Cell Tissue Res (1987) 248:439–448

Cell and Tissue Research

© Springer-Verlag 1987

A Golgi study of the isthmic nuclei in the pigeon (*Columba livia*)

Onur Güntürkün

Experimentelle Tierpsychologie, Psychologisches Institut, Ruhr-Universität Bochum, Bochum, Federal Republic of Germany

Summary. The isthmic nuclei of the pigeon were studied with the use of three different Golgi techniques. The nucleus isthmo-opticus (IO) consists of a single cell type in which all dendrites of one neuron take the same direction and ramify at identical distances from the perikaryon to form dense dendritic arborizations. The cell bodies of the IO neurons form two parallel layers. The dendrites of these neurons always extend to the area between the two layers so that the dendritic arborizations of opposite neurons overlap. A model of the cellular organization of the IO was constructed based upon these morphological characteristics. The neurons of the n. isthmi/pars parvocellularis (Ipc) have oval perikarya and long, smooth, infrequently branching dendrites. All neurons except those at the borders of the nucleus show the same dorsoventral orientation in their dendritic arborizations and together with their afferents seem to have a columnar organization. The dendrites of the neurons located at the margin of the nucleus ramify within the Ipc along its border. The n. semilunaris (Slu) consists of neurons with round somata that have on an average three dendrites with small spines. The axons leave the nucleus from the medial side and join the lemniscus lateralis. The neurons of the n. isthmi/pars magnocellularis (Imc) comprise a generalized isodendritic type resembling the cells of the reticular formation. Axons from the tectum penetrate the nucleus, making numerous en-passant contacts with several neurons.

Key words: Isthmic nuclei – Golgi study – Centrifugal system – Optic tectum – Reticular formation – Pigeon

According to Ariëns Kappers et al. (1936), the isthmic nuclei of birds consist of the four midbrain structures: n. isthmo-opticus (IO), n. isthmi/pars parvocellularis (Ipc), n. isthmi/pars magnocellularis (Imc) and n. semilunaris (Slu, Fig. 1).

The IO is one of the best studied examples of a nucleus manifesting a high rate of naturally occurring cell death during ontogeny. About 60% of the original IO neurons degenerate between the 12th and 16th days of incubation in the chick (Clarke and Cowan 1976). Clarke (1985) suggests that aberrant neuronal connections are eliminated by this cell loss. The IO is part of the topographically organized avian centrifugal optic system. It constitutes the tegmental part of a feedback circuit consisting of a projection from the retinal ganglion cells to the contralateral tectum, the efferents of which in turn project to the ipsilateral IO from which a back-projection leads to the contralateral retina (McGill et al. 1966a, b). Electrophysiological (Miles 1972a, b; Holden and Powell 1972; Pearlman and Hughes 1976) and behavioral experiments (Rogers and Miles 1972; Shortess and Klose 1977; Kniepling 1978) suggest that the IO serves to enhance the detection of moving objects and discrimination performance in dim-light situations.

Ipc, Slu and Imc have reciprocal and topographical connections with the ipsilateral optic tectum (Showers and Lyons 1968; Hunt and Künzle 1976; Hunt et al. 1977). Due to the hodological similarities and the equivalence of the transmitters in these nuclei, Künzle and Schnyder (1984) postulated that the isthmus-tegmentum complex is homologous in mammals, birds and reptiles. According to their study the Ipc would be comparable to the n. parabigeminalis of the rat, while Imc and Slu would be homologous to the dorsal or ventral parts, respectively, of the lateral periparabigeminal tegmentum. Despite this importance of the isthmic nuclei for a comparative analysis of the midbrain, information about their neuronal morphology are, with the exception of the IO, completely lacking (Cowan 1970; Angaut and Repérant 1978; Crossland 1979). The present study therefore describes the cellular characteristics of the isthmic nuclei on the basis of Golgi preparations.

Materials and methods

Three different Golgi techniques were applied to the brain material of ten adult homing pigeons (one to three years of age) of both sexes: Golgi-Cox, rapid Golgi and a Golgi technique developed by Mestres (Mestres and Lafarga 1972). The Golgi-Mestres procedure, which was employed with two brains, will be briefly summarized here: the animals were anesthetized (Mallin and Delius 1983) and perfused intracardially first with saline heated to 40° C and then with a fixation solution containing potassium dichromate (3%), paraformaldehyde (1%) and chloral hydrate (1.6%) dissolved in 0.12 M phosphate buffer (pH 7.4). The brains were quickly removed and postfixed for 4 h in the same fixative. Then, 2-mm thin sections of the brains were immersed for two days in a 6% potassium dichromate solution, which was renewed every day and kept at room tem-

Send offprint requests to: Onur Güntürkün, Experimentelle Tierpsychologie, Psychologisches Institut, Ruhr-Universität, D-4630 Bochum, Federal Republic of Germany

