On the extrinsic eye muscles of the whale, with special remarks upon the innervation and function of the musculus retractor bulbi

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While I was engaged in the anatomical study on the visual organs of the whale, special attention was directed to the musculi palpebrales, which are in the cetacea, as some anatomists said, of an unique existence throughout the animal kingdom. Next to that, my special interest was rendered to the well-developed musculus retractor bulbi, the existence of which is never characteristic for the cetacea, but is rather common for almost all vertebrates except the cyclostoma and fishes (Haller v. Hallerstein, 1934; Franz, 1934 etc.)[1]. Meanwhile I encountered in the whale a peculiar feature concerning the innervation of the retractor bulbi and tried to explain it by various means of researches, which will be related in order in the following paragraphs. As the result, I came to the conclusion that the innervation of the cetacean retractor bulbi is never essentially different from that in other vertebrates, though it exhibits a noteworthy peculiarity at first sight.

Relating to this problem, I tried to know the functional meaning of this muscle and studied also its original nucleus in the brain-stem, experimenting on the cat.

At the end, my observations on the sensory nerves of the retractor and of other extrinsic eye muscles in the cetacea will be mentioned.

MATERIALS

MYSTACOCETI:

1) Sei whale (Balaenoptera borealis, Lesson): adult 1 (45 feet, female), fetus 1 (7 feet, male)
2) Blue whale (B. musculus, L.): fetuses 2 (6 feet, female; 7 feet, male)
3) Fin whale (B. physalus, L.): fetuses 3 (3 feet, male; 8 feet, female; 13 feet, male)

1) Even among the fishes some teleostei are said to have slight indication of this muscle.

ODONTOCETI:

4) Sperm whale (Physeter catodon, L.): fetuses 2 (3 feet, female; 5 feet, male)
5) Pilot whale (Globicephalus melas, Traill): adult 1 (17 feet, male)
6) A dolphin (Prodelphinus caeruleo-albus, Meyen): adults 2, fetuses 3.

Other mammals used for comparison:

1) cats 5 2) dogs 2 3) rabbits 2

1. *The extrinsic eye muscles of the whale*

In the cetacea the extraocular muscles consist of two oblique, four straight ones and of the retractor bulbi. Of them, it is noteworthy that the greater part of each of four recti muscles extends forwards over the eyeball and inserts into the eyelid, delivering only a small muscle branch to the eyeball (Fig. 1, 2). While the ocular portions

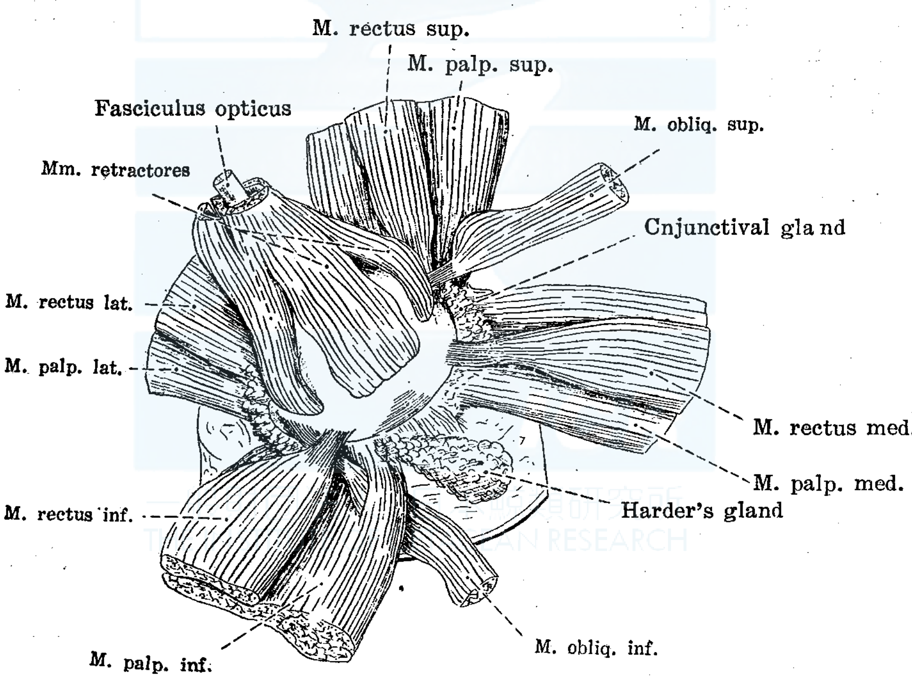


Fig. 1. Extrinsic eye muscles of Globicephalus melas (17 feet, male) (left eye)

of the recti muscles are relatively well preserved in the Globicephalus, they are very rudimentary in the Sei and other baleen whales. For this reason, these muscles of the cetacean eye do not deserve well the name "Mm. recti bulbi", but the name "Mm. palpebrales" is for them more preferable, as Weber (1886) and Pütter (1903) called them.

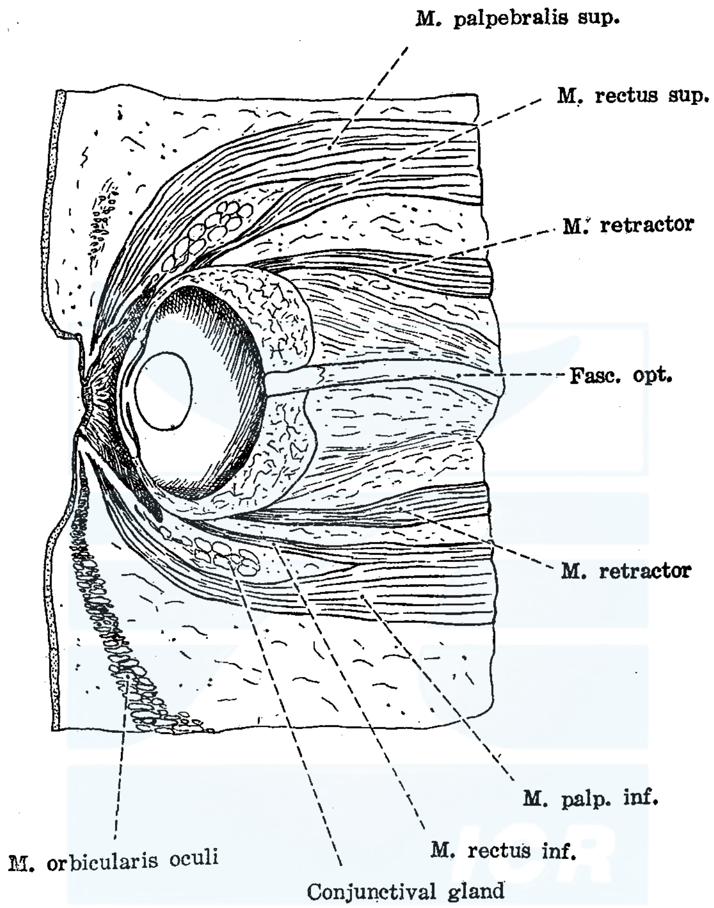
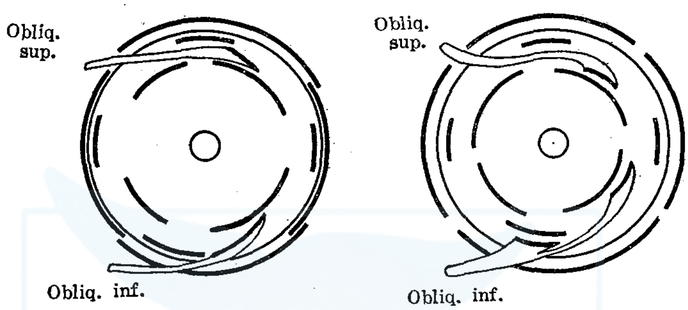


Fig. 2. Median section through eye and palpebrae of Globicephalus melas

The peculiarity of the musculi palpebrales of the cetacea has been well known since Weber, but the meaning of it is not yet fully determined. Weber was of the opinion that they might serve for the mechanical protection of the eyeball against water pressure, while Pütter ascribed them a hydrodynamic function, assuming that they might efficiently work against cooling down of the eyeball producing heat by their contraction.

The smallness of the ocular attachments of the recti muscles is generally thought to have much to do with the decline of the oculomotor function in the whale.

Concerning the obliqui muscles nothing special is found in the cetacean eye, except that the ocular insertion of the inferior obliquus is sometimes divided into two portions, as shown in Fig. 3.



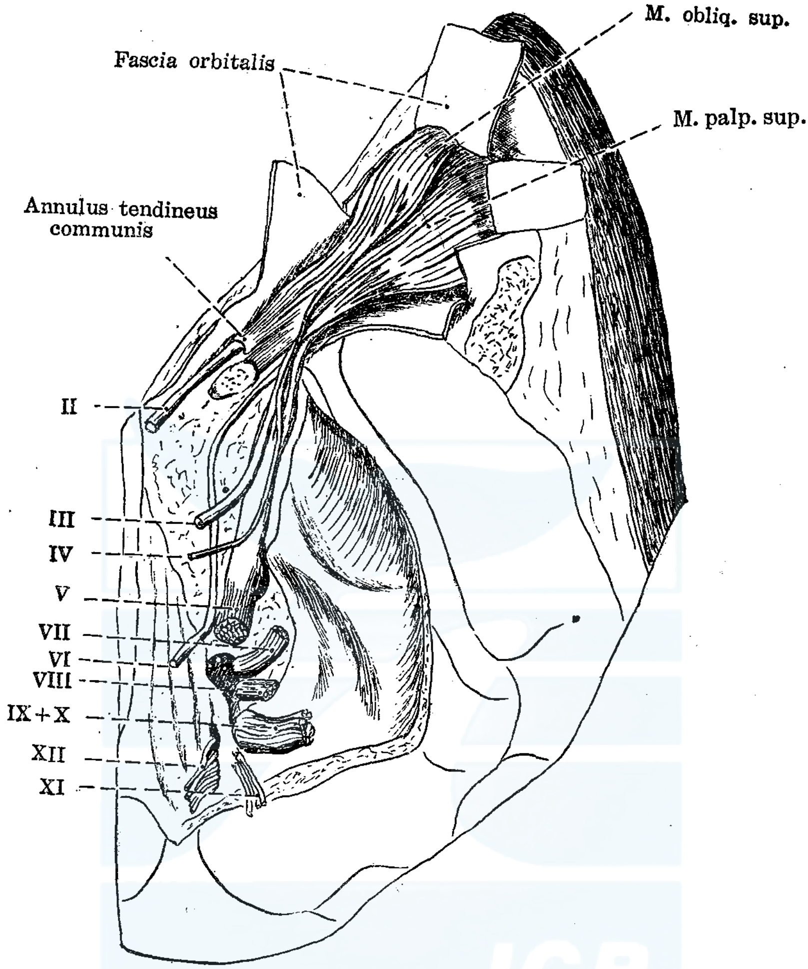
a, fetus of Sei whale b, adult Sei whale

Fig. 3. Diagram to show the insertions of the oblique muscles (right eye, posterior view)

The retractor bulbi will be described at length later on.

