ISSN 0044-3107 · Z. mikrosk.-anat. Forsch. · Leipzig · **101** (1987) 2 · S. 339–362

Distribution of Monoamine-Containing Neurons in the Brain of the Weakly Electric Teleost, *Eigenmannia lineata* (Gymnotiformes: Rhamphichthyidae)

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(Received June 28, 1986)

With 8 Figures and 1 Table

Key words: Teleost brain – Monoamines – Fluorescence microscopy – *Eigenmannia* – electric fish

Summary

The distribution of neurons and fibres containing monoamines (MA, that is noradrenaline, dopamine, and serotonin) was studied in the brain of the weakly electric fish, *Eigenmannia lineata*, by formaldehyde-induced fluorescence histochemistry.

Control experiments using a catecholamine-precursor (Dopa), a MA-depleting (reserpine), and a MA-accumulating (nialamide) drug, together with microspectrofluorometric measurements, allowed to distinguish specific (MA) from unspecific (for example lipofuscine) fluorescence. High Performance Liquid Chromatography (HPLC) assays of MA of untreated brains yielded 313 ± S.E. 24 ng/g brain tissue noradrenaline, 96 ± S.E. 19 ng/g dopamine, and 71 ± S.E. 12 ng/g serotonin (N = 12 in each case).

The highest density of MA-perikarya was found, as in other species, in the diencephalon: in the region of the nucleus praeopticus periventricularis (npp), in the nucleus ventromedialis (nvm), in the nucleus posterior periventricularis (nppv), and in the hypothalamic nucleus recessus lateralis (nrl) and nucleus recessus posterior (nrp). The mesencephalic torus semicircularis, the "super-laminated" key structure of sensory-motor integration in gymnotids, contained monoamines in the large T-cells of layer VI.

Both types of cells of the medullary pacemaker nucleus (pm) of the electric organ, the smaller pacemaker and the larger relay cells, showed specific, yellow fluorescence indicating the presence of monoamines.

Fluorescent MA-fibres in the frontal, medial and lateral parts of the telencephalon connected with hypothalamic and midbrain areas. Several electroreceptive layers of the torus semicircularis (layers V, VIII, IX, XI, XIII) showed a clearly recognisable and in some parts dense network of MA-fibres. Only few fluorescent fibres occurred in the massive corpus cerebelli (which is mixed electro-/mechanoreceptive), in the second order electroreceptive lobus lineae lateralis posterior and in the medulla oblongata (ventrolateral to the raphe region, especially in the frontal medulla at the level of the torus).

Introduction

The biogenic monoamines noradrenaline (NA), dopamine (DA) and serotonin (5-HT) are transmitter substances in the autonomous and/or central nervous system of vertebrates. The classic technique to visualize monoamine-containing neurons is the formaldehyde-induced fluorescence (FIF; FALCK et al. 1962).

In the mammalian brain NA-neurons mainly occur in the pons and the medulla as well as in the locus coeruleus. NA-fibres project to the forebrain, to the cerebellar cortex, to the hippocampus, and to the spinal cord. Dopaminergic neurons are mainly confined to the midbrain, anterior to the majority of noradrenergic neurons, especially the substantia nigra and globus pallidus, with fibres projecting to the corpus striatum (and other areas). 5-TH-neurons are found in significant numbers in the upper brainstem, especially the raphe system. Other 5-HT-neurons are found in ventral parts of the median forebrain bundle.

The question of specific functions of monoaminergic neuronal networks is still open. Peripheral NA (and adrenaline) of the autonomous nervous system is important for the fight-or-flight response in emergency situations; a similar role is assumed for central NA (such as the regulation of arousal and mood). Dopamine, for which receptors are known only in the brain, plays an important role in motor control (DA loss: desease Parkinsonism; SCHÖNHÖFER and SCHWABE 1984). Serotonin, like NA, seems to be involved in the maintenance of "normal behaviour" or body functions, such as sleep, body temperature, and sensory perception (see, for example, BURGEN and MITCHELL 1978, JULIEN 1985).

Physiological and behavioural studies made use of certain "psychoactive drugs" (psychopharmaka), which influence the monoamine metabolism. In the sunfish (*Lepomis gibbosus*), reserpine-induced release of central monoamines (NA, DA and 5-HT) caused an increase of the frequency of aggressive and nest-building behaviour (KRAMER 1973), while the DA-antagonist chlorpromazine reduced aggression and nest-building, without affecting the sexual tendency (KRAMER 1973). Chlorpromazine reversibly reduced the electric organ discharge (EOD) frequency of *Apteronotus albifrons* (KRAMER 1984), a South American knife fish (Gymnotiformes). The electric organ discharge is part of a system involved in communication as well as in active orientation (reviews: SZABO et al. 1973, SCHEICH 1982, BULLOCK 1982).

Only few studies have described the MA-distribution of the entire teleost brain (BERTLER et al. 1963, LEFRANC et al. 1969, PARENT et al. 1978, WATSON 1980, EKSTRÖM and VAN VEEN 1982, PARENT and NORTHCUTT 1982, KOTRSCHAL and ADAM 1983, KAH and CHAMBOLLE 1983; for reviews see SANTER 1977 and PARENT et al. 1984). Several studies analysed the MA content of parts of the teleost brain, especially the diencephalon (BAUMGARTEN and BRAAK 1967, BRAAK and BAUMGARTEN 1967, VIGH-TEICHMANN et al. 1969, EKENGREN 1975, SWANSON et al. 1975, FREMBERG et al. 1977, TERLOU et al. 1978, BATTEN et al. 1979, EKSTRÖM and VAN VEEN 1982).

None of these is on gymnotids or on any other electric fish. MALER et al. (1981) described the distributions of acetylcholinesterase and choline acetyl transferase in the cerebellum of a gymnotid fish.

It is particularly interesting to study the central monoaminergic system in the weakly-electric fish *Eigenmannia* for the following reasons: 1. *Eigenmannia's* EOD is involved in social signalling during reproductive behaviour (HOPKINS 1974, HAGEDORN and HEILIGENBERG 1985), a traditional field of MA-function (VAN OORDT, in press). 2. The descending information modulating the EOD-frequency converges on an ana-

tomically identified, medullary pacemaker nucleus which is a group of electrotonically coupled cells controlling the electric organ discharge in a 1:1-fashion (SZABO and ENGER 1964, BENNETT et al. 1967, ELEKES and SZABO 1981, 1982, 1985). 3. The paths of ascending electrosensory information, on entering the brain via the anterior lateral line nerves (SZABO 1974), including processing centres in the hind- and midbrain, have largely been elucidated (review: SCHEICH and EBBESSON 1983). 4. Specific electric stimuli cause stereotyped EOD (that is, pacemaker) frequency changes (the jamming avoidance response, JAR; reviews: HEILIGENBERG 1977, BULLOCK 1982, SCHEICH 1982) which depend in strength on the sexually dimorphic EODs (KRAMER 1985).

Material and Methods

The distribution of MA-containing neurons in the brains of *Eigenmannia lineata* (commercially obtained from Laetitia, Columbia in South-America; determined by F. Kirschbaum) was studied.

1. Experimental techniques

1.1. General histology

Complete series of 10–20 μm transversal and sagittal sections of 20 *Eigenmannia* brains or whole decalcified heads were stained according to the methods of Klüver-Barrera, Masson-Goldner, or Azan (ROMEIS 1968), or silver-impregnated (FRASER 1963). The mechanical stage of a microscope (Leitz Ortholux II) was modified by an additional stage for fine movements. X- and Y-axis movements were recorded by an X-Y-plotter, via two potentiometer-controlled D.C.-circuits. This facilitated the recording of brain structures on paper using a cross-hair microscope eyepiece.