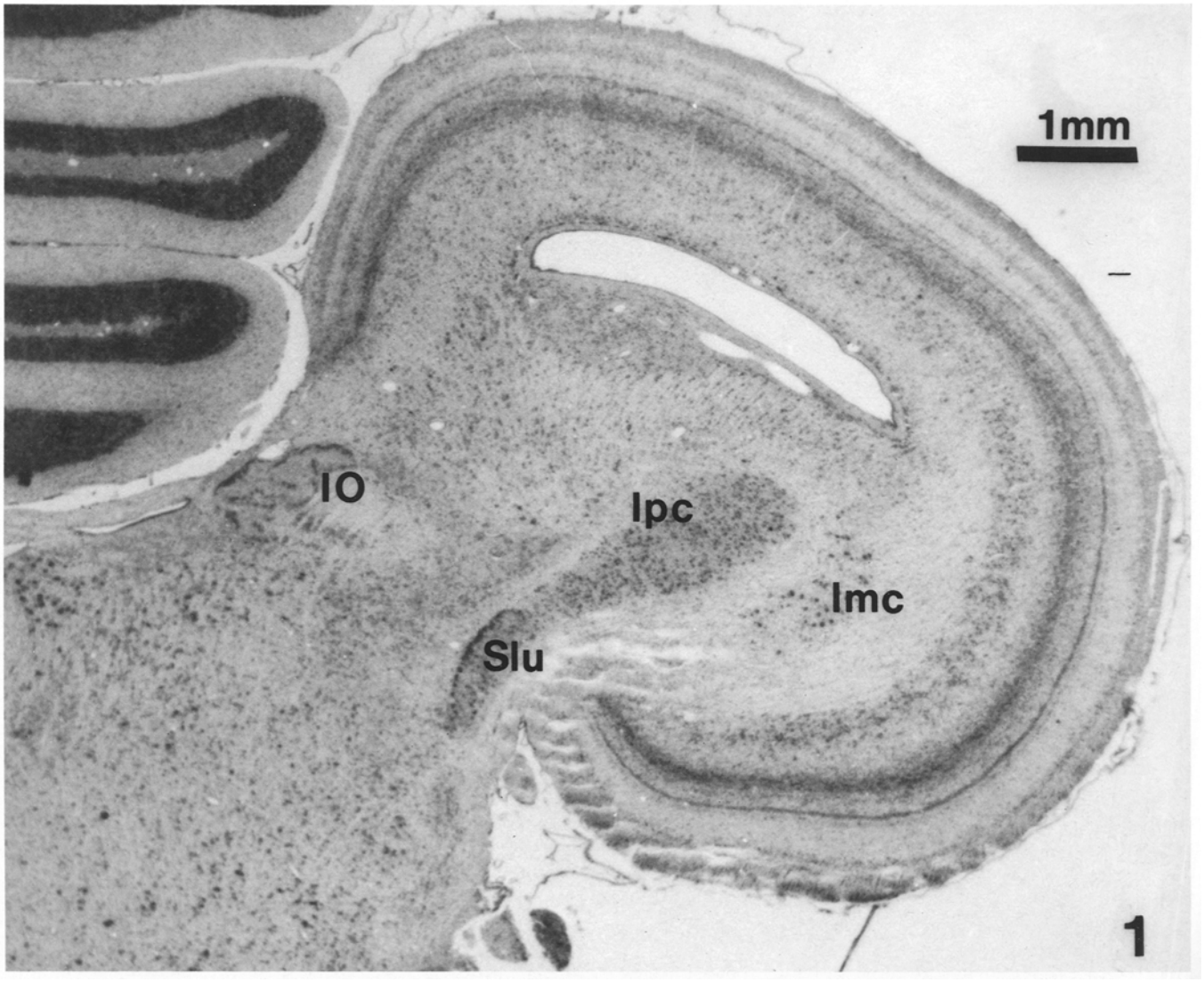


Fig. 1. The location of the isthmic nuclei in the pigeon. Frontal section, stained with cresyl-violet, that corresponds to the A 2.50 plane of the Karten and Hodos pigeon brain atlas (1967). *Imc* n. isthmi/pars magnocellularis; *Ipc* n. isthmi/pars parvocellularis; *IO* n. isthmo-opticus; *Slu* n. semilunaris; *TO* tectum opticum

perature in the dark. The sections were subsequently briefly washed in 0.5% silver nitrate solution and immersed for 36 h in 1% silver nitrate. After celloidin embedding, the blocks were cut into 100-µm thick sections.

The rapid Golgi impregnation described by Valverde (1970) was employed using five animals. Sections from three pigeon brains, stained according to the Golgi-Cox technique, were processed according to Ramón-Moliner (1970). Celloidin embedding was used throughout and 100-µm thick sagittal as well as frontal sections were made. To confirm the identification of anatomical structures the pigeon brain atlas of Karten and Hodos (1967) and series

Fig. 2. Rapid Golgi-impregnated neurons of the IO (n. isthmo-opticus)

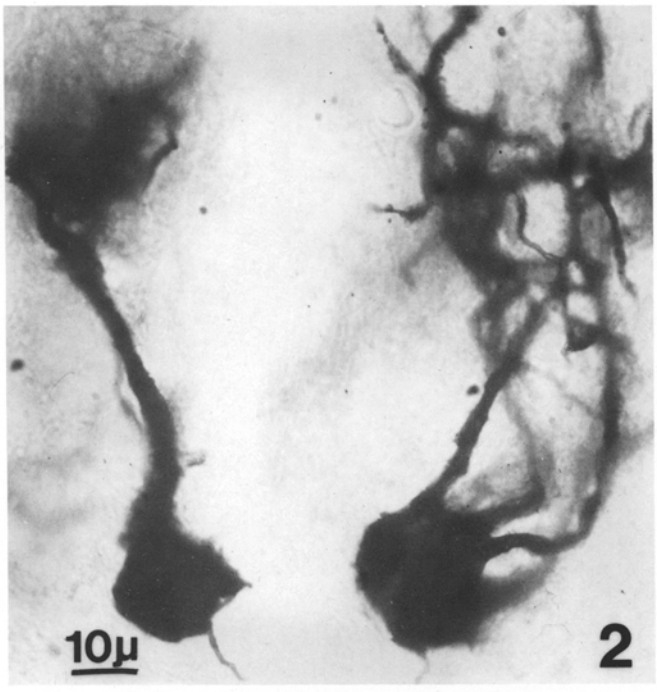
Fig. 3. Photomontage of a group of IO neurons in which the upper cell is located in the opposite layer to the lower three neurons. Note the area of dense dendritic arborizations between the neurons of different layers. Rapid Golgi impregnation

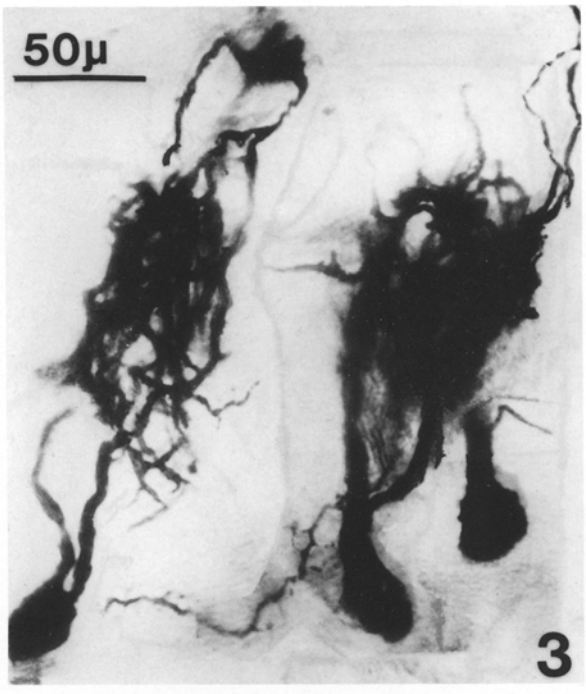
Fig. 4. Somatic spines (*arrows*) on IO neuron. Rapid Golgi

Fig. 5. Simplified model of the cellular organization of the IO. Only two cell rows that are separated by dendritic arborizations are shown. The axons entering the system are presumably of tectal origin

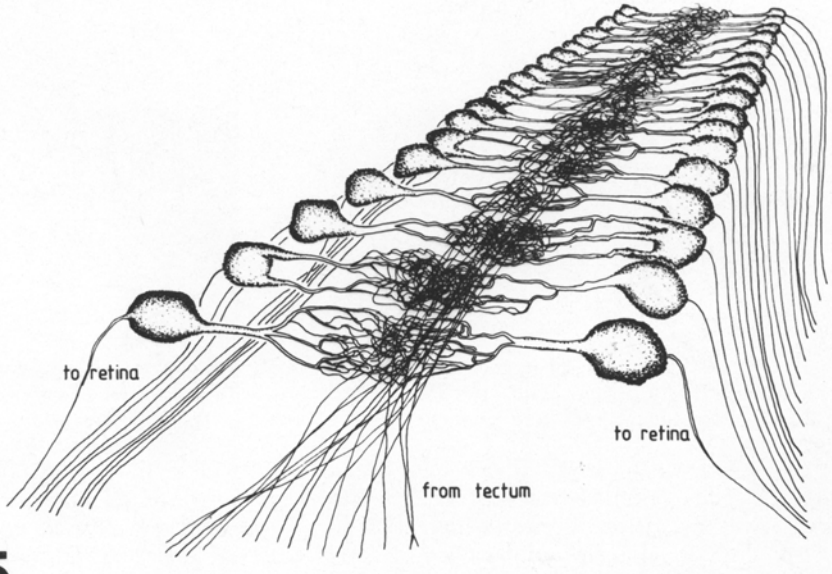
Fig. 6. Spines (*arrows*) and thin appendages on dendrites of a rapid Golgi-impregnated IO neuron

