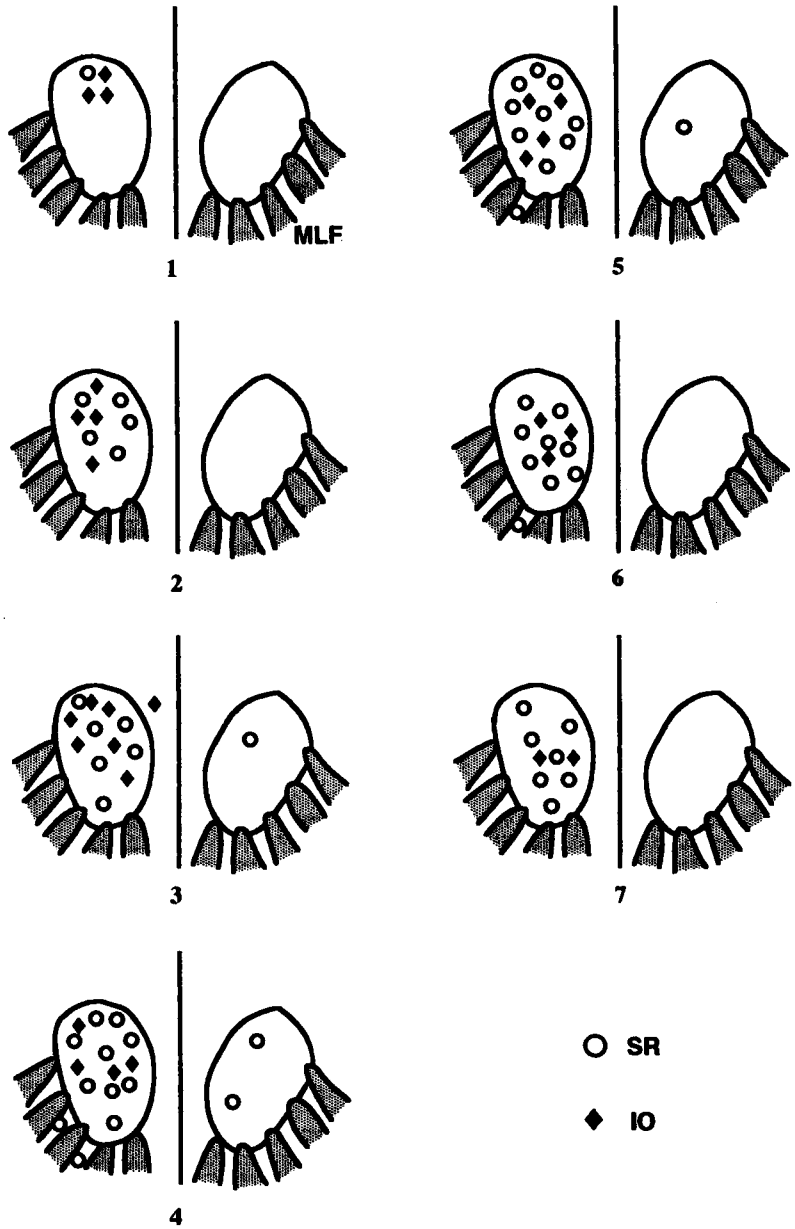

Figure 3. Camera lucida drawings showing the locations of the labeled motoneurons after injecting FG into the left SR, and DiI into the right IO (experiment number 14). Note that IO motoneurons are exclusively ipsilateral, those of SR are almost contralateral with few neurons scattered among the fibers of the medial longitudinal fasciculus, and no double labeled motoneurons are found.

Table I. Total number of perikarya in the motoneuron pool of SR.

Experiment	FG			DiI		
number	Ips.	Cont.	Total	Ips.	Cont.	Total
1	23	351	374	21	406	427
2	18	323	341	25	301	326
3	13	266	279	16	319	335
4	16	315	331	12	279	291
5	20	293	313	11	282	293
6	15	305	320	12	269	281
7	31	394	425	26	317	343
8	11	280	291	10	259	269
9	17	294	311	23	311	334
10	10	288	298	18	303	321
11	25	310	335	13	299	312
12	12	276	288	15	291	306
Average	17.6	308	325.6	16.8	302.9	319.7
(percentage)	5.4	94.6	100	5.3	94.7	100

Cont., contralateral; DiI, 1,1` - dioctadecyl 3,3,3`,3` - tetramethylindo-carbocyanine perchlorate; FG, Fluoro-Gold; Ips., ipsilateral; SR, superior rectus muscle.