THE INNERVATION of the obliqui and recti muscles is in the whale intrinsically the same as in other animals; namely the inferior obliquus and all the recti except the lateral rectus are supplied by the oculomotorius, while the superior obliquus and the lateral rectus are innervated respectively by the trochlearis and the abducens. These muscles and nerves are illustrated in Fig. 4 (a-g). Fig. 5 (a-e) shows the intramuscular distribution of nerve fibres in each muscle. Fig. 6 is a diagram showing the innervations.

GANGLION CILIARE. In old times, more than a century ago, Burns (1832) and Rapp (1837) could not find the ciliary ganglion in Phocaena communis, but Stannius (1842) saw it in the same porpoise (cited from Schwalbe, 1879). Weber (1886), not finding it in Hyperoodon and other toothed whales, thought that this ganglion might be missing or at least very rudimentary in them. In the whales treated in the present work, both in the baleen and toothed ones, the existence of this ganglion was ascertained, though they are usually very small in size (Fig. 5, c). The radix brevis, connecting this ganglion with the trunk of the oculomotor nerve, consists of one or two thin bundles, sometimes very short, while in other cases it is considerably longer.



a

Fig. 4. Extrinsic eye muscles and their innervations of the Sei whale (fetus, 7 feet) (right eye)

The radix longa, the connection with the ophthalmic nerve, is always present, while the sympathetic root could not be seen.

The size of this ganglion is as follows;

1)	Blue whale	(fetus, 6 feet, left)	$3 \times 1.8 \times 1.5$ mm
2)	,, ,,	(,, 7 feet, l.)	$1.1 \times 0.8 \times 0.8$ mm
3)	Fin whale	(,, 8 feet, l.)	$3 \times 2 \times 1.2$ mm
4)	,, ,,	(,, 13 feet, right)	$1.7 \times 1.3 \times 1.0$ mm
5)	Sperm whale	(,, 3 feet, r.)	$1.5 \times 1.0 \times 0.8$ mm

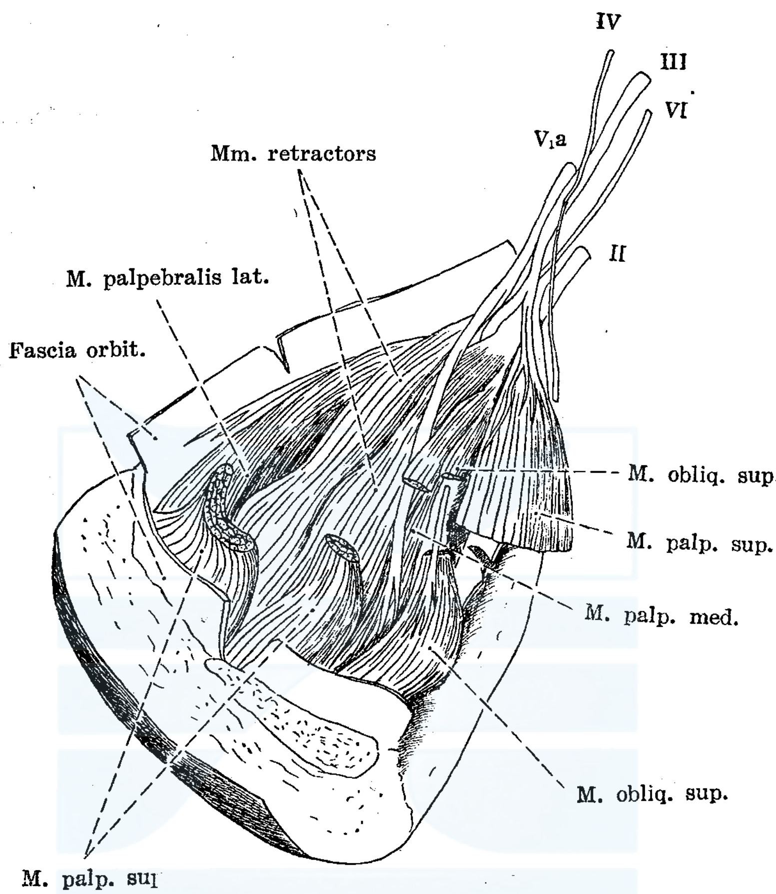


Fig. 4. b

Comparison with the ciliary ganglion of the cat ($3.5 \times 1.9 \times 1.5$ mm; $3.0 \times 1.8 \times 1.5$ mm), dog ($3.0 \times 1.7 \times 1.5$ mm) and of the rabbit ($0.8 \times 0.6 \times 0.5$ mm) shows how small it is in the whale.

2. General view of the retractor bulbi

The retractor bulbi is in the whale, as illustrated in Figs. 1 and 2, composed of not very distinctly separated four portions. They insert to the eyeball, as shown in Fig. 7, nearer the posterior pole of the eyeball than the recti muscles, and each portion is situated between two of the latters. So I would call them respectively Pars superior medialis, Pars superior lateralis, Pars inferior medialis and Pars inferior lateralis. As generally known, the retractor is well developed

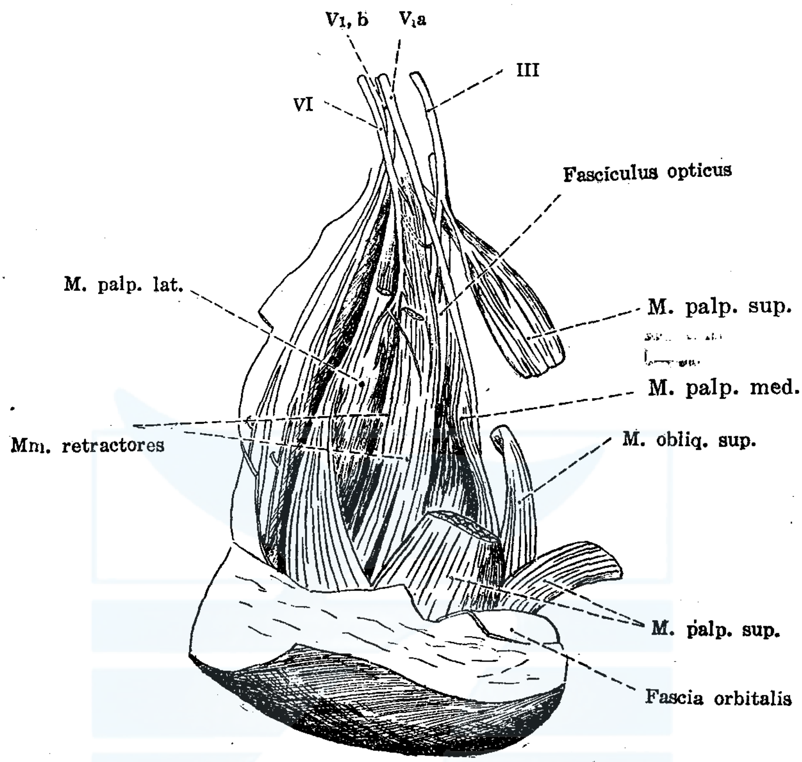


Fig. 4. c

in amphibia and reptilia, while in birds the musculus pyramidalis and musculus buralis s. quadratus are probably homologous to it. Also in mammals the retractor has a wide distribution; only a few of them including man are devoid of this muscle. According to Haller v. Hallerstein, these exceptional mammals are Orycteropus, Pteropus and Primates[1].

As in the whales, the mammalian retractor is often divided into four portions. But it is sometimes not readily divisible into portions, for example in some domestic animals such as horse, ox, sheep and pig.

Many authors have studied the retractor, calling it with various names, for instance, m. retractor bulbi s. oculi, m. suspensor[ius] oculi, m. choanoides, Grundmuskel, muscle en étonnoir, posterior rectus etc.

1) Nussbaum (1893) and Fleischer (1907) described as anomalous cases a rudimentary retractor in the human being.

