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The Eye Muscles and their Innervation in the Gobiid Fish *Tridentiger trigonocephalus*

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Abstract The morphology and innervation of the six oculomotor muscles in the gobiid fish *Tridentiger trigonocephalus* are described. Every rectus muscle is composed of two types of muscle fibres. Muscles attach onto the cartilaginous or fibrous sclerotica. Oblique muscles attach onto the ethmoidal plate; recti muscles attach onto the parasphenoid or a thick fibrous membrane. There is no myodome. The common oculomotor nerve is composed of four bundles, the trochlear and the externus of two. The two kinds of fibres of the lateral rectus and the two distinct bundles of the nerve VI suggest a possible homology between this muscle in fishes and the lateral rectus+retractor bulbi in mammals.

The dorsolateral position of the eyes and the platytrabic form of the skull in gobiids led us to study the extraocular (oculomotor) muscles and their innervation. In spite of a good number of works dealing with this subject in fishes (Van Gehuchten, 1895; Allis, 1897, 1902; Norris and Hughes, 1920; Norris, 1925; Oliva, 1965; Sterling, 1977; Freihofer, 1978; Easter, 1979; Graf and McGurk, 1985; Thomot and Bauchot, 1985), there is no data concerning the gobiids.

Material and methods

We used juveniles of *Tridentiger trigonocephalus* (Gill), and notably a specimen of 32 mm total length, on which our description is based.

The study of histological series (after fixation in Bouin's fixative, 0.01 mm sectioning and staining by cresyl violet), and the method of graphical reconstruction allowed us to establish the disposition of each oculomotor muscle from origin to insertion and to follow the pathway of the nerves III, IV and VI from their central nervous system nuclei to the innervated muscles.

Results

1. Oblique muscles. The fibres of these muscles show no visible differences in their aspect, coloration or volume. The obliquus inferior is slightly longer (1.2 mm) than the superior (1.12 mm). Their fixation on the skull is situated in an anteromedial zone of the eye-socket, without any anterior myodome, on the cartilaginous ethmoidal horizontal plate, in front of the anterior border of the cartilaginous mesethmoid.

A) Obliquus superior (O. S.) (Figs. 1a–c, 2): Its proximal region is divided into three fascicles, each of which has its proper fixation on the skull. The most lateral fascicle lies most rostrally and its fixation on the ethmoidal plate is inside the sagittal plane. The middle fascicles are slightly more posterior and are fixed in the sagittal region just after crossing the sagittal plane. The most medial and most caudal fascicles are fixed on the ethmoidal plate in the contralateral region, after crossing the sagittal plane dorsally to the horizontal part of the ethmoidal plate and anterior to the mesethmoid. The general orientation of the muscle is vertical. It is directed upward and slightly laterocaudally. It runs medial to the medial rectus (D. Int.) and lateral to the olfactory nerve behind its foramen. The muscle runs to the anteromedial limit of the eyeball, adheres to the dorsal surface of the cartilaginous ring of the sclerotica and, a little more posteriorly, inserts on the fibrous sclerotica in the anterodorsal region of the eye.

B) Obliquus inferior (O. I.) (Figs. 1b–d, 2): Its fixation on the skull is situated in the sagittal region on the horizontal part of the cartilaginous ethmoidal plate, a little posterior to the zone of fixation of the middle fascicles of the superior obliquus. Its general orientation is horizontal. It is directed laterocaudally, runs ventral to the medial rectus (D. Int.), then approaches the anteroventral limit of the eyeball and, more caudally, in the middle region of the eye, crosses the inferior rectus (D. Inf.) Most caudally, it inserts on the cartilaginous ring of the sclerotica, near the medial border in the ventrocaudal region of the eyeball. This zone of fixation is 0.3 mm caudal to that of the rectus inferior on the same cartilaginous ring of the sclerotica.

2. Recti muscles. They show two types of fibres each with a different aspect, coloration and volume. These differences are more visible in some muscles, but not always along their whole length. The superior and inferior recti have a length (1.3 and 1.18 mm) comparable to that of oblique muscles, while the lateral and medial recti are almost twice as long as these (2.6 and 2.2 mm). There is no posterior myodome and the zones of fixation of these muscles on the skull are far from one another. The cranial fixation of the inferior recti is not made on a skeletal element but on a thick conjunctival membrane.

