

Anatomy. — *Neurobiotactic influences in the arrangement of midbrain and 'tween-brain centres.* By C. U. ARIËNS KAPPERS.

Dedicated to the memory of CLARENCE LUTHER HERRICK and to CHARLES JUDSON HERRICK on the fiftieth anniversary of the foundation of the Journal of Comparative Neurology.

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The influence of the direction from which stimuli reach ganglioncells, on the location of these cells, so evident in the motor nuclei of the bulb and in cell groups connected with the acoustic system, is also demonstrated in higher centres, especially in the mid- and tweenbrain of Teleosts, so well described already by C. L. HERRICK ('92).

A striking example is the development of the *torus longitudinalis*.

In lower fishes such as the Plagiostomes the roof of the midbrain shows a very simple structure, as a symmetric vaulting over the spacious midbrain ventricle or ventriculus opticus. In the dorsal midline, where both sides meet, this roof is thinner than laterally. Already in Ganoids, (Acipenser, JOHNSTON '01 and Polyodon, HOCKE HOOGENBOOM, '16) but especially in Teleosts a symmetric intraventricular longitudinal ridge of small cells appears under the midline, which acquires its greatest volume over the posterior commissure (Megalops and Monopterus, fig. 1), decreasing gradually in a backward direction and finishing some distance before the caudal end of the optic ventricle (Periophthalmus, fig. 2).

This structure, derived from the deeper parvocellular elements of both halves of the tectum, is not equally thick in all Teleosts. The midbrain roof being the most important centre of optic impulses, FRANZ ('12) was inclined to believe that the degree of development of the *torus longitudinalis* depends on the size of the optic nerve or optic tectum. He based this opinion on the small size of this torus in a blind fish (Trypauchen) and its large size in Raniceps.

Direct connections of the *torus longitudinalis* with the optic nerve, however, have never been observed, and — although this torus may be quite large in some fishes with large eyes (c.f. Megalops, fig. 1), in several fishes with even larger optic nerves, such as Orthogoriscus mola (c.f. also BURR, '28), Exocoetes evolans, and Periophthalmus, the torus is even less developed than in Monopterus and Raniceps. Besides, according to our ('06), WALLENBERG's ('13) and JANSEN's ('29) experience, the size of the *torus longitudinalis* is not in the least influenced by atrophy of an eye and amongst the blind fishes examined by CHARLTON the torus is quite large in Troglichtys rosae ('33, fig. 8). Consequently a direct relation between the size of the torus and visual projection does not exist.

Which then is the factor that determines its development? First of all

I wish to emphasize that this subtectal mass develops from the medial part of the deep parvocellular layer of the tectum (SARGENT, '03), whereas the optic fibres chiefly end in the superficial layers. Secondly I can confirm KUDO's statement ('23) that the torus longitudinalis receives a bundle of fibres from the cerebellum (tr. cerebello-tectalis or: tr. cerebello-toralis). After its origin from the corpus (= vermis) cerebelli, probably from PURKINJE cells, this bundle runs forward medially and dorsally to the lateral lemniscus joining the tecto-cerebellar tract (fig. 3, Belone) which originates from the fronto-lateral part of the tectum (see fig. 1, Monopterus) ending in the corpus cerebelli (cf. WALLENBERG '13). The toral fibres continue their course underneath the ventricle (see Periophthalmus, fig. 3) to enter the torus frontally and laterally to the commissura posterior (Monopterus fig. 1, similarly in Raniceps).

TUGE ('34b), who also traced a cerebello-tectal bundle (in addition to a larger tecto-cerebellar tract) in *Carassius auratus*, found the cerebello-tectal fibres in this animal mingling with the lemniscus bundle, to enter the lateral part of the tectum. "None of them were found farther orad." We could, however, trace some fibres in the rather small torus longitudinalis of this animal on the level of the commissura posterior, where both halves of the torus join. In fig. 5 of his '35 paper TUGE also draws these fibres. Caudally both halves of the torus are pushed wide apart by the pressure of the large valvula cerebelli on the tectum.

As another bundle that may influence the development of the torus longitudinalis we may consider a strand of fibres arising from the frontal subtectal region on the level of the commissura posterior. KUDO ('24), who was the first to trace this bundle, found it strongly developed in *Raniceps*. According to MEADER ('34), this bundle is not constant, but KUDO found it also in *Motella*.

The cerebello-toral fibres are strongly developed in *Monopterus* with its large torus and small tectum and also in *Raniceps* and *Megalops*. Most of them end in the homolateral, about one fifth or less in the contralateral torus half (see fig. 1: *Monopterus*).

The fact that this tract enters the torus in the region above the commissura posterior explains the greater size of the torus of this level. The rest of its fibres runs backwards in the torus, terminating gradually among its cells. These cells, first described by SALA ('95), are small and also because of the form of their short dendrites closely resemble the granular cells of the cerebellum. As already stated by KUDO ('23) in most fishes their axiscylindres are unmyelinated (see *Megalops*, fig. 1) or surrounded by some myelinated fibres only (*Scardinius*¹⁾).

¹⁾ The fact that, wherever myelinated fibres run together with unmyelinated ones, they tend to acquire a sheathlike arrangement round the unmyelinated fibres is very striking also in the comm. habenularum of *Plagiostomes* and in the fasc. retroflexus of several animals (cf. KAPPERS, HUBER and CROSBY '36). They form a sort of sheath round the unmyelinated fibres (l.c. fig. 437) and it is not unlikely that this arrangement is to be explained by the same influence that acts in the peripheral accumulation of the myeline sheath.

In *Gobius* (fig. 1) only we found them provided with some myeline. As already stated by SALA ('95), RAMON ('99) and KUDO ('24) these axiscylindres run dorsally into the superficial layer of the tectum associating their impulses with those of the optic radiation and contributing considerably to the thickness of its superficial layer, especially in the medial part of the tectum (see fig. 1, *Gobius*). This is very evident also in *Raniceps* (KUDO). — Laterally the thickness of this superficial layer of the tectum decreases.