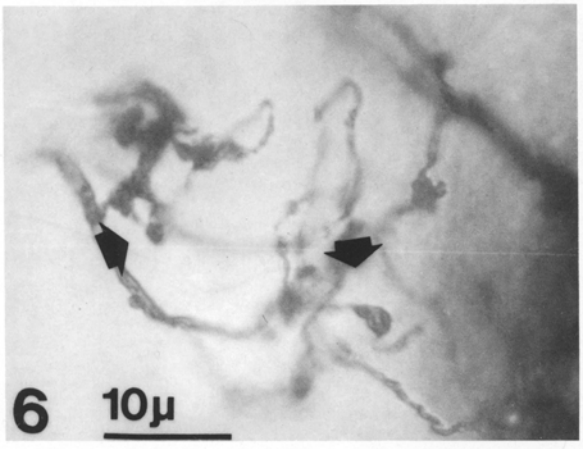
Fig. 7. Spine (*arrow*) on the axon hillock of a rapid Golgi impregnated IO neuron

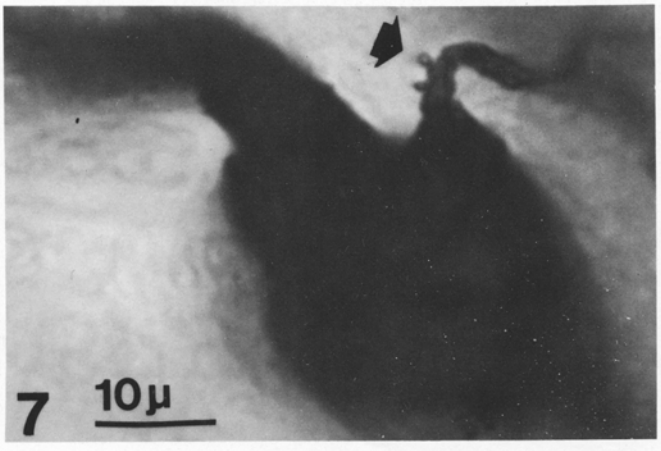

10µ
2

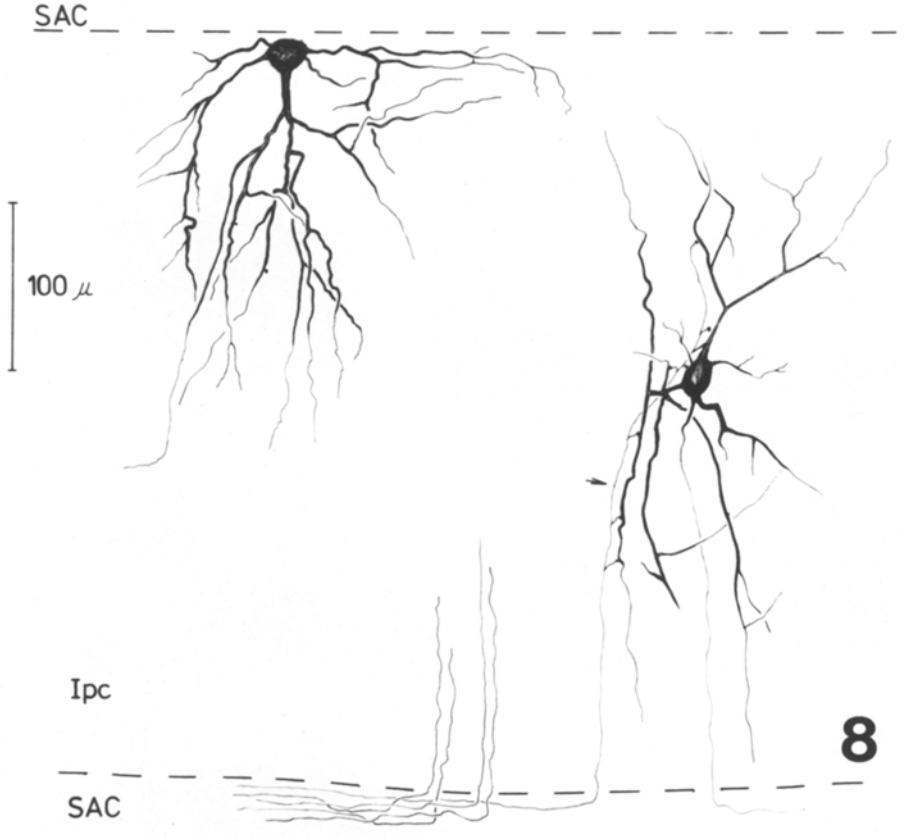

50µ
3


10µ
4

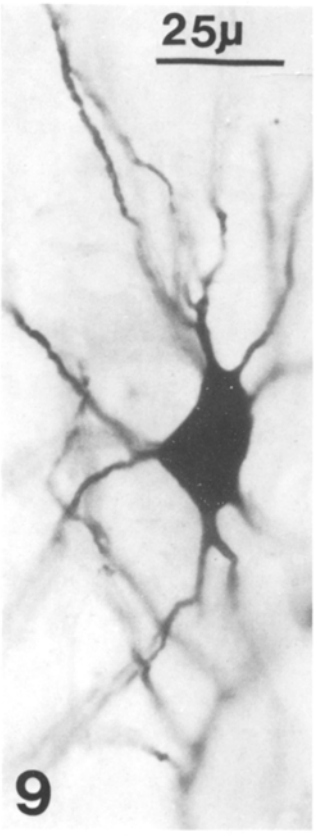

to retina
to retina
from tectum
5


6
10µ

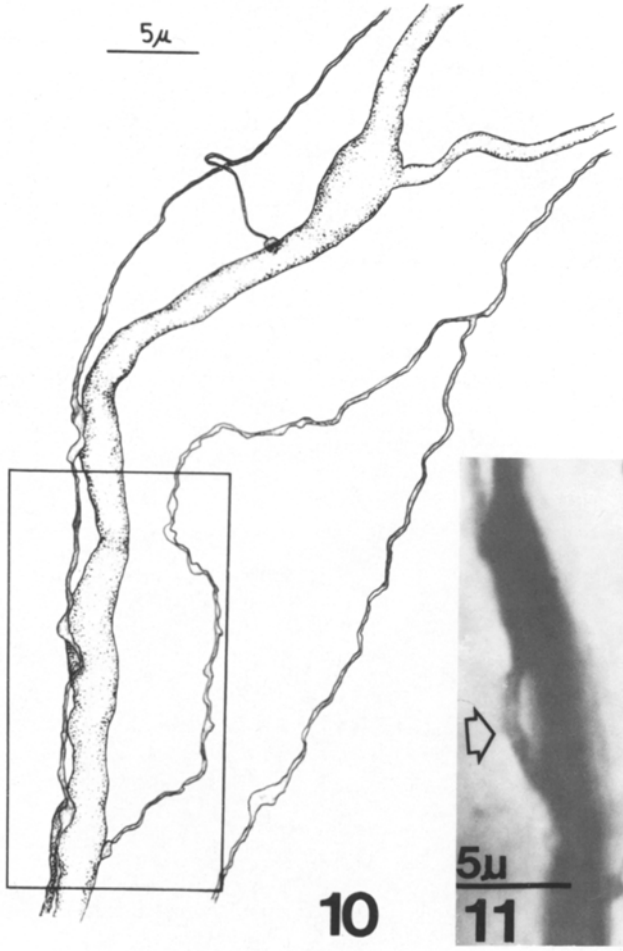

7
10µ



8

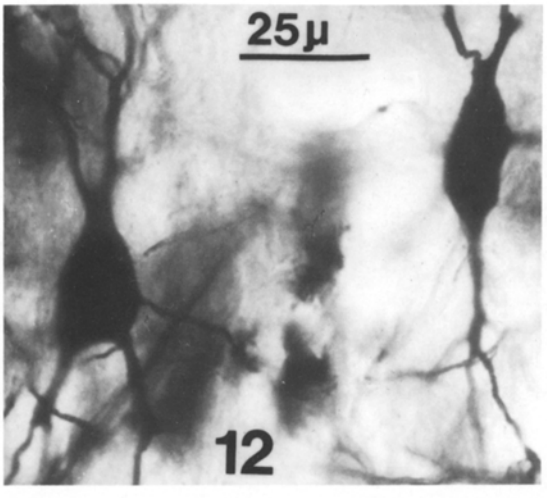


9

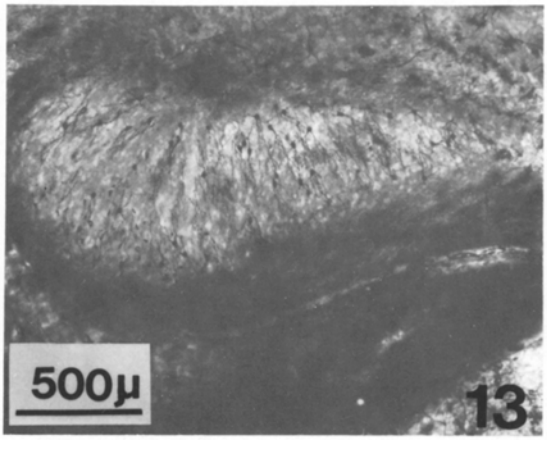


10

11



12



13

of sections of control pigeon brain were used. For these sections three adult pigeons were perfused with saline heated to 40° C and then with 4% paraformaldehyde. The brains were embedded in paraffin, and 20-μm thick saggital as well as frontal sections were cut and stained with cresyl violet or Klüver-Barrera Nissl/myelin staining, respectively.

Results

From the three Golgi techniques employed the Golgi-Cox method was the most reliable. It consistently impregnated a large number of neurons throughout the entire brain. Although it was particularly useful for a general classification of cell types, it gave only poor results in the impregnation of dendritic details, such as small arborizations or spines. With the rapid Golgi technique the dendritic morphology could be clearly visualized, but generally the axons were only impregnated for the first 20 to 30 μm. The Golgi Mestres technique yielded the best impregnations of dendrites and spines and was also particularly successful in visualizing a number of different axon tracts in the tegmental area. Unfortunately, in different parts of the brain such as in the telencephalon, impregnated neurons were rather scarce and were located generally in the outer "corticoid" areas.

Topography

In an anterior to posterior direction the localization of the isthmic nuclei extends in the lateral tegmental field from the most rostral part of the commissura posterior to the level of the n. trochlearis. The IO consists of a small group of cells situated in the dorsolateral tegmentum, just medial to the optic tectum and possesses a highly convoluted lamina made up of two layers of medium-sized perikarya. The Ipc is also situated in the lateral tegmental field ventral to the IO and is composed of medium-sized cells, which are arranged in dorsoventrally radiating rows. At its rostral extent, the nucleus appears in frontal sections as a dorsally flattened oval, which increases caudalward in size to assume an elliptical appearance. The Imc is a mass of large multipolar cells lying ventrolateral to the Ipc and embedded completely in the white matter of the optic tectum. This nucleus assumes in frontal sections an archiform shape, with the concave aspect dorsal and the convex aspect ventral. The Slu is situated medial to Imc and Ipc and lateral to the path of the ascending fibers of the lateral lemniscus. By virtue of similarities in size and staining the Slu appears in frontal sections as a medial extension of the Ipc, only separated by a small portion of the fibers of the brachium colliculi superiores.

