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Published in:
Brain Research

DOI:
[10.1016/0006-8993\(81\)90210-9](https://doi.org/10.1016/0006-8993(81)90210-9)

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
1981

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Luiten, P. G. M. (1981). Afferent and efferent connections of the optic tectum in the carp (*Cyprinus carpio* L.). *Brain Research*, 220(1), 51-65. [https://doi.org/10.1016/0006-8993\(81\)90210-9](https://doi.org/10.1016/0006-8993(81)90210-9)

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AFFERENT AND EFFERENT CONNECTIONS OF THE OPTIC TECTUM IN THE CARP (*Cyprinus carpio* L.)

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(Accepted November 6th, 1980)

Key words: afferents — efferents — carp — horseradish peroxidase

SUMMARY

The afferent and efferent connections of the tectum opticum in the carp (*Cyprinus carpio* L.) were studied with the HRP method. Following iontophoretic peroxidase injections in several parts of the tectum anterograde transport of the enzyme revealed tectal projections to the lateral geniculate nucleus, dorsal tegmentum, pretectal nuclei, nucleus rotundus, torus longitudinalis, torus semicircularis, nucleus isthmi, contralateral tectum and to the mesencephalic and bulbar reticular formations.

Tectal afferents were demonstrated by retrograde HRP transport in the area dorsalis pars centralis of the telencephalon, torus longitudinalis, torus semicircularis, nucleus isthmi, nucleus profundus mesencephali, several pretectal nuclei, dorsomedial and dorsolateral thalamic nuclei, nucleus of the posterior commissure, mesencephalic and bulbar reticular nuclei and nucleus ruber. Visuo-cerebellar circuitry was investigated by means of peroxidase injections in the various parts of the cerebellum. These experiments revealed indirect retino- and tecto-cerebellar pathways via the pretectal nuclei and the nucleus isthmi.

INTRODUCTION

The neuroanatomy of the visual system in vertebrates has recently received new inputs due to the unique technical possibilities offered by the intracellular transport methods. Unlike the situation for several other vertebrate classes^{9,11,34}, our knowledge especially of non-retinal tectal inputs for teleost fish is far from complete^{12,14,29}. The existence of such connections in fish, however, is known on the basis of electrophysiological data showing that the activity of tectal cells can be influenced by various non-visual stimuli²⁴, perhaps by way of tegmental²⁵ or even spinal structures²⁴.

Special interest in tectal connections in our laboratory originates from electrophysiological investigations on the respiratory control system in carp. It was found that HRP injections at sites of cell groups with a respiratory rhythmic activity in mesencephalic and diencephalic parts of the brain resulted in extensive labeling of structures in the optic tectum². Apart from these physiological data the importance of the optic tectum in visually mediated respiratory behavior was also assessed by tectal ablation studies³¹.

Recordings we made from respiratory rhythmic neurons in the rostral aspects of the tectum and mesencephalic tegmentum² followed by peroxidase injections resulted in labeling of several tectal connections. A more detailed interpretation of these results, however, is hampered by the limited information available on visual system anatomy. In particular, there is also a need for data on connections between tectum and cerebellum in the carp since Karten and Finger¹⁵ and Finger⁶ provide strong evidence for the absence of a direct pathway between these two important brain centers in catfish. Such a connection was long believed to be present as the tractus tecto-cerebellaris.

In the present study the input and output channels of the optic tectum in teleost fish were investigated after iontophoretic injections of horseradish peroxidase in the optic tectum and analysis of the retrograde and anterograde transport. Although several degeneration studies reported on tectal projections in teleost fish^{5,10,29,30} an effort is made to give a more detailed description of the course of tectal efferents in carp based on anterogradely transported HRP.

To obtain data on the visuo-cerebellar interconnections, HRP injections were also placed in several parts of the cerebellum.

MATERIALS AND METHODS

All experiments were performed on 3-year-old specimens of *Cyprinus carpio* L. measuring about 30 cm in length and obtained from hatcheries of the Netherlands Organization for the Improvement of Inland Fishery. The results of the tectal connections are based on 18 successful experiments. Additional information on the visual pathways related to the cerebellum is provided by seven relevant experiments of a larger series of HRP injections in the corpus cerebelli.

The animals were deeply anesthetized in a 1:15,000 solution of MS-222 (Sandoz) in tap water. The brain was exposed and a glass micropipette with a tip diameter varying between 10 and 50 μm and filled with a 10 % HRP (type VI, Sigma) solution in 0.01 M NaCl or 0.05 M Tris·HCl buffer (pH = 8.2) was positioned in a part of the tectum or in the cerebellar corpus with the aid of a hydraulic micromanipulator.