1.2. Fluorescence microscopy

The Falck-Hillarp method of Formaldehyde-Induced Fluorescence (FIF, FALCK and OWMAN 1965) or its modification by LORÉN et al. (1976) was applied to the brains of 21 animals (9–11 cm body length, 1.9–4.7 g body weight). Six animals were treated with the combination of the CA-precursor L-Dopa (Sigma; 133 mg/kg i.m.; 24 h before sacrifice) and with the MAO-inhibitor nialamide (Sigma; 570 mg/kg i.m.; 4 h before sacrifice). One animal was kept in water with nialamide (12.5 mg/100 ml) 10 h before sacrifice. These substances increased the MA-concentrations in the tissues. The slices were examined in an Ortholux II fluorescence microscope (Leitz) using Leitz filter set D (Excitation: BP 355–425, beam splitter: RKP 455, barrier filter LP 460).

The controls for specificity of fluorescence were the following: 1. Administration of reserpine (Serpasil, Ciba; 10 mg/kg i.m.; 18 h before sacrifice or 50 mg in 4 l water; 10 h before sacrifice) depleted the monoaminergic neurons and allowed to assess the weak background fluorescence. 2. In brains not exposed to the formaldehyde gas, only weak fluorescence was observed.

1.3. HPLC

Monoamine-concentrations were determined electrochemically after separation by High Performance Liquid Chromatography (HPLC; KISSINGER et al. 1981) in eleven *Eigenmannia* brains.

1.4. Microspectrofluorometry (MSF)

The emission spectra of green- and yellow-fluorescent perikarya and of varicose fibres were measured in six brains by microspectrofluorometry using an MPV-2 microphotometer (Leitz) equipped with xenon high pressure lamp (Osram, XBO 75), filter set D (Leitz), photomultiplier (EM 9558) and an S 20 cathod. The aperture could be closed to 2–3 μm. Measurements from 430–700 nm were made

in 2 nm steps. Calibration of the photomultiplier and correction of the spectra were according to specifications in "Leitz-Mitteilungen" (16/01.76).

2. Discrimination of specific from unspecific fluorescence

Structures containing substances other than MA also showed yellow fluorescence, for example histamine and lipofuscine. These will be considered as unspecifically fluorescent. Lipofuscine-containing cells were identified in ungassed control sections; mast cells (containing histamine) were recognized from neurons by Nissl staining.

In contrast to NA- and DA-fluorescence, serotonin fluorescence is fast-fading in UV-light (Falck and Owman 1965), and granular in appearance (Braak and Baumgarten 1967). In this study, clear serotoninergic neurons were only found in two anatomically defined brain areas in nialamide treated animals. (In these cases, the use of filter set H and I (Leitz), the transmission maxima of which best match the excitation and emission maxima of 5-HT, resulted in bright yellow fluorescence). 5-HT may often go undetected due to the low yield of 5-HT and 5-HTP fluorescence after standard FIF treatment (Björklund et al. 1975).

In the following anatomical description of monoaminergic neurons no attempt was made to distinguish between the catecholamines (CA) (noradrenaline, dopamine, and their common precursor Dopa) and serotonin, all of which show green to yellow fluorescence after Falck-Hillarp treatment.

High CA-concentrations may cause a subjective shift of the colour of the fluorescence from green to yellow (Falck and Owman 1965), so that CA at high concentrations can not be discriminated from serotonin but still by its slow fading compared with serotonin. As shown by a more sensitive (immunocytochemical) method serotonin also occurs in nerve cell groups which show strong green to yellow fluorescence after FIF-treatment although it is not clear whether the FIF-fluorescent cells, or adjacent cells, are involved (Bonn, in preparation). At present, the occurrence of 5-HT/5-HTP and one of the catecholamines in the same perikaryon cannot be excluded (Ekengren 1975). 5-HTP is rapidly transformed to 5-HT by 5-HTP- or Dopa-decarboxylase; the emission maximum of both is at 520 nm (Braak and Baumgarten 1967, Björklund et al. 1975). 5-HT was never detected in axons; this is probably due to fading caused by the relatively long illumination time during and before the MSF measurement. Therefore, specifically fluorescent perikarya and axons will be referred to as MA-neurons in this report.

Results

1. External morphology

The brain of *Eigenmannia* (Fig. 1), like that of all South-American gymnotoids, is especially large: close to 2.8% of the body weight (Scheich and Ebbesson 1983) compared to 1.7% in the goldfish (Bonn, submitted). This brain size is due to the large structures receiving electrosensory input, such as the posterior lateral line lobe, the torus semicircularis (covered by the cerebellum and the tectum opticum), and the cerebellum (Fig. 1).

The posterior lateral line lobe (LLLp, Fig. 1) is the target of electrosensory information carried by the anterior lateral line nerve (NLLa; Szabo 1974). This lobe is a lateral and posterior expansion of the medulla only found in weakly electric (Mormyriformes, Gymnotiformes) and electroreceptive teleosts, such as the Siluriformes (McCormick 1982). The caudal lobe (Lc), the cerebellum (cc), the torus semicircularis (ts), and the optic tectum (to) represent higher order stations within the electrosensory pathway (Scheich and Ebbesson 1983).

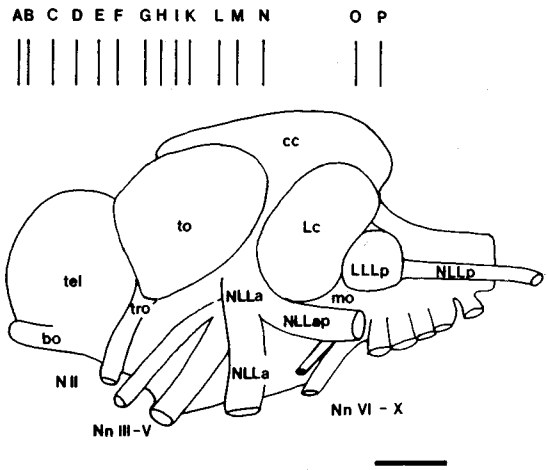

Fig. 1. Lateral view of *Eigenmannia's* brain. Planes of frontal sections refer to Fig. 2. Unless otherwise indicated, dorsal is up in all figures

For the nomenclature of the forebrain structures the study by PETER and GILL (1975) was used while for the mid- and hindbrain anatomy we referred to HARDER (1975), HEILIGENBERG (1977), HEILIGENBERG et al. (1981), MALER et al. (1974, 1982), RETHELYI and SZABO (1973), and SCHEICH and EBBESSON (1983). In cases of disagreement on nomenclature a choice had to be made (as indicated).

Anatomical abbreviations

bo	Bulbus olfactorius
ca	Commissura anterior
cc	Corpus cerebelli
co	Chiasma opticum
cp	Commissura posterior
dc	Area dorsalis telencephali pars centralis
dd	Area dorsalis telencephali pars dorsalis
di, Di	Diencephalon
dl	Area dorsalis telencephali pars lateralis
eg	Eminentia granularis
flm	Fasciculus longitudinalis medialis
hy	Hypophysis
Lc	Lobus caudalis
lel	Lemniscus lateralis
LLLp	Lobus lineae lateralis posterior
mes	Mesencephalon
mo	Medulla oblongata
na	Nucleus anterior
ng	Nucleus glomerulosus
Nn	Nervi craniales
NLLa	Nervus lineae lateralis anterior
NLLap	Nervus lineae lateralis anterior pars posterior

NLLp	Nervus lineae lateralis posterior
npe	Nucleus praeeminentialis
npo	Nucleus praeopticus
npp	Nucleus praeopticus periventricularis
nppv	Nucleus posterior periventricularis
nrl	Nucleus recessus lateralis
nrp	Nucleus recessus posterior
nvm	Nucleus ventromedialis
nm	Nucleus medialis
pm	electric pacemaker nucleus
ppm	Pre-pacemaker nucleus
PVO	Paraventricular organ
PRO	Preoptic recess organ
tel	Telencephalon
tl	Torus longitudinalis
to	Tectum opticum
ts	Torus semicircularis
tro	Tractus opticus
trol	Tractus olfactorius
va	Valvula cerebelli
vd	Area ventralis telencephali pars dorsalis
vl	Area ventralis telencephali pars lateralis
vv	Area ventralis telencephali pars ventralis

2. Distribution of monoaminergic neurons and fibres in the brain

2.1. Telencephalon

In *Eigenmannia's* whole telencephalon unspecific, yellow-fluorescent perikarya (probably mast cells) were found, especially in ventral and ventrolateral parts. Some of these cells were close to blood vessels.