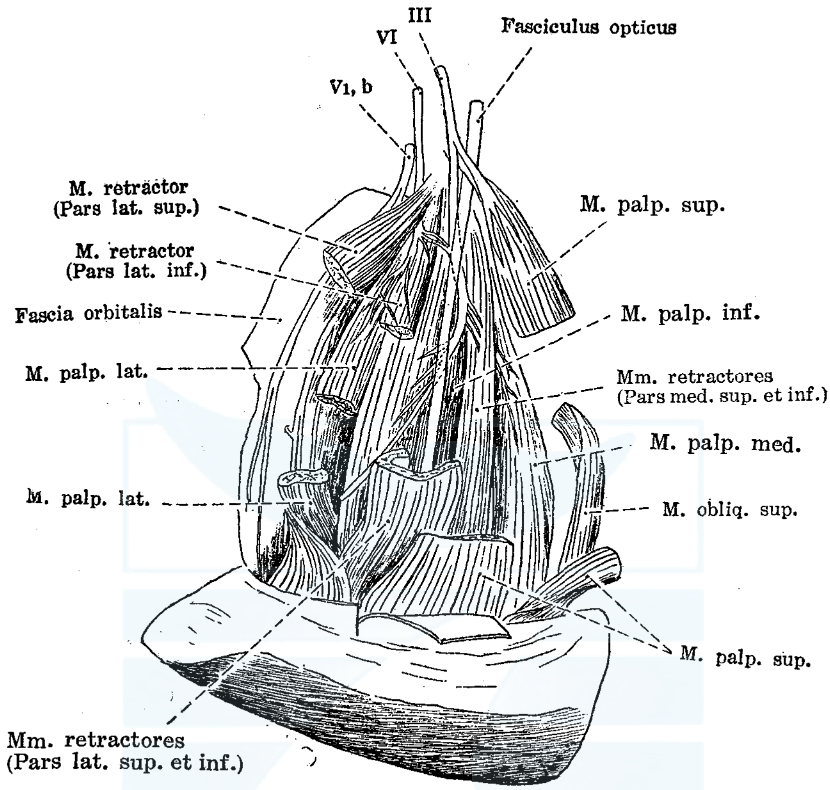


Fig. 4. d

3. *Historical review on the motor innervation of the retractor bulbi*

Before mentioning the nerves of the retractor in the whale, I will review briefly the literature of the problem for various kinds of animals. Concerning lower vertebrates, previous authors said unanimously that it is supplied by the abducent nerve (Corning, 1902; Nishi, 1922, 1938). As to the mammals, however, remarkable discrepancies have prevailed among the authors, of which the details were already reported by Hopkins (1919) and Cords (1924). Table 1 represents the brief summary of them. As shown in this table, the authors might be classified into two groups, the one saying that the retractor is innervated merely by branches from the abducens, and the other attributing two or more nerve sources for this muscle. It is interesting to note that many of veterinary anatomists belong to the latter group. Most of them insisted on the dual innervation by the abducens

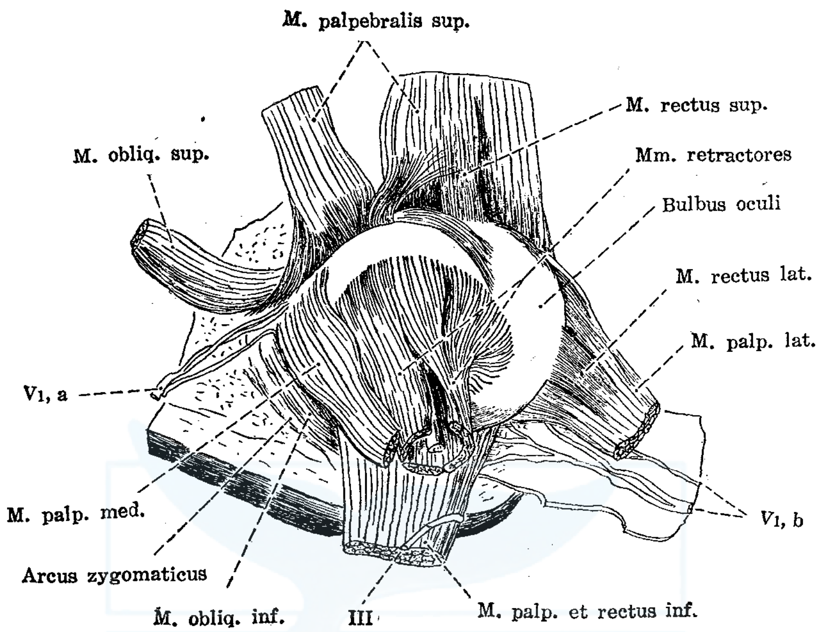

M. palpebralis sup.
M. rectus sup.
Mm. retractores
Bulbus oculi
M. obliq. sup.
M. rectus lat.
M. palp. lat.
V1, a
M. palp. med.
V1, b
Arcus zygomaticus
M. obliq. inf.
III
M. palp. et rectus inf.

Fig. 4. e

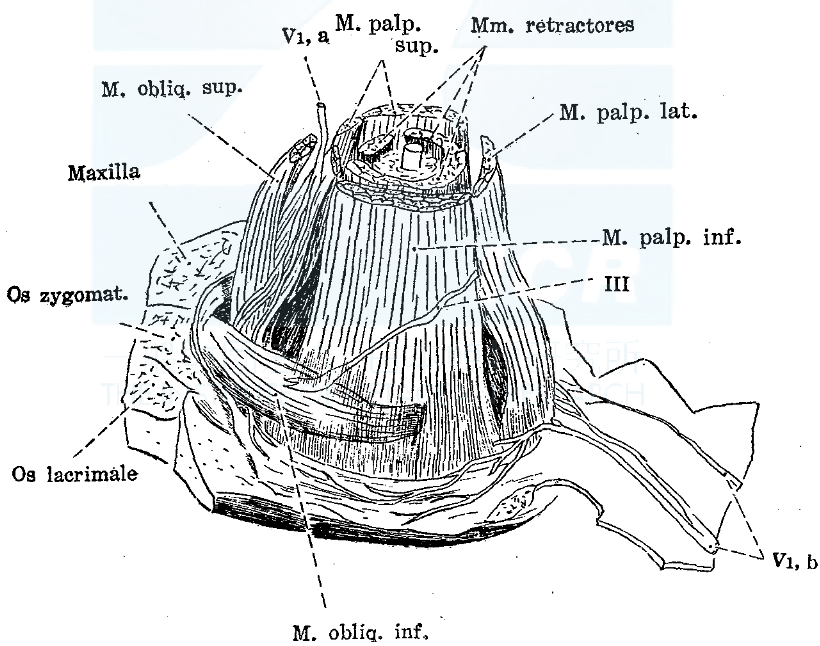

V1, a
M. palp. sup.
Mm. retractores
M. obliq. sup.
M. palp. lat.
Maxilla
M. palp. inf.
III
Os zygomat.
Os lacrimale
V1, b
M. obliq. inf.

Fig. 4. f

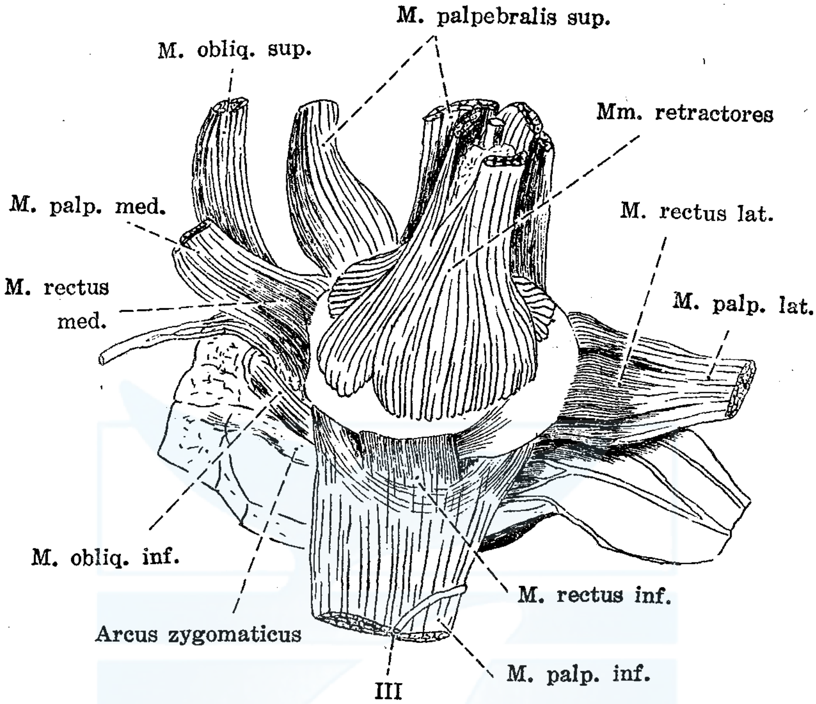


Fig. 4. g

and the oculomotorius.

This remarkable disagreement attracted naturally the attention of some anatomists, and especially Hopkins and Cords, in order to decide this problem, dissected many kinds of mammals repeatedly, using the binocular microscope. They found then no indication of filaments either from the superior or from the inferior division of the oculomotor nerve to the retractor, and so concluded that the mammalian retractor is supplied exclusively by the abducent nerve just like in lower vertebrates. They said with confidence that all the statements attributing the oculomotorius or other motor source were incorrect for this muscle.

4. Motor innervation of the cetacean retractor bulbi

As shown in Table 1, Rapp (1837) and Stannius (1842) stated that the retractor of Phocaena communis is supplied by the abducent nerve[1].

1) They described also a nerve supply from the ophthalmic nerve. About such a sensory innervation I will state later in Chapter 8.

Weber (1886) mentioned the same for Hyperoodon and other whales, and Cords (1924) was also of the same opinion, when he dissected a young specimen of Delphinus phocaena.

In the present study, however, an interesting fact was seen that the retractor of the whale, especially its medial portions receive decidedly branches from the inferior division of the oculomotor nerve, while the lateral portions of this muscle are supplied without doubt by branches of the abducens (Figs. 5, 8 and 9 a). I confirmed this fact in all the whales treated in the present paper. There exists, concerning this point, no exception, although the branches are quantitatively variant to some extent according to individuals or to species.