Neuronal morphology

N. isthmo-opticus (IO)

The IO consists of a single cell type with rounded to oval perikarya of 15–20 μm diameter. Generally, one to two dendrites arise from one pole side of the soma but in a few cells up to five dendrites were observed (Fig. 2). There is no apparent correlation between the number of dendrites and the location or orientation of the neurons within the nucleus. The dendritic trunk has a smooth surface with few spines and generally follows a straight course after arising from the soma. In cells with more than one dendrite these always extend in the same direction and ramify at a distance of 50–100 μm beyond the perikaryon into numerous branches, which ramify into shorter segments resembling the "claws" observed by Cowan (1970). Since most of these segments branch inward to the center of the arborization, they form a highly packed, spherical network of about 50–70 μm diameter. Within this arborization sphere many spines and appendages of different sizes can be seen, so that a clear distinction between spines, appendages and small dendritic segments is often difficult. Most spines are localized on the distal ends of the dendrites (Fig. 6). In some of the neurons somatic spines can also be observed and a few cells even exhibit spines on the axon hillock (Figs. 4, 7). The axons emerge from the soma or from the first segment of the dendritic trunk. For at least the first impregnated 50 μm the axons coursed in the direction opposite to the dendrites.

As described on the basis of Nissl-stained material the IO consists of a convoluted lamina made up of two layers of neurons, which are separated from each other by a narrow, distinct area of dendrites and axons. This organization can be clearly seen in the Golgi-stained material. The perikarya of impregnated IO neurons form two parallel rows each representing one of the IO layers. The dendrites of these neurons always extend to the area between the two layers so that the dense dendritic arborizations of opposite neurons overlap completely (Fig. 3). On the basis of these observations a model of the cellular organization of the IO was drawn, which illustrates schematically a small part of the double layer. To simplify, only two of the opposing cell rows, separated by the dendritic arborizations and the afferent axons from the tectum, are shown (Fig. 5).

Fig. 8. Diagrammatic camera lucida drawing of two Ipc cells (n. isthmi/pars parvocellularis), which are located at the border or in the center of the nucleus. The axons (*arrow*) shown to enter the nucleus from the ventral part are presumably of tectal origin

Fig. 9. Golgi-Mestres-stained Ipc neuron

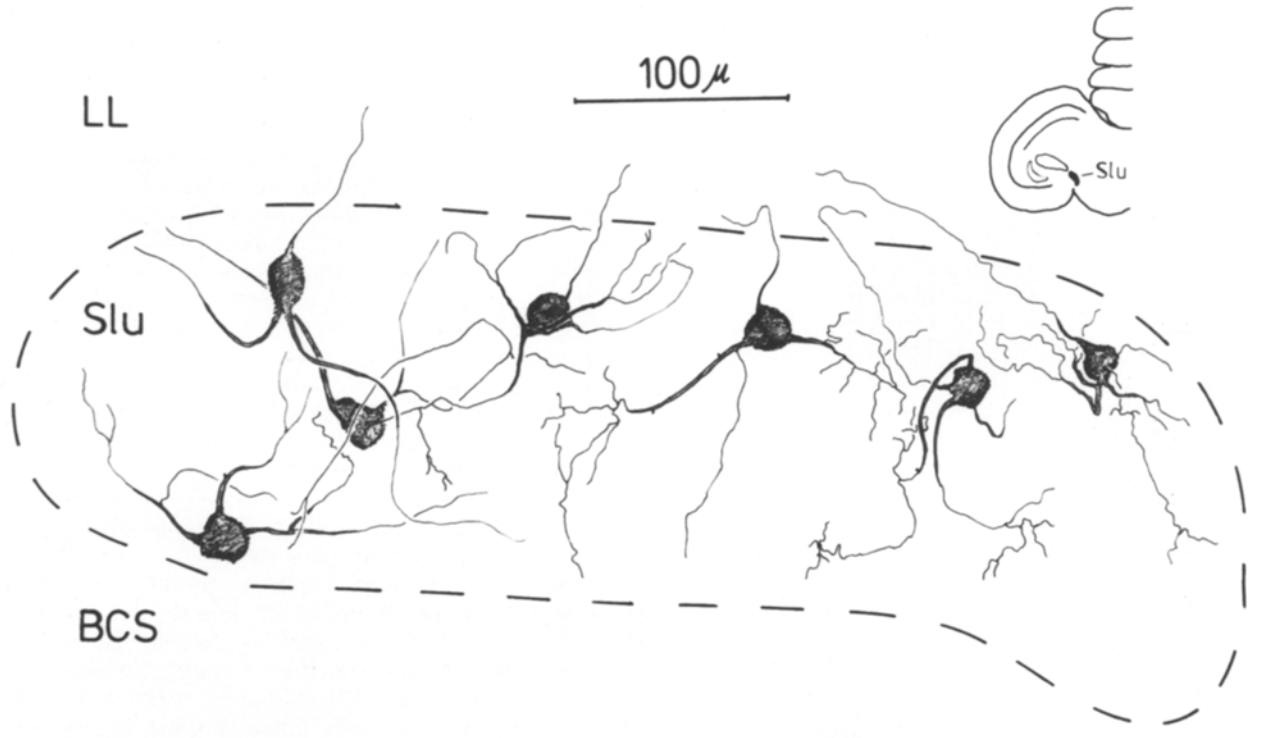
Fig. 10. Diagrammatic reconstruction of afferent axons that make several synapses along Ipc dendrite