The prevailing transverse spread of these fibres also shows a certain resemblance to the transverse spread of the axiscylindres of the granular cells in the molecular layer of the cerebellum; with this difference, however, that the torus fibres do not dichotomize. Even the topographic relation of the torus longitudinalis to the tectum, strongly resembles the topographic relation of the granular masses to the molecular layer as found in the cerebellum of *Plagiostomes*¹⁾.

Although the spatial economy of the Teleostean brain case in larval life may favour the intraventricular outgrowths in Teleosts²⁾, it is evident that the direction, location and degree of this outgrowth is determined by the influence of the fibres reaching it from the ventricular side, which also explains the greatest development of the torus at the level where these fibres enter it.

Whereas the intraventricular outgrowth of the torus shows the neuro-biotactic influence of tecto-petal fibres arising in the cerebellum, the development of the *valvula cerebelli* shows the same influence exercised by cerebello-petal fibres originating from the midbrain. Contrary to *Plagiostomes* in most Teleosts (and in Ganoids, JOHNSTON '01, HOCKE HOOGENBOOM, '16) a part of the cerebellum grows out underneath the midbrain roof pushing forward the thinned hindwall of the tectum.

This *valvula cerebelli* derives from the basal part of the corpus (= vermis) cerebelli. The size of the subtectal part or *valvula* varies greatly in different Teleosts. In some fishes such as *Lophius*, *Periophthalmus* (fig. 2) and *Hippocampus*, it only consists of one impair lobule. In others, the number of impair lobuli increases (e.g. *Perca*, fig. 2), and in others again paired lobuli develop on each side of the impair one filling up the posterior part of the optic ventricle. (*Belone*, fig. 2.)

¹⁾ This cytological resemblance between distant territories with related functions is not exceptional. The typical structure of the "cerebellar crest" covering the bulbar centres of the lateral line organs and the resemblance of the protopathic substantia gelatinosa in the spinal cord, the spinal trigeminus nucleus and the substantia gelatinosa accompanying the solitary tract in man are other examples of homologous functions determining homologous structures in different regions. A similar observation is made by DE CRINIS for mammals (Journ. f. Psych. und Neur., 1934, 45).

²⁾ Spatial economy acts a part also in the development of the forebrain in these animals as it does in birds.

The frontal direction and the degree of this outgrowth is determined by a fibre tract reaching the cerebellum chiefly from the nucl. lateralis valvulae, the tr. tegmento-cerebellaris (tr. teg. cer. fig. 2). This nucl. lateralis valvulae (n. lat. val.) is intimately related to end stations of the lateral lemniscus; the torus semi-circularis and ganglion isthmi, and to HERRICK's anterior gustatory nucleus. Contrary, however, to higher vertebrates the lateral lemniscus of fishes has to do chiefly with stimuli resulting from the lateral line organs, which are not concerned in hearing but which serve a static function. For this static function the tegmentum mesencephali is the chief projection and correlation centre. From it impulses are conducted chiefly to the basis of the cerebellum, which also receives some direct lateral nerve fibres (ADDISON, '23; PEARSON, '36).

An other bundle, not reaching the valvula but the corpus cerebelli from a frontal centre is the tecto-cerebellar tract, whose cerebellopetal course has been proved by WALLENBERG ('13) and a smaller bundle arising from the ganglion isthmi — a static centre intercalated between the tectum and corpus cerebellum. Of all these systems the tegmento-mesencephalic tract, however, sends its fibres into the valvula cerebelli and the intraventricular outgrowth of the valvula, specially the development of its lateral lobes runs parallel to the development of this system ¹⁾ (Belone, fig. 2). This is most conspicuous in such fishes as the Cyprinoids and Siluroids (HERRICK '05) whose gustatory system is so strongly developed and in Mormyridae, whose lateral nerves are hypertrophic and whose valvula cerebelli acquires an enormous size (FRANZ '11, STENDELL '14, BERKELBACH VAN DER SPRENKEL '15, SUZUKI 32c).

In addition to these two instances of neurobiotactic influence on the configuration of the midbrain I shall mention two examples of this influence in the diencephalon. The first of these concerns the development of the *nucleus rotundus*, a prominent nucleus in the ventral thalamus of most Teleosts, first described by FRITSCH ('78) and whose relations to an other thalamic nucleus, the *nucleus anterior*, has been elucidated by FRANZ ('12), who was the first to show that these two nuclei are closely related structures and who — on account of their internal glomerular structure, first noted by BELLONCI ('85) and CATOIS (l.c. '02, p. 104, fig. 27) — classified them together under the name of corpus glomerulosum. Both nuclei are characterized by a number of central glomeruli consisting of axonic endfeet of various origin, synapting with tufts of dendrites arising from peripheral cells.

The nucleus anterior of Teleosts, which has nothing in common with the homonymous nucleus of mammals, is located dorso-frontally under the

¹⁾ This system connecting the valvula cerebelli with the nucl. lateralis valvulae should be well distinguished from the brachium conjunctivum or tr. cerebello-tegmentalis which arises farther backward in the corpus cerebelli, ending (after having crossed) in the basis of the mid- and 'tweenbrain.

frontal part of the tectum, medially to the posterior pole of the lateral geniculate nucleus, with which it is connected by internuclear fibres (HOLMGREN, '20; MEADER, '34) and laterally to and behind the region of the medial optic ganglion described by WALLENBERG ('13) and also observed by MEADER ('34, p. 378). The nucleus anterior itself does not receive optic fibres¹). Dorsally to the nucleus anterior most fibres of the commissura horizontalis arise and end. This commissure is also connected with the caudoventral or rotundus part of the corpus glomerulosum, which practically is intercalated in this bilateral connection between the frontal tectal (and pretectal) areas of the midbrain, the projection centres of the frontal visual field (LUBSEN, '21; STRÖER, '39), so important for the capture of food.