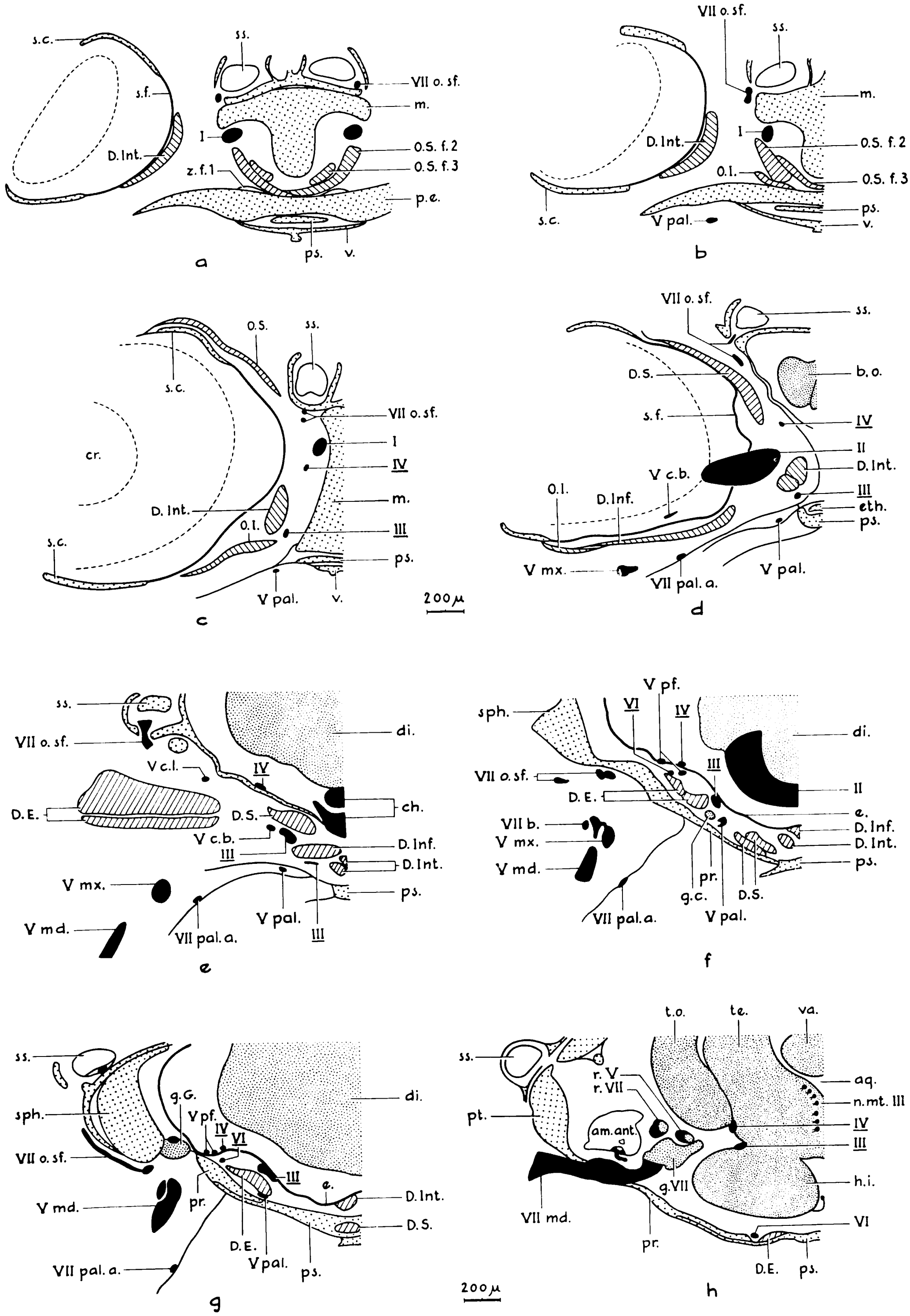
A) Superior rectus muscle (D. S.) (Figs. 1d, e, 2): Its skull fixation is in a short gutter near the sagittal plane situated about 0.4 mm posterior to the caudal border of the eyeball and 0.1 mm posterior to the optic chiasma, on the parasphenoid. The gutter becomes blind posteriorly and in this way forms something like a little individual myodome. The muscle has a general orientation in an oblique dorsolatero-anterior direction. It first runs laterally for 0.03 mm and then dorsomedially to the eyeball, without crossing any other muscle. Anteriorly, it becomes thicker, adheres to the surface of the fibrous sclerotica in the dorsomedial part of the eyeball and attaches to the cartilaginous ring of the sclerotica on the middle dorsal portion of the eye.