Fig. 11. Photomicrograph of two afferent axons (*open* and *black arrow*) shown in the framed area of Fig. 10

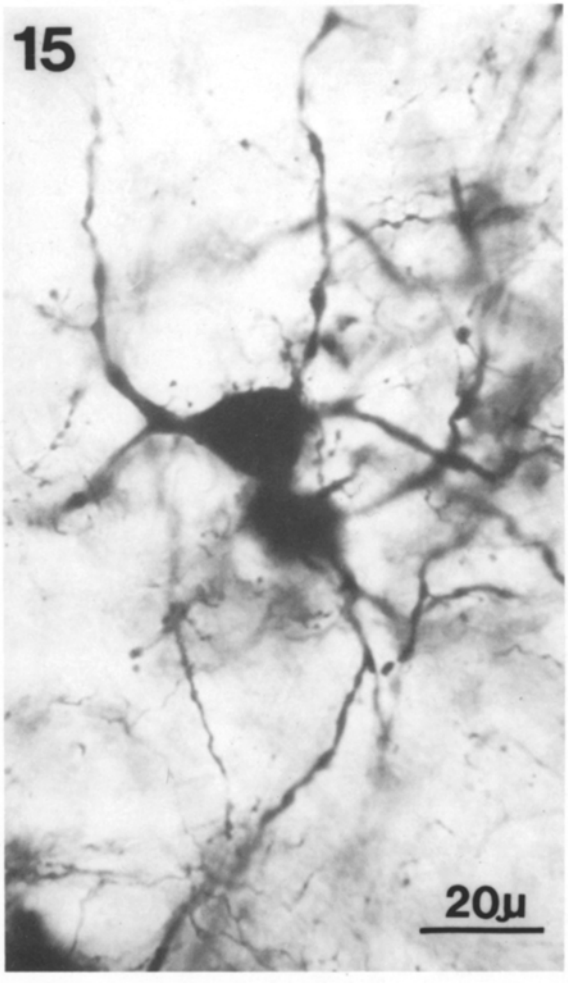
Fig. 12. Two Golgi-Mestres-stained Ipc neurons

Fig. 13. Rapid Golgi-stained Ipc neurons in a frontal section shown at low magnification. Note the virtually equal orientation of all cells. Dorsal is upward and lateral is to the left. The section corresponds to the A 3.00 plane of the pigeon brain atlas

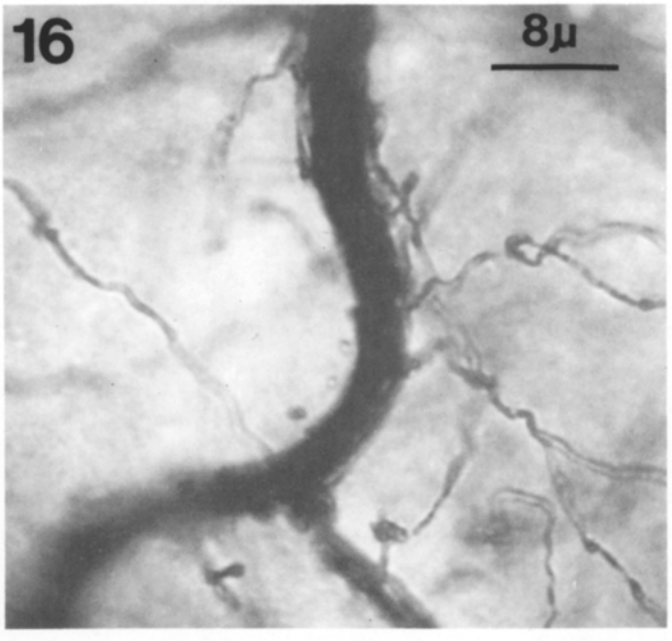
14



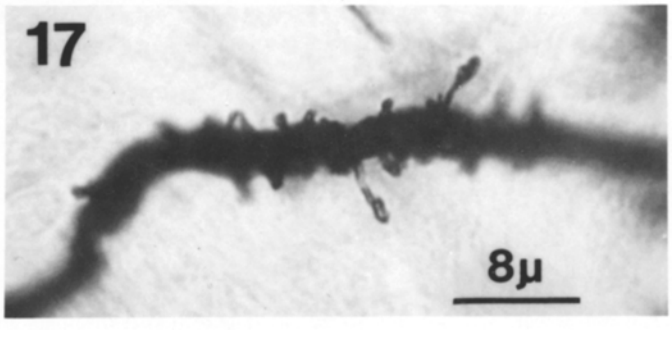
15



16



17



N. isthmi/pars parvocellularis (Ipc)

The Ipc consists of a single cell type with round perikarya 20 μm in diameter. All somata and most of the dendrites are completely free of spines (Figs. 9, 12). On an average five thin (2–4 μm), sparsely branching dendrites leave the soma and ramify up to a distance of 150–200 μm mainly to the dorsal and ventral side of the perikaryon, so that a single Ipc neuron occupies approximately a cylindrical volume with a diameter of about 150 μm and a height of 300–400 μm (Figs. 8, 9, 13). This differs only in neurons that are located in the marginal part of the nucleus, so that the dorsal or ventral part of the dendritic arborizations does not traverse the borders of the Ipc but instead ramifies within the nucleus along its border to other structures, as shown in Fig. 8. Within the nucleus, afferent axons of presumably tectal origin (Hunt et al. 1977) follow the same dorsoventral orientation as the Ipc dendrites (Fig. 8) and make numerous axodendritic en-passant contacts along the entere length of the neurons, resembling climbing fibere in the cerebellum (Figs. 10, 11). Afferent axons were observed to terminate on several Ipc-neurons along their course through the nucleus. These axons seem to follow a columnar organization of the Ipc, since they only contact those neurons that lie along a narrow dorsoventrally oriented path.

N. semilunaris (Slu)

The neurons of the Slu have round somata with a diameter of 20 μm and on an average three sparsely branching dendrites (Figs. 14, 16). Mushroom-shaped dendritic spines, which reach a length of up to 6 μm, can be detected in all impregnated neurons (Fig. 17). The axons of the neurons enter the lemniscus lateralis, which courses medially from the Slu, while the afferent axons invade the nucleus from the brachium colliculi superioris (BCS), which lies laterally (Figs. 14, 16).

