

Anatomy. — *The eye-muscle nerves of petromyzonts, especially in their general morphological significance.* By J. L. ADDENS. (Central Dutch Institute for Brain-Research, Amsterdam.) (Communicated by Prof. B. BROUWER.)

(Communicated at the meeting of June 30, 1928).

The nuclei and roots of the eye-muscle nerves of petromyzonts, as compared with those of gnathostomes, show a number of differences, which, apart from their systematic value, give rise to some not unimportant conclusions of a general morphological nature. Hitherto these peculiarities were quite insufficiently known or erroneously interpreted. That there is not spoken here of a comparison between cyclostomes and gnathostomes, but between petromyzonts and gnathostomes, is due to the fact that in the other group of cyclostomes, the myxinoids, eye-muscle nerves as well as eye-muscles are totally lacking ¹).

For the present research were used a transverse, a longitudinal and a horizontal series through the brain of the adult *Petromyzon fluviatilis*, all three stained with EHRLICH's haematoxylin. Thickness of sections 18 μ .

To easier understand the following the reader is referred especially to figs. 1 and 2, representing longitudinal reconstructions of the motor nuclei and roots of *Petromyzon fluviatilis* and *Selache maxima*, resp., made after the method devised by KAPPERS. The chart of the shark *Selache maxima* was introduced to make possible the comparison with a less specialized lower vertebrate. Attention is also called to fig. 9, a part of fig. 1 two times enlarged, and with the intracerebral course of the roots indicated.

The remark must yet be made that in the ensuing speculations the cyclostomes, in accordance with the current view, are regarded as the most primitive craniotes extant, though in some respects strongly specialized, and in others reduced. In as far as the latter applies to the eyes, it is of special importance for the conclusions here arrived at regarding the eye-muscle nerves. TRETJAKOFF (1927), it is true, maintains that the eyes of petromyzonts are entirely normal, but, in my opinion, there are several characters suggesting that these organs once possessed a stronger development, among others, their smallness, the total lack of muscle-fibres within them, and the incompleteness of the tectum opticum. Moreover, the very rudimentary condition of the eyes of myxinoids gives additional weight to the surmise that also in petromyzonts, so closely resembling them in structure and life-habits, the visual powers are on the wane.

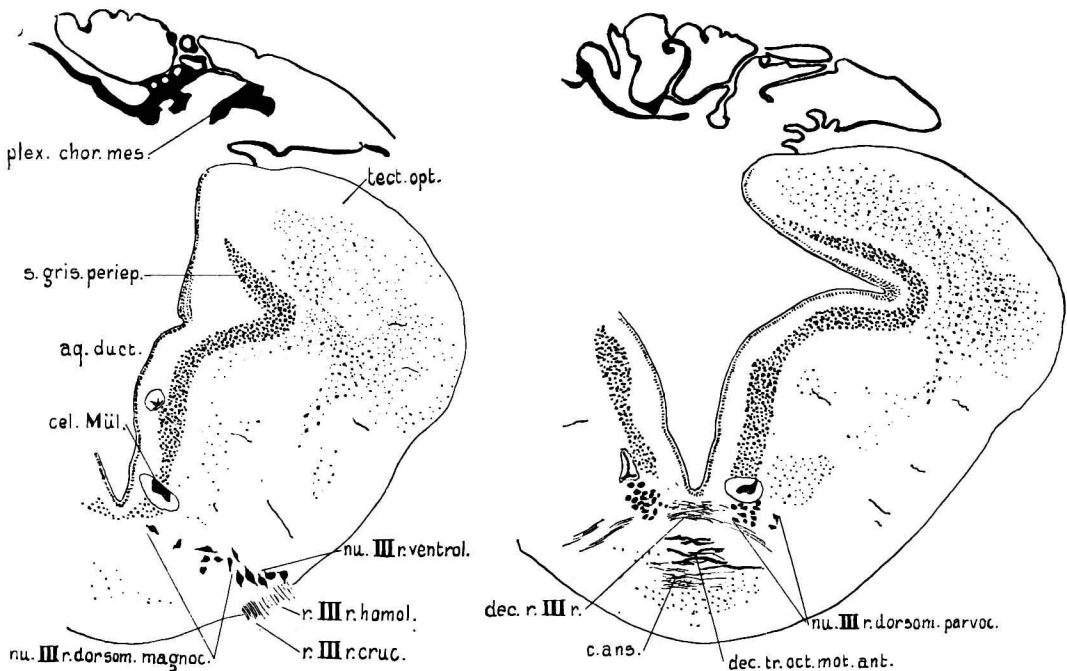
I now proceed to treat of the nuclei and roots of the three eye-muscle

¹) The statement of some text-books that in myxinoids the eyes themselves are entirely absent, is not correct. The eyes and optic nerves are constantly present, although utterly rudimentary and perhaps no longer functional.

of two widely separated divisions, a rostral and a caudal. Of these two nuclei the rostral, which is situated at the same place as the single nucleus of the other vertebrates, is by far the more voluminous. The caudal nucleus, made up of but a small number of cells, lies far back at the level of the beginning of the trigeminal motor nucleus. The root arising from this caudal third nucleus, does not join that from the rostral or principal nucleus, but issues separated from the latter, in what manner we shall see later on.

Under the present heading I shall only deal with the rostral third nucleus and root, as the caudal ones are more aptly discussed together with the abducens.

In the rostral oculomotor nucleus two subdivisions are to be distinguished: a small ventrolateral and a large dorsomedial nucleus (figs. 1, 3 and 4).