B) Inferior rectus muscle (D. Inf.) (Figs. 1d, e, 2). Its cranial fixation is not on a skeletal element but on a thick conjunctival membrane, in tight connection with the ectomeninges. This fixation is ventral to the chiasma and is situated about 0.05 mm dorsorostrally to the fixation of the superior rectus muscle. In this region, the fibers pass out of the sagittal plane and cross the fibres of the contralateral muscle.

The general orientation of this muscle is in an oblique latero-ventro-rostral direction. It runs laterally, reaches the ventromedial border of the eye without crossing any other muscle, then adheres to the ventral limit of the eyeball. From there it passes laterorostrally, dorsally to the inferior obliquus and attaches onto the cartilaginous ring of the sclerotica, near its medial border, in the mid-ventral region of the eye. This fixation is slightly posterior to that of the superior obliquus and 0.3 mm anterior to that of the inferior obliquus on the same ring of the sclerotica.

C) Lateral rectus muscle (D. E.) (Figs. 1e–h, 2): Its cranial fixation is the most posterior of all extraocular muscles, beyond the level of the caudal border of the hypothalamus, beyond the vascular sack and even the roots of the otic nerve VIII.

Fig. 1. Transversal sections of the head of *Tridentiger trigonocephalus* at different levels, from rostral (a) to caudal (h), in the region of the extraocular muscles and oculomotor nerves. The muscles are represented by hatchings, nerves in full black, cartilage and bone by loose dottings, central nervous system and ganglia by thick dottings. The levels of the sections are pointed out in Fig. 2 by parallel lines, with the letter of the corresponding transverse section in Fig. 1. am.ant., anterior ampulla of the membranous labyrinth; aq., aqueduct of the mesencephalon; b.o., olfactory bulb; ch., optic chiasma; C.H., Haller's campanula; cr., lens; D.E., lateral rectus muscle; di., diencephalon; D.Inf., inferior rectus muscle; D.Int., medial rectus muscle; D.S., superior rectus muscle; e., ectomeninge; eth., ethmoid; g.c., ciliary ganglion; g.G., Gasser ganglion; g.VII., ganglion of the VIIth nerve (facialis); h.i., inferior lobe of the hypothalamus; n.mt.III, motor nucleus of the IIIrd nerve; m., mesethmoid; O.I., inferior oblique muscle; O.S., superior oblique muscle; O.S.f.2, second fascicle of the superior oblique muscle; O.S.f.3, third fascicle of the superior oblique muscle; p.e., ethmoidal plate; pr., prootic; ps., parasphenoid; pt., pterotic; r.c.l., radix ciliaris longa; r.V., root of the Vth (trigeminal) nerve; r.VII., root of the VIIth (facial) nerve; s.c., cartilaginous ring of the sclerotica; s.f., fibrous sclerotica; sph., sphenotic; s.s., sensory canal; te., tegmentum; to., optic tectum; v., vomer; va., valvula cerebelli; z.f.1, fixation zone of the first fascicle of the superior oblique muscle; V c.b., ciliaris brevis ramus of the V; V c.l., ciliaris longus ramus of the V; V md., mandibularis branch of the V; V mx., maxillaris branch of the V; V pal., palatine branch of the V; V pf., profundis branch of the V; VII b., buccalis branch of the VII; VII md., mandibularis branch of the VII; VII o.sf., ophthalmic superficialis branch of the VII; VII pal.a., anterior palatin branch of the VII.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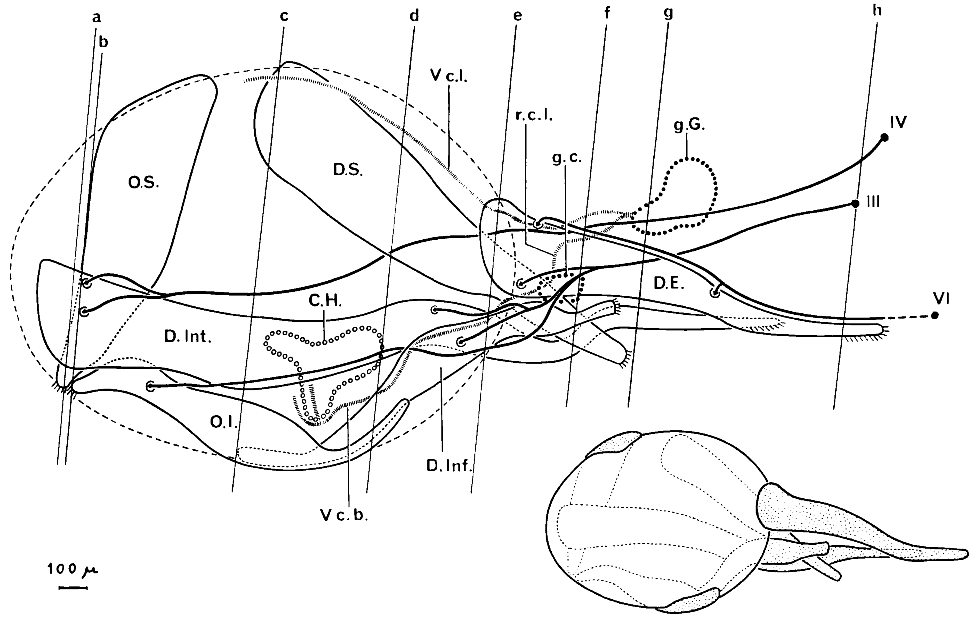