A current generator was connected to a silver wire inserted in the micropipette and to another wire in the water surrounding the animal. A positive DC current of 1.5–2.0 μA , 1 sec on — 1 sec off, was then applied to the micropipette during 20 min total on-time, for iontophoretical peroxidase delivery.

Following iontophoresis the electrode was left in situ for 10 min to prevent loss of peroxidase during retraction.

A second set of large injections was obtained by inserting air-dried HRP around the tip of a glass micropipette into the optic tectum after which the tracer dissolved in the surrounding nervous tissue.

Following the injections the skull was closed with dental cement and the animals were allowed to survive for 3–20 days at 18 °C. Optimal results were obtained after survival times of 12–15 days.

The long survival times necessary to obtain adequate retrograde labeling may have produced a considerable shrinking of the observed injection site, thereby hampering the interpretation of the experiments. The experiments using iontophoretic HRP delivery and short survival times, however, showed that such shrinking of the actual size of the injection site during the survival period is minimal, apparently due to the low temperature of the survival tanks. The animals were perfused with teleost saline containing heparine, followed by a 2% paraformaldehyde, 1% paraformaldehyde–4% glutaraldehyde, or 4% glutaraldehyde solution in phosphate buffer (0.1 M; pH = 7.4). The brains were then embedded rapidly in 20% gelatin. The trimmed gelatin block was immersed in the same fixative overnight at 4 °C. Prior to sectioning at 40 μ m on a freezing microtome, the blocks were immersed for 2 h in a 30% sucrose solution.

Every second section was stained for HRP according to the diaminobenzidine method of Graham and Karnovsky⁸ or the modified procedure of Malmgren and Olsson²⁰ and counterstained with cresyl violet. In the later cases the adjacent sections were stained according to the benzidine-diHCl procedure of de Olmos and Heimer³ or Mesulam²¹. Especially the procedure of de Olmos and Heimer³ proved to be extremely sensitive and powerful.

RESULTS

As has been reported before¹⁹, injection of HRP in teleost nervous tissue results in both retrograde labeling of fibers and somata of afferent neurons and in anterograde labeling of efferent fibers.

Application of the sensitive HRP procedure of de Olmos and Heimer³ might give rise to labeling of collateral connections, which might hamper an adequate interpretation. In that sense one might describe tectal efferents that in fact are collaterals of, e.g., retino-tectal fibers. These problems of interpretation, however, were overcome: (1) by section-to-section tracing of filled fibers to determine possible sites of axonal branching; (2) by comparing results obtained with the de Olmos and Heimer technique with series treated according the diaminobenzidine procedures of Graham and Karnovsky⁸ or Malmgren and Olsson²⁰, and (3) by paying adequate attention to the fiber diameters of the various labeled tracts. In all of the cases in this study, the combination of the variously treated sections led to a clear and easily distinguishable picture of labeled fiber tracts. It should be noted, however, that although the HRP technique applied to teleost material results in a substantial labeling of efferents, further study using anterograde transport of radioactive tracers would be of great value for the evaluation of the efferent projections described in the present paper.

Fig. 1. Photomicrograph of retrogradely labeled afferents in the torus longitudinalis following a deep tectal injection of horseradish peroxidase. Scale bar = 50 μ m.

Injections in deeper tectal layers resulted in labeling of afferents and efferents that to a certain degree differed from the results of more superficial injections. These differences in the results are exemplified by two representative cases of a deeper (Fig. 2) and a more superficial peroxidase injection in the tectum (Fig. 3).

The connections found in this study will be described according to the following classification: (a) telencephalic afferents, (b) retino-tectal projections, (c) the descending tecto-bulbar fiber system and related connections, (d) the complex of tractus mesencephalo-cerebellaris and horizontal commissure, and (e) a diverse group of thalamic and midbrain connections. Cerebellar pathways considered to be involved in the visual circuitry are described separately.

Telencephalic afferents

Following HRP injections into the deeper tectal layers a group of cells in the ipsilateral telencephalon became labeled with the tracer. Although we never observed a clear staining of fibers connected to these afferents, somata in the central telencephalon, which is called the area dorsalis telencephali pars centralis^{23,26}, became labeled. These cells are medium sized, approximately 15 μ m in diameter, and are part of a relatively cell sparse area surrounded by cell-dense dorsal and lateral telencephalic areas.