Only MA-fibres, but no MA-perikarya were found in the telencephalon (tel). MA-fibres were present in ventral areas of the bulbus olfactorius (bo) (Fig. 2A) which in *Eigenmannia* is juxtaposed to the ventro-frontal parts of the tel (Fig. 1). At the posterior part of the bo these fibres ran into the medial area of the tel.

In the frontal tel MA fibres occurred in the lateral parts of the area dorsalis (dl) and area ventralis (vl) (Fig. 2B, 4A and B), and also in more medial areas where the fibres were aligned vertically (Fig. 2C and 4C). More caudally the number of MA-fibres increased with the majority of the fibres located medially, adjacent to the first

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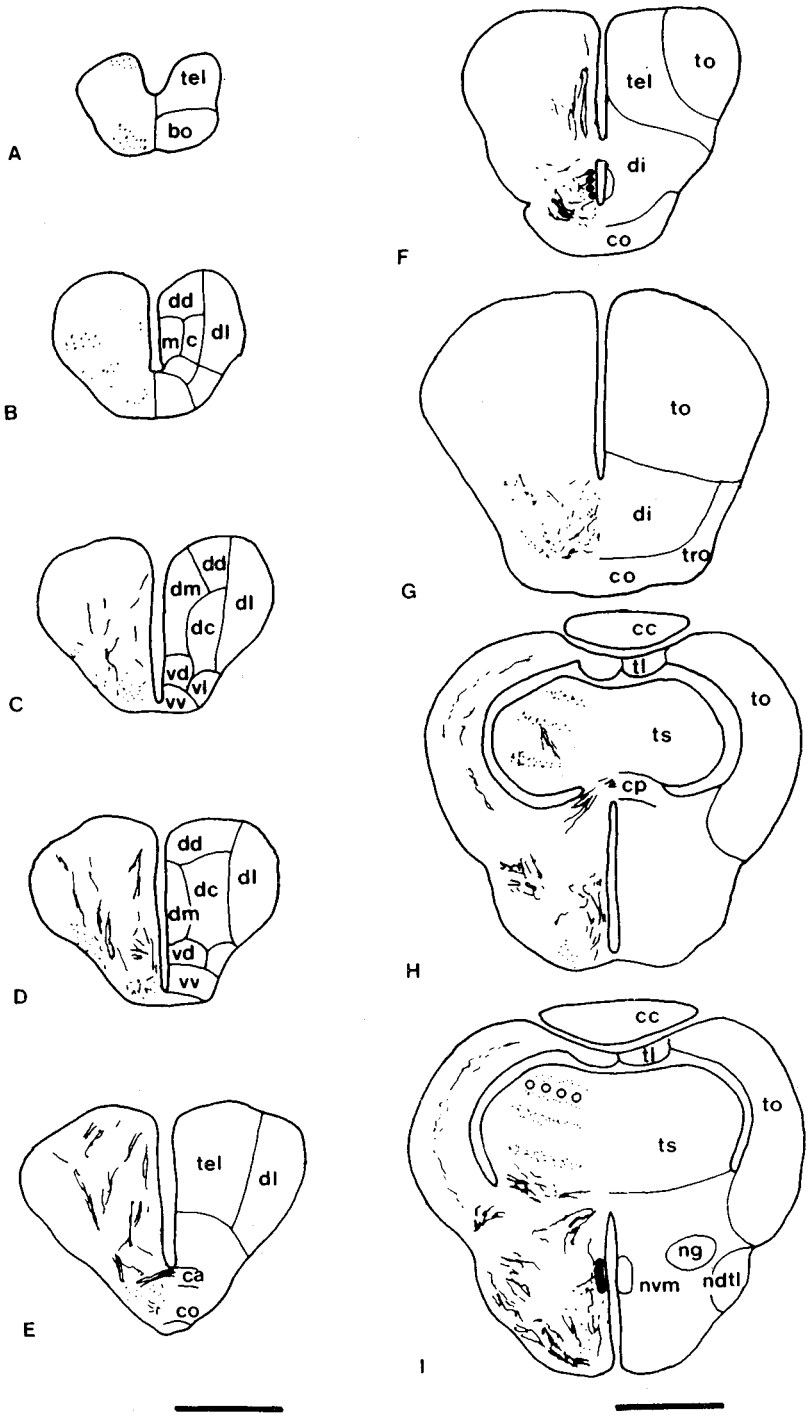
Fig. 2. Frontal sections of the *Eigenmannia* brain in rostro-caudal order. The left half of each section schematically shows the distributions of MA-containing neurons (filled circles), of MA-fibres (dots or lines), and of 5-HT-containing yellow-fluorescent perikarya (open circles). The right half of each section shows the locations of the major anatomical structures. Bar = 0.5 mm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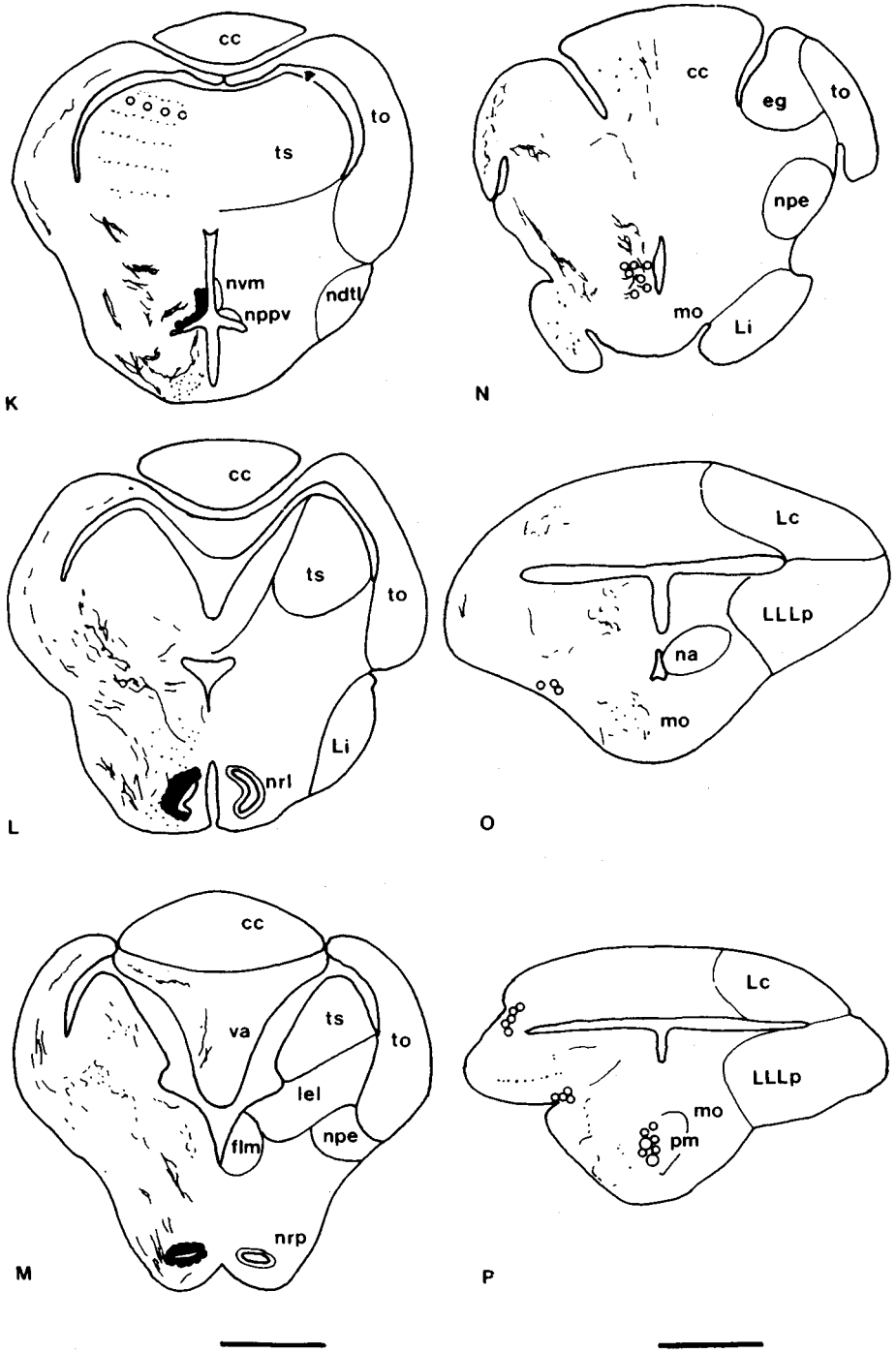
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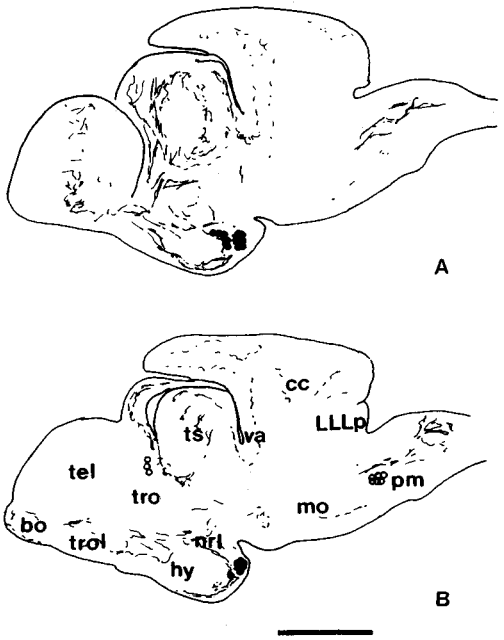