Fig. 2. Extraocular muscles and oculomotor nerves of *Tridentiger trigonocephalus*. Top: Graphical reconstruction in lateral projection made from transverse sections of the head. Parallel lines correspond to the levels illustrated in Fig. 1. Bottom: Representation, in lateral view, of the disposition of the extraocular muscles in their relation to the eyeball. As for abbreviations, see Fig. 1.

This fixation is situated in an anteroposterior shallow gutter on the posterior part of the parasphenoid, near the sagittal plane and is contiguous to its contralateral homologue from which it is only separated by a thin septum. These two gutters are posteriorly covered by the ventromedial region of the prootic and opisthotic and make a little cavity which is blind posteriorly and may be considered the counterpart of a little individual myodome special to the two lateral recti.

The general orientation of the lateral recti muscles is horizontal. They run anteriorly and progressively laterally. Their gutters are separated by a median thickening of the parasphenoid, about 0.4 mm from their caudal end. A little farther (0.8 mm), in the same horizontal plane, they lie between the parasphenoid and the ectomeninge, lateral to the medial zone of fixation of the medial recti. From this region, the lateral recti take an oblique orientation dorso-latero-rostrally. They leave their parasphenoid gutter, adhere to the intracranial surface of this bone and, dorsally, to that of the prootic, progressively farther from the ectomeninge. The lateral recti pass laterally to the ciliary ganglion and, about 0.1 mm in front of the anterior border of the prootic, they bend laterally and a little rostrally to reach the eyeball and attach onto the lateroposterior region of the cartilaginous ring of the sclerotica.

D) Medial rectus muscle (D. Int.) (Figs. 1a–g, 2): It is the longest of all extraocular muscles (2.6 mm). Its general orientation is horizontal, with a thin and long caudal region (1.5 mm) made of two contiguous dorsal and ventral fascicles, as well as a thicker and shorter (1.1 mm) rostral one, in which the two fascicles mingle.

For almost all its length (except in the 0.16 mm most anterior), the caudal part is situated very near the sagittal plane, from which it is separated only by a thin septum. The dorsal fascicle caudally becomes rapidly thinner and, after about 0.8 mm, lies like the ventral one, under the inferior recti. Here, it divides into several bundles of fibres, each fixing onto a thick conjunctival membrane in tight contact with the ectomeninge. This fixation is a little more caudal than that of the inferior recti and lies a little behind the optic chiasma. At this same level, the caudal end of the superior rectus ventrally crosses the ventral fascicle of the medial rectus and attaches more caudally in a cavity of the parasphenoid, near the sagittal plane. The ventral fascicle is thicker and extends more caudally and ventrally until it reaches the parasphenoid where it divides into bundles which attach to a shallow gutter situated near the median thickening of the parasphenoid. This gutter is not blind caudally; it lies in the same horizontal plane as its contralateral equivalent and between the gutters in which lie the lateral recti present in the rostral part of their horizontal path. The ventral fascicle anteriorly contacts the ectomeninge and then, more caudally, lies between it and the parasphenoid.