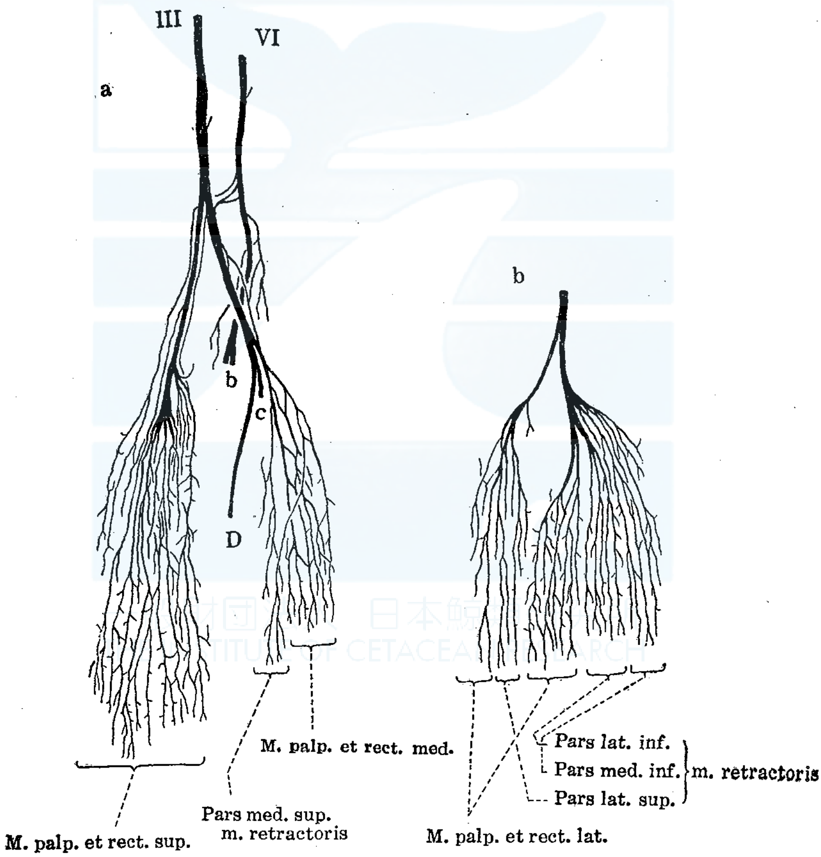


Fig. 5. (1) Motor innervation of the extrinsic eye muscles (fetus of the Fin whale, 13 feet, male) (right eye)

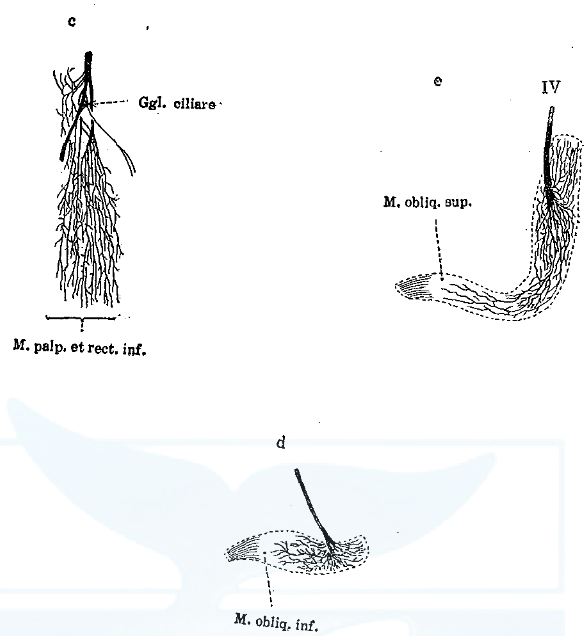


Fig. 5. (2)

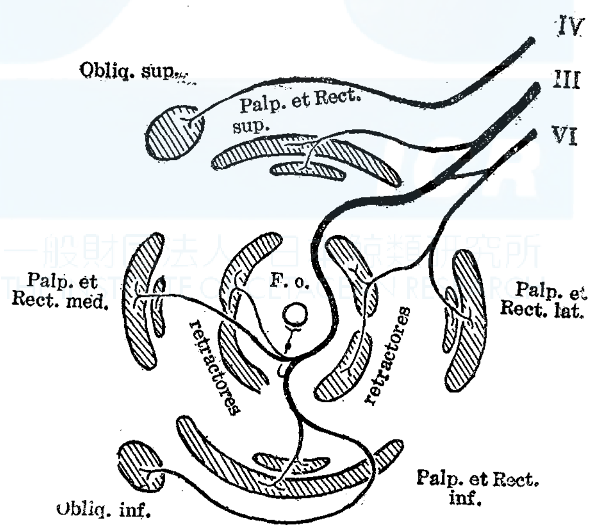
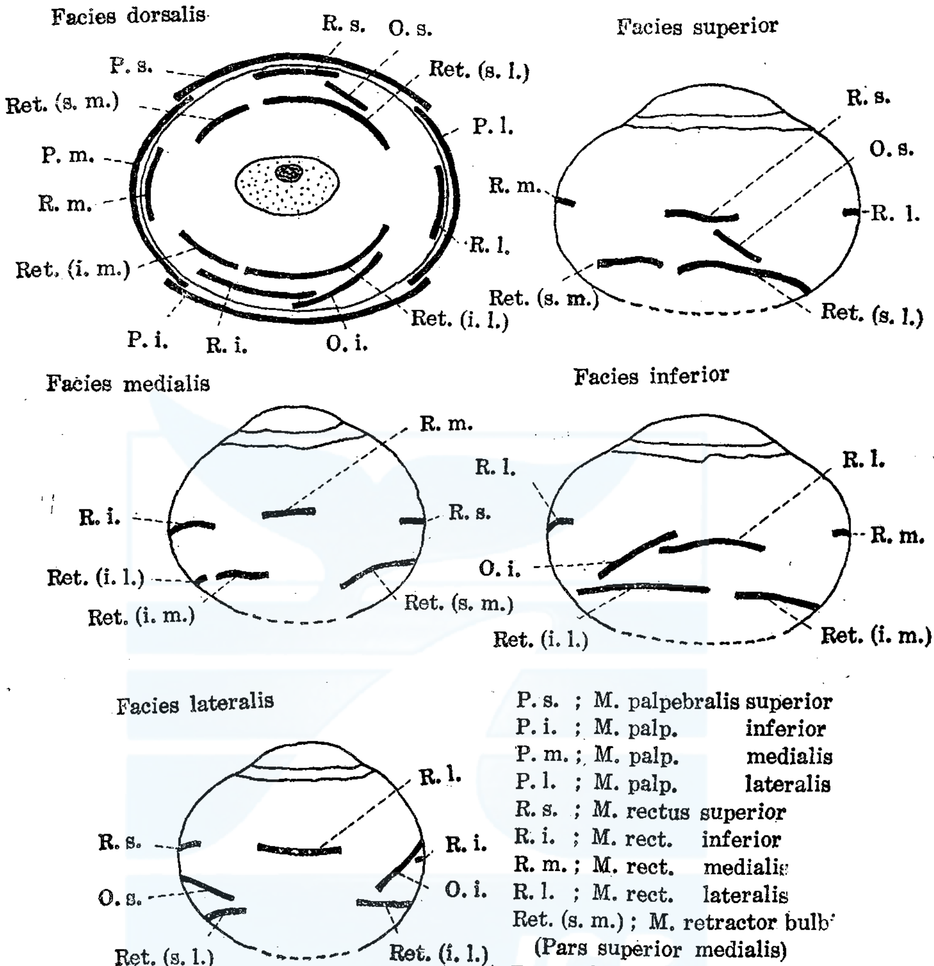


Fig. 6. Diagram to show the innervation of the extrinsic eye muscles in the whale (left eye, anterior view)



P. s.	; M. palpebralis superior
P. i.	; M. palp. inferior
P. m.	; M. palp. medialis
P. l.	; M. palp. lateralis
R. s.	; M. rectus superior
R. i.	; M. rect. inferior
R. m.	; M. rect. medialis
R. l.	; M. rect. lateralis
Ret. (s. m.)	; M. retractor bulbi (Pars superior medialis)
Ret. (s. l.)	; 〃 (P. sup. lat.)
Ret. (i. m.)	; 〃 (P. inf. med.)
Ret. (i. l.)	; 〃 (P. inf. lat.)

Fig. 7. Insertions of the extrinsic eye muscles of the whale (Fetus of Sei whale, 7 feet) (right eye)

Moreover, in all cases an anastomsis is existent between the trunk of the abducens and the inferior division of the oculomotor nerve near the top of the orbital cone. The anastomosing nerve bundle comes proximally from the abducens and passes distally into the oculomotorius. It is illustrated in Fig. 5, 8 and 9 a. Fig. 9 b is a simplified diagram to show the relation.

Table 1.

Opinions of the previous authors upon the innervation of M. retractor bulbi in mammals

VI (N. abducens) only		VI and other nerves		
Authors	Materials	Authors	Innervation	Materials
		Rapp (1838)	VI + V_1	Phocaena comm.
Stannius (1846)	(comparative anatomy)	Stannius ('42)	〃 + 〃	〃
		Chauveau ('57)	VI + III	domestic animals
Foltz ('62)	horse, rabbit			
Owen ('68)	(comp. anat.)	Krause ('68)	{ III only VI only	rabbit etc. cat, young ox
Milne-Edwards ('76)	(comp. anat.)	Gurlt ('73)	VI + III	(comp. anat.)
		Schwalbe ('79)	VI + III	sheep, ox, dog, rabbit etc.
Wilder & Gage ('86)	domestic animals			
		Leisering ('85)	〃 + 〃	domestic animals
Weber ('87)	Phocaena comm., Sei whale			
Motais ('87)				
Mivart ('89)	cat	Ellenberger & Baum ('91, '96)	III only	dog
		Frank ('94)	VI + III	domestic animals
Nussbaum ('93)	(comp. anat.)			
		Reute ('97)	〃 + 〃	fetus of pig
		Bradley ('97)	〃 + 〃	(veterinary anat.)
Gegenbaur ('98)	(comp. anat.)			
		Varaldi ('99)	〃 + 〃	(〃 〃)
		Du-Bois Reymond & Silex ('99, '07)	〃 + 〃	dog, cat, rabbit
Corning ('02)	dog, cat	Reighard etc. (1901)	III only	cat
		M'Fadyan ('02)	VI + III	horse
Wiedersheim ('06)	(comp. anat.)	Struska ('03)	〃 + 〃	domestic animals
		Martin ('04)	〃 + 〃	〃 〃
		Share-Jones ('06)	III+IV+VI	horse
		Fleischer ('07)	III only	man (anomaly)
Montane-Bourdelle ('13)	domestic animals	Ellenberger & Baum ('08, '12)	VI + III	domestic animals
		Strangeway ('09)	VI + x (III ?)	(veterinary anat.)
Hopkins ('17)	horse, ox, sheep, pig, dog, cat, rabbit, etc.	Zimmerl ('09)	VI + III	(〃 〃)
		Bensley ('10)	〃 + 〃	rabbit
Cords ('24)	many kinds of mammals including Phocaena comm.	Bradley ('12)	III only	dog
		Sisson ('14)	VI + III	domestic animals
Key-Åbergs ('34)	rabbit			
Imai ('34, '36)	monkey, cat			