Retino-tectal projection

The results of this study on the structure and course of the retino-tectal part of the optic nerve is in general agreement with the description of the optic nerve

Fig. 2. Series of transverse sections from rostral (A) to caudal (F) with diagrammatic charting of fiber and cell labeling following HRP injections in the deeper strata of the optic tectum.

projection as studied by degeneration and autoradiographic techniques. The retino-tectal projection can be clearly divided in a dorsomedial and a ventrolateral root which splits just anterior to the nucleus rotundus and nucleus geniculatus. After entering the brain the dorsomedial root turns dorsad lateral to the preoptic region and then fans out over the dorsal and more rostral aspects of the tectum. The ventrolateral bundle runs caudal and supplies the more lateral and caudal parts of the optic tectum.

Fig. 3. Diagrammatic charting of transverse sections from rostral (A) to caudal (G) with the anterograde and retrograde labeling after an HRP injection in the more superficial strata of the optic tectum.

Consequently, rostral and caudal HRP injections are reflected in the larger quantity of fiber labeling in the dorsomedial or ventrolateral optic roots respectively. Both roots consist of a large proportion of coarse fibers and a smaller quantity of fine fibers. Within the tectum, thick fibers run as condensed bundles in the stratum opticum, both in the dorsomedial and in the ventrolateral roots and fine fibers run in the stratum fibrosum et griseum superficiale.

The tecto-bulbar fiber system and related connections

The second large fiber system that becomes labeled after tectal injections is the extensive fiber system that connects the tectum with the midbrain and bulbar reticular formation. Over a short distance various other tectal connections share the course of this fiber system. Within the tectum, the tecto-bulbar pathway runs in the stratum periventriculare, then traverses the torus semicircularis and reaches the ventrolateral tegmental surface (Fig. 3E). The bulk of the tecto-bulbar pathway consists of efferent tectal fibers and is called the tractus tecto-bulbaris. The tract is composed of both a crossed and an uncrossed component. The crossing fibers run to the midline, decussate in the commissura ansulata and immediately turn caudal occupying a medial position in the floor of the midbrain tegmentum (Fig. 3F). At this level, some of the fibers move dorsad to end in fine branches within the mesencephalic reticular formation. The larger quantity of tecto-bulbar fibers, however, do not cross the midline but run caudad as the tractus tecto-bulbaris rectus which, during its course through the brain stem, takes a position just lateral to its contralateral counterpart. Throughout the midbrain and bulbus, fibers emerge from the tecto-bulbar tracts and branch into fine twigs in the various divisions of the reticular column (Fig. 4). No fiber labeling could be detected beyond the level of nucleus reticularis inferior. Beside the major tecto-bulbar pathway described above, another smaller branch of the tecto-bulbar tract descends from the rostromedial tectum. Here bundles of fine fibers leave the tectum parallel to the dorsomedial optic tract, but then turn caudad at the dorsal tegmental surface and join the tractus mesencephalo-cerebellaris anterior. Although the majority of these labeled fiber bundles will give rise to the commissure horizontalis (see next paragraph), the most medial fascicle descends medially joining the tractus tecto-bulbaris just rostral to the commissura ansulata (Fig. 3E).

Although the tractus tecto-bulbaris is mainly efferent in character a number of somata mainly in the ipsilateral and occasionally in the contralateral reticular formation of midbrain and medulla oblongata were also labeled with HRP. They constitute an afferent bulbo-tectal projection via the tractus tecto-bulbaris.

The intratectal part of the tecto-bulbar tract is shared by various midbrain connections. A considerable number of fibers enter the torus semicircularis immediately after leaving the tectum. The afferent portion of these fibers soon reaches their parent cell bodies in the lateral border of the torus (Fig. 3E). Since this retrograde labeling did not occur after HRP injection in the rostral parts of the tectum it cannot be excluded that we are dealing with labeling of afferents to the torus longitudinalis whose fibers run via the optic tectum¹⁴.

Fig. 4. Photomicrograph of anterogradely labeled fibers leaving the uncrossed tecto-bulbar tract towards their termination field in the superior reticular nucleus. Scale bar = 200 μ m.

Tectal efferents run more medially and project on the central core of the torus. A few fibers can be followed farther as afferents that spring from labeled somata ventromedial to the nucleus lateralis valvulae and close to the oculomotor nuclei. Some other fibers end as efferents in the nucleus lateralis valvulae.