The rostral part of the muscle begins at the level where the optic nerve passes out of the eyeball; posteriorly it lies between the mesethmoid and the ventromedial border of the eye. More rostrally, the muscle progressively approaches the sclerotica and the inferior oblique muscle; it crosses this muscle dorsally and the superior oblique muscle ventrolaterally. The medial rectus muscle adheres to the surface of the sclerotica in the angle between the two oblique muscles and attaches onto the anteromedial part of the eyeball. This fixation on the fibrous sclerotica occupies a large caudal area: more than 0.25 mm from the rostromedial border of the cartilaginous ring.

3. Extraocular (oculomotor) nerves. The extraocular nerves (III, IV and VI) show differences in their thickness and length. The thickest is the (common) oculomotor (III) which innervates four of the six muscles. The trochlear (IV) and the abducent (VI) innervate one muscle each and have about the same diameter but differ in their length, the IV being the longer. From the motor nuclei, the caudal and most ventral is that of the VI (in the ventral region of the medulla oblongata) while those of the nerves III and IV are contiguous in the caudal part of the tegmentum, the trochlear one being more posterior.

A) Oculomotor (III) nerve (Figs. 1c–h, 2): This nerve, which innervates four of the six extraocular muscles, is the thickest of the three oculomotor nerves.

1) Nucleus and intracerebral pathway: At the level of the anterior part of the valvula cerebelli and of the inferior lobes of the hypothalamus, near the median plane of the tegmentum and the ventricular lining of the mesencephalon, lies a group of voluminous nerve cells from which start the fibres of nerve III (Fig. 1h). These nerve cells have the same location as those described by Graf & McGurk (1985) in *Carassius auratus*, which form the four sectors of the nucleus of the IIIrd nerve. From this nucleus, the axons run ventrolaterally and reach the border of the brain between the bases of the tegmentum and the inferior lobes of the hypothalamus, at the level of the rostral border of the valvula cerebelli and the foramen of the mandibular nerve of the facial nerve (VII).

2) Extracerebral pathway: The nerve runs rostroventrally and is almost straight until the level of the optic chiasma. On the first 0.25 mm, it runs near the limit of the diencephalon; more rostrally, it passes laterally and, about 0.64 mm from its way out of the brain, it lies between the brain and the prootic, medially to the lateral rectus muscle from which it is separated by the ectomeninges. More rostrally, it goes through the ectomeninge and then lies ventromedially to the lateral rectus muscle and dorsomedially to the ciliary ganglion with which it is in tight contact. Here, it gives off a bundle which, a little more rostrally (0.12 mm), innervates the superior rectus muscle. Then it passes through the ciliary ganglion and out with the ramus ciliaris brevis ventrally, from which it is rapidly separated before dividing into a dorsal and ventral branch. The dorsal branch is subdivided immediately into two bundles: a ventral one which penetrates the inferior rectus dorsally and a dorsal one which penetrates the medial rectus muscle about 1.1 mm in front of its skull fixation. The long ventral branch runs ventromedially under the inferior rectus in its proximal region (under the medial rectus) and then rostrally near the sagittal plane on 0.24 mm. It runs progressively along the level of the optic nerve as it passes out from the eyeball. The ventral branch follows the ventromedial border of the medial rectus muscle until the level at which the latter crosses dorsally the inferior oblique that it innervates about 0.36 mm from its cranial fixation.

B) Trochlear (IV) nerve (Figs. 1c–h, 2): It innervates only one extraocular muscle, the inferior oblique. It has a small diameter and is the longest of the three oculomotor nerves.

1) Nucleus and intracerebral pathway: The motor nucleus of the nerve IV is made of a group of voluminous nerve cells, with the form of a

gamma, situated near the mesencephalic ventricular lining, a little caudally to the nucleus of the IIIrd nerve. From this nucleus, the fibres first run rostromedially. They reach the median linie in a region rostral to the valvula cerebelli and anterodorsal to the commissura gustatoria. They then continue contralaterally in a latero-caudal direction, describing an arc with an anterior convexity. They then follow the contralateral motor nucleus medio-ventro-caudally and leave the brain in the dorsolateral region of the brainstem, at the same level as the Vth nerve, about 0.16 mm from the posterolateral border of the optic tectum, lateral to the cerebellum (Fig. 1h). Thus, the fibres of nerve IV cross the contralateral ones in a transverse tube situated about 0.1 mm in front of the motor nucleus in the valvula cerebelli.