N. isthmi/pars magnocellularis (Imc)

The neurons of the Imc show a great variability in shape and size of their perikarya (Fig. 18). The diameters of the somata range from 12 to 50 μm. The neurons have on an average five to six dendrites without a preferred orientation within the nucleus. There is a considerable variance in the diameters (3 to 8 μm) and length (up to 250 μm) of the dendrites. Most of them are densely covered with spines (Fig. 19). Some dendrites leave the borders of the nucleus and penetrate into the neighboring stratum album cellulare (SAC) or the Ipc. The axons of Imc neurons could not be followed for a sufficient distance to allow a definite description of their terminations but most of them seemed to course laterally towards the ipsilateral tectum (Fig. 20). The afferent axons from the tectum enter the Imc from its ventral and lateral sides, terminate within the nucleus without any orientational preference on a large number of different cells and leave the Imc at its medial side to join the fibers of the BCS (Fig. 20).

Discussion

All impregnated neurons in the n. isthmo-opticus (IO) had a uniform overall morphology with short dendrites and dense dendritic arborizations. This concurs with the results of Cowan (1970), Angaut and Repérant (1978) and Crossland (1979). The latter author additionally observed at the border of the IO a second type of neuron with long and infrequently branching dendrites. In none of the examined sections could a cell with these characteristics be observed within the nucleus. Since reticular neurons close to the IO border showed the characteristics that Crossland (1979) described, it seems possible that he inadvertently ascribed these tegmental neurons to the IO.

As already described by McGill et al. (1966a, b), Holden and Powell (1972) and Clarke and Caranzano (1985), the IO consists of a highly convoluted lamina in which two perikaryal layers are separated by a neuropil of dendrites and axons. These observations were confirmed in the present Golgi study in which the perikarya of impregnated neurons were found to be located in two parallel rows in which the dendrites of neurons from opposing layers ramify toward the middle of the two layers. Axons that were observed to run through this interjacent area of dense dendritic arborizations are presumably of tectal origin since Angaut and Repérant (1978) reported that the tectal projections terminate almost exclusively in a topographically organized axo-dendritic fashion and make up the greatest proportion of the afferents of the IO.

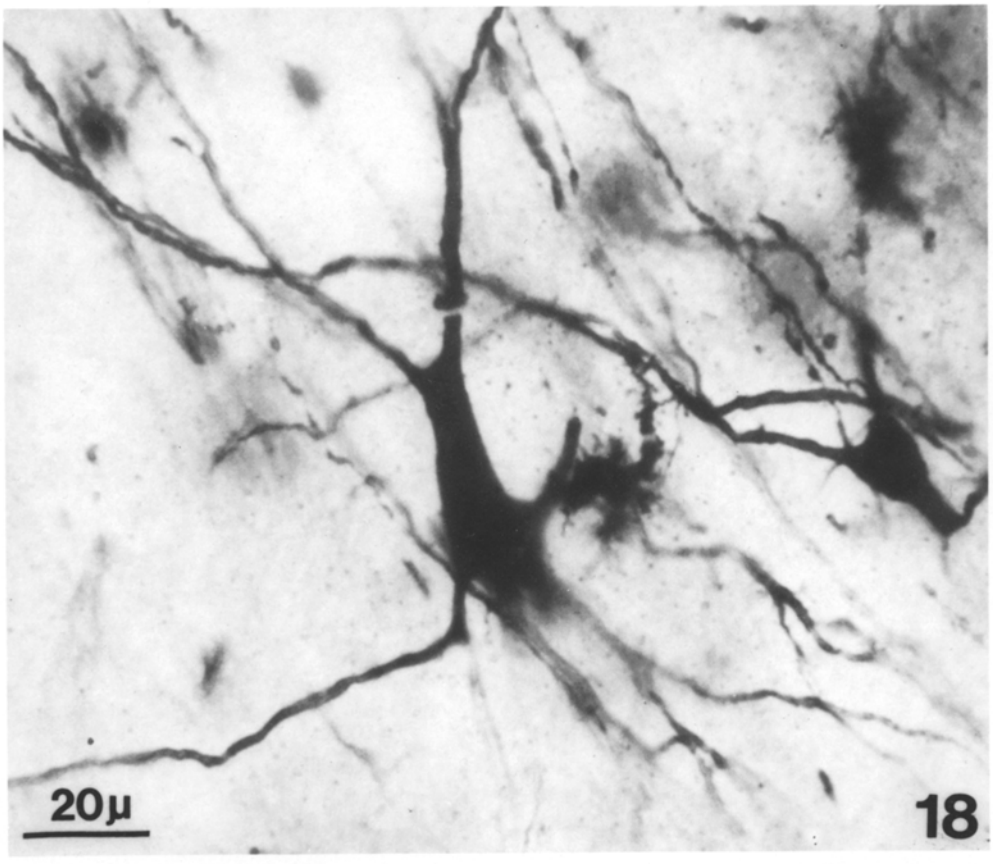
Holden and Powell (1972) observed that afferent fibers from the same portion of the tectum were always found to terminate in adjoining regions of both layers. Neurons in opposing layers were reported to have receptive fields of similar types and in adjacent sections of visual space. Since cells in both layers seem to share similar afferents and visual properties, the functional significance of this duplication is not clear. Holden and Powell (1972) supposed that the IO neurons in opposing layers exert a dichotomous excitatory or inhibitory effect on the amacrine cells of the retina. This hypothesis seems to be unlikely since Miles (1972b) observed a rather uniform disinhibition of retinal ganglion cells after electrical stimulation of the contralateral IO. Maturana and Frenk (1965) and Hayes and Holden (1983) described a dichotomy in the synaptic connections of IO axons in the retina. They form either convergent or divergent terminal branches, which synapse on amacrine cells. In the convergent terminal type, the axon ends in several branches, which usually synapse on only one ama-

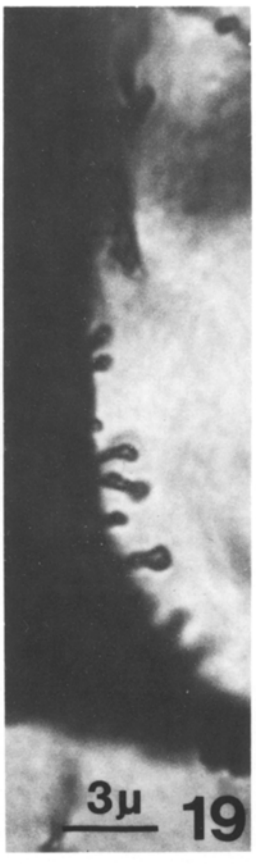
Fig. 14. Diagrammatic camera lucida drawing of different neurons in the Slu. The axons coursing upward enter the lemniscus lateralis (*LL*). Frontal section corresponding approximately to the A 2.25 plane of the pigeon brain atlas (Karten and Hodos, 1967). For orientation, see small *insert* to the right. *BCS* brachium colliculi superioris