A second group of connections that is related to the tectobulbar pathway is formed by afferents from the nucleus profundus mesencephali and the nucleus isthmi (Fig. 3F). The nucleus profundus mesencephali (Fig. 3E) is situated at the ventromedial border of the torus semicircularis dorsolateral and also rostral to the nucleus isthmi. Labeling of nucleus profundus afferents only occurred following the more superficial injections of the tracer in the tectum. Such injections also resulted in labeling of a small number of cells in the contralateral nucleus profundus. These contralateral tectal afferents cross the midline in the commissura ansulata. The nucleus isthmi connection consists of an afferent and an efferent component. The tectoisthmic efferents seem to reach the core while the afferent somata (Fig. 2E) have a more peripheral position in the nucleus.

Tractus mesencephalo-cerebellaris and commissura horizontalis (Figs. 2 and 3)

Fascicles of fine fibers leave the stratum periventriculare at the anterior end of the tectum and turn caudad along the dorsal surface of the tegmentum to form a considerable part of the tractus mesencephalo-cerebellaris anterior (or tractus tecto-cerebellaris). Fine fibers from the medial parts of the tectum join the tractus mesencephalo-cerebellaris after it leaves the dorsal tegmental surface and takes a more ventral position. At the level where the commissura horizontalis traverses the nucleus

glomerulosus, labeled fiber bundles leave the tractus mesencephalo-cerebellaris and split into two parts. One part joins the dorsal ascending commissura horizontalis. These recurrent fibers can be followed as tectal efferents into the core of the ipsilateral nucleus rotundus (Fig. 2B). The other part traverses the nucleus glomerulosus ventrad (Fig. 3D) and constitute the ventral part of the commissura horizontalis. These fibers ascend medially, decussate posterior to the optic chiasma and descend again in the contralateral part of the commissura horizontalis. These crossed fibers can be followed up to the glomerular complex where the horizontal commissure traverses the nucleus glomerulosus dorsad and then turns rostrad again to terminate in the core of the contralateral nucleus rotundus. Although most of the fibers are efferent, some of them appear to be afferent and originate from cells of the nucleus preglomerulosus (Fig. 3C).

Other thalamic and midbrain connections

Intertectal connections. A number of fine fibers traverse the stratum periventriculare and ascend parallel to the ventrolateral optic root. These fibers decussate caudal to the optic chiasma, and accompany the contralateral ventrolateral optic root to reach the central layers of the contralateral tectum opticum. This connection has been described before as the commissura transversa. A number of fibers in this commissura does not reach the contralateral tectum, but terminates in the ventral aspects of the contralateral torus semicircularis (Fig. 3C). More or less parallel to the commissura transversa runs the commissura minor (Fig. 2B). This commissure contains efferent fibers that terminate diffusely in the medial aspects of the pretectal area.

Another group of intertectal fibers runs via the lamina commissuralis tecti which connect the tectal halves dorsally. Labeled fibers traverse the longitudinal tori and can be followed into the stratum album centrale of the contralateral tectum. Most of these intertectal fibers proved to be efferent of nature, although occasionally labeled somata were observed in the deep layers of the contralateral tectum.

Together with the latter group of intertectal fibers run the axons that sprout from afferent somata in the ipsilateral torus longitudinalis (Fig. 1). While the labeled somata in the torus were always situated in the more dorsal aspects, we also observed a number of efferent terminal structures in the more ventral granular layer of the ipsilateral torus.

Connections with the mesencephalic tegmentum (Fig. 2C). A condensed fascicle of coarse fibers emanates from the tectum at the level of the commissura posterior, runs medially and can be followed to labeled somata in the nucleus of the posterior commissure and dorsal aspects of the tegmentum both ipsi- and contralaterally. Apart from these afferents a number of fibers form efferent projections to the dorsal tegmentum. A considerable part of this fiber bundle, however, runs caudally and reaches parent cell bodies in a nucleus made up of large somata which we consider as the nucleus ruber¹. This is a circumscribed cell population ventral to and more or less continuous with the mesencephalic reticular formation (Fig. 5).

Connections between tectum and thalamus. A limited number of somata became retrogradely labeled in the periventricular thalamic nuclei (or dorsomedial optic

Fig. 5. Photomicrograph of labeled somata in the nucleus ruber following a deep tectal injection of HRP. Scale bar = 200 μ m.

nucleus of Ebbesson⁴; dorsolateral, dorsomedial and preoptic thalamic nuclei of Schnitzlein²⁸). These thalamo-tectal fibers follow a very diffuse course and consequently cannot be described in detail. Reciprocal tecto-thalamic efferents to these thalamic nuclei were hard to establish with certainty.