2) Extracerebral pathway: The IVth nerve runs forward in a horizontal plane, between the optic tectum and the tegmentum. About 0.26 mm from its exit from the brain, it is dorsal to the point of emergence of the IIIrd nerve, under the ventral border of the optic tectum. The IVth nerve continues forward in the same position for 0.28 mm and then goes laterorostrally. It crosses the nerve VI and the radix longa, lateral to the ectomeninge and stays in a medial position. More rostrally, it is medial to the lateral rectus muscle and, about 1.40 mm from its exit from the brain, pierces the dura mater, medial to the superior rectus and a little in front of the level of the optic chiasma. It is then medial to the superior rectus and dorsal to the optic nerve in the region where the later penetrates the sclerotica. More rostrally, the IVth nerve runs between the sagittal plane and the medial border of the eyeball dorsal to the medial rectus mucle. About 2.5 mm from its exit from the brain, it is lateroventral to the olfactory nerve, dorsomedial to the medial rectus and under the superior oblique muscles. Here, it divides into two branches, superior and inferior. The first one follows the medial surface of the superior oblique, running between this and the olfactory nerve. About 0.28 mm from its origin, it pierces the superior oblique at a point dorsal to the region where it divides itself into three fascicles. This branch seems to be connected with the most laterocaudal fascicle of this muscle. The inferior branch follows the medial surface of the superior oblique and pierces it just ventral to the region where the two other fascicles are separated, ventral to the olfactory nerve. The existence of these two terminal branches of the IVth nerve, innervating two regions of the superior oblique muscle in *Tridentiger trigonocephalus*, and the presence in *Carassius auratus* of two sectors in the motor nucleus of the IV (Graf & McGurk, 1985) suggest that each branch has its own proper intracerebral nucleus.

C) Abducens (VI) nerve (Figs. 1f–h, 2): This nerve innervates only one extraocular muscle, the lateral rectus, has a small diameter (comparable to that of the IVth nerve) and is the shortest of the three oculomotor nerves.

1) Nucleus and intracerebral pathway: The point of exit of the VIth nerve is the most posterior of the three oculomotor nerves, about 0.5 mm behind the level of the nuclei of the IIIrd and IVth nerves. It is situated in the ventrolateral region of the brain stem, at the same level as the more dorsal anterior root of the VIIIth nerve, about 0.08 and 0.12 mm behind the caudal borders of the vascular sack and the inferior lobes of the hypothalamus. In the brain stem, the fibres run dorso-medio-rostrally from a group of voluminous nerve cells and are caudorostrally elongated in exactly the same position as that of the two sectors nucleus of *Carassius auratus* (Graf and McGurk, 1985).

2) Extracerebral pathway: The nerve VI first runs under the inferior hypothalamic lobes before reaching the ectomeninge, near the gutter of the parasphenoid located by the lateral rectus muscle. It pierces the meninges about 0.72 mm in front of its point of emergence, runs lateral to the lateral rectus and then, about 0.2 mm in front of its foramen and ventral to the nerves III and IV, gives off a medial branch which pierces the lateral rectus on its lateral border. More rostrally (0.08 mm) and laterally, the VIth nerve dorsally crosses the ramus palatinus of the V, ventral to nerve III and then follows the lateral rectus. About 0.32 mm in front of its first branch, the VIth nerve ventrally crosses the radix longa and nerve IV and adheres to the dorsal surface of the lateral rectus. It then ventrally crosses the ramus ciliaris longus and pierces the lateral rectus about 1.5 mm in front of its exit from the brain, just before the lateral bending of this muscle (i.e. about 0.16 mm from its fixation to the sclerotica).