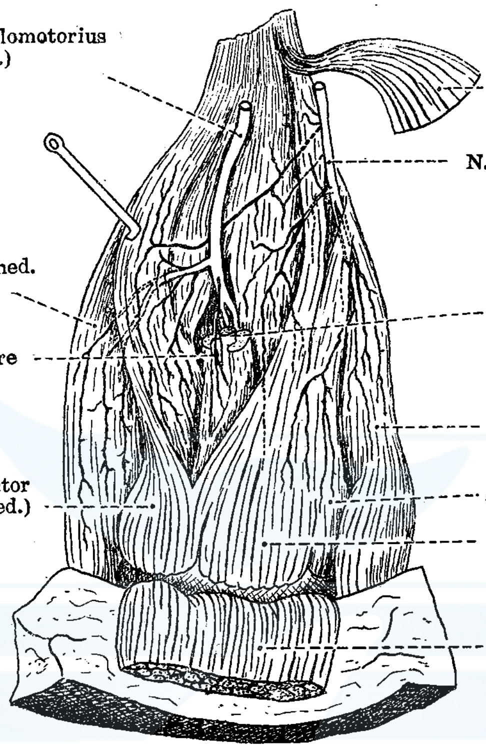
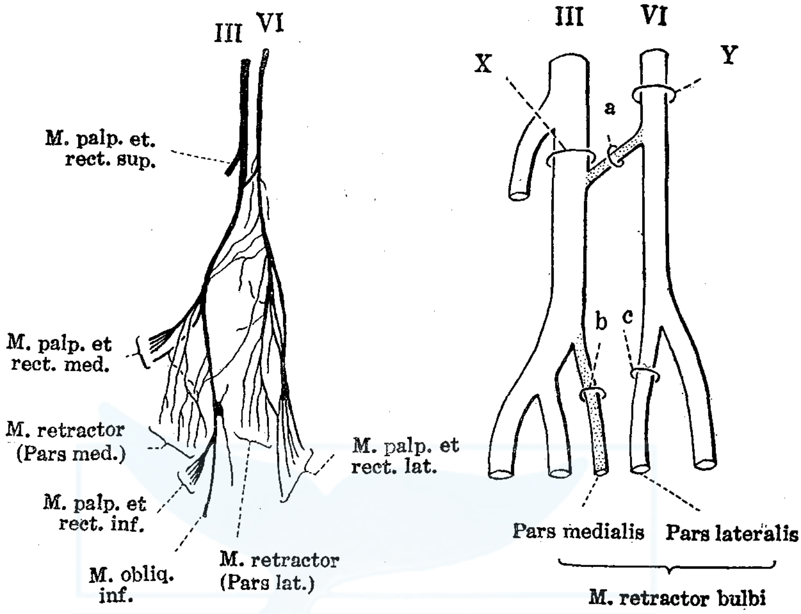


Fig. 8. Innervation of M. retractor bulbi (1)
Fetus of Blue whale (7 feet) (left eye)

Now, it occurs naturally the question whether the nerve fibres of the anastomosis (*a* in Fig. 9 b) continue directly into the branches of the oculomotor nerve to the medial portions of the retractor (*b* in the same figure). In other words, the branches in question may belong intrinsically to the abducens, like the branches to the lateral portions, passing only temporarily via the oculomotorius. But because of the close adhesion of fiber bundles, it was impossible for me to separate and trace the distal extention of the bundle *a* macroscopically. So, I tried to settle the problem from various viewpoints.

A. CALCULATION OF NERVE FIBERS

First of all, the nerve fibres were calculated in the anastomosis and in the branches of the oculomotorius going to the retractor. The result upon a fetus of the Blue whale is shown in Table 2. The medullated fibers of the bundle *a* amount to 768, while those of the bundle *b* are 806, exceeding thus the former by about 5%. If Kölliker



a, Fetus of Blue Whale b, Scheme

Fig. 9. Innervation of M. retractor bubli (2)

(1867) and Sherrington (1894) be right in their remarks that the nerve fiber does not bifurcate during its course in relatively thick nerve trunk, which is macroscopically recognizable, one could admit that at least some of the fibers in *b* are probably derived from the oculomotor nerve itself. But my further calculation of fibers in the trochlear nerve in the same whale, showed that the nerve trunk contains in the distal part more fibers than in the proximal part, the difference amounting to 10% approximately.

Moreover, I found in a cat that a distal portion of the abducens possesses about 20% more fibers than a proximal portion. And as between the two points examined no addition of nerve fibers from outside to the nerve trunk occurred, this increase of nerve fibers in number is very probably due to bifurcation or dichotomizing of a nerve fiber within the nerve trunk. Eccles and Sherrington (1930) insisted statistically, on the branching of both the afferent and efferent fiber within the nerve trunk with unequivocal illustrations of bifurcating fibers. Other authors such as Dunn (1902), Björkmann and Wohlfart (1936), Takagi (1948) etc. have also suggested or confirmed the increase of nerve fibers distalwards in the nerve trunk.

Table 2.

Fiber-analysis of N. III and N. VI of a Blue whale fetus
(6 feet, left eye)

Parts as shown in Fig. 9, b	total number of nerve fibres	thickness* of a fiber	number of fibres of each thickness	% to the total number
X	9247	thick	401	4
		medium-sized	5791	63
		fine	3055	33
Y	7041	thick	199	3
		med.-sized	4512	64
		fine	2330	33
a	769	thick	34	4
		med.-sized	549	71
		fine	186	25
b	806	thick	18	2
		med.-sized	548	72
		fine	204	26
c	1160	thick	18	2
		med.-sized	901	78
		fine	241	20

* thick fibres: larger than 5.0 μ (in diameter)
medium-sized f.: between 5.0 and 2.5 μ (〃)
fine fibres: smaller than 2.5 μ (〃)

Anyway, now that the distal increase of nerve fibers in number along the nerve trunk is certain, all the nerve fibers in the bundle *b* of the whale may possibly be derived from the anastomosis *a*, though at the same time we cannot deny also the possibility that some of the fibers in *b* may belong originally to the oculomotorius. Thus it became clear that the numerical calculation of nerve fibers does not afford any reliable basis to decide the problem.

B. FIBER-ANALYSIS OF THE NERVE BUNDLES IN QUESTION

As the second step, fiber-analysis was undertaken upon the nerve bundles in question. Namely, all of the fiber-constituents were classified into three classes according to their diameter; thick, medium-sized and thin fibers, each being respectively more than 5 μ, between 5 and 2.5 μ and less than 2.5 μ in diameter. I determined the number of fibers belonging to each class in the bundles *a*, *b*, Y and X as indicated in Fig. 9 b. My data are given in Table 2. Fig. 10 shows the result diagrammatically. Thus, the bundle *b* displays nearly the same fiber-composition as the bundle *a* and also the same as the trunk of the abducens (Y). If otherwise the trunk of the oculomotor nerve (X) exhibited a different fiber-composition from these three, it would tell almost undoubtedly that the bundle *b* is nothing but the distal extention of the bundle or anastomosis *a*.

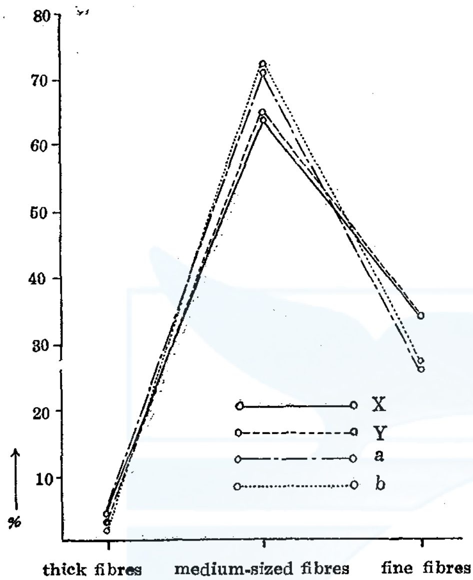


Fig. 10. Fiber-analysis of N. III and N. VI of a Blue Whale fetus

In reality, however, a striking resemblance was found to exist as to the fiber-composition between the abducens (Y) and the trunk of the oculomotorius (X), and therefore, it became impossible for me to know the relation between the bundles *b* and *a* by means of the fiber-analysis[1].

C. NERVE ENDINGS OF THE ABDUCENS, COMPARED WITH THOSE OF THE OCULOMOTORIUS

Thirdly, nerve endings were examined in each of the eye muscles in the whale. For, if there be, concerning this point, any noticable difference between the abducens and the oculomotorius, though this assumption is rather unplausible, it might be helpful for determining the nature of the bundle *b*, which innervates the medial portions of the retractor. Some of the nerve endings stained by the Bielschowsky method are illustrated in Fig. 11 (m. palpebralis lat.), in Fig. 12 (m.

1) Fig. 10 shows that the bundle *b* contains somewhat less fibers of larger diameter than the bundle *a*. It may be caused by the distal caliber-decrease of nerve fibers testified by Eccles, Sherrington (1930), Björkmann and Wohlfart (1936).