Figs. 3 and 4. *Petromyzon fluviatilis*. Cross-sections through the mid-brain at the level of the front and hind parts, resp., of the rostral third nucleus. $\times 40$. cel. Müll, Müllerian cell; c. ans., commissura ansulata; dec. r. III r., decussation of the rostral third root; nu. III r. dorsom. magnoc., big-celled part of the dorsomedial rostral third nucleus; nu. III r. dorsom. parvoc., small-celled part of the dorsomedial rostral third nucleus; nu. III r. ventrol., ventrolateral rostral third nucleus; r. III r. cruc., crossed rostral third root; r. III r. homol., direct rostral third root.

The ventrolateral division lies close to the periphery of the mesencephalon, rather remote from the median plane. In the sagittal series it was noticed that a number of its cells, partly or even completely, lay a little outside the brain (fig. 5), but this could not be found either in the transverse or in the horizontal series. JOHNSTON (1902) observed also that in *Lampetra wilderi* some of the oculomotor cells project beyond the contour of the brain.

The cells of the ventrolateral nucleus are big, and stain intensely with haematoxylin, whereas those of the dorsomedial are smaller, and stain fainter. By these two differences the nuclei under discussion can always be clearly delimited, although they touch each other.

The dorsomedial nucleus can be subdivided into two zones, inasmuch as the cells of its hind dorsal part are smaller, and much more closely packed together than those of its foremost ventral part.

The fibres originating in this rostral oculomotor-complex, leave the brain in two bundles, viz., a slender compact bundle, which crosses, and a much broader bundle made up of loosely arranged fibers, which is uncrossed. These bundles are adjacent, the small crossing one occupying the medial position. The decussating fibres come exclusively from the dorsomedial nucleus, although many of the fibres from this nucleus show a direct course. The remainder of the homolateral fibres arises in the ventrolateral nucleus. The decussation of the oculomotor takes place at the hindmost level of the nucleus, and is best seen in horizontal sections (fig. 6).

The most conspicuous feature of the rostral third nucleus is the extremely ventral position of its lowest cells. In gnathostomes also this nucleus sometimes may stretch far ventrally, but never reaches the periphery of the brain, let alone that it extends beyond this boundary. Since, as

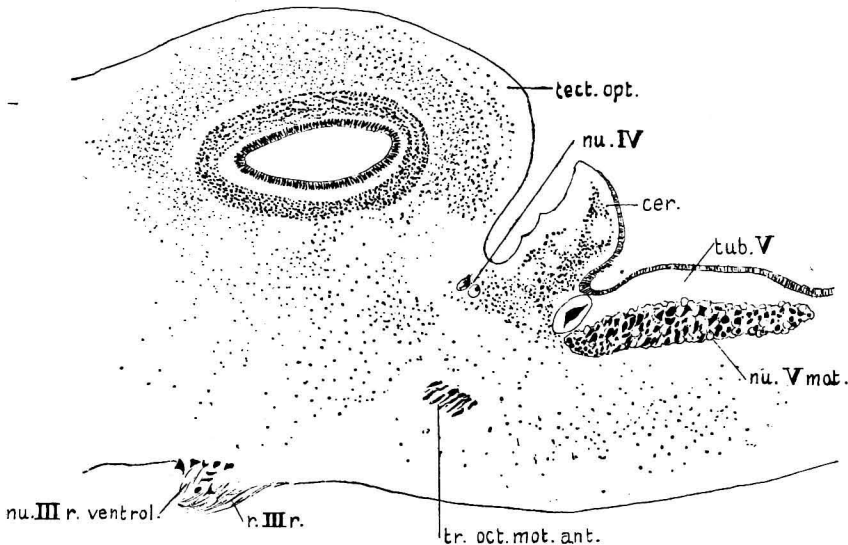


Fig. 5. *Petromyzon fluviatilis*. Parasagittal section through the mid-brain and the beginning of the oblongata. $\times 40$. nu. III r. ventrol., ventrolateral rostral third nucleus; r. III r., rostral third root; tub. V, tuberculum trigemini.

remarked above, petromyzonts besides primitive also show secondary characters, we shall have to inquire, every time we encounter a deviation from the general vertebrate type, whether this is due to primitiveness or to secondary modification. Is, then, the ventral position of the third nucleus primitive or secondary? Before this question can be answered, we must

consider what criteria in general are available regarding the primitiveness of the position of nuclei. For want of room, however, something can be said here only about the embryological criterion.

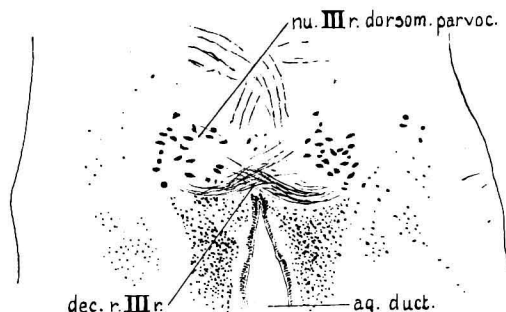


Fig. 6. *Petromyzon fluviatilis*. Horizontal section through the mid-brain at the level of the decussation of the rostral third root. $\times 40$. nu. III r. dorsom. parvoc., small-celled part of the dorsomedial rostral third nucleus; dec. r. III r. decussation of the rostral third root.