Table II. The cell constituents of the superior rectus subnucleus.

Experiment	Right side			Left side		
number	SLCi	SLCc	DLC	SLCi	SLCc	DLC
1	15	345	6	14	397	9
2	16	299	2	23	321	2
3	10	316	3	14	264	2
4	8	311	4	13	276	3
5	5	287	6	16	278	4
6	8	301	4	12	266	3
7	18	386	8	25	311	6
8	9	279	1	9	257	2
9	19	290	4	13	307	4
10	6	299	4	16	286	2
11	11	308	2	22	296	3
12	14	275	1	9	288	3
Average	11.6	308	3.7	15.5	295.6	3.6
(percentage)	3.59	95.25	1.16	4.93	93.93	1.14

DLC, double labeled cells; SLCc, single labeled cells on the contralateral side; SLCi, single labeled cells on the ipsilateral side.

SR motoneurons (Fig. 3). In the rostral third, they were concentrated dorsally, while in the middle and caudal thirds, most of them were observed in the center. In all regions, the SR motoneurons were mixed with those of the IO, and there were no definite boundaries for each subnucleus. In spite of this neuronal intermingling, no double labeled cells were seen after injecting the tracers into SR and the ipsilateral / contralateral IO.

Quantitative analysis

The total number of the labeled perikarya in the SR motor neuron pool (i.e., the sum of the ipsilateral and contralateral groups labeled by the same tracer as they supply the same muscle) ranged from 269 to 427 cells with an average of 322.7±40.1 cells. The contralateral population constituted 92.3% to 96.2% with an average of 94.65%, while the ipsilateral population constituted 4.8% to 7.7% with an average of 5.35% (Table I).

The ipsilaterally projecting population consisted of 5 to 25 neurons with an average of 13.5, representing 4.26% of the total number of the labeled cells in the SR subnucleus of the oculomotor nucleus. The contralaterally projecting group had 257 to 397 labeled neurons with an average of 301.8, representing 94.59% of the total number of the labeled cells in the SR subnucleus of the oculomotor nucleus. The number of the bilaterally projecting (to both SR) cells ranged from 1 to 9 cells with an average of 3.65 cells. Their percentage varied from 0.3% to 2.0% with an average of 1.15% (Table II). The majority of the labeled cells were large and medium sized, while few cells were of the small type. Most of the double labeled cells were of the medium or small sized variety.

The total number of the IO motoneurons ranged from 112 to 137 cells with and average of 122.8; all of them were ipsilateral (Table III). No bilaterally projecting (to SR and IO) neurons were found.

Table III. Number and location of labeled motoneurons supplying the extraocular muscles of the upward gaze.

Experiment	SR			IO			DLC	
number	Ips.	Cont.	Total	Ips.	Cont.	Total	Ips.	Cont.
13	14	329	343	112	0	112	0	0
14	19	360	379	131	0	131	0	0
15	31	418	449	108	0	108	0	0
16	13	297	310	126	0	126	0	0
17	20	348	368	137	0	137	0	0

Cont., contralateral; DLC, double labeled cells; IO, inferior oblique muscle; Ips., ipsilateral; SR, superior rectus muscle.

There were very evident significant differences between the ipsilateral and contralateral populations of the SR, between the counts of the unilaterally projecting (i.e., single labeled) cells and the bilaterally projecting (i.e., double labeled) neurons in the SR subnucleus, and also between the total number of the motoneurons controlling the SR and that of the IO. However, there was no significant difference in the counts of the FG labeled neurons and the DiI labeled neurons ($p < 0.05$).

DISCUSSION

In this study, we used the recently introduced fluorescent tracers Fluoro-Gold and DiI for investigating the motor neuron pool of the superior rectus muscle (SR) of albino rats. They have several advantages [12, 15, 26, 33]. Firstly, their spread into injected muscles is rapid and greater than other neuroanatomical tracers as horseradish peroxidase (HRP). Consequently, not only the axon terminals around the injected site, but also the other ramifications supplying the other parts of the muscle - inaccessible to the micropipet - could be labeled. In other words, fluorescent tracers migrate much more readily through the tissue and ensure satisfactory labeling of the neurons in the motor neuron pool of the injected muscle [10], and hence quantitative analysis can be effected with great reliability. Secondly, they do not diffuse outside the labeled perikarya, and therefore cross labeling of adjacent neurons - which has been frequently reported with other fluorescent tracers as nuclear yellow [4] - does not occur. Thirdly, their fluorescence is clear and persistent. This alleviates the fears of fading which results in inaccurate quantitative data. Fourthly, they have different excitation wave lengths and fluoresce different colors. This enabled us to inject the SR of both sides simultaneously and observe the bilaterally innervating neurons in one and the same section by changing the filters. Fifthly, the micromolecules of the fluorescent tracers are more readily uptaken by the axon terminals than the macromolecules of HRP. Thus, the probability - that the smaller neurons with finer axons can be visualized by fluorescent tracers - is greater. Finally, these tracers fill the entire perikarya as well as their neurites. This facilitates measuring the soma size and quantitative comparison between different neurons.