Fig. 3. Distribution of MA-containing neurons in two paramedian sagittal sections (A, B) of the *Eigenmannia* brain. Bar = 0.5 mm

ventricle (Fig. 2C and D, 4C). The still vertically arranged fibres connected to the ventro-lateral area (vl). Some fluorescent axons ran horizontally through the commissura anterior (ca, Fig. 2E). In a caudal, ventral area of the tel at the level of the chiasma opticum, co, (Fig. 2F) some MA-fibres were seen. The dorsomedial part of the caudal telencephalon contained many MA-fibres in vertical configuration (Fif. 3). This arrangement could be followed caudally to the level of the frontal tectum opticum.

2.2. Diencephalon

MA-perikarya: The preoptic-hypothalamic area contained the highest density of monoaminergic neurons. The most rostral green-fluorescent MA-neurons were located next to the third ventricle in the frontal diencephalon (Fig. 2F; 5A, B). These neurons in the wall of the preoptic recess belong to the npp which is part of the preoptic recess organ (PRO, VIGH-TEICHMANN et al. 1969). Most of these MA-neurons sent fluorescent club-like protrusions into the lumen of the third ventricle. The neurons of the PRO located slightly rostral to the chiasma opticum (co) and beneath the nucleus praeopticus (npo) were non-fluorescent. More caudally, MA-perikarya occurred in the paraventricular organ (PVO), that is in the nucleus ventromedialis

thalami (nvm, Fig. 2I; 5A, B), in the nucleus posterioris periventricularis (nppv; Fig. 2K, 5C), in the nucleus recessus lateralis (nrl, Fig. 2L; 5D), and in the nucleus recessus posterior (nrp; Fig. 2M, 5E).

MA-fibres: A great number of MA-fibres was found in dorsal, medial and ventral parts of the anterior diencephalon (di), at its maximum cross-sectional area (Fig. 2F;

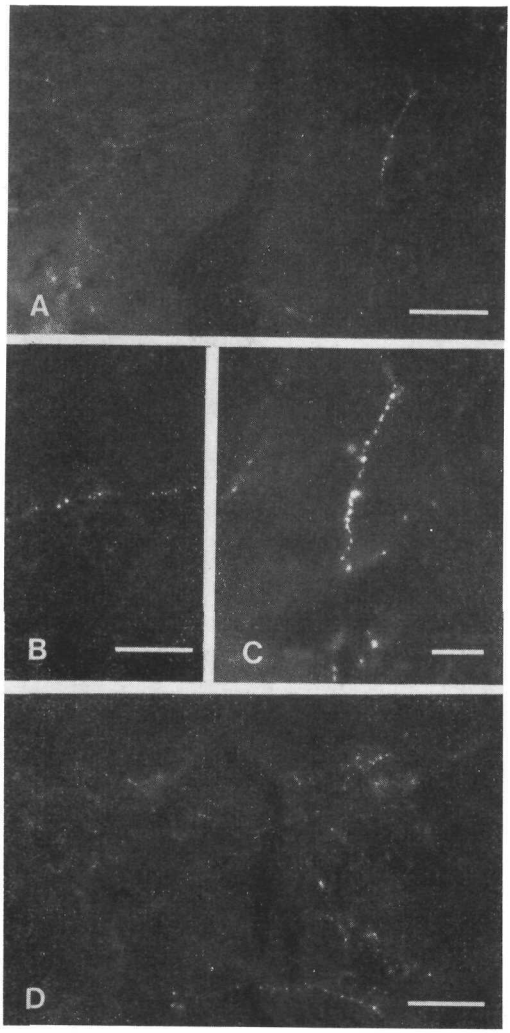

Fig. 4. Catecholaminergic fluorescence in sagittal sections through *Eigenmannia's* telencephalon; bar = 50 μm

A) Varicose fluorescent fibres in the ventral telencephalon
B) NA-containing varicose fibre in the telencephalon
C) Magnification of A, showing an NA-containing varicose fibre with typical bead-like structure (bar = 20 μm)
D) MA-fibres in the medial tel, adjacent to the border of the ventricle

5F, H, I). In the medial part of the di, MA-axons occurred mainly in medial, dorsomedial and ventral areas (Fig. 2I). The fluorescent nerve endings surrounded the nuclei of the PRO and PVO where MA-fibres connect the nucleus ventromedialis, the nuc. post. periventricularis, the nuc. recessus lateralis and the nuc. rec. posterior. In the ventral, medial diencephalon ascending or descending fluorescent fibres appeared in a V-shaped configuration in the cross-section; other fibres were running horizontally. In the caudal diencephalon many MA-fibres were seen over the whole extent of the ventral hypothalamus (Fig. 2K, 5G). The lobus inferior (Li; Fig. 2L–N) contained only few fibres.

2.3. Mesencephalon

MA-perikarya: Equidistant, yellow-fluorescent perikarya (T-cells) occurred in the upper third of the dorsal torus semicircularis (ts) in lamina VI (Fig. 6B). The granular and fast fading fluorescence indicates serotonin. These cells were the only fluorescing perikarya in the whole mesencephalon.

MA-fibres: Green-fluorescent fibres occurred in several parts of the mesencephalon (mes). In the frontal mes, MA-fibres occurred at the level of and within the commissura posterior (cp, Fig. 2H). Scattered MA-fibres were also seen in the stratum fibrosum et griseum centrale of the tectum opticum (to, Fig. 6A).

The rostral parts of the ts (which are completely covered by the to) contain a clearly recognisable and in some parts dense network of fluorescent fibres (Fig. 6D). These fibres were found in layers V, VII, IX and XI (possibly also X) in the rostral, medial and caudal torus (Fig. 6C–F). In the caudal torus some MA-fibres also occurred in lamina XIII (Fig. 6F). Some of the caudal fibres projected ventrally to or from the diencephalon. MA-fibres of the lemniscus lateralis (lel; Fig. 2K, M) projected to or from the caudal ts (Fig. 2M).