According to the rule of recapitulation, motor nuclei which have shifted phylogenetically, will indicate their original location in the embryonic condition. The nearer, therefore, a nucleus lies in the adult to the place where it arose in the embryo, the more primitive its position. So migrations during ontogenesis are recapitulations of phylogenetic migrations. We must be here, of course, on our guard against cenogenesis: notwithstanding that a nucleus phylogenetically has shifted, it may already at its first appearance occupy its final place, or even arise at a quite different location from its original one.

The development of the motor nuclei of petromyzonts unfortunately is wholly unknown, but regarding higher vertebrates we are rather well-informed in this respect.

BOK (1915), especially, in his research on the development of the chick's brain has put the thesis that all motor cells originate as a single longitudinal column dorsal to the fasciculus longitudinalis medialis.

This thesis, however, is not tenable to its full extent, as is apparent from later work (URRA, 1922; BECCARI, 1923; TELLO, 1923), which my own researches confirm. In the first place, it must be remarked that the column in question is not continuous longitudinally, since several nuclei are isolated from the very first. A more serious objection is that the oculomotor and trigeminal nucleus do not arise medially, but laterally near the outer border of the brain, at least become visible as such here for the first time. URRRA found even that in the youngest stages of the chick some cells of the third nucleus protrude outside the brain, just as described above for the adult *Petromyzon*. In the further course of development they migrate to their final dorsal position.

If this were a phenomenon of recapitulation, we would be bound to

conclude that in primitive forms the place of the third nucleus was ventral, petromyzonts even nowadays showing this primitive location.

Notwithstanding that ontogeny points to primitiveness, I am inclined to regard the extremely ventral site of the third nucleus as secondary, and that for two reasons. First, because also the fifth nucleus, as mentioned above, arises laterally, and yet its original position is dorsal, as evidenced by the condition in lower vertebrates in general, inclusive of the petromyzonts themselves (see fig. 2 for the Selachii). So, phylogenetically, BOK's thesis may be right. Secondly, doubt is raised by the curious extra-cerebral situation of part of the cells.

I am of opinion, therefore, that it is more plausible to ascribe the character just discussed to a secondary shifting in a ventral direction, in consequence of the weakening of the optic impulses. The remark must be made, however, that the reflex pathways to the eye-muscle nuclei of petromyzonts are insufficiently known.

At this point it may be stated that nothing suggesting the presence of a nucleus of EDINGER-WESTPHAL was found. In this nucleus in all probability the greater part of the intrinsic eye-musculature (cf. BROUWER, 1918) is localized. Intrinsic eye-muscles as well as a ganglion ciliare are totally lacking in petromyzonts, as would be in keeping herewith.

Before proceeding to the caudal oculomotor nucleus and root, which are better discussed together with the abducens, I turn to the trochlear nerve.

The Trochlear Nerve.

The nucleus of the fourth nerve is very strangely located, inasmuch as it lies in the cerebellum, dorsal to the sulcus limitans therefore (figs. 5 and 7). Consequently it is not indicated within the chart, but above it.

The trochlear cells, which stain intensely with haematoxylin, are small and strongly elongated horizontally, i.e., in the direction of the axones going out from them. The axones leave their cells at the medial side, and cross above the ventricle. Having traversed the heterolateral nucleus, they collect to form the root, which emerges a fair distance in front of the nucleus in the usual dorsal position (fig. 8).

In two respects the location of the trochlear nucleus is noteworthy.

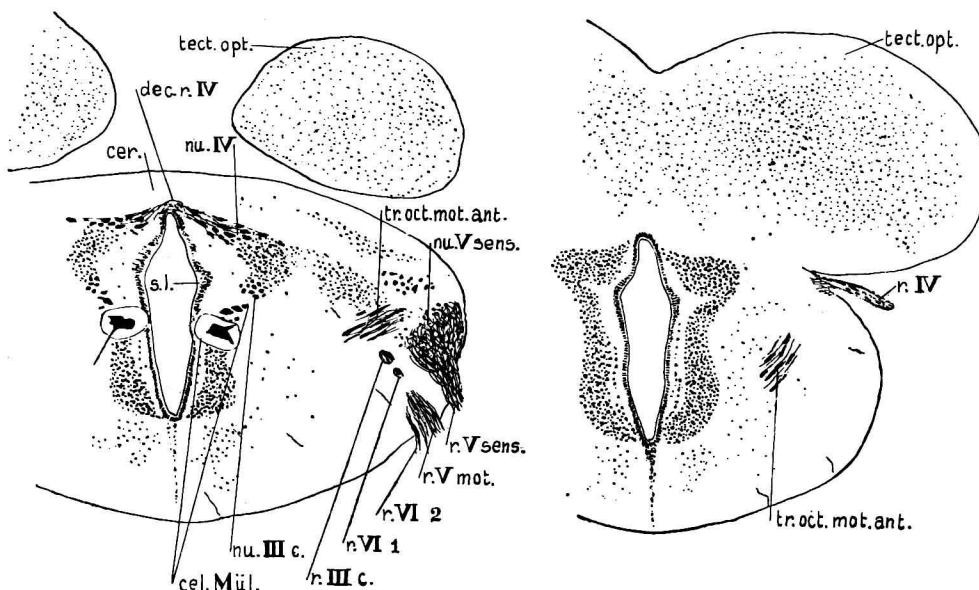
Firstly, because nowhere else is this nucleus encountered in the cerebellum, dorsal to the sulcus limitans, and secondly, because in no other group does it lie at so caudal a level.

Are these two features primitive or secondary?

Those investigators who have pronounced an opinion on the position of the trochlear nucleus of petromyzonts (TRETJAKOFF, 1909; KAPPERS, 1912, 1920) hold that both peculiarities are primitive. In this I can but partly agree with them.