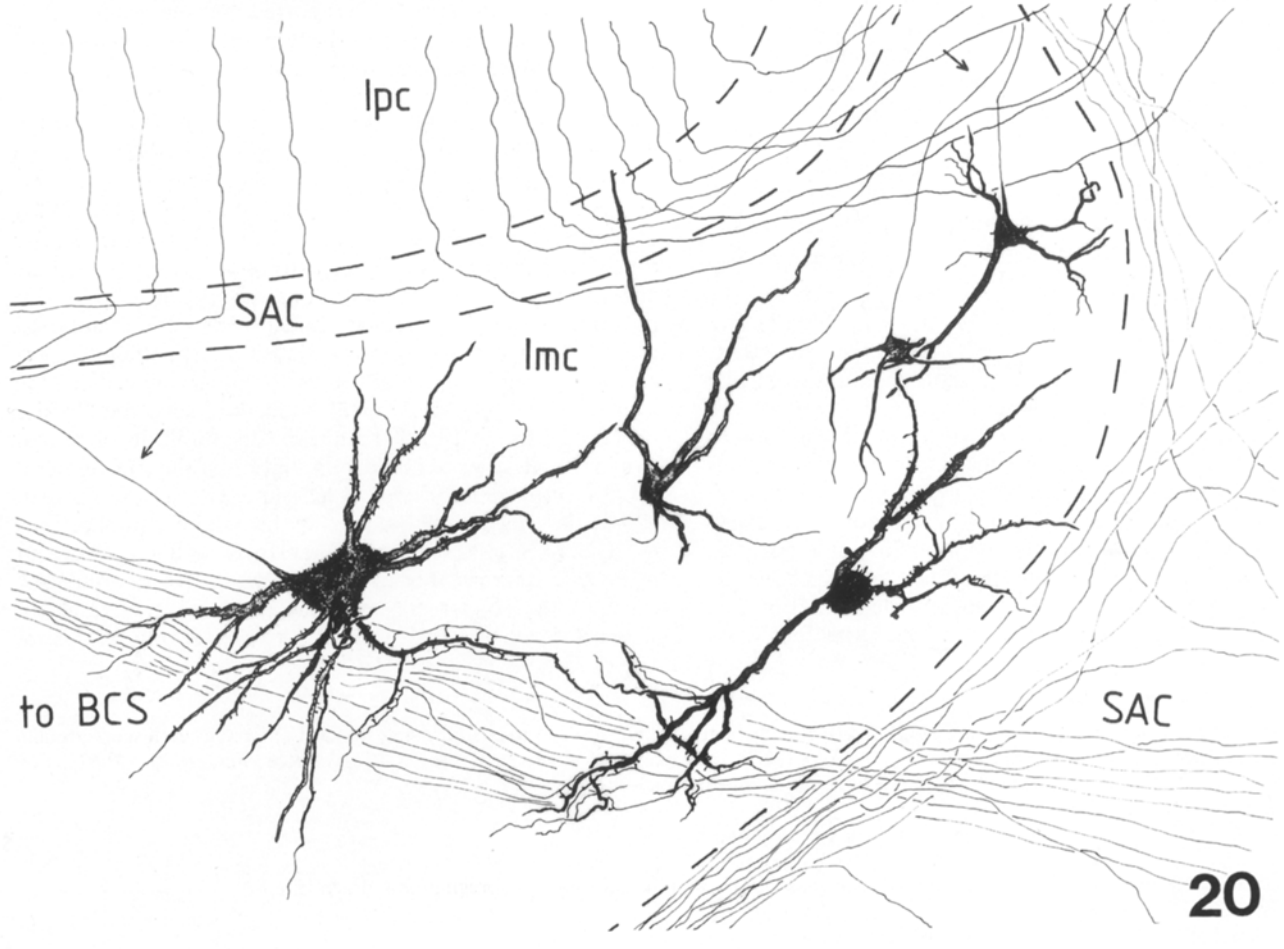
Fig. 15. Rapid Golgi-impregnated neurons of the Slu (n. semilunaris)

Fig. 16. Axons of presumably tectal origin make numerous contacts on a rapid Golgi-impregnated Slu dendrite

Fig. 17. Dendritic spines on a rapid Golgi-impregnated Slu neuron


20µ
18


3µ
19


Ipc
SAC
Imc
to BCS
SAC
20

crine cell in the inner nuclear layer. In the divergent terminal type, the fibers give off branches that make successive synapses with several amacrine cells at the boundary between the inner nuclear layer and the inner plexiform layer. From these observations it seems possible to speculate that the duplicated structure of the IO may correspond to the two different types of retinal innervation.

The results of the Golgi impregnations demonstrate that the n. isthmi/pars parvocellularis (Ipc) consists of a single cell type that shows a uniform columnar orientation within the nucleus. This concurs with the observations of Streit et al. (1980), who found radially arranged columns of retrogradely labeled neurons in the Ipc after small injections of tritiated glycine in the ipsilateral tectum. Hunt et al. (1977) demonstrated that the neurons in the small rostral part of the Ipc are GABAergic, while those in the larger caudal part are glycinergic. In the presently studied Golgi material no morphological differences could be observed between caudal and rostral Ipc neurons so that these transmitter heterogeneities do not seem to be correlated with differences in the shape of the neurons.

Ariëns Kappers et al. (1936) suggested that the n. semilunaris (Slu) is innervated by fibers of the lateral lemniscus. This concurs with observations of Erulkar (1955), Harman and Phillips (1967) and Newman (1970), who recorded auditory-evoked potentials from this nucleus. On the other hand, neither Wallenberg (1898), Boord (1968) nor Correia et al. (1982) found any anatomical evidence for a projection of the lateral lemniscus to the Slu. This accords with the observations of the present study in which none of the afferent axons to the Slu entered the nucleus from the medial side where the path of the lateral lemniscus is located, but from the direction of the optic tectum, lateral to the nucleus. Many axons of Slu neurons were observed to enter the lateral lemniscus. Since hodological studies gave no evidence for a participation of this nucleus in ascending auditory projections to thalamic or telencephalic structures (Karten 1967; Schall et al. 1986), the axons of the Slu neurons seem to follow the path of the lateral lemniscus for only a short distance to leave it and to enter the optic tectum (Showers and Lyons 1968).

According to Seller (1981), electrical stimulation of the Imc leads to vocalizatory responses. Showers and Lyons (1968) observed rapid pupil dilations and constrictions after the same procedure, while Phillips (1964) elicited crouching after Imc stimulation. This confusion concerning the function of the Imc can be partly resolved when the afferents and the morphological details of this nucleus are closely inspected. The projection of the tectum to the Imc arises mainly from the deeper tectal layers (Hunt and Künzle 1976) in which the cells respond to visual, somatosensory and auditory stimuli (Cotter 1976). In the Golgi sections many tectal axons were observed to cross the Imc on their way to the brachium colliculi superioris thereby synapsing on a large number of different cells. This presence of probable multimodal afferents could account for the conflicting results after stimulating this nucleus.

The morphological details of the Imc neurons match perfectly the criteria formulated by Ramón-Moliner and Nauta (1966) for the neurons of the reticular formation. According to Ramón-Moliner (1962) neurons with these "isodendritic" characteristics generally have afferent connections of heterogeneous origin. It is conceivable that the resemblances in the morphology between reticular and Imc neurons match functional similarities. The reticular formation is thought to be involved in the control of the activity level of the structures on which it projects (Scheibel 1981). By analogy to this function one can speculate that the Imc could also modulate the gross activity level of its main efferent structure, the optic tectum.

Acknowledgements. I am especially grateful to P. Mestres for introduction to the Golgi techniques, thus providing a new field of enthusiasm. I also thank J.D. Delius and J. Emmerton for critically reading the manuscript and H. Rohmann for typing it. The research was supported by the Deutsche Forschungsgemeinschaft through its Sonderforschungsbereich 114.