▶

Fig. 5. MA-containing, fluorescent neurons in the diencephalon of *Eigenmannia*; transversal sections; bar = 50 μm

A), B) MA-neurons in the recessus preopticus bordering the third ventricle. Note fluorescent nerve endings in the nucleus preopticus (npo; arrow-heads) and club-like protrusions of some neurons into the third ventricle (arrows). B) is about 100 μm caudal to A)

C) MA-containing neurons in a transversal section through the nucleus ventromedialis (nvm) and the nucleus posterior periventricularis (nppv)

D) MA-containing perikarya in the nucleus recessus lateralis (nrl) of the periventricular organ (PVO); transversal section; bar = 20 μm

E) MA-neurons in the nucleus recessus posterior (nrp); transversal section; bar = 50 μm

F) MA-fibres in the ventrolateral diencephalon of *Eigenmannia*; transversal sections; bar = 50 μm

G) Photomontage of MA-fibres in the ventrolateral, caudal diencephalon at the level of the entry of the optic tract into the brain; transversal section; bar = 50 μm

H), I) MA-containing fibres in the ventral diencephalon, dorsal to the chiasma opticum (co) which is not fluorescent

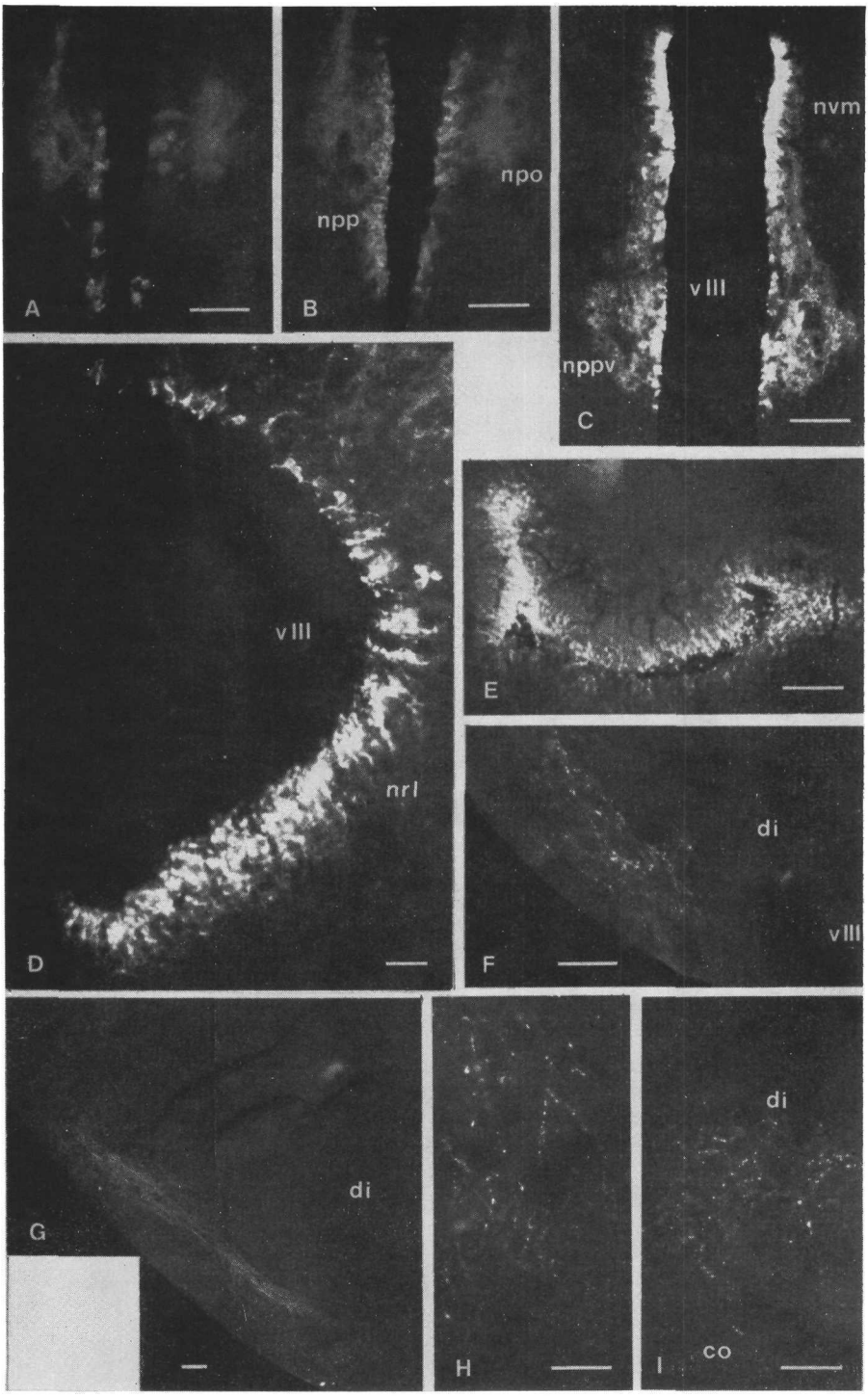

Fig. 5

In the mesencephalic tegmentum MA-fibres were present in the region of the prepacemaker nucleus (ppm; HEILIGENBERG et al. 1981) whereas in the caudal mesencephalon many MA-fibres occurred in the mediodorsal region, especially near the third ventricle (v III). Some of these fibres coursed towards the lateral parts of the midbrain (Fig. 2I).

2.4. Rhombencephalon

MA-perikarya: In the frontal brain stem of nialamide-treated animals, a group of yellow-fluorescent 5-HT-perikarya occurred in the raphe-region on both sides of the midline (Fig. 7A). Some of these neurons had brightly yellow-fluorescent proximal axon parts but only weak fluorescence more distally. As far as they could be followed these axons projected towards the ventral medulla.

The medullary pacemaker nucleus (pm) which commands the electric organ contains two types of cells: the large relay neurons, and the smaller pacemaker neurons (ELEKES and SZABO 1981, 1982, 1985; Fig. 7G). Both types of cells were yellow-fluorescent (Fig. 2O; 7D, E, F). The fluorescence was distributed in granules over the whole perikarya and faded fast during illumination indicating the presence of MA (see Material and Methods). Ungassed control sections and reserpine-treated brains showed no fluorescence (Fig. 7F).

Other yellow-fluorescent perikarya occurred in the following regions: 1. the lateral wall of the medulla oblongata (mo; Fig. 2O), 2. near the lateral extent of the fourth ventricle, 3. in the lobus caudalis (Lc), near the lobus lineae lateralis posterior (LLLp), and 4. at the border of the LLLp and the dorsolateral parts of the mo. The number of these yellow-fluorescent cells was greatly reduced in ungassed controls.

MA-fibres: Only few vertically oriented MA-fibres were found in the corpus cerebelli (cc) and in the valvula cerebelli (va; Fig. 2M). Similarly poor in MA-fibres were the middle layers of the lobus lineae lateralis posterior (LLLp; Fig. 2N). The ventral molecular layer of the LLLp, the ventral part of the hindbrain, and the medulla oblongata (mo; Fig. 7B, C) contained only few green-fluorescent fibres ventro-

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Fig. 6. Monoamine containing neurons in the mesencephalon of *Eigenmannia*; bar = 50 μm. Roman numbers in toral sections indicate the laminae as described by SCHEICH and EBBESSON (1983)

A) Varicose fluorescent axons in the medial layers of the tectum opticum (to), mainly in the stratum fibrosum et griseum centrale; transversal section, FIF

B) Yellow-fluorescent neurons in lamina VI containing T-units (SCHEICH and EBBESSON 1983), of the medial torus semicircularis (ts); transversal section

C), D) Transversal section through the frontal ts with fluorescent MA-fibres in lamina XI. The position of D) is indicated in C)

E) Transversal section through the frontal ts showing fluorescent fibres in the lamina IX