It does not seem doubtful to me that the situation in the cerebellum is secondary. As intimated above, in petromyzonts nothing is known about

the development of the motor nuclei, but in gnathostomes, as far as investigated, the trochlear nucleus always arises in the same way as the



Figs. 7 and 8. *Petromyzon fluviatilis*. Cross-sections through the oblongata and cerebellum at the level of the fourth nucleus and through the mid-brain at the level of the emergence of the fourth root, resp. $\times 40$. nu. III c., caudal third nucleus; r. III c., caudal third root; r. VI 1, foremost sixth rootlet; r. VI 2, hindmost sixth rootlet; s. l., sulcus limitans.

rest of the nuclei, i.e., in the basal plate, consequently beneath the sulcus limitans. It can be neurobiotactically explained, moreover, why this nucleus should have moved into the cerebellum, as set forth below.

The second peculiarity, the caudal position, must be accounted for inversely, for, as KAPPERS has convincingly pointed out, a caudal location of the trochlear nucleus is archaic. This topic may again be briefly discussed.

In the majority of vertebrates the fourth nucleus is situated immediately behind the third; only exceptionally are these nuclei separated by a more or less extensive interval, as especially in urodeles (RÖTHIG, 1913) where the trochlear nucleus lies almost as caudally as in petromyzonts. This nucleus, in all cases in which its ontogeny was investigated¹⁾, was found to arise a little caudal to the third nucleus, shifting forwards towards the latter as development proceeds. The assumption that a caudal position of the trochlear nucleus is primitive is further substantiated by the fact, discovered by TSUCHIDA (1906), and confirmed by KAPPERS (1912) and VAN VALKENBURG (1912), that in man frequently a part of the nucleus lies separately at a more caudal level (nucleus trochlearis posterior).

Although all this speaks strongly in favour of the primitiveness of a

¹⁾ For full literature, as for all problems touched upon in this preliminary communication, the reader is referred to a forthcoming more complete account.

caudal situation of the trochlear nucleus, yet it is very questionable if this feature, in its full extent, may be attributed to primitiveness, as the embryonic interval between the third and fourth nucleus is always quite small, and in no way so extensive as in adult petromyzonts and urodeles. The caudal position of the fourth nucleus in these forms will, therefore, probably be due partly to backward shifting.

The Oculomotor-abducens Nerve.

I now proceed to the common treatment of the caudal oculomotor and abducens nerves, which henceforward, as forming a single nerve-stem, will be designated as the oculomotor-abducens.

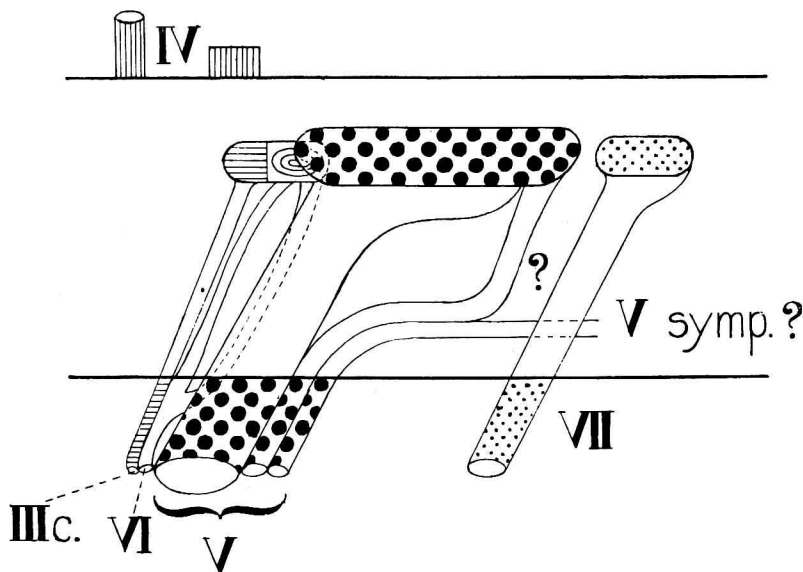


Fig. 9. *Petromyzon fluviatilis*. A part of fig. 1 two times enlarged with the course of the roots indicated. IIIc., caudal third root.

The information available in literature about this nerve, or better said, about the abducens, since it has not been hitherto recognised that oculomotor elements are present in it, is utterly confused, and for the greater part wrong. A knowledge of the anatomical details involved is gained most easily by a survey of the scheme of fig. 9.

Ventromedially and adjacent to the rostral end of the trigeminal nucleus, which consists of big cells, there is found a column of much smaller cells (fig. 10). In its greater part, however, this column extends in front of the fifth nucleus (fig. 7). By the size of the composing cells it can be divided into two parts, the foremost and shorter part being made up of somewhat smaller elements than the hindmost and longer.

To say it at once, without giving reasons for the present, the foremost component of the column in question is the caudal oculomotor nucleus spoken of above, the hindmost the abducens nucleus.