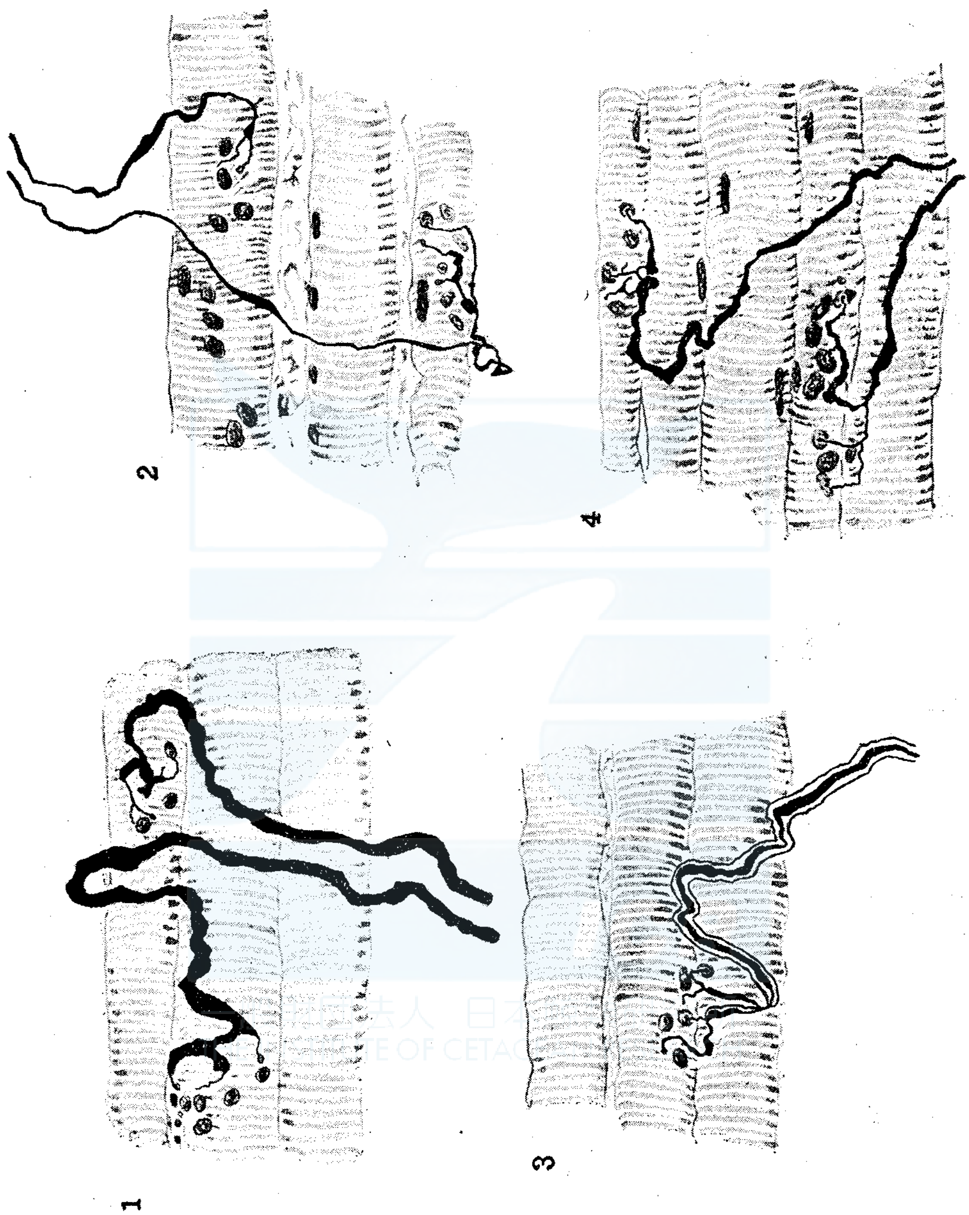


Fig. 11. Nerve endings in M. palbebralis lateralis of Prodelphinus caeruleo-albus

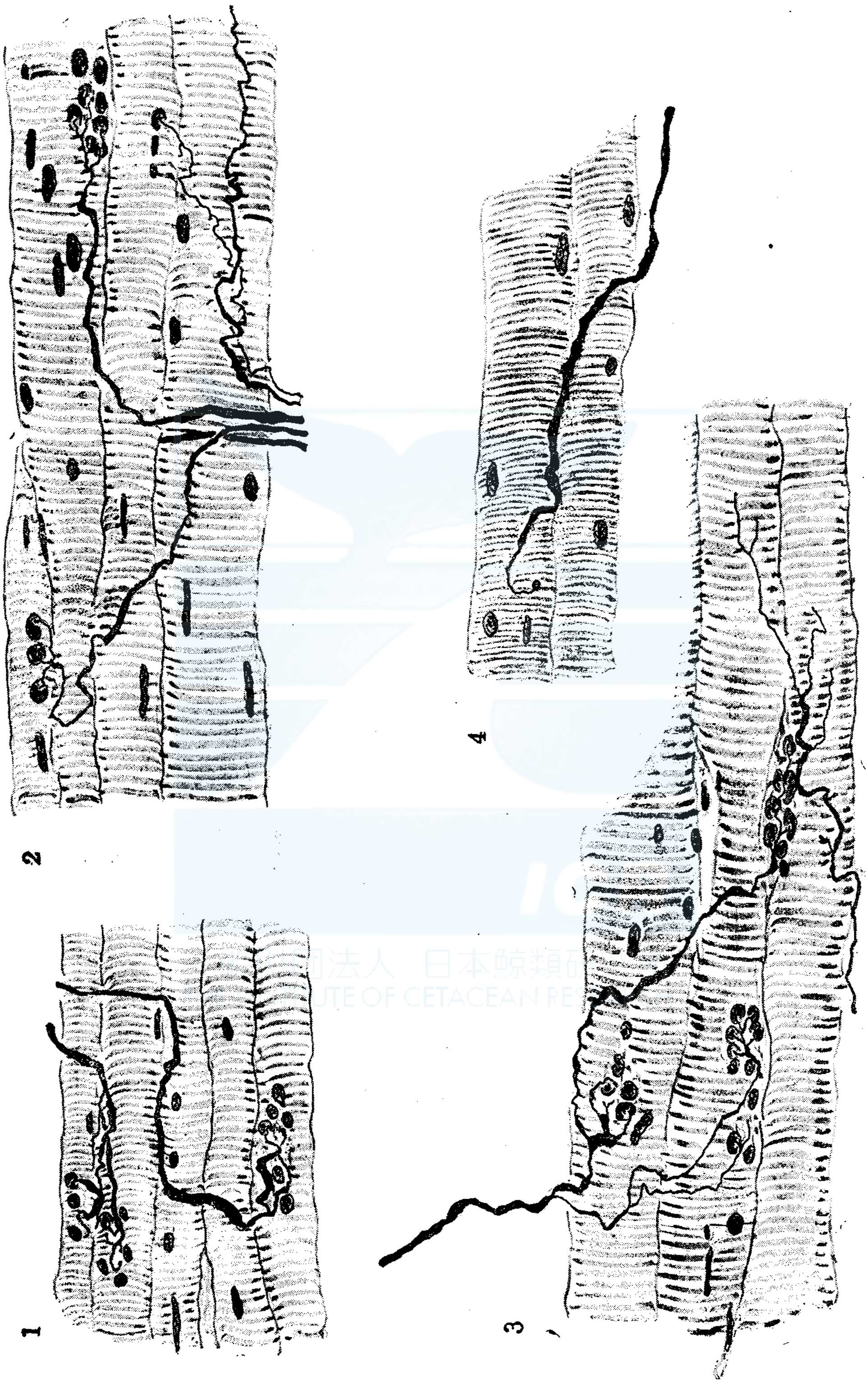


Fig. 12. Nerve endings in M. palpebralis medialis of Prodelphinus caeruleo-albus

a, Pars medialis b, Pars lateralis

Fig. 13. Nerve endings in M. retractor bulbi of *Prodelphinus caeruleo-albus*

palp. med.) and in Fig. 13 (m. retractor bulbi). A precise description of these endings and the comparative anatomical discussions upon them are not needed here, for we find no remarkable difference or peculiarity, compared with them in other animals.

The motor nerve endings in the extrinsic eye muscles have been studied by many authors, viz. Retzius (1892), Hamada (1928), Hines (1931), Woollard (1931), Yokomatsu (1932) etc., for various kinds of animals, but never for the whale. In the huge amounts of literature, however, no remarkable difference has ever been reported as to the anatomy of nerve endings between the trochlearis, the abducens and the oculomotorius. For, all of the previous authors who have studied this problem treated always the eye muscles as a whole, without paying attention to each muscle separately. I myself compared the terminal branchings, terminal buttons etc. between the abducens in m. palpebralis lateralis and pars lateralis m. retractoris bulbi and the oculomotorius in m. palpebralis medialis. But I failed to see any noteworthy difference between the two. All of these muscles exhibited very similar nerve endings, notwithstanding whether the examined muscle bundle belongs to pars medialis of the retractor, the medial palpebralis, to the lateral palpebralis or to pars lateralis of the retractor. The same histological research was performed also on the extraocular muscles of the cat, but with the similar results.

D. MICRODISSECTION OF THE NERVE BUNDLES IN A DOLPHIN, PRODELPHINUS CAERULEO-ALBUS

A kind of the sharply snouted dolphin, Prodelphinus caeruleo-albus Meyen, is very common to the sea near Izu Peninsula. And a good opportunity was given me to dissect the extrinsic eye muscles of this dolphin, and I found that, though the relations of nerves and muscles in question are quite the same as in other whales, branches from the oculomotorius to the retractor are relatively simple in this dolphin and the distance between the anatomosis *a* and the branching of bundle *b* is considerably shorter than in other whales. So I endeavoured to separate and trace the distal course of the bundle *a* along the oculomotor nerve. Using sharp pointed pincettes and needles under the binocular microscope, the bundle *a* was dissected distalwards. The result is shown in Fig. 14, which indicates clearly that the branches innervating the medial portions of the retractor are really continuous with the abducent nerve via the anastomosis.

Thus finally I believe to have succeeded in proving that all portions of the retractor are innervated also in the whale by the abducens, though some of the nerve fibers supplying the medial portions of this muscle run temporarily in the trunk of the *oculomotorius* and look like branches from the latter apparently.