Projection to the lateral geniculate nucleus. One of the shortest connections found in this study is formed by an efferent projection to the lateral geniculate nucleus. This nucleus is situated in the rostral thalamus immediately lateral to the optic tract where it reaches the tectum. The geniculate projection is formed by coarse fibers that run via the marginal layer of the tectum and is strictly ipsilateral.

Connections between tectum and pretectal nuclei. In the transition area between tectum and thalamus, various groups of labeled somata could be detected. Several names have been given to these nuclei by various authors such as area pretectalis and nucleus pretectalis²⁸, nucleus opticus pretectalis dorsalis, ventralis and medialis²⁷, nucleus pretectalis²² and pretectal cell group numbers 1 and 27. Apart from these afferents an efferent tectal projection to the dorsal pretectal nucleus was observed.

Visuo-cerebellar connections (Fig. 6). In none of the tectal injection cases was there evidence for direct cerebello-tectal connections. Two HRP injections in the corpus cerebelli provided some information on direct cerebello-tectal projections (Fig. 6A). This might, however, be mistaken for some incompletely labeled efferents directed towards the torus longitudinalis¹⁴.

More clearly present, however, is an indirect visuo-cerebellar circuitry. Following HRP injections in the corpus cerebelli, large numbers of cells in the dorsal and ventral pretectal nuclei were retrogradely labeled, beside a smaller amount of somata

Fig. 6. Diagrammatic charting of HRP labeling following an injection in the corpus cerebelli from rostral (A) to caudal (C). Only labeling considered to be relevant to the visual system has been indicated.

in the optic nucleus of the posterior commissure (terminology of Repérant and Lemire²⁷). The pretecto-cerebellar projection has been reported before by Finger and Karten⁷ who described the dorsal and ventral pretectal nuclei as pretectal group 1 (P1) and 2 (P2), respectively. The labeled fibers that sprout from these cells constitute the afferent bulk of the tractus mesencephalo-cerebellaris anterior which courses caudad in the mesencephalic tegmentum and passes medial and slightly caudal to the nucleus lateralis valvulae on its way to the cerebellar corpus. Having a projection to cerebellum and oculomotor nuclei cell group P2 or ventral pretectal nucleus is considered to be equivalent to the nucleus of the basal optic root⁷.

A second category of visual cerebellar afferents is formed by retrogradely labeled somata in nuclei that are described in previous paragraphs as being related to the tectum. Most prominent is a clear isthmo-cerebellar pathway. Its fibers pass dorsal to the lemniscus lateralis in a medial direction, traverse the mesencephalic reticular formation and join the huge tractus mesencephalo-cerebellaris anterior in a cerebello-petal direction (Fig. 6B).

DISCUSSION

The efferent tectal connections described in this study to a considerable degree confirm the previous descriptions of Ebbesson and Vanegas⁵, Grover and Sharma¹⁰ and Sligar and Voneida³⁰. The retrograde labeling of tectal afferents reveal a number of input channels to the optic tectum, some of which have not been reported in teleost fish. The main afferent source to the tectum formed by the retinal projection has been described in such detail before that it will not be further discussed here.

A major group of tectal afferents in the central nervous system originate from neurons in the nucleus isthmi, nucleus profundus mesencephali and torus semicircularis. All these nuclei are known to be involved in vestibular, lateral line or gravistatic functions¹⁷. Afferents from these nuclei supply the tectum with gravistatic information perhaps necessary to discriminate moving visual stimuli from movements of the body. Reciprocal efferents from tectum to the nucleus isthmi and the torus semicircularis indicate that such processes also may take place in tegmental centers as has been established before by Page and Sutterlin²⁵.

The tectal afferent cell groups in the pretectal, preoptic and tegmental nuclei in cyprinoid teleost fish are all known to receive a projection from the retina²⁷. This suggests that these nuclei allow other sources of information to integrate with retinal information before it reaches the optic tectum. This view, however, is highly simplified since only a low percentage of pretectal and preoptic cells seem to project to the tectum. Data on the significance of a complicated pretectal and preoptic system in teleosts is scarce. Vanegas and Ebbesson³² in a degeneration study found only a minor telencephalic projection to the dorsomedial preoptic nucleus, while Ito and Kishida¹³ did not establish retrograde labeling in one of these nuclei after telencephalic HRP injections. However, the present study, as well as previous ones^{6,7,15}, demonstrates that projections of nuclei in the pretectal area to the cerebellum are present. Furthermore, in a recent study Finger and Karten⁷ conclude that the pretectal cell group 2 (P2),

which probably is identical to the ventral pretectal nucleus in our study, constitutes the homologue of the accessory optic nucleus as exists in reptiles, birds and mammals.