Discussion

The extraocular muscles proceed from the three or four anterior somites and more precisely from their dorsal zone. This last one is itself subdivided into superior or tectocranial and inferior or basicranial parts (Bjerring, 1977). We are far from an agreement among authors as to the correspondence of the different extraocular muscles and the cranial metameres (Allis, 1897; Neal, 1914, 1918; Kesteven, 1945; Bjerring, 1977). Neal (1896), on the basis of innervation, considered the superior oblique (nerve IV) and the lateral rectus (nerve VI) as ventral. The same author, in 1918, divided each myotome into dorsal and ventral parts and gave the following correspondence:

dorsal premandibular myotome: superior and medial rectus (III)
ventral premandibular myotome: inferior rectus and inferior oblique (III)
dorsal mandibular myotome: superior oblique (IV)
ventral mandibular myotome: lateral rectus (VI)
ventral hyoid myotome: lateral rectus (VI)

whereas Bjerring (1977) considered only the inferior oblique as ventral (basicranial) and all other extraocular muscles as dorsal (tectocranial). Our material, using juveniles and not embryos of *Tridentiger*, does not allow us to solve the question.

The presence of two types of fibres in the extraocular rectus muscles of *Tridentiger trigonocephalus* seems to be shared by a lot of other teleostean fishes and even by some other species of vertebrates, as is shown by histochemical and ultrastructural studies. Recent studies on lamprey extraocular muscle distinguish either two (Nakado and Aoki, 1982) or three (Witalinski and Labuda, 1982) types of muscle fibres. In *Carassius* and *Rana*, Kilarsky and Bigaj (1969) have shown two functionally different categories of fibres in the oculomotor muscles: red (slow) and white (fast). Kordylewski (1974) and Davey et al. (1975) studied the ultrastructure of these two types of fibres in *Gobio gobio* and in *Carassius*. Two types of fibres were also described in extraocular muscles of amphibians (Nowogrodzka-Zagorska, 1974) and selachians (Witalinski and Loesch, 1975) and in the lateral rectus of *Cephaloscyllium isabella* (Housley and Montgomery, 1984). In reptiles and birds, Kaczmarski (1969, 1970) and Alvarado-Mallart (1972) found three types of fibres and in mammals, Pachter (1982) described six types of fibres of these muscles. For Kilarski and Bigaj (1969): "Slow fibers would be responsible for a tonic muscle action in pursuit movements as well as for the slow phase of labyrinthine reflexes. White fibers would be responsible for extremely rapid jerking movements of the eyeball, such as occasionally be observed in fishes." More cautiously, Davey et al. (1975) wrote: "The connection, if any, between the two types of muscle fibre and fast and slow movements of the eye produced naturally, it not known for any species". Nevertheless, it is probable that this complex muscle organization is needed for precise and multiple movements in these animals.

The absence of anterior and posterior myodomes as shown in *Tridentiger trigonocephalus*, is often found in teleosts (Daget, 1964) but the individual fixation of the rectus muscles is rare. In *Gobius* sp. and some other teleost species as in *Tridentiger*, the dorsal part of the myodome of the Salmonidae is only present and houses the lateral rectus (Holmgren and Stensiö, 1936).

The fixation of the obliques, as seen also in the young of *Ameiurus nebulosus*, is made on the ethmoidal plate (Kindred, 1919), while in juvenile *Anguilla vulgaris* it occurs on the internasal septum (Norman, 1926). In *Nannocharax fasciatus*, the superior oblique attaches onto a sagittal membrane separating the median cavity in the internasal zone, while the shorter inferior obliques attach to the ethmoidal plate (Daget, 1961).

The cranial fixation of the superior oblique through three distinct fascicles, the most medial inserted in the contralateral region, after crossing it symmetrically, has not been described in other species; the functional significance of this anatomical organization is not clear.

The lateral rectus is composed of one bundle only. The subdivision of this muscle into two branches in *Chlamydoselachus anguineus* seems to be specific of this shark (Nishi, 1922).

In its caudal moiety, the medial rectus muscle is made of two fascicles of different lengths. The shorter is attached to a conjunctival membrane and the longer to the parasphenoid (named synpterygoid by Kesteven, 1945). This organization has not been described in other species, either, and suggests that these two fascicles could be homologous to two different muscles associated during phylogenesis.

The cranial fixation of some muscles (superior rectus, dorsal fascicle of the medial rectus) on a conjunctival membrane and not on a rigid skeletal element raises questions concerning the efficiency of these muscles. This organization has already been pointed out in other species for oblique (Daget, 1961, in *Nannocharax fasciatus*) and rectus muscles (Omarkhan, 1948; Daget and D'Aubenton, 1960, in Mormyroidei).

The fixation to the eyeball, either on the fibrous part of the sclerotica (medial rectus and superior oblique) or on the cartilaginous ring of the sclerotica (other muscles), has not been described in other species.