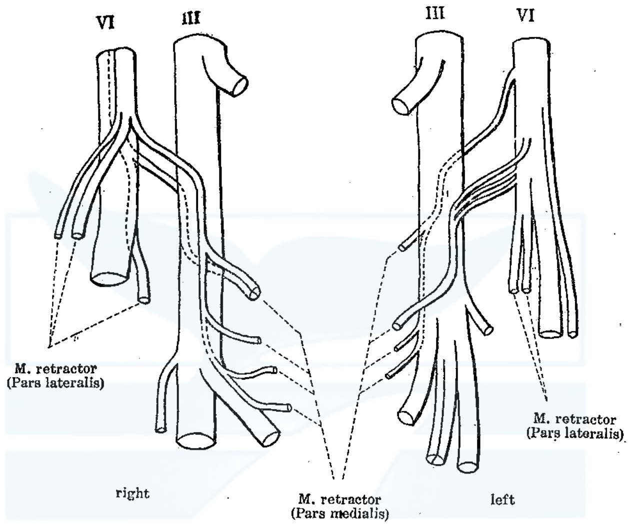


Fig. 14. Innervation of the M. retractor bulbi of Prodelphinus caeruleo-albus

5. Comparative anatomical study upon the innervation of the retractor bulbi

Then it occurred to me the question, whether the same relation holds good also in other animals. If so, the divergent statements of the previous authors reviewed in Chapter 3 might be easy to understand. In other words, if the anastomosis *a*, being situated in the depth of the orbita, be missed in observation, the peripheral branches would be taken very possibly for branches of the oculomotor nerve itself. For this sake the eyes of cats, dogs and rabbits were dissected with greatest caution. But, as shown in Figs. 15 and 16, such relations as seen in the whale were never present in these animals. Neither the anastomosis between the abducens and the oculomotorius nor branches which, arising from the latter, innervate the retractor were found. Hence this type of innervation of the retractor is for

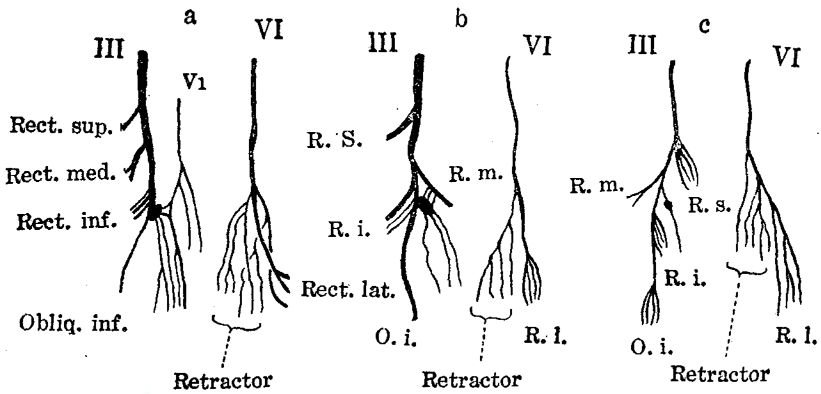


Fig. 15. Innervation of the M. retractor bulbi of cat (a), dog (b) and rabbit (c)

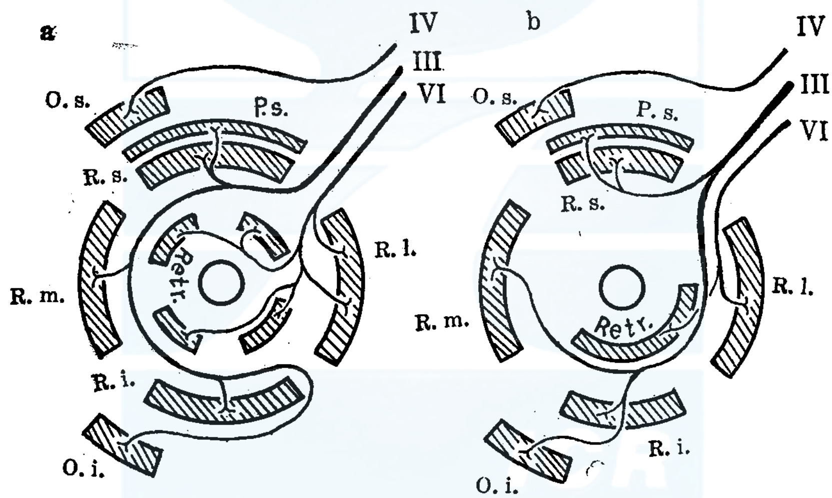


Fig. 16. Diagram to show the innervation of the extrinsic eye muscles of cat (a) and rabbit (b) (left eye, anterior view)

the present to be considered as peculiar to the whales[1].

Additionally I wish to mention a bold assumption upon the cause why a number of authors such as Schwalbe (1879), Du-Bois Reymond (1907) etc. have incorrectly thought of the dual innervation of the retractor from the abducens and the oculomotorius. In the mammals

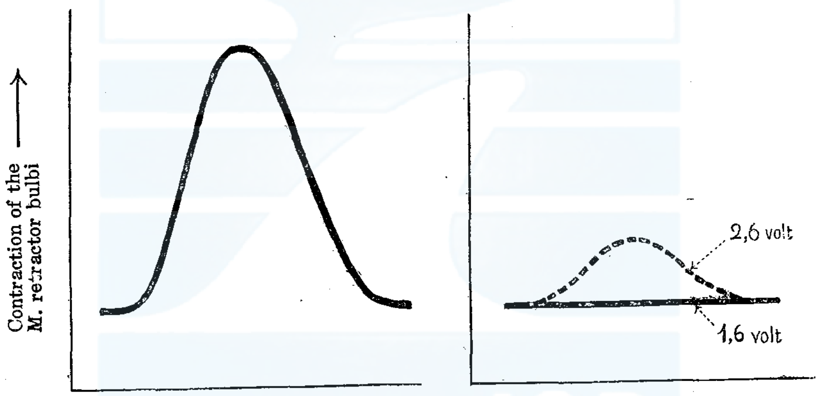
1) For me it is difficult to understand, why Rapp, Stannius, Weber and Cords did not find this peculiarity in the whale. Phocaena and Hyperoodon which they used as the materials may lack in this peculiaritry. But I can hardly surmise such a possibility.

examined by me, cat, dog and rabbit, some of the nervi ciliares breves arising from the ciliary ganglion go winded around the retractor or penetrate this before they reach the optic nerve. Because of this somewhat confusing course, they might have been taken as terminating in the retractor itself[1].

6. *Physiological studies upon the retractor bulbi of the cat*

A. INNERVATION OF THE RETRACTOR

According to Hopkins and Nishi, Foltz (1862) and Key-Abergs (1934) examined physiologically the innervation of the retractor respectively in the horse and in the rabbit. I myself carried out a few physiological experiments upon the retractor bulbi of the cat. The result is shown in Fig. 17. When the trunk of the abducens is stimulated with electri-



a. Electric stimulation of the N. abducens

b. Electric stimulation of the N. oculomotorius

Fig. 17. Experimental study upon the innervation of the M. retractor bulbi (cat)

city, the retractor contracts intensely, while it does not show any contraction by stimulation of the oculomotor nerve. This observation is quite consistent with the macroscopic dissection illustrated in Fig. 15. In Fig. 17 *b* one sees a slight contraction of the retractor by stimulation of the oculomotorius. Perhaps, this may be due to collateral current, presence of which could be proven with the tester.

1) Cords said the same thing, too, though briefly (p. 243, foot-note 2).

B. THE FUNCTION OF THE RETRACTOR BULBI

Together with the above mentioned experiments, I attempted to know the real function of the retractor muscle, for the name "m. retractor bulbi s. oculi" is one which was given by the anatomists such as Stannius, Benz, Gegenbaur etc. probably from purely morphological standpoint, and we have had seemingly no definite, physiological proof to show the appropriateness of this name. According to Cords, some authors assumed other functions for this muscle; for example, Milne-Edwards, Stannius, Straus-Durkheim, Le Double, Ellenberger-Baum thought that it might merely cooperate with the recti muscles. Motais and Martin supposed, on the other hand, that it might serve to support the eyeball for the purpose to allow the higher activity of the straight and oblique muscles (m. suspensorius oculi).

To answer this problem, I stimulated the nerves and muscles individually with the electrode, examining the movements of the eyeball. The details of my results are omitted here. The conclusive remarks are represented by Fig. 18; that is, the recti and obliqui muscles rotate the eyeball by their contraction, but do not retract the eyeball at all, while the retractor muscle pulls backward the eyeball strikingly, without causing any rotation.

	Retraction of the Bulbus oculi	Rotation of the Bulbus oculi
When the straight or oblique muscle contracts	+++	±
When the M. retractor bulbi contracts	±	+++

Fig. 18. Experimental study upon the function of the M. retractor bulbi (cat)

Thus, it became doubtless that the retractor bulbi serves almost exclusively for the retraction of the eyeball; in other words, it deserves the name quite adequately also from the physiological aspect.

7. *Motor nucleus of the retractor bulbi in the brain-stem*

The intramedullar location of the motor nucleus for the retractor bulbi has not yet been determined. According to Kappers, Huber and Crosby (1936), some authors have accounted the so-called accessory nucleus of the abducens for it. But this nucleus, which generally exists in mammals including man (Terni, Preziuss, Addens etc.), and on the other side interpreted as the "dorsal facial nucleus" (van Valkenberg, Kappers), does not seem in reality to send fibers either in the facial or in the abducent nerve. Furthermore, if we recollect that the retractor bulbi is absent in the primates including man, while this cell group is well developed in them, it is quite unreasonable to regard those nerve cells as the nucleus innervating the retractor. In my opinion, such a nucleus may exist somewhere in the brain-stem, probably occupying a portion in the nucleus nervi abducentis. The reason, why I supposed so, is thus:

The fibers of the abducens going to the retractor amount to about 2,000 in a fetus of the Blue whale, making nearly one third or one fourth of all the fibers of this nerve (Table 2), and they can be followed proximalward as relatveiy definite parts within the trunk of the abducens[1]. In other words, the nerve fibers supplying the retractor are well localized within the abducens. I guess, such a localization may also exist in its original nucleus.

So I studied at first the comparative anatomy of the abducens nucleus by serial sections stained with the Pal-Weigert method, paying special attention to the morphological difference of this nucleus between animals with and without the retractor muscle. But no remarkable difference could be found, which is available for this purpose[2].

Secondly, I performed degeneration-experiments using a few cats as the material. Because of technical difficulty, however, the operative removal of the retractor bulbi was not successful. So the lateral rectus muscle of one side was extirpated together with its nervous insertions; the retractor with its nerves remained intact. After the lapse of ten or fourteen days the cat was killed and the brain-stem was fixed in alcohol, 20 μ thick sections were prepared serially and stained with thionin. At the same time, utilizing the osmic acid, the retrograde degeneration of the lateral rectus fibers of the abducens and the intactness of the retractor fibers were examined. The serial sections of the brain-stem revealed, however, no marked change either in the root fibers of the abducens or in the nerve cells of the original nucleus of the abducens.