According to FRANZ' researches the nucleus anterior is the phylogenetically oldest part of the corpus glomerulosum. In Physostomes, where the nucleus rotundus part of the corpus glomerulosum fails, it is very large (see also JEENER, '30). Among the Physoclists the rotundus part may fail or be little developed in the Anacanthini. In Acanthopterygi the rotundus part acquires its greatest extension, while the dorso-frontal anterior nucleus decreases.

We have been able to reexamine the relations of the corpus glomerulosum system in a great number of Teleosts. Our results largely agree with FRANZ'.

In *Amia*, *Lepidosteus*, and many Physostomes (pike, herring, carp, eel, *Silurus*) the anterior nucleus is well developed, while a glomerular rotundus nucleus as it appears in the higher Teleosts in the caudo-ventral part of the thalamus, is absent. A glomerular rotundus nucleus does not, however, fail in all Physostomes²). In Megalops it is even very large.

Among the Anacanthini which we examined it is present in *Exocoetes*, *Scomber*, *Ctenolabrus*, *Gadidae* and *Pleuronectidae*. In the Acanthopterygii the rotundus part is well developed, in the Plectognath *Tetrodon* and in the Lophobranchs *Syngnatus* (see fig. 3) and *Hippocampus* it attains its greatest size.

The nucleus anterior in these animals is much reduced and what is left of it is connected by a stalk-like elongation with the glomerular substance of the nucleus rotundus (see fig. 3, *Syngnatus*), as described by FRANZ.

While the decrease of the anterior nucleus accompanying the increase of the rotundus nucleus suggests that the development of the rotundus takes place at the expense of the anterior, the question arises what is the

1) According to FRANZ ('12), HOLMGREN ('20) this nucleus is also connected with the commissura minor of C. L. HERRICK, which may act a similar part in connection with the anterior nucleus as the comm. horizontalis does in connection with the rotundus nucleus.

2) It may not be superfluous to state that the air-bladder itself has nothing to do with this nucleus which is very large even in the *Pleuronectidae* where the air-bladder is atrophic. *Symbranchus* whose airbladder is equally atrophic also possesses a rotundus nucleus.

C. U. ARIËNS KAPPERS: NEUROBIOTACTIC INFLUENCES IN THE
ARRANGEMENT OF MIDBRAIN AND 'TWEEN-BRAIN CENTRES.

Dedicated to the memory of CLARENCE LUTHER HERRICK and to CHARLES JUDSON
HERRICK on the fiftieth anniversary of the Journal of Comparative Neurology.

Fig. 1. Transverse sections of the tectum opticum and torus longitudinalis of *Megalops cyprinoides* and *Monopterus javanensis*. Horizontal section of the tectum and torus longitudinalis of *Gobius spec.*

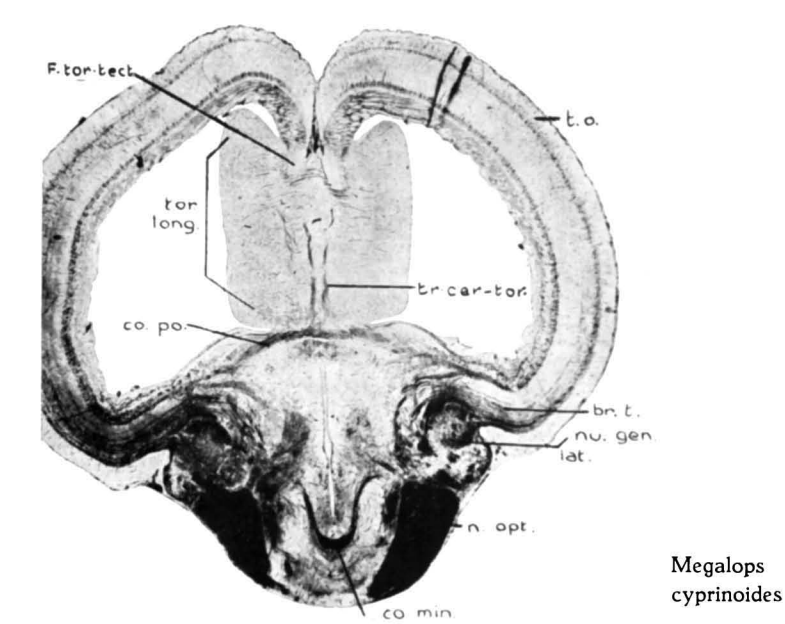
br. t. = brachium tecti (= fibr. geniculo-tectales); co. h. = comm. horizontalis; co. min. = comm. minor (C. L. HERRICK); co. po. = comm. posterior; dec. N. IV = decussatio N. trochlearis; f. c. t. = fascic. cerebello-toralis; f. retrofl. = fasc. retroflexus; f. tor. tect. = fibrae toro-tectales; f. t. c. = fasc. tecto-cerebellaris; la. co. tecti = lamina commissuralis tecti; n. opt. = nervus (tractus) opticus; nu. gen. lat. = nucleus geniculatus lateralis; nu. me. V = nucleus mesencephalicus trigemini; t. o. = tectum opticum; tor. long. = torus longitudinalis; tr. = tractus cerebello-toralis (= f. c. t. = fasc. cerebello-toralis); tr. opt. m. = tr. opticus medialis.

Fig. 2. Sagittal section of the cerebellum, midbrain and lobus inferior hypothalami of *Perca fluviatilis* and *Belone belone*.