HRP injections in the deep tectal layers resulted in retrograde labeling of somata in the central core of the ipsilateral telencephalon which confirms the previous report of Ito and Kishida¹². Moreover, in our material indirect telencephalic connections with the optic tectum are suggested by bilateral projections from the tectum to the nucleus glomerulosus and preglomerulosus (or nucleus rotundus of Ebbesson and Vanegas⁵). Ito and Kishida¹³ report a projection from the latter nucleus to the telencephalon. Furthermore, a reciprocal connection from telencephalon to the nucleus preglomerulosus is described by Vanegas and Ebbesson³³.

Both tectal and cerebellar injections of HRP demonstrate that no direct tecto-cerebellar connections are present. The material, however, revealed various well developed pathways for indirect cerebellar connections with the visual system. The main cerebellar afferent fiber system from anterior parts of the brain, called the tractus mesencephalo-cerebellaris originates in the pretectal nuclei that surround the nucleus rotundus, which is in agreement with earlier reports^{6,7,15}. Since some of these pretectal nuclei receive a projection from the retina^{6,27}, the tractus mesencephalo-cerebellaris anterior probably constitutes the main cerebellar input channel for visual information. The isthmo-cerebellar projection may constitute a second, more indirect, circuit for visual information to reach the cerebellum. In teleost fish, as in various other vertebrate classes^{11,16}, the core of the nucleus isthmi receives a considerable projection from the tectum opticum (see also ref. 5). The functional character of an isthmo-cerebellar projection remains obscure as the nucleus is also involved in the processing of information on body posture.

The indirect visual pathways to the cerebellum, however, support the view of Kotchabhakdi¹⁸, who states that retinal information is probably processed in other brain parts before it reaches the cerebellum.

ABBREVIATIONS

C Ans commissura ansulata; Cb corpus cerebelli; CH commissura horizontalis; CM commissura minor CP commissura posterior; CT commissura transversa; Dc area dorsalis telencephali pars centralis; Dd area dorsalis telencephali pars dorsalis; Dld area dorsalis telencephali pars lateralis; DLv area dorsalis telencephali pars lateralis ventralis; Dm area dorsalis telencephali pars medialis; FLM fasciculus longitudinalis medialis; L Inf lobus inferior; LL lemniscus lateralis; nCP nucleus of the posterior commissure; nDL nucleus dorsolateralis thalami; nDM nucleus dorsomedialis thalami; nG nucleus glomerulosus; nGL nucleus geniculatus lateralis; nH nucleus habenularis; nI nucleus isthmi; nLV nucleus lateralis valvulae; nMV nucleus motorius nervi trigemini; nOC nucleus oculomotorius; nPd nucleus pretectalis dorsalis; nPv nucleus pretectalis ventralis; nPG nucleus preglomerulosus; nPM nucleus profundus mesencephali; nPO nucleus preopticus; nR nucleus rotundus; nRM nucleus reticularis mesencephali; nRS nucleus reticularis superior; nRub nucleus ruber; N II nervus opticus; N V nervus trigeminus; N VII nervus facialis; SAC stratum album centrale; SFGS stratum fibrosum et griseum superficiale; SG stratum granulosum; SM stratum marginale; SO stratum opticum; SPV stratum periventriculare; TrO tractus opticus; TGS tractus gustatorius secundus; TL torus longitudinalis; TMCa tractus mesencephalo-cerebellaris anterior (or tractus tecto-cerebellaris); TO tectum opticum; TSC torus semicircularis; TTBa tractus tectobulbaris pars anterior; TTBC tractus tectobulbaris cruciatus; TTBr tractus tectobulbaris rectus; Valv Cb valvula cerebelli.

ACKNOWLEDGEMENTS

The author expresses his gratitude to Dr. C. M. Ballintijn and Dr. E. Kicliter for fruitful discussions and constructive criticism on the manuscript. We are indebted to Mrs. J. Poelstra-Hiddinga and Mrs. A. de Ortega for their secretarial assistance.

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