It seems, injuries on such peripheral extremities of root fibers do not bring forth any remarkable tigrolysis in their original nerve cells. But the cells in the rostral portion of the abducens nucleus showed a

1) In the abducent nerve of the cat, I found the retractor supplying fibers numbered about 300, occupying approximately one fourth of the total fibers of about 1200.

2) Concerning the comparative anatomical study of the nucleus n. abducentis, Fuse's detailed work published in 1912 teaches us very much.

slight tencency of tigrolysis on the operated side, whereas the caudal portion looked perfectly intact. At present I am inclined to think, that the rostral part of this nucleus may supply fibers to the lateral rectus, while the caudal portion may send them to the retractor muscle. Naturally I can have no definite opinion upon this problem.

8. *Sensory fibers of the retractor bulbi and of other extrinsic eye muscles in the whale*

Though the retractor bulbi is said to have no sensory innervation (Huber, 1899, 1900, etc.), I observed in this muscle of the whales as well as of the cat many nerve endings, which are very much like the sensory ones. Some of them are illustrated in Fig. 13 (*b*, 2, 3). These endings, especially that shown in Fig. 13, *b*, 3 resembles to a high degree the grape-like ending (terminaison en grappe) described by Tschiriew (1879), who explained them as a young, undeveloped form of the motor end-plate. Retzius (1892) too called such endings as "atypical" motor ones. On the other hand, Bremer (1882), Huber (1899), etc, took them, being situated epilemmally, for sensory endings in the skeletal muscles, and also in Dogiel's excellent work on the sensory endings in the extrinsic eye muscles (1906) similar endings were described as sensory and illustrated very precisely. Though some recent anatomists, Hines (1931) etc., were of the opinion that those endings, lying sometimes hypolemmally or coming from an axis cylinder which constitutes a medullated nerve fiber continuing to motor end-plates, might be motor in nature, it is more generally believed that at least some of those grape-like endings are of the sensory character (Kulchitsky, 1925; Hinsey, 1927; Woollard, 1931 etc.)[1,2].

My macroscopical observations upon the sensory nerves to the retractor of the whale, are shown in Fig. 19; the ophthalmic nerve (V_1 in this figure) is seen supplying thin branches to the retractor[3]. In

1) Boeke (1927) said that, though the most of grape-like endings are either motor or sensory, some of them are of the sympathetic nature.

2) In relation to the sensory endings in the extrinsic eye muscles, Cooper, Daniel and Whitteridge's recent paper (1949) is very important. By recording impulses in the nerve from the inferior obliquus of goats during stretch or active contraction of the muscle, they obtained physiological evidence for the presence of proprioceptors in this muscle. They ascribed however such a proprioceptive function to the muscle spindles.

3) The ophthalmic nerve of the whale is composed of two main branches. One of them takes the course similar to the nasociliary nerve in other mammals and man (V_{1a} in Fig. 19), while the other appears to correspond to the lacrimal nerve (V_{1b} in Fig. 19).

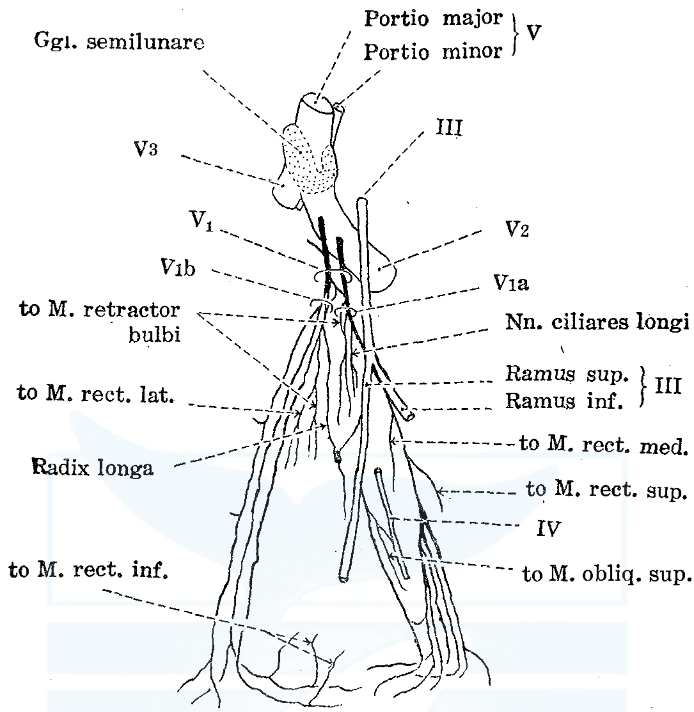
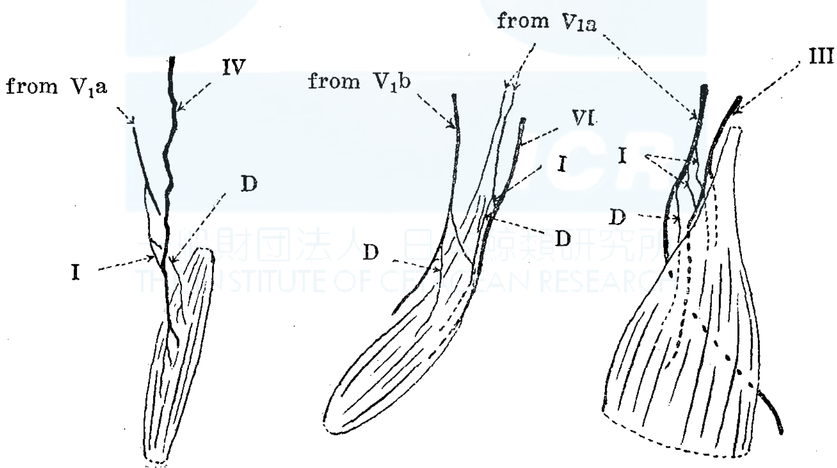


Fig. 19. Sensory innervation of the external eye muscles of the whale (1) (Fetus of the Sperm whale)



M. obliq. sup. M. rectus lat. M. rectus sup.

D: direct insertion I: indirect insertion

Fig. 20. Sensory innervation of the external eye muscles of the whale (2)

this figure, furthermore, the sensory branches to other extrinsic eye muscles are illustrated. Examining these nerves, a remarkable feature quite different from the case in man is noticed. For, as described well in Schwalbe's textbook (1881), in man the sensory fibers to the extrinsic eye muscles, branching from the trunk of the ophthalmic nerve near the sinus cavernosus or at the entrance of the orbita, go immediately into the trunk of the oculomotorius, trochlearis or of the abducens and run together with those motor nerves until their destinations. In the whale, on the contrary, the sensory nerves course independently for a long distance until very near their insertions to the muscle. Though sometimes they run along with the motor nerves, the adhesion or union takes place only in the very vicinity of their terminations (indirect insertion in Fig. 20). Even in such cases, some of the sensory nerves reach the muscle quite independently from the motor nerves (direct insertion in Fig. 20).

Concerning the sensory fibers of the extrinsic eye muscles of rabbit, cat and monkey, Tozer and Sherrington (1910) stated that nearly all of them run from beginning to end of their ocurse within the motor nerves such as trochlearis, oculomotorius and abducens, while the trigeminal nerve has nothing to do with the sensory innervation of these muscles. Woollard (1931) and Hines (1931) also said the same for rabbit, dog, cat, rat etc. Their reason for this conclusion is, that almost all of the intramuscular nerve endings, both of motor and sensory nature, disappeared, after the motor nerves were severed at their exits from the brain-stem. According to Hines, those sensory nerves have their origin in the upper portion of the nucleus mesencephalicus of the trigeminal nerve.

In the present work no definite evidence was obtained to settle the problem, whether the extraocular muscles of tne whale receive also such sensory fibers other than the above mentioned branches issuing from the ophthalmic nerve.

Summary

1) The musculi palpebrales of the cetacean eye are of an unique existence throughout the animal kingdom. The motor innervation of them is quite the same as that of four straight muscles, which insert to the eyeball; namely, the lateral palpebralis is supplied by the abducens, while the other three are innervated by the oculomotorius.

2) The musculi obliqui and the innervations of them show nothing

peculiar in the cetacea, with one exception that the ocular insertion of the inferior obliquus is sometimes divided into two portions.

3) The ciliary ganglion, the presence of which has not yet been clarified in the cetacea, exists in all of Mystaco- and Odontoceti treated in the present work, though always rather in vestigial conditions.

4) The retractor bulbi is remarkably well developed in the whales, and is divided into four portions: Pars superior medialis and lateralis, Pars inferior medialis and lateralis.

5) The retractor bulbi of the whale is apparently innervated doubly by the abducens and by the oculomotorius, each nerve supplying the lateral and medial portions of this muscle respectively. But the branches innervating the medial portions are, though they appear to arise from the oculomotorius, nothing but fibers which belong essentially to the abducens and have coursed only temporarily in the trunk of the oculomotorius. Namely, all the portions of the retractor are supplied in the whale exclusively by the abducens just like in all other animals, whose retractor receives direct branches from the abducens only. Such a temporary course of the abducens fibers via the oculomotorius trunk is very peculiar for the cetacea.

6) The name "musculus retractor bulbi" is appropriate for this muscle, as my experiments on the cat's eye resulted, that its contraction caused a striking retraction of the eyeball, while the recti and obliqui muscles brought forth merely rotating movements of the eyeball.

7) There seems to be some possibility that the nerve cells supplying motor fibers to the retractor are localized in the caudal part of the nucleus n. abducentis.

8) The retractor bulbi as well as the other extrinsic eye muscles receives in the whale sensory innervation from the ophthalmicus.

9) The sensory nerves of the extrinsic eye muscles show in the cetacea a different feature from those in man. In the former they run from the ophthalmic nerve quite independently until their insertions to the muscles, while in the latter the sensory nerves course nearly through the whole length united with the motor nerves, viz. oculomotorius, trochlearis, and abducens.

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