F) Photomontage of transversal sections through the caudal ts

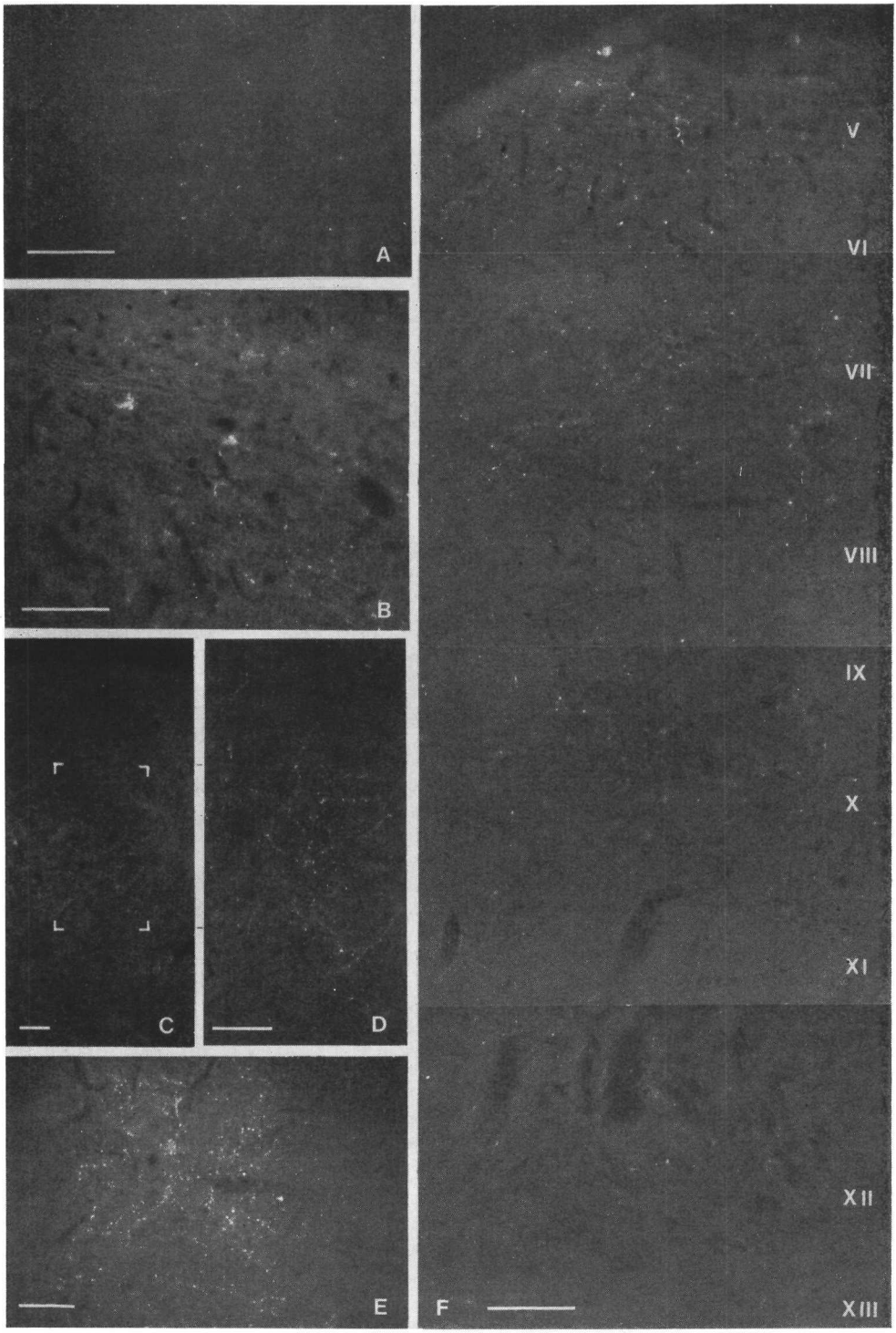

Fig. 6

lateral to the raphe region. The number of these fibres was maximal in the frontal medulla at the level of the caudal ts.

3. MA-concentrations in the brain of Eigenmannia

The concentrations of the biogenic amines NA, DA and 5-HT were determined electrochemically after separation by High Pressure Liquid Chromatography (HPLC; Tab. 1). Adrenaline (A) was below the detection limit of about 4 ng/g wet weight.

Table 1. Mean values (± standard error, SE) of weight (W), brain weight (BW), and concentrations of the monoamines noradrenaline (NA), dopamine (DA), and serotonin (5-HT). N is number of brains or parts of brains used

N	W	BW	NA	DA	5-HT	NA/DA
	(g)	(mg)	(ng/g wet weight)			
12	1.95	32.4	313	96	71	3.3
(SE)	0.4	3	24	19	12	
telencephalon ($N = 3$)			238 ± 62	37 ± 22	62 ± 44	8.4
di-/mesencephalon ($N = 3$)			372 ± 110	33 ± 15	40 ± 21	11.0
cerebellum/medulla ($N = 3$)			172 ± 31	25 ± 3	39 ± 19	6.7

The noradrenaline (NA) content was significantly greater than the dopamine content ($p < 0.01$; $N = 12$; Wilcoxon test), as determined in whole brains.

Statistical comparisons of the MA-contents between parts of the brains were not carried out because of the low number of fish studied ($N = 3$). Maximum NA-con-

►

Fig. 7. Monoaminergic fluorescence in the hind-brain of *Eigenmannia*; bar = 50 μm

A) Transversal section through the raphe region. Yellow-fluorescent 5-HT-neurons (fast fading) along the ventral sulcus medianus (arrows). Note the short fluorescent axons projecting laterally (arrow-heads)

B) Transversal section with MA-fibres in the ventrolateral medulla oblongata (mo), at the level of the raphe. These fibres form a dense network in the ventral hindbrain

C) Green-fluorescent MA-fibres in the ventral mo with bundle like appearance in rostrocaudal extension; transversal section

D) Yellow-fluorescent, MA-containing perikarya in the medullary pacemaker nucleus of *Eigenmannia*. R = relay neuron, P = pacemaker neuron; transversal section; bar = 50 μm

E) Yellow-fluorescent pm-neurons with granules in the perikarya

F) Pm-neuron in the brain of a reserpine-treated fish. Note the absence of fluorescent granules in the perikaryon

G) Frontal section of pm neurons. Note the relay- (R) and pacemaker-neurons (P) surrounded by myelinated nerve fibres (semithin section, 2 μm; Richardson stain; bar = 20 μm