In the present study, the majority of the neurons controlling this vertical yoke muscle were observed on the contralateral side while the remainder lay on the homolateral side of the injected muscle. Although the percentages may differ according to the technique and the type of species investigated, our results are in consensus with previous reports of Garcia et al. [10], Glicksman [11], and Oda [21]. This pattern of topographic distribution is similar to that of the cat [1, 6, 8, 18, 32]. However,

Warwick [35] reported that the organization of the neurons innervating the SR is different in other mammals as the monkey where they reside exclusively on the contralateral side.

The existence of few SR-projecting neurons in the homolateral oculomotor nucleus of some species was rationalized from a developmental point of view [13, 14, 24, 28]. In the early developmental stages, the motor neuron pool of the SR is essentially homolateral. However, as development proceeds, these neurons migrated to reach their definitive destination in the contralateral oculomotor nucleus. Due to differential migration rate, some motoneurons did not cross the midline. We think that some of these latter neurons have -instead of crossing to the opposite side - sent a branch or axonal collateral, in addition to supplying the original ipsilateral SR, to the contralateral muscle. On the other hand, some of the migrated neurons have intermingled with the fibers of the medial longitudinal fasciculus. This gives a clue to existence of few labeled neurons on the contralateral side among the fibers of the medial longitudinal fasciculus. A similar topographic observation have been reported after injecting a tracer into or transecting the innervating fibers of the medial rectus [1, 9, 35], superior oblique [10, 11], the inferior rectus, levator palpebrae and the lateral rectus muscles [10].

We found that the motoneurons in the SR subnucleus did not form a well defined group, but they were relatively separated from each other by intercellular spaces that differed stereotaxically from one plane to another. This can be explained by the fact that, in the rat, the motoneurons innervating a given extraocular muscle tend to cluster together, but the resulting ensembles intermingle with each other so that it would be arbitrary to trace neat boundaries defining the territories corresponding to the various muscles. This might have resulted from the greater inferior motility and development of the rat's extraocular musculature [25], which is cramped by the large cornea that occupies nearly half the eyeball. This absence of clear division of the oculomotor nucleus into distinct groups of neurons was also observed by Garcia et al. [10] and Oda [21].

Regarding the neuronal control of conjugate movements, it has been reported that vertical and oblique monocular movements [2] can be elicited on unilateral stimulation at the level of the oculomotor nucleus. However, paralysis of the vertical gaze is caused by bilateral lesions. Bilateral lesions (1 cm) within the pretectum caudal to the rostral interstitial nucleus of the medial longitudinal fasciculus or midsection of the posterior commissure result in paralysis of upward gaze. In an attempt to prove the existence - in the oculomotor nucleus - of common motor supply to the extraocular muscles that control the upward gaze, different fluorescent tracers were injected simultaneously into the rat's SR of one orbit and the IO of the opposite side, a marked degree of overlap was found between the 2 neuronal

groups, but no double labeled cells were found. This indicates that these functionally associated groups which coordinate the upward gaze innervate their respective muscles exclusively. This observation also denotes that coordination is mediated by a different set of interneurons. This confirms the previous finding of Garcia et al. [10]. A similar finding was reported by Kondo et al. [18] who investigated the common innervation of the vertical yoke muscles in cats. However, concerning the function of the bilaterally projecting neurons in the present study, we believe that they are not somatomotor. Should these neurons be motor to the SR, their stimulation would enforce both SR to pull the eyeballs simultaneously upwards and inwards, an action which does not occur in normal rats. On the other hand, Akagi [1] and Garcia et al. [10] reported that gamma neurons [26] - which mediate the gamma reflex that subdues the muscle tension to the control of the descending motor pathways - might be found among the labeled perikarya in the oculomotor nucleus of the rat [10], cat [1] and rabbit [1]. However, an electrophysiologic study is necessary to clarify their exact nature and physiologic role in ocular movements and/or reflexes.

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