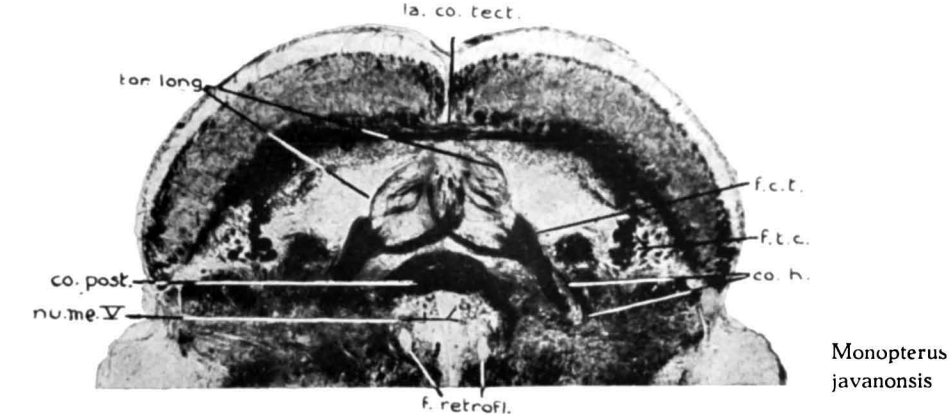
cer. = corpus cerebelli; Co. tr. = comm. transversa; dec. br. c. = decussatio brachii cerebelli; f. cer. = fasc. cerebello-hypothalamicus; f. cer. tect. = fasc. cerebello-tectalis; f. teg. cer. = fasc. tegmento-cerebellaris; g. ist. = ganglion istmi; lem. l. (lat.) = lemniscus lateralis; lob. inf. = lobus inferior hypothalami; lob. lat. valv. = lobus lateralis valvulae; N. III d.l. and v.m. = nucl. oculomotorius dorso-lateralis and ventro-medialis; nu. l. valv. = nucl. lateralis valvulae; tr. cer. lob. = tract. cerebello-lobaris; t. cer. tect. et tect. cer. = tractus cerebello-tectalis et tecto-cerebellaris; t. (tr.) ist. tect. = tractus istmo-tectalis et tecto-istmicus; tr. N. valv. desc. = tractus descendens nucl. valvulae lateralis; str. gr. and str. m. = stratum granulosum and moleculare valvulae cerebelli; t. t. b. cr. and r. = tract. tecto-bulbaris cruciatus and rectus; t. teg. cer. = tract. tegmento-cerebellaris; v. c. and valv. cer. = valvula cerebelli.

Fig. 3. Sagittal sections of the thalamus and tectum of *Syngnathus acus*, the lower figure is the most lateral one. To the right: transverse section of the cerebellum, tectum and lobus inferior hypothalami of *Scardinius erythrocephalus*.

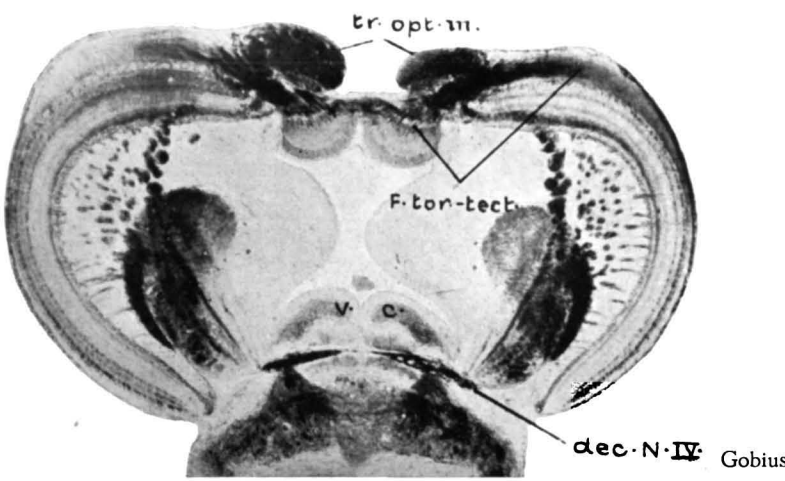
cer. = corpus cerebelli; co. hor. = comm. horizontal; cor. glom. = corpus glomerulosum; n. cer. hyp. = nucleus cerebellaris hypothalami; n. lat. v. = nucl. lateralis valvulae; n. rot. = nucl. rotundus (= pars rotunda cor. glom.); p. ant. = pars anterior (nucl. anterior) corpi glomerulosi; t. = tectum opticum; tr. lob. rot et rot. lob. = tr. lobo-rotundus et rotundo-lobaris; v. c. = valvula cerebelli.