From the caudal oculomotor nucleus one rootlet departs, from the abducens nucleus two. The foremost of the two sixth rootlets, during its

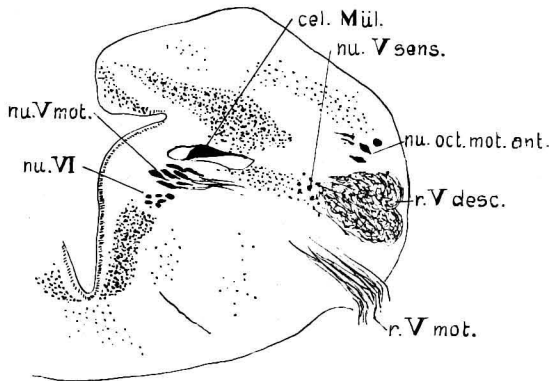


Fig. 10. *Petromyzon fluviatilis*. Cross section through the oblongata at the level of the sixth nucleus $\times 40$.

intracerebral course, is situated close to the oculomotor rootlet, the hindmost, however, more separately. The third and foremost sixth rootlets, on leaving the brain, unite, and a little outside the brain the hindmost sixth rootlet joins them. Thus these three fibre-bundles form one stem, the oculomotor-abducens, the abducens of my predecessors. It runs but for a short distance independently, and soon unites with the motor trigeminal. Its further course could not be followed in the series at my disposal, since they only contained the brain with the proximal nerve-stumps. Regarding this, however, we are informed long ago by the researches of PAUL FÜRBRINGER (1875), a brother of the renowned comparative anatomist MAX FÜRBRINGER. In the orbit the oculomotor-abducens, as appears from P. FÜRBRINGER's description of *Petromyzon marinus*, has left the trigeminus, and again has become independent.

Here it divides into two branches, one of which goes to the rectus posterior s. externus, the usual abducens muscle, whilst the other innervates the rectus inferior, which in all other vertebrates is supplied by the oculomotor.

The correctness of P. FÜRBRINGER's observations is not to be doubted. M. FÜRBRINGER (1897) and CORNING (1902) confirmed them for the same species (*marinus*). I, too, could by dissection of a large specimen of *Petromyzon marinus* ascertain this mode of innervation, and NISHI (1922) found the same in *Entosphenus japonicus*.

Petromyzon fluviatilis behaves somewhat differently in this respect, according to the recent papers of TRETJAKOFF (1926, 1927). Though here, too, the rectus inferior is mainly supplied by the oculomotor-abducens, it still gets a small twig from the rostral oculomotor¹⁾.

It will be clear by now, how I was led to interpret the so-called abducens

¹⁾ TRETJAKOFF, of course, speaks simply of oculomotor and abducens.

as an oculomotor-abducens. This conception was, quite naturally, arrived at by combining the fact that two parts could be seen in the nucleus of this nerve with the aberrant territory of its innervation.

According to this supposition, a part of the oculomotor-cells, and just the one innervating the rectus inferior, has migrated backwards, and joined the abducens nucleus. In *Petromyzon marinus* this process has been complete, in *Petromyzon fluviatilis* some of the rectus inferior cells have remained in their old centre. Thence the twig found by TRETJAKOFF.

If it might be objected that this is too extensive a migration, it can be immediately replied that the abducens nucleus, about whose identity no doubt is possible, must have shifted forwards over at least the same distance, as a comparison between the charts of *Petromyzon* and *Selache* shows. In the latter form the sixth nucleus approximately exhibits its original position, as will be argued presently. Likewise the sixth root here emerges at its original level.

Of course, the hypothesis just put forward only can be regarded as proved, when it is established that during development cells from the third nucleus migrate backwards, and join the sixth nucleus; but, as remarked, nothing is known about the ontogeny of the motor nuclei of petromyzonts.

It may now be mentioned briefly what was known heretofore about the so-called abducens.

P. FÜRBRINGER (1875) described the course of the nerve in the orbit, and discovered the remarkable innervation, whilst AHLBORN (1883), for the first time, observed its emergence close in front of the trigeminus. Thus, it was the central relations which hitherto were not elucidated. According to AHLBORN, the root springs from the foremost part of the trigeminal nucleus, JOHNSTON (1902, 1905) maintains that the sixth nucleus occupies its usual place, and TRETJAKOFF wholly arbitrarily assumes that it lies in the hindmost part of the trigeminal nucleus.

The only author that saw the oculomotor-abducens column, without noticing, however, two parts in it, was TRETJAKOFF, according to whom the fibres arising from it run forwards, and emerge with the rostral oculomotor. Consequently he considers this cell-group in its entirety as an oculomotor nucleus (his dorsal oculomotor nucleus). I could find no trace of such fibres.

The numerous efforts hitherto made to explain why the so-called abducens of petromyzonts in addition to its own accustomed muscle, the rectus posterior, innervates the rectus inferior, cannot all be reviewed here.

P. FÜRBRINGER and others have tried to solve this enigma by supposing that some of the eye-muscles of petromyzonts are not homologous with their namesakes in the rest of vertebrates.

P. FÜRBRINGER, for instance, assumes that the rectus posterior and inferior of petromyzonts have united in gnathostomes to form one muscle: the rectus posterior of the latter. Thus in them but one muscle would be supplied by the abducens. The rectus anterior of petromyzonts at the same

time would have split up into the rectus anterior and inferior of gnathostomes, the latter supplanting the homonymous muscle of petromyzonts.

PLATE, in his recent text-book of General Zoölogy (1922, 1924), has put forward a different explanation, though he, too, regards the innervation of the rectus inferior by the abducens as a primitive cyclostome feature. In gnathostomes the muscle in question would have shifted forwards into the territory of the oculomotor, where this nerve would have taken over the task of the abducens. But, although in petromyzonts the rectus inferior is situated somewhat further back than in gnathostomes, this difference is much too slight to make acceptable such an explanation.

PLATE's hypothesis rests on the principle that changes of innervation during phylogenesis are possible, a phenomenon designated by the name of secondary, collateral or heterotopic innervation, which last term, as the most characteristic, will be used by me throughout.