The innervation of the superior oblique by the IVth nerve, of the lateral rectus by the VIth nerve and of the other four muscles by the IIIrd nerve is common among vertebrates. This scheme is different from that of the cyclostomates, in which the nerve VI innervates two muscles, the lateral and inferior recti (Furbringer, 1875).

The contralateral position of the motor nucleus of the IVth nerve, seen in *Tridentiger trigonocephalus* and also present in other species, seems to be a neuroarchitectural organization of general occurrence in fishes. In comparison, observations in the frog (Schwalbe, 1879) or in the cat (Destombes et al., 1979) show that the VIth nerve innervates two muscles originating from the hyoid somite (the lateral rectus and the retractor of the eyeball), an arrangement that does not occur in fishes. It is nevertheless to be noted that, in *Tridentiger*, the VIth nerve innervates, through two distinct branches, two regions of the lateral rectus far from each other. These regions are made of two types of muscular fibres. Is there a homology between the lateral rectus of *Tridentiger* and the ensemble lateral rectus+retractor bulbi of other groups of vertebrates? In favour of this hypothesis is the fact that, while the motor nucleus of the IIIrd nerve is made of four distinct sectors corresponding to the four innervated muscles, the rostrocaudally elongated motor nucleus of the VI, like that in *Carassius auratus* (Graf and McGurk, 1985) suggests an analogy with the organization of evolved vertebrates. Hosokawa (1951), after Allis (1897), gave a table of the different innervations of the retractor bulbi (also named musculus suspensorius oculi, musculus choanoides or posterior rectus), notably in mammals. He has shown that in whales this innvervation, though apparently made by fibres of both nerve III and nerve VI, is actually only due to some fibres of nerve VI which, after an anastomosis, follow the fibres of nerve III to reach their target. In the whales as in the cat (Destombes et al., 1979), the motor nucleus of the VI is made of two sectors, each giving a fascicle innervating either the lateral rectus or the retractor of the eyeball. These two sectors could be related to the double origin (mandibular and hyoid) of the lateral rectus muscle and its innervation, as given by Allis (1897) and Neal (1918).

Conclusions. There is no myodome for the oculomotor muscles in *Tridentiger trigonocephalus*. The obliquus superior is divided into three parts, each of which is independently attached to the ethmoidal plate; the most posterior part is attached to the contralateral part of the plate after crossing with its opposite counterpart. The recti are composed of two kinds of muscle fibres, some of which are attached to the parasphenoid and others onto a thick conjunctive membrane contiguous with the ectomeninge. All oculomotor muscles are attached to the eyeball on the cartilaginous ring of the sclerotica, except for the superior obliquus and the rectus externus, which are attached to the fibrous sclerotica itself.

The common oculomotor nerve (III) is composed of four bundles, one for each innervated muscle. Its motor nucleus lies in the tegmentum, near the mesencephalic ventricular lining, just in front of the cerebellar valvula. The motor nucleus of the trochlear nerve (IV) is contiguous with, but slightly posterior to the motor nucleus of nerve III; it innervates the superior obliquus by two bundles which enter the region where it is divided into three sections. The motor nucleus of the external oculomotor nerve (VI) is the most ventral and posterior; it innervates the rectus externus by two bundles.

The existence of two terminal bundles in nerves IV and VI suggests that each has its origin in a special part of the corresponding motor nucleus. The fact that the rectus externus is comprised of two kinds of fibres and is innervated by two distinct nerve bundles suggests a possible homology between this muscle in *Tridentiger trigonocephalus* and the rectus externus and retractor bulbi muscle in mammals.

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シマハゼの眼筋と神経分布

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シマハゼ *Tridentiger trigonocephalus* の6つの動眼筋の形態と神経分布を調べた．直筋はすべて2つのタイプの筋線維からなっている．各筋肉は軟骨性又は線維性の鞏膜に付着し，また頭骨側では斜筋は篩骨板に，直筋は副蝶形骨又は肥厚した線維性膜に付着する．動眼筋室は前後とも見られない．動眼神経は4本の束からなり，滑車神経と外転神経はそれぞれ2本の束からなる．側直筋に2種類の筋線維があることと，第6脳神経が2本の束からなることは，魚類におけるこの筋肉が哺乳類の側直筋＋眼球牽引筋と相同であることを示唆している．