Megalops
cyprinoides

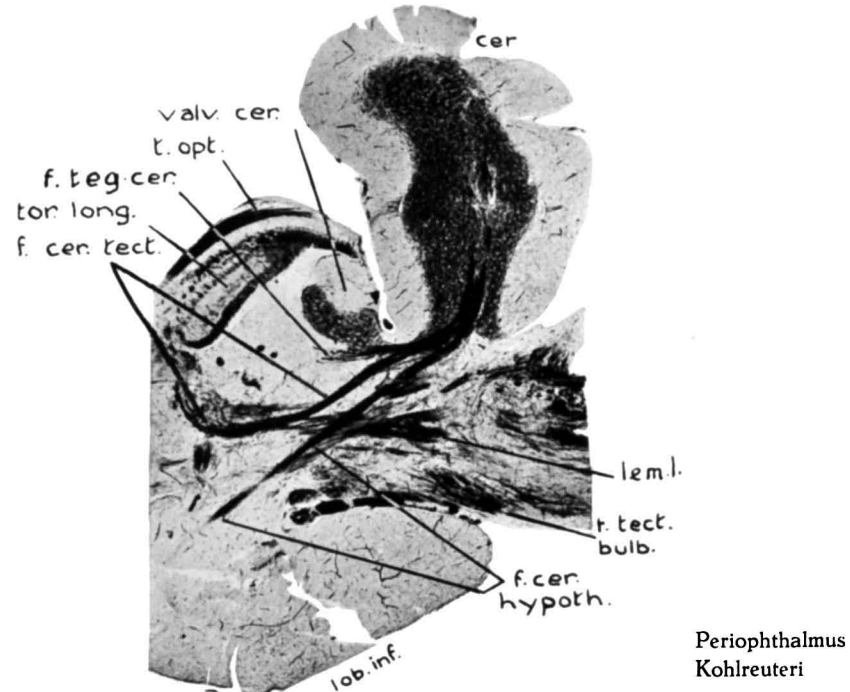


Monopterus
javanensis

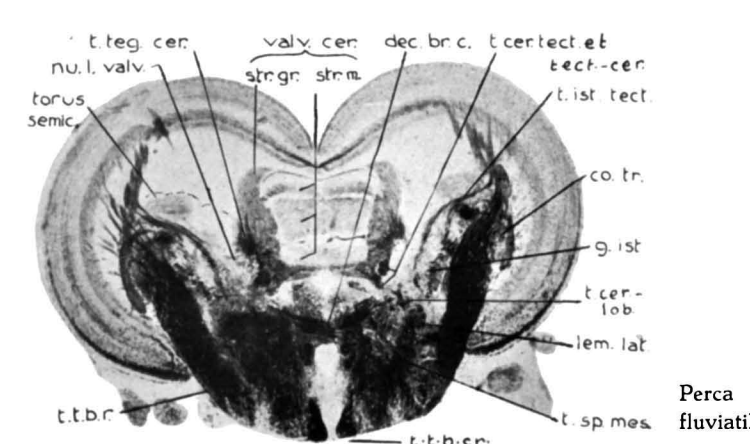


dec. N. IV. Gobius

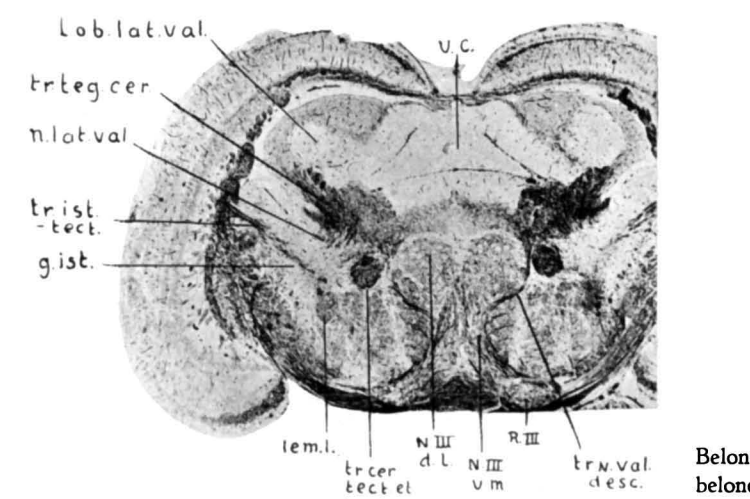
Fig. 1.



Periophthalmus
Kohlreuteri



Perca
fluviatilis



Belone
belone

Fig. 2.

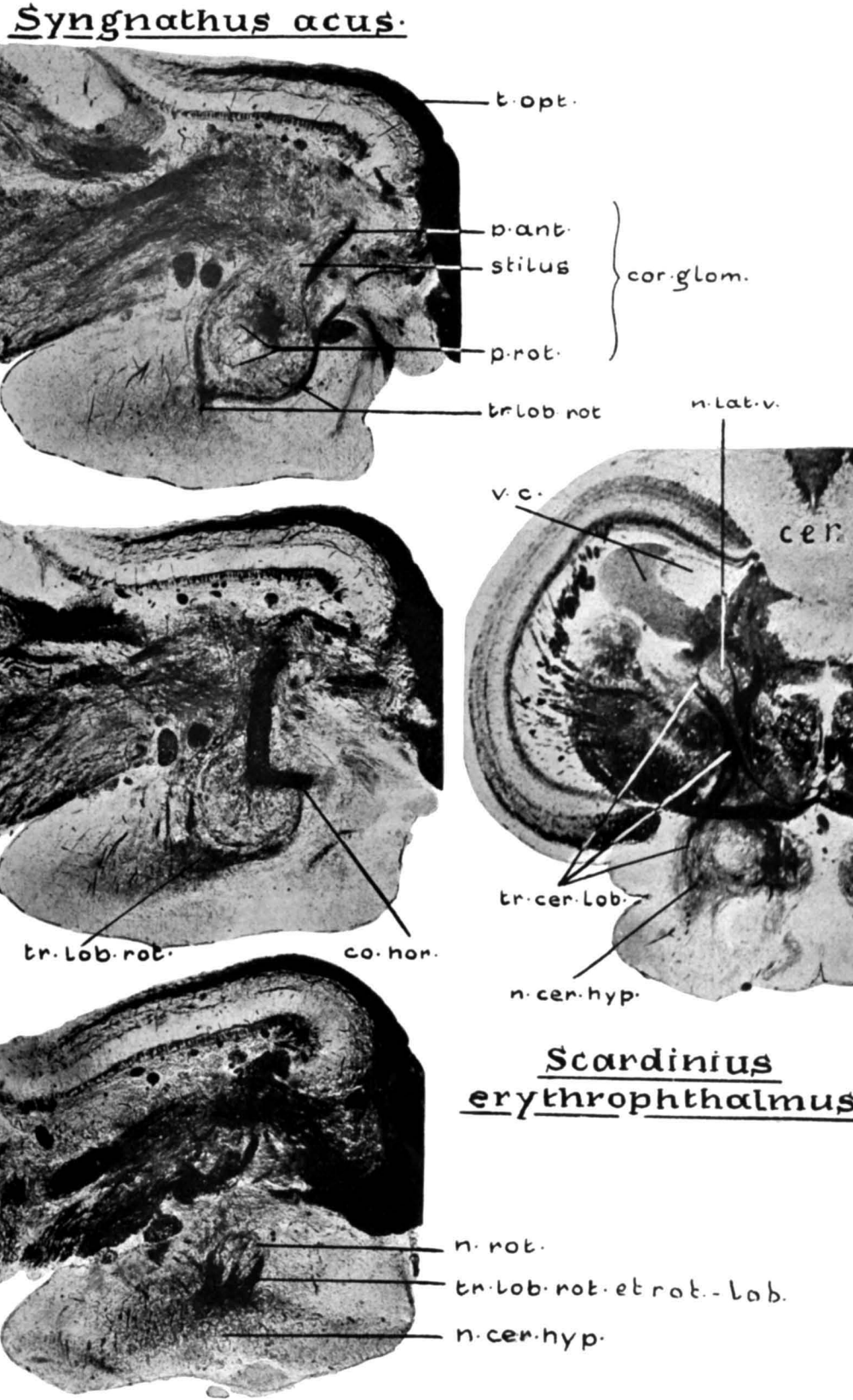


Fig. 3.

reason of the caudo-ventral displacement and accumulation of this glomerular system?