Finally there is an explanation by MOŽEJKO (in "BRONN's Klassen und Ordnungen"), very intricate and far-fetched, but nevertheless accepted by TRETJAKOFF, which cannot be dealt with here.

CORNING (1902) alone has surmised, in what direction at least, the solution of the problem lay, viz., in supposing that intracranially oculomotor fibres have joined the abducens.

To the phenomenon that within the central nervous system a part of one nerve unites with another, and emerges with it, I should like to give the name of *central anastomosis*. Nerves, therefore, are not fixed units, not even the so strongly individualized cranial nerves. An investigation, extending over the motor nuclei and roots of all the vertebrate groups, has revealed to me other instances of this phenomenon, though it is not frequent.

In two respects this principle of central anastomosis is of importance.

In the first place, from the standpoint of pure morphology, whereby here is understood the mere establishing of homologies. FÜRBRINGER, and following him the school of GEGENBAUR in general, was of opinion that during phylogeny the innervation of muscles never changed, and so would be an infallible guide in tracing the homology of the latter. This view rested on the now obsolete HENSEN doctrine that motor cell and muscle-fibre are connected from their earliest ontogenetic appearance. Although all comparative anatomists will be agreed as to the correctness of FÜRBRINGER's rule in the overwhelming majority of cases, many among them, as apparent from the foregoing, ascribe a more or less important rôle to secondary or heterotopic innervation, as especially EDGEWORTH (1911), who enumerates a whole series of examples. E. HUBER¹⁾, on the contrary, has even most recently defended the absolute validity of FÜRBRINGER's doctrine. In a series of studies on the facialis musculature

¹⁾ See for E. HUBER's writings on this topic the list of literature in HUBER and HUGHSON (1926).

he, by electrically stimulating or cutting the facialis, reached the result that the alleged additional supply of these muscles by the plexus cervicalis or trigeminus is due to peripheral anastomoses.

My own attitude in this matter is conciliatory.

On the one hand I am of opinion that EDGEWORTH goes too far. Not to speak of erroneous observation, I believe that a number of cases of heterotopic innervation is but seeming, and once will be eliminated by the demonstration of peripheral, or perhaps central anastomoses, as done in the present research for the rectus inferior of petromyzonts. Moreover, there is another complication by which a false appearance of heterotopic innervation can be raised, viz., that fibres in the course of evolution transferred their place of exit from ventral to dorsal. To this I presently shall return.

On the other hand, however, I cannot entirely agree with E. HUBER. Without doubt, there are cases in which in the course of time the nerve supply of muscles has undergone alteration. The most striking and certain example, known to me, is brought out by a comparison of the innervation of the tail of urodeles and reptiles with that of mammals (v. SCHUMACHER, 1909). The spinal cord in the first-named animals continues backwards to the tip of the tail, giving off in each segment a pair of caudal nerves. In mammals, on the contrary, the caudal part of the spinal cord is reduced, and along with it the last tail-nerves, so that the number of caudal vertebrae is from three to six times more numerous than that of the tail-nerves. In the embryo these tail nerves which have vanished in the adult, are still laid down, but soon they disappear. The innervation of the muscles of the last tail-segments, consequently, must have been taken over by more rostral tail-nerves.

Thus having considered the significance the principle of central anastomosis may have in the controversy regarding the phylogenetic constancy of innervation, I turn to the second theoretical point for which the phenomenon is of importance. KAPPERS has put forward the law that nerve-fibres which conduct impulses at the same time or shortly one after the other in the same direction, tend to group together in bundles. This he called *fasciculation*. In the special case of motor fibres the simultaneousness of excitation would be brought about by the circumstance that the uniting fibres innervate closely collaborating muscles. As we shall see presently, however, the simultaneousness may have another cause.

Is, then, the union of oculomotor and abducens fibres described above, a case of fasciculation?

This would not seem quite impossible, although in no event is it a striking illustration of the principle. The caudal oculomotor goes to the rectus inferior, the abducens to the rectus posterior. P. FÜRBRINGER (1875) as well as TRETJAKOFF (1926) states that in Petromyzon the eye-ball is turned backwards by the rectus posterior, and downwards and at the same time a little *backwards* by the rectus inferior. Thus, these two muscles may collaborate to some extent; if here, however, stronger than in gnathostomes

in general I should not venture to say for the moment. In a forthcoming more complete account I hope to be in a position to say something more regarding this point.

It is apparent from the foregoing that the positions of both the abducens and of the caudal oculomotor nucleus of *Petromyzon* are held by me to be secondary. For the abducens nucleus this is easily demonstrated. Mainly by the researches of STREETER (1908) in man, but also by those of BOK (1915) on the chick's development, the nucleus in question is known to arise in the position characteristic for adult selachians (see fig. 2 for *Selache*). It follows, furthermore, from the development of the muscle localized in the sixth nucleus, that the latter is rather to be expected on the level of the facialis than on that of the trigeminal nucleus, this muscle, the rectus posterior, being formed by the upper part of the hyoid myomere, the myomere of the facialis.

The location of the caudal oculomotor nucleus, likewise, is not a primitive character. As an argument can be adduced that in those gnathostomes where the ontogeny of the third nucleus was studied, never did some of its cells arise more caudally and apart from the rest. It is possible, moreover, to ascribe this caudal position to neurobiotactic influences, and to the same that have brought about the location of the abducens and trochlear nuclei.

Which neurobiotactic factors, then, have been operative here ?