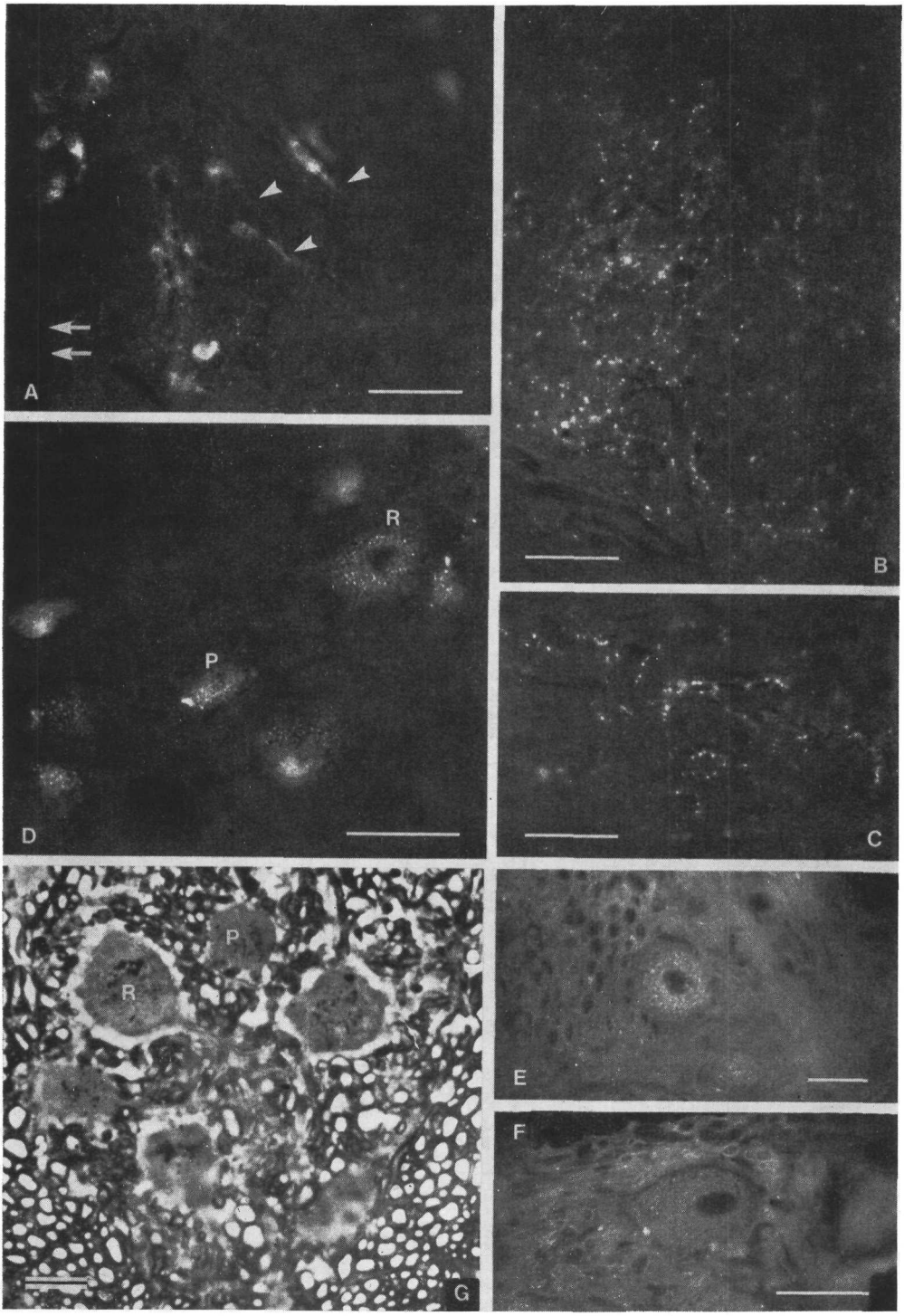

Fig. 7

centrations were found in the di and mes, while 5-HT was most concentrated in the tel. The DA-concentration was lower in the corpus cerebelli and medulla compared with the di-mesencephalon and telencephalon (Tab. 1).

4. Microspectrofluorometry

Green- and yellow-fluorescent neurons and fibres were studied by means of microspectrofluorometry (MSF) in the preoptic recess organ, paraventricular organ, nuc. recessus lateralis, nuc. rec. posterior and pacemaker nucleus in order to discriminate specific (aminergic) from unspecific fluorescence (non-aminergic content). Unspecific fluorescence (Fig. 8D); ungassed and gassed yellow fluorescent cells and fibres) had its emission maximum at 462 nm and was characterized by a steep decline of fluorescence at greater wavelengths. All green fluorescent cells, and most of the green- to yellow-fluorescent fibres and perikarya (including the pm-neurons) had peaks at 470 to 476 nm (Fig. 8A–C), and therefore are regarded as CA-specific (CA and precursors; BJÖRKLUND et al. 1975). The emission spectra of the green-fluorescent perikarya

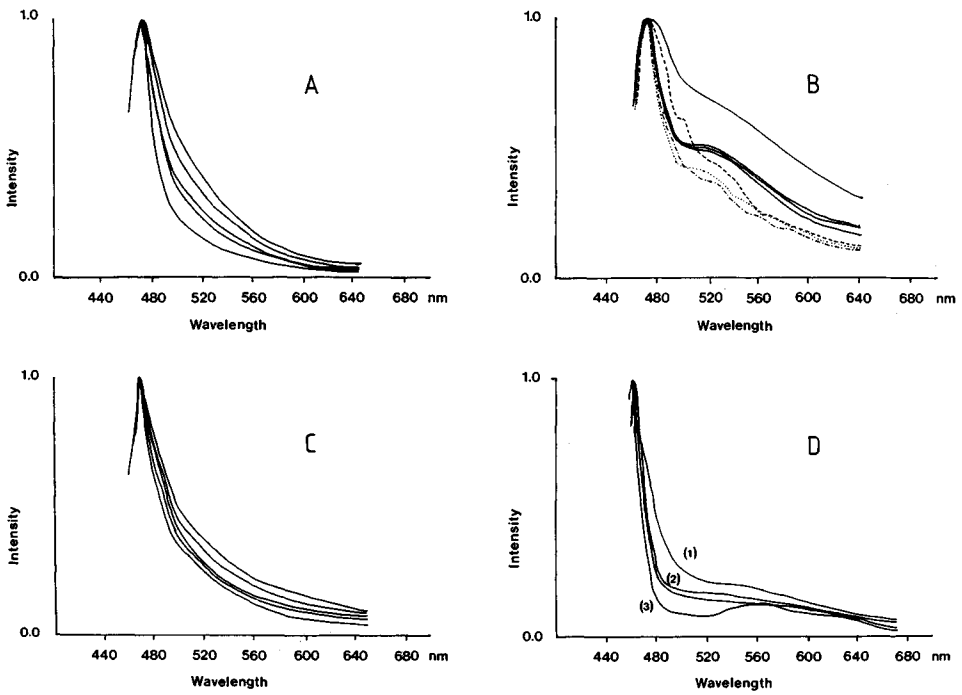

Fig. 8. Emission spectra of fluorescent neurons in the brain of *Eigenmannia*

A) Green-fluorescent perikarya

B) Yellow-fluorescent perikarya, including those of the pacemaker nucleus (dashed lines)

C) Varicose fluorescent fibres

D) Unspecific fluorescent neurons from formaldehyde-treated material (1, 3) and from ungassed controls (2)

(Fig. 8A) are almost identical to the spectra of the green-fluorescent fibres (Fig. 8C), while the spectra of the green- to yellow-fluorescent perikarya show more intense fluorescence above 500 nm (Fig. 8B). What appears like a weak secondary peak at about 520 nm was only found in the spectra of the yellow-fluorescent perikarya of Fig. 8B and may indicate 1) high CA-concentrations (as explained in Material and Methods), 2) small amounts of 5-HT (because of its rapidly fading fluorescence at 520–540 nm), or 3) products from chemical sidereactions and oxidation (BJÖRKLUND et al. 1975). On the second assumption these yellow-fluorescent neurons would contain both CA and 5-HT (see Discussion).

Discussion

The overall intensity of fluorescence in the brain of *Eigenmannia* was weaker than in the brain of the goldfish (BONN 1983), as also confirmed by HPLC measurements of amine concentrations. The absolute and relative NA content was lower in *Eigenmannia's* brain, as shown by the NA- to DA-concentration ratios which were 2.5 in *Eigenmannia* compared with 4 in *Carassius* (BAUMGARTEN 1972, BONN 1983).

The MA-distribution in the brain of *Eigenmannia lineata* is similar to that of several other teleosts, such as *Lepomis*, *Myoxocephalus*, *Lepisosteus* and *Blennius* (PARENT et al. 1978, SANTER 1977, WATSON 1980, PARENT and NORTHCUTT 1982, KOTRSCHAL and ADAM 1983).

The absence of fluorescent perikarya in the telencephalon of *Eigenmannia* agrees with all other reports on teleosts; the fluorescent nucleus described in the tel of *Anguilla* by FREMBERG et al. (1977) was identified as autofluorescent in a later study (PARENT and NORTHCUTT 1982).

Also the MA-fibre distribution observed in *Eigenmannia's* bulbus olfactorius and telencephalon was similar to that of other teleosts. While in *Lepomis* (PARENT et al. 1978) the main CA-fibre occurrence was reported in the area dorsalis tel. pars lateralis (dl) a more scattered picture was described for *Anguilla* (FREMBERG et al. 1977), and a dense network was observed in the frontal tel in *Myoxocephalus* (WATSON 1980). A network of 5-HT-fibres in the dl, as shown in *Lepomis* (PARENT et al. 1978) and *Carassius* (KAH and CHAMBOLLE 1983), was not found in the brain of *Eigenmannia* (present study; this difference may be due to the fast fading of the 5-HT-fluorescence). In *Carassius* these 5-HT-fibres are believed to originate in the raphe-region of the medulla and to project to the telencephalon via the tegmentum, dorsal diencephalon and the median forebrain bundles (KAH and CHAMBOLLE 1983).

A bundle-like appearance of MA-fibres in *Eigenmannia's* middle tel, from which the fibres spread radially, had already been observed in the eel (LEFRANC et al. 1969). These fibres were described to be of extratelencephalic origin. In contrast to *Carassius* (BONN 1983) the commissura anterior of the *Eigenmannia* brain contains fluorescent MA-fibres.

MA-fluorescence also occurred in the frontal diencephalic areas, which correspond to the PRO (VIGH and VIGH-TEICHMANN 1973) or to the nucleus recessus preopticus

(nrpo of EKENGREN 1975), while in the habenula no fluorescence was found. This agrees with the results of EKSTRÖM and VAN VEEN (1982) on *Ictalurus* but not with those of FREMBERG et al. (1977) on *Anguilla*.