In connection with this we must realize that the ventro-caudal accumulation of glomeruli resulting in the formation of the rotundus nucleus takes place in the caudal end of a strand of cells formerly described by us as *nucleus prerotundus* because this column commences at some distance in front of the rotundus region. It, however, is not only in this sense that the name prerotundus is appropriate to this strand of cells, the name happens to be appropriate also in so far as its caudal pole serves as a basis for the formation of the rotundus nucleus. The small cells of the nucl. prerotundus (also in its caudal pole) receive fibres from the tr. olfacto-hypothalamicus lateralis.

The first form in which the glomerular rotundus nucleus develops is such that a small number of glomeruli appear amongst the small cells in the caudal pole of the prerotundus nucleus. This arrangement is seen in some Physostomes (carp, c.f. also SHELDON, '12) and also in the Physoclist, *Ammodytes tobianus*.

In the higher fishes the number of these central glomeruli in the rotundus nucleus increases, and the cells move more and more to the periphery, their dendrites entering the glomerular centre where they synapt with the afferent olfactory fibres, with tecto-rotundus fibres and with fibres of the horizontal commissure, originating on the contralateral side. In several Acanthopterygei especially in Plectognathi and Lophobranchi the small cells have nearly all migrated to the periphery forming a cellular capsule around the glomerular centre. This gradual accumulation of the small cells, part of which may have shifted from the anterior nucleus to the periphery of the glomerular mass of the rotundus has been observed also in Japanese fishes by our former collaborator, Prof. SUZUKI ('32 a).

While the dendrites of these cells enter the glomerular centre, their axiscylindres run downward and backward ending in the hindpole of the lobi inferiores¹⁾. Similar exones arise from the peripheral cells of the nucl. anterior, forming a thalamo-lobar tract. Contrary, however, to the nucleus anterior the nucl. rotundus also receives a large number of fibres arising in the lobi inferiores and ending among the central glomeruli (see also HOLMGREN '20). These fibres²⁾ originate in a large mass of cells located in the postero-lateral part of the lobi inferiores, rightly described by GOLDSTEIN ('05) as nucl. cerebellaris hypothalami (fig. 3 n. cer. hyp.). The chief afferent connection of this nucleus is obviously made by a tract that

¹⁾ SUZUKI ('32 a) rightly observed that this tr. rotundo-lobaris is best developed in such fishes where the peripheral cell mass of the rotundus is well developed.

²⁾ HOLMGREN ('20) considers these fibres as homologous to the mammillo-thalamic tract (Vicq d'Azyr) of Mammals, an opinion which we cannot share since the caudo-lateral part of the lobi inferiores, where most of these fibres arise, is by no means to be compared with the corpus mammillare. It does not receive fornix fibres but fibres from the nucl. lateralis valvulae in front of HERRICK's secondary gustatory nucleus.

arises from the cerebellum and the nucleus lateralis valvulae, immediately in front of HERRICK's secondary gustatory nucleus (the Rindenknotten of German authors). In our microphotograph of *Scardinius* (fig. 3) the whole course of this tract, already observed by EDINGER ('96) and HERRICK ('05, p. 420) is seen in one section and is labelled as tr. cerebello-lobaris (tr. cer. lob.). This connection, which may run both ways¹), is very distinct also in HOLMGREN's figs. 87, 88, 89 of *Callionymus* and in SUZUKI's picture of *Plecoglossus altivelis* (32 b., fig. 6).

It includes also fibres of the tertiary gustatory tract described by C. J. HERRICK ('05) but the fact that the nucleus lateralis valvulae is so closely connected with the cerebellum and also sends descending fibres in the fasc. long. posterior (tr. n. valv. desc. in Belone, fig 2) makes it evident that the cerebello-hypothalamic tract has a prevailing static function.

We do not believe that this static function has to do with gustatory impulses only. We are more inclined to assume that the location of the small celled secondary gustatory nucleus immediately behind the nucl. lateralis valvulae is an expression of the fact that in fishes, where taste buds are spread over a large part of the body, taste also has a directive influence. HERRICK himself ('05) emphasized the close relation of his secondary gustatory nucleus to the nucleus lateralis valvulae (l.c. p. 419 and 452) and of his tertiary gustatory tract to cerebello-lobar and lobo-cerebellar fibres. The addition of gustatory impulses to this tract may explain that this tract has its greatest development in Cyprinoids and Siluroids where taste is most developed. (ADDISON, '23) and where the nucl. lateralis valvulae and the valvula cerebelli are also very large.

I therefore believe that the addition of static projections to the lobi inferiores has to be considered chiefly responsible for the development of the lobo-rotundus system and the caudo-ventral displacement of the glomerular body, the more so as the lobi inferiores also receive a descending geniculate bundle. This may also explain that the lobo-rotundus tract and the nucleus rotundus are well developed in Megalops, and Lophobranchi whose gustatory system is not nearly so strongly developed as in Cyprinoids and Siluroids.

So much is sure that — whereas the fixation of the dorso-frontal part of the corpus glomerulosum (or nucleus anterior) may be explained by its connections with the pretectal and anterior tectal area — the increase of the glomerular system in the caudo-ventral rotundus nucleus partly at the expense of nucl. anterior has to be explained by the increasing influence of the caudo-lateral part of the lobi inferiores on this system, and the structural accommodation to these impulses in the more differentiated Teleosts.

The various stimulations correlated in the rotundus part of the corpus glomerulosum are affected, partly by lobo-cerebellar fibres, partly by the lobo-bulbar fibres arising in the hypothalamus and ending on the level of the trigeminus nucleus (basi-quintal tract of WALLENBERG, '31). According to HOLMGREN ('20) collaterals of the tr. lobo-rotundus also take a descending course.