The close spatial relationship of all three nuclei to the cerebellum provides us with a key. The caudal third nucleus lies just beneath this part of the brain, the sixth immediately behind, and the fourth even within it. The afferent pathways to the cerebellum of petromyzonts are almost exclusively of octavolateral nature. So it is justified to ascribe the position of the three nuclei at the same longitudinal level to the neurobiotactic influence of static and lateralis stimuli, which prevailed over the agency of the optic system.

The second peculiarity of the oculomotor-abducens calling for comment, is the lateral emergence of its root. As aforesaid the latter leaves the brain in as lateral a position as the motor trigeminus. In gnathostomes, without exception, the oculomotor and the abducens emerge ventrally, which is deemed a typical feature of so-called somato-motor nerves. Probably also this peculiarity is secondary, as it is not at all impossible to account for it by fasciculation, on the basis of the specialized manner of life of these animals.

This explanation, however, can only be given with great reserve. A little digression on the feeding habits of petromyzonts is necessary to this end.

The petromyzonts are predatory. They attack fishes, even very big ones. With its oral funnel the lamprey fixes itself to its prey, and by the rasping movements of the so-called tongue, which is provided with teeth, it reduces the tissues of its victim to a fine pulp, which is then swallowed.

The so-called tongue is supplied by the trigeminus, whence appears that this organ has nothing to do with a genuine tongue. While the lamprey is

feeding, the prey, roused by pain, will carry with it the aggressor in convulsive movements. So the eye-muscle nerves, which mainly receive static and lateralis impulses, will be stimulated simultaneously with the trigeminus, which moves the tongue.

If the union of oculomotor-abducens and trigeminus actually is a consequence of simultaneousness of stimulation, then, in this case, as alluded to above, the simultaneousness may not be ascribed to the contraction of closely collaborating muscles, since it cannot be seen how eye-movements could be of any avail to the lamprey while feeding. The contraction of the one group of muscles merely entails that of the other. But, as stated, the above explanation is only given with all due reserve. It is possible, after all, that any weak nerve, for some reason or other coming into the vicinity of a strong nerve-stem, may unite with it.

However this may be, the lateral emergence of the oculomotor-abducens is a remarkable fact, and of great interest from the point of view of pure morphology also. It stands not alone as an instance of the phenomenon of a nerve transferring its place of exit from ventral to lateral or dorsal. The spinal accessory and a part of the vagus have arisen in like manner, as was brought to light during my researches on the phylogeny of the motor cranial nerves of vertebrates, already mentioned above.

Something may yet be said here on the origin of the accessory. This nerve until now was, following GEGENBAUR and FÜRBRINGER, generally interpreted as a branch of the vagus which had gained during evolution a more or less pronounced independence. The musculature supplied by it, the trapezius musculature, in keeping herewith is regarded as a derivative of the branchial muscles, as seemed proved by the embryological researches of EDGEWORTH (1911). It was, however, found out by me that the accessory is nothing else but fibres of one or more of the foremost spinal nerves which instead of a ventral have assumed a dorsal exit, and have joined the vagus. So there is ground for presuming that EDGEWORTH was mistaken in his researches on the development of the trapezius. In justification of this surmise I can appeal to a paper of VÖLKER (1908) on the development of the occipital region of *Larus ridibundus*, which clearly describes and figures that the trapezius is formed by the fusion of split-off portions of the occipital myotomes.

For want of room it cannot be further pointed out what theoretical significance the phenomenon of nerves taking on a dorsal exit instead of a ventral has, for instance, for the so-called "four-root" or American theory about the division of the nervous system. It may only be mentioned that in this manner, too, a fallacious appearance of heterotopic innervation can be raised, inasmuch as nerves which really are identical, may seem quite different by their changed mode of exit. The translocation in question probably is caused by fasciculation, but about this no more can be said for the moment.

Let us now summarize what was described or argued in the above.

For the first time a plausible explanation was given of the strange fact, discovered by P. FÜRBRINGER in 1875, that in petromyzonts the abducens not only innervates the rectus posterior, but also the rectus inferior, viz., by making it probable that the abducens of these animals is not a pure abducens, an oculomotor bundle having become associated with it within the brain. To this and similar phenomena the name of *central anastomosis* was given.

Furthermore, an endeavour was made to explain the deviations from the general vertebrate type which petromyzonts exhibit in the structure of their eye-muscles, on the basis of secondary modification, mainly as the effect of a diminution of their visual powers. The characters thus interpreted, are no less than six in number :

1. The extremely ventral or even extracerebral situation of the lowest rostral oculomotor cells.
2. The presence of a caudal third nucleus, united with the sixth.
3. The location of the fourth nucleus in the cerebellum.
4. The extremely rostral position of the sixth nucleus.
5. The union of the caudal third and sixth roots to form an oculomotor-abducens, emerging close in front of the trigeminus.
6. The lateral emergence of the oculomotor-abducens.

The extremely caudal position of the fourth nucleus, moreover, is probably but partly a consequence of primitiveness.

It was possible to attribute most of these peculiarities to neurobiotaxis, and two of them perhaps to fasciculation. It may be insisted how a comparison of the charts of Petromyzon and Selache not only strikingly demonstrates the existence of the shifting phenomenon, but also conveys an impression over what considerable distances the migrations of the nuclei may extend.