References

Angaut P, Repérant J (1978) A light and electron microscopic study of the nucleus isthmo-opticus in the pigeon. Arch Microsc Morph Exp 67:63–78

Ariëns Kappers CU, Huber GC, Crosby EC (1936) The comparative anatomy of the nervous system of vertebrates, including man. Hafner Publ Comp, New York

Boord RL (1968) Ascending projections of the primary cochlear nuclei and nucleus laminaris in the pigeon. J Comp Neurol 133:523–530

Clarke PGH, Caranzano F (1985) Dendritic development in the isthmo-optic nucleus of chick embryos. Dev Neurosci 7:161–169

Clarke PGH, Cowan WM (1976) The development of the isthmo-optic tract in the chick, with special reference to the occurrence and correction of developmental errors in the location and connections of isthmo-optic neurons. J Comp Neurol 167:143–164

Correia MJ, Eden AR, Westlund KN, Coulter JD (1982) Organization of ascending auditory pathways in the pigeon (*Columba livia*) as determined by autoradiographic methods. Brain Res 243:205–212

Cotter JR (1976) Visual and non-visual units recorded from the optic tectum of *Gallus domesticus*. Brain Behav Evol 13:1–21

Cowan WM (1970) Centrifugal fibres to the avian retina. Br Med Bull 26:112–119

Crossland WJ (1979) Identification of tectal synaptic terminals in the avian isthmo-optic nucleus. In: Granda AM, Maxwell JH (eds) Neural Mechanisms of Behavior in the Pigeon. Plenum Publishing Press, New York, pp 267–286

Erulkar SD (1955) Tactile and auditory areas in the brain of the pigeon. J Comp Neurol 103:421–452

Harman AL, Phillips RE (1967) Responses on the avian midbrain,

Fig. 18. Neurons of the Imc (n. isthmi/pars magnocellularis) with typical dendritic characteristics in Golgi-Mestres impregnations. Note the presence of neurons of different size

Fig. 19. Dendritic spines on Imc cell. Rapid Golgi

Fig. 20. Diagrammatic camera lucida drawing of different neurons in the Imc, the axons of which (*small arrows*) take a course in the direction of the ipsilateral tectum (*right side*) or leave the nucleus together with tectal fibers. Afferent axons from the stratum album centrale (*SAC*) enter the nucleus and make numerous contacts on different neurons. *BCS* brachium colliculi superioris, *Ipc* n. isthmi/pars parvocellularis

thalamus and forebrain evoked by click stimuli. Exp Neurol 18:276–286
Hayes BP, Holden AL (1983) The distribution of centrifugal terminals in the pigeon retina. Exp Brain Res 49:180–197
Holden AL, Powell TPS (1972) The functional organization of the isthmo-optic nucleus in the pigeon. J Physiol (London) 223:419–447
Hunt SP, Künzle H (1976) Observations on the projections and intrinsic organization of the pigeon optic tectum: an autoradiographic study based on anterograde and retrograde, axonal and dendritic flow. J Comp Neurol 170:153–172
Hunt SP, Streit P, Künzle H, Cuénod M (1977) Characterization of the pigeon isthmo-tectal pathway by selective uptake and retrograde movement of radioactive compounds and by Golgi-like horseradish peroxidase labeling. Brain Res 129:197–212
Karten HJ (1967) The organization of the ascending auditory pathways in the pigeon (*Columba livia*). I. Diencephalic projections of the inferior colliculus (nucleus mesencephali lateralis, pars dorsalis). Brain Res 6:409–427
Karten HJ, Hodos W (1967) A Stereotaxic Atlas of the Brain of the Pigeon. The Johns Hopkins Press, Baltimore, Maryland
Kniepling RR (1978) No deficit in near-field visual acuity of pigeons after transection of the isthmo-optic tract. Physiol Behav 21:813–816
Künzle H, Schneyder H (1984) The isthmo-tegmentum complex in the turtle and rat: a comparative analysis of its interconnections with the optic tectum. Exp Brain Res 56:509–522
Mallin HD, Delius JD (1983) Inter- and intraocular transfer of colour discriminations with mandibulation as an operant in the head-fixed pigeon. Behav Anal Lett 3:297–309
Maturana HR, Frenk S (1965) Synaptic connections of the centrifugal fibers in the pigeon retina. Science 150:359–361
McGill JI, Powell TPS, Cowan WM (1966a) The retinal representation upon the optic tectum and isthmo optic nucleus in the pigeon. J Anat 100:5–33
McGill JI, Powell TPS, Cowan WM (1966b) The organization of the projection of the centrifugal fibres to the retina in the pigeon. J Anat 100:35–49
Mestres P, Lafarga M (1972) Cholinesterase activity in the perineural net. Ann Histochem 17:135–139
Miles FA (1972a) Centrifugal control of the avian retina. III. Effects of electrical stimulation of the isthmo-optic tract on the receptive field properties of retinal ganglion cells. Brain Res 48:115–129
Miles FA (1972b) Centrifugal control of the avian retina. IV. Effects of reversible cold block of the isthmo-optic tract on the receptive field properties of cells in the retina and isthmo-optic nucleus. Brain Res 48:131–145
Newman JD (1970) Midbrain regions relevant to auditory communication in songbirds. Brain Res 22:259–261
Pearlman AL, Hughes CP (1976) Functional role of efferents to the isthmo-optic nucleus. J Comp Neurol 166:123–132
Phillips RE (1964) 'Wildness' in the mallard duck: effects of brain lesions and stimulation on 'escape behavior' and reproduction. J Comp Neurol 1964:139–156
Ramón-Moliner E (1962) An attempt at classifying nerve cells on the basis of their dendritic patterns. J Comp Neurol 119:211–227
Ramón-Moliner E (1970) The Golgi-Cox technique. In: Nauta WHJ, Ebbeson SOE (eds) Contemporary Research Methods in Neuroanatomy. Springer-Verlag, Berlin, Heidelberg, New York
Ramón-Moliner E, Nauta WJH (1966) The isodendritic core of the brain stem. J Comp Neurol 126:311–336
Rogers LJ, Miles FA (1972) Centrifugal control of the avian retina. V. Effects of lesions of the isthmo-optic nucleus on visual behavior. Brain Res 48:147–156
Schall U, Güntürkün O, Delius JD (1986) Sensory projections to the nucleus basalis prosencephali of the pigeon. Cell Tissue Res 245:539–546
Scheibel AB (1981) The problem of selective attention: a possible structural substrate. In: Pompeiano O, Ajmone Marsan C (eds) Brain mechanisms and perceptual awareness. Raven Press, New York, pp 319–326
Seller TJ (1981) Midbrain vocalization centres in birds. TINS 4:301–303
Shortess GK, Klose EF (1977) Effects of lesions involving efferent fibers to the retina in pigeons. Physiol Behav 18:409–414
Showers MJC, Lyons P (1968) Avian nucleus isthmi and its relation to hippus. J Comp Neurol 132:589–616
Streit P, Knecht E, Cuénod M (1980) Transmitter related retrograde labelling in the pigeon optic lobe: a high resolution autoradiographic study. Brain Res 187:59–67
Valverde F (1970) The Golgi method. A tool for comparative structural analysis. In: Nauta WJH, Ebbesson SOE (eds) Contemporary Research Methods in Neuroanatomy. Springer Verlag, Berlin Heidelberg New York, pp 12–31
Wallenberg A (1898) Die secundäre Acusticusbahn der Taube. Anat Anz 14:353

Accepted October 7, 1986