1) Cf. WALLENBERG '07, p. 37 and WALLENBERG '31, p. 260—261.

The last example of a shifting to be mentioned here concerns the *hypothalamic hypophysary nuclei*. As is well known in Mammals the hypophysary nuclei may be divided into three groups, a basal supra-optic and paraventricular magnocellular nucleus and some parvocellular tuberal groups, the former being located in the preinfundibular, the latter in the postinfundibular region of the hypothalamus. Of the two magnocellular nuclei the supraoptic one is chiefly concerned with the hypophysary function, influencing water- and salt metabolism.

Ontogenetically and phylogenetically both magnocellular nuclei derive from a continuous mass of large cells, the so-called preoptic magnocellular nucleus of fishes. From the descriptions by JOHNSTON ('01), RÖTHIG ('11), SHELDON ('12), CHARLTON ('32), KAPPERS ('34) and BOON ('38) it appears that in its primitive form this nucleus presents itself as a mass of magnocellular elements, located in front and above the optic chiasm.

In some Teleosts a part of the cells of this nucleus shifts backward along the hypothalamo-hypophyseal bundle to acquire a far more caudal position near the hypophyseal stalk (Gadus, RÖTHIG, '11; Sarda, CHARLTON, '32; Belone, KAPPERS, '34). In Mammals (rabbit, dog, apes and man) also a part of the basal hypophyseal nucleus shifts over the optic chiasm to form a postchiasmatic parahypophyseal nucleus.

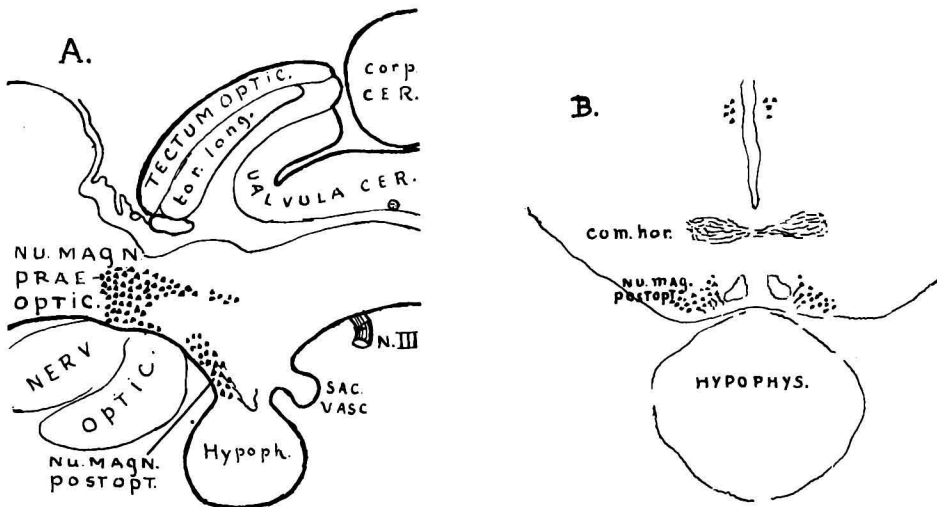


Fig. 4. A. Sagittal section of the brain of Sarda, after CHARLTON, showing the location of the preoptic and postoptic magnocellular nuclei. B. Transverse section of the brain of Belone showing the location of the postoptic magnocellular nucleus on the level of the hypophysis.

The shifting of these cells in the direction of their effector, the hypophysis, is a most interesting phenomenon. Whereas other migrations in the central nervous system, proceed in the same direction in which the dendrites of their cells (the chief receptors of the impulses) grow out, the

shifting of this hypophysary nucleus apparently occurs in the direction of its axiscylindres, thus approaching the effector, the hypophysary gland.

A similar migration in an axonic direction is observed in the onto- and phylogenetic development of the autonomic system of the viscera. It is a well known fact that the postganglionic cells of the sympathetic chain develop either from the neural crest (MÜLLER and INGVAR, '23), or, more probably from the spinal cord itself along the ventral roots (KUNTZ and BATESON, '20, JONES, '37) or both ways (KUNTZ, '29; TERNI, '31). Whatever may be the case, all postganglionic cells in the embryo (as in adult primitive vertebrates) are located near the spinal cord or bulb. Later in development (similarly in higher vertebrates compared with lower ones) an ever increasing number of the cells shifts into the direction of their effectors and, migrating along the axonic fibre strands, acquires a juxta-mural or an intramural position.

Since this proces of migration apparently is the opposite of what usually occurs in the central nervous system, there must be a special reason for it. This reason is to be found in the different ways in which reflexes are effected in the central and autonomic nervous systems. Whereas in the central nervous system reflex action occurs through the transmission of the stimulus to the dendrites (or body) of the cells, LANGLEY and ANDERSEN ('94) pointed out that the majority of the reflexes in the visceral autonomic system are *axon reflexes*, i.e. reflexes initiated by impulses originating in the effector. Reaching the postganglionic cells by way of their axons these impulses spread again to the effector by means of collaterals. These antidromic or axon reflexes according to our opinion ('08) are responsible for the antidromic shifting of autonomic cells towards their effector.

In his lecture on the autonomic nerves given at *Amsterdam* ('05) LANGLEY said: "from the axon reflex we naturally pass to consider whether any reflex in the usual sense occurs in the other visceral ganglia". He then further stated: "No reflex action is obtained from them which cannot reasonably be referred to an axon reflex" (l.c. p. 16). — Although this may be exaggerated, the prevalence of axon reflexes in the sympathetic nervous system is very likely also owing to the fact that whereas in the somatic roots the number of sensory fibres usually exceeds the number of motor fibres, the number of sensory visceral fibres in the rami albi is far less than of the preganglionic ones, (1 : 8 approximately). — Considering the fact that the number of postganglionic fibres again exceeds at least thirty times the number of preganglionic ones (RANSON and BILLINGSLEY, '18) it is not at all surprising that most reflexes occurring in the viscera are axonic ones, thus explaining also the migration of the postganglionic cells in the direction of the effector.