Finally, attention is directed towards the two principles of pure morphological nature arrived at in this paper, partly on the basis of the above facts. First, that even the so strongly individualized cranial nerves are not fixed units, which, apart from the doctrine of neurobiotaxis and fasciculation, is of importance in the problem of heterotopic innervation, and secondly, that the place of exit of roots may change from ventral to dorsal. It could only be cursorily touched upon what significance the latter phenomenon has in various morphological problems.

LITERATURE CITED.

- AHLBORN, F. (1883). Untersuchungen über das Gehirn der Petromyzonten. Zeitschr. wiss. Zool. Bd. **39**, p. 191—294.
- BECCARI, N. (1923). Intorno al primo differenziamento dei nuclei motori dei nervi cranici. Mon. zool. Ital., Anno **34**, p. 161—166.
- BOK, S. T. (1915). Die Entwicklung der Hirnnerven und ihrer zentralen Bahnen. Die stimulogene Fibrillation. Fol. Neuro-Biol., Bd. **9**, p. 475—565.
- BROUWER, B. (1918). Klinisch-anatomische Untersuchung über den Oculomotoriuskern. Zeitschr. ges. Neurol. und Psych., Bd. **40**, p. 152—193.

- CORNING, H. K. (1902). Ueber die vergleichende Anatomie der Augenmuskulatur. *Morph. Jahrb.*, Bd. 29, p. 94—140.
- EDGEWORTH, F. H. (1911). On the morphology of the cranial muscles in some vertebrates. *Quart. Journ. micr. sc.*, Vol. 56, p. 167—316.
- FÜRBRINGER, M., (1897). Ueber die spino-occipitalen Nerven der Selachier und Holocephalen und ihre vergleichende Morphologie. *Festschr. Gegenbaur*, Bd. 3, p. 349—788.
- FÜRBRINGER, P. (1875). Untersuchungen zur vergleichenden Anatomie der Muskulatur des Kopfskelets der Cyclostomen. *Jenaische Zeits.*, Bd. 9, p. 1—93.
- HUBER, E. and HUGHSON, W. (1926). Experimental studies on the voluntary motor innervation of the facial musculature. *Journ. comp. Neur.*, Vol. 42, p. 113—163.
- JOHNSTON, J. B. (1902). The brain of *Petromyzon*. *Journ. comp. Neur.*, Vol. 12, p. 1—86.
- (1905). The cranial nerve components of *Petromyzon*. *Morph. Jahrb.* Bd. 34, p. 149—203.
- KAPPERS, C. U. ARIËNS (1912). Weitere Mitteilungen über Neurobiotaxis. VII. Die phylogenetische Entwicklung der motorischen Wurzelkerne in *Oblongata* und *Mittelhirn*. *Fol. Neuro-Biol.*, Bd. 6, p. 1—142.
- (1920). Die vergleichende Anatomie des Nervensystems der Wirbeltiere und des Menschen. I. Haarlem (De Erven F. BOHN).
- MOZEJKO, B., in „BRONN's Klassen und Ordnungen des Tierreichs". Bd. 6. Abt. 1. Pisces. Buch 1. Leipzig (Akad. Verlagsges.) 1924.
- NISHI, S. (1922). Beiträge zur vergleichenden Anatomie der Augenmuskulatur. *Arb. Sendai*, H. 7, p. 65—82.
- PLATE, L. (1922, '24). Allgemeine Zoologie und Abstammungslehre. I and II. Jena (G. FISCHER).
- RÖTHIG, P. (1913). Contributions upon Neurobiotaxis (The arrangement of the motor nuclei in *Myxine glutinosa*, in *Cryptobranchus*, *Necturus*, *Rana fusca* and *Bufo*). *Proc. Kon. Akad. Amsterdam*, Vol. 16, p. 296—305.
- SCHUMACHER, S. v. (1909). Die segmentale Innervation des Säugetierschwanzes als Beispiel für das Vorkommen einer „Kollateralen Innervation". *Anat. Hefte*, Bd. 40 (H. 120), p. 47—94.
- STREETER, G. L. (1908). The nuclei of origin of the cranial nerves in the 10 mm. human embryo. *Anat. Rec.*, Vol. 2, p. 111—115.
- TELLO, J. F. (1923). Les différenciations neuronales dans l'embryon du poulet, pendant les premiers jours de l'incubation. *Travaux Cajal*, T. 21, p. 1—93.
- TSUCHIDA, U. (1906). Ueber die Ursprungskerne der Augenbewegungsnerve und über die mit diesen in Beziehung stehenden Bahnen im Mittel- und Zwischenhirn. *Arb. Zürich*. H. 2, p. 1—205.
- TRETJAKOFF, D. (1909). Das Nervensystem von *Ammocoetes*. II. Gehirn. *Arch. mikr. Anat.*, Bd. 74, p. 636—779.
- (1926). Das Skelett und die Muskulatur im Kopfe des Fluszneunauges. *Zeitschr. wiss. Zool.*, Bd. 128, p. 267—304.
- (1927). Das periphere Nervensystem des Fluszneunauges. *Zeitschr. wiss. Zool.*, Bd. 129, p. 358—452.
- URRA, F. M. (1922). Über die embryonale Entwicklung des Oculomotoriuskerns. *Von Graefe's Arch. Ophthalm.*, Bd. 107, p. 123—147.
- VALKENBURG, C. T. VAN (1912). On the splitting of the nucleus trochlearis. *Proc. Kon. Akad. Amsterdam*, Vol. 14, p. 1023—1026.
- VÖLKER, O. (1908). "Contributions to the knowledge of the development of the occipital region in the gull" (in Czechian). *Czechian Acad. Prague*, II, Vol. 17, p. 1—47.