Also STIEMENS ('34) in her work on the phylogenetic development of the vagus and sympathetic system considers the antidromic reflex as responsible for the increasing peripheral displacement of thoracic and abdominal postganglionic cells in the series of Vertebrates, in the direction of their effectors, a process that runs parallel with the phylogenetic increase of intestinal activity.

Since, however, the hypothalamic cells referred to are also to be con-

sidered as autonomic cells, comparable to postganglionic visceral elements, their migration in the direction of the hypophysis confirms our explanation ('08) of the peripheral migration of the postganglionic cells of the viscera.

LITERATURE.

- ADDISON ('23), *J. Comp. Neur.* **36**; BELLONCI ('84—'85), *Mem. R. Acc. dei Lincei*, Roma, Serie IV, **1**; BOON ('38), *Dissertatie* Amsterdam, *Acta Psych. et Neur.* **18**; BRICKNER ('29), *J. Comp. Neur.* **47**; BURR ('28), *J. Comp. Neur.* **45**; CATOIS ('02), *Bull. Scient. de la France et de la Belgique* **36**; CHARLTON ('32) *J. Comp. Neur.* **55**; CHARLTON ('33), *J. Comp. Neur.* **57**; EDINGER ('96) *Vorlesungen über den Bau der nervösen Centralorgane des Menschen und der Tiere*, Leipzig; FRANZ ('11), *Zool. Jahrb. Abt. Anat. u. Ontog.* **32**; FRANZ ('12), *Folia Neurobiol.* **6**; FRANZ ('13), *Anat. Anz.* **45**; FRITSCH ('78), *Untersuchungen über den feineren Bau des Fischgehirns*, Berlin; GOLDSTEIN ('05), *Arch. mikr. Anat.* **66**; HERRICK, C. L. ('92), *J. Comp. Neur.* **2**; HERRICK, J. C. ('05), *J. Comp. Neur.* **15**; HOLMGREN ('20), *Acta Zool.* **1**; HOOGENBOOM ('16), *Dissertatie* Amsterdam, *Zeitschr. mikr. anat. Forsch.* **18**; JANSEN ('29), *Proc. Kon. Akad. v. Wetensch.* **32**; JEENER ('30), *Proc. Kon. Akad. v. Wetensch.* **33**; JONES ('37), *Anat. Rec.* **70**; JOHNSTON ('01), *Zool. Jahrb. Abt. Anat. u. Ontog.* **15**; KAPRERS ('06), *J. Comp. Neur.* **16**; KAPPERS ('08), *Engl. J. of Physiol.* **37**; KAPRERS ('34), *Zeitschr. mikr. anat. Forschung* **36**; KAPPERS, HUBER and CROSBY ('36), *The comparative anatomy of the nervous system of Vertebrates, including man*, Macmillan Comp. New-York; KRAUSE ('98), *Arch. mikr. Anat.* **51**; KUNTZ ('29), *The autonomic nervous system*, London; KUNTZ and BATESON ('20), *J. Comp. Neur.* **32**; KYOZO KUDO ('23), *Anat. Anz.* **56**; KYOZO KUDO ('23a), *Proc. Kon. Akad. v. Wetensch.* **26**; KYOZO KUDO ('24), *Anat. Anz.* **57**; LANGLEY ('05), *The autonomic nervous system Vereen. Secties v. Wetenschapp. Arbeid*, Amsterdam; LANGLEY and ANDERSEN ('94), *Engl. J. of Physiol.* **16**; LUBSEN ('21), *Ned. Tijdschr. v. Geneesk.* **11A**; MEADER ('34), *J. Comp. Neur.* **59**; MÜLLER and INGVAR ('23), *Arch. mikr. Anat.* **99**; NEUMAYER ('95), *Arch. mikr. Anat.* **44**; PARKER ('03), *U.S.A. Fish Comm. Bull.* for 1902; PEARSON ('36), *J. Comp. Neur.* **64** and **65**; RADL ('15), *Morph. Jahrb.* **49**; RAMON, P. ('99), *Rev. trimestr. microgr.* **4**; RAMSAY ('01), *J. Comp. Neur.* **11**; RANSON and BILLINGSLEY ('18), *J. Comp. Neur.* **29**; RÖTHIG ('11), *Folia Neurobiol.* **5**; SALA ('95), *Arch. ital. de Biol.* **24**; SARGENT ('03), *Mark Anniversary Vol.* Boston; SHANKLIN ('34), *Acta Zool.* **15**; SHANKLIN ('35), *Trans. Roy. Soc. London* **224B**; SHELDON ('12), *J. Comp. Neur.* **22**; SPRENKEL, BERKELBACH VAN DER ('15), *J. Comp. Neur.* **25**; STENDELL ('14), *Abhandl. Senckenb. Naturf. Ges. Frankfurt a/M.* **36**; STENDELL ('14), *Anat. Anz.* **46**; STIEMENS ('34), *Verhand. Kon. Akad. v. Wetensch. Amsterdam, 2de Sectie*, **33**; STRÖER ('39), *Zeitschr. f. Anat. u. Entw. Gesch.* **110**; SUZUKI ('32a), *Saito, Ho-On-Kai, Sendai* **8**; SUZUKI ('32b), *Saito, Ho-On-Kai, Sendai* **8**; SUZUKI ('32c), *Annot. Zool. Japon.* **13**; TUGE, HIDEOMI ('29), *Report Tohoku Imp. Univ. Sendai* **4**; TERNI ('31), *Zeitschr. f. Anat. und Entw. gesch.* **96**; TUGE I (34a), *J. Comp. Neur.* **60**; TUGE, HIDEOMI II (34b), *J. Comp. Neur.* **60**; TUGE, HIDEOMI III ('35), *J. Comp. Neur.* **61**; WALLENBERG ('07), *Anat. Anz.* **31**; WALLENBERG ('13), *Névraxe* **14**; WALLENBERG ('31), *Arch. f. Psych. u. Nervenkr.* **94**.