The strong fluorescence in parts of *Eigenmannia's* paraventricular organ (PVO as defined by VIGH-TEICHMANN and VIGH 1983), the perikarya of which are in the subependymal region contacting the third ventricle, is characteristic of all teleosts studied so far (BERTLER et al. 1963, BAUMGARTEN and BRAAK 1967, EKENGREN 1975, FREMBERG et al. 1977, TERLOU et al. 1978, WATSON 1980, EKSTRÖM and VAN VEEN 1982, KOTRSCHAL and ADAM 1983). Especially strong fluorescence is typical for the rostrally situated nuclei ventromedialis and periventricularis posterior (nvm and nppv; homologous to the PVO pars anterior of EKSTRÖM and VAN VEEN 1982), and the nucleus recessus lateralis (nrl) and posterior (nrp), and was also found in *Eigenmannia*. While in the lobus inferior (Li) of *Lepomis* (PARENT et al. 1978) a rich MA-innervation was reported, the Li of *Eigenmannia* only contained a few MA-fibres. According to BAUMGARTEN and BRAAK (1967) these fibres probably were axonal projections of hypothalamic cerebrospinal-fluid-contacting-(CSF)-cells (Fig. 3B) in *Carassius*. The assumed role of these (CSF) cells is receptive and/or neurosecretory, or integrative in association with adjacent neural tissue (VIGH-TEICHMANN and VIGH 1983).

Eigenmannia's tectum opticum showed scattered MA-fibres in middle layers only, as also observed in *Carassius* (BONN 1983), *Lepisosteus* (PARENT and NORTHCUTT 1982), and *Lepomis* (PARENT et al. 1978) while in *Blennius* (KOTRSCHAL and ADAM 1983) a homogeneous MA-distribution in all tectal layers occured. MA-fibres parallel to the layers of the to were reported in *Myoxocephalus* (WATSON 1980).

Eigenmannia's torus semicircularis (ts) is huge compared with that of *Carassius* or any other fish studied with respect to the MA-distribution. In *Eigenmannia* the ts is a coordinative midbrain center for ascending electrosensory information and descending electromotor commands. It consists of 15 layers (SCHEICH and EBBESSON 1983); its dorsal part receives afferent input from the Lobus lineae lateralis posterior (LLLp), from the Lobus caudalis (Lc), from the trigeminal nuclei, and from the ipsilateral tectum opticum (to). The efferents of the dorsal torus semicircularis project to lateral regions of the diencephalon, to the tectum opticum, to the Lobus lineae lateralis posterior, to the pretectal area and to the inferior olive (CARR et al. 1981). The ventral part of the torus gets input from ordinary lateral line receptors and the auditory system, the dorsal part exclusively receives electrosensory information (CARR et al. 1981). As described before, MA-fibres occurred in layers V, VII, IX, XI (possibly X) which are the main layers receiving electrosensory input (SCHEICH and EBBESSON 1983), as well as in the ventral torus. The large T-cells of layer VI which are part of the fast-conducting, electrosensory T-system are MA-perikarya.

In the hindbrain of *Eigenmannia*, and of the closely related electric fish, *Gymnotus carapo*, another transmitter system, the acetylcholinesterase-(AChE) and choline acetyl transferase-(CAT)-activities were studied (MALER et al. 1981). In *Eigenmannia* the AChE-activity was weakest in the corpus cerebelli, stronger in the ventral molecular layer of the Lobus lineae lateralis posterior (LLLp) and strongest in the dorsal

molecular layer. The CAT-activity in the LLLp was four times stronger than in the cerebellum or twice as strong compared with the Lobus caudalis. Weak MA-fluorescence in these brain areas, as found in the present study, together with these reports on the AChE-activity, suggest transmitters other than MA.

The rhombencephalon of gymnotids consists of the cerebellum (three parts: valvula, va, corpus cerebelli, cc, and lobus caudalis, Lc), and the multilayered posterior lateral line lobe (LLLp) which is a dorsolateral protrusion of the medulla, partly covered by the Lc (MALER et al. 1974). These areas are greatly enlarged in gymnotids, and the LLLp works as a first order station for electrosensory input (MALER et al. 1974). In the LLLp seven layers and four different cell types were described, some of these connected with the three different types of electroreceptors (SCHEICH 1977, MALER 1979, MALER et al. 1981). Functionally the LLLp can be subdivided into four segments which represent somatotopic maps of the electroreceptors on the body surface (CARR et al. 1982). Efferents of the LLLp project to 1. the nucleus praeeminentialis dorsalis, and 2. to the laminae 3, 5, 6, 7, 8b and 8d of the dorsal torus semicircularis (nomenclature of MALER et al. 1982), or to the layers III, V, VII, IX and XI (SCHEICH and EBBESSON 1983). According to MALER (1979) descending electrosensory information ends in the deepest (molecular) layer of the LLLp.

The occurrence of MA-neurons in the raphe region of *Eigenmannia* agrees well with other reports (*Lepomis*: PARENT et al. 1978; *Carassius*: BAUMGARTEN and BRAAK 1967; *Anguilla*: LEFRANC et al. 1969) although the MA-neurons in *Eigenmannia* did not reach such rostrocaudal extent as in *Lepisosteus* (PARENT and NORTHCUTT 1982).

Apart from the yellow-fluorescent cells of the medullary pacemaker nucleus (pm), there were some medullary MA-fibres in vertical configuration which might originate in the raphe region and could connect the medulla oblongata with the corpus cerebelli.

The neurons of the pacemaker-(pm)-nucleus (the large relay-neurons, about 60 μm in diameter, and the smaller pacemaker-neurons, about 30 μm in diameter; ELEKES and SZABO 1981, 1982) showed MA-specific fluorescence for two reasons: 1. an enhancement of the yellow fluorescence in nialamide-treated animals was observed; 2. no fluorescence in ungassed or reserpine-treated brains was detected. The emission maxima of about 470 nm suggest CA and CA-precursors. The presence of a weak secondary peak around 530 nm in yellow-fluorescent cells (Fig. 8B) suggest faded 5-HT as 5-HT-cells show emission maxima at 520–530 nm (BJÖRKLUND et al. 1975). On this assumption the pm-neurons would contain 5-HT in addition to CA or its precursors. EKENGREN (1975) suggested the presence of CA and 5-HT in the same neuron for the roach (*Leuciscus*) brain. BOER et al. (1984) have shown DA and 5-HT to coexist in the cerebral giant ganglion of the snail *Lymnaea*.

The MA-fibres connecting the hypothalamus with hindbrain areas might correspond at least partly to the fibres of the pre-pacemaker nucleus (ppm) labelled retrogradely by injecting HRP into the pacemaker nucleus (pm) by HEILIGENBERG et al. (1981).

From the locations of MA-neurons one may suggest that important electrosensory and electromotor brain areas (reviews see BELL 1979, BULLOCK 1982, SCHEICH and EBBESSON 1983) contain monoaminergic transmitters.

A highly simplified picture is given here. The electrosensory lateral line nerve (NLLa) projects to the Lobus lineae lateralis posterior (LLLp) in the rhombencephalon. This lobe in the dorsolateral portion of the mo is the first order electrosensory station in the brain of *Eigenmannia* (Maler et al. 1981) and, as first shown here, contains (although only few) MA-fibres. Efferents from the LLLp go to the highly laminated dorsal part of the mesencephalic torus semicircularis (ts) the electrosensory layers of which also contain MA-fibres, and to other brain areas via lemniscal fibre bundles. Among other structures, the output of the ts is relayed to the pacemaker nucleus (pm), which also contains monoamines.

The only functional evidence to date, concerning a possible role of MA in the electromotor system, is the observation that chlorpromazine, a dopamine antagonist, reversibly reduces the EOD-frequency (Kramer 1984). The present observations on the rhombencephalon and the torus show that some electrosensory brain centers and areas of sensory-motor integration, as well as the pacemaker nucleus itself, contain monoamines in *Eigenmannia lineata*. Future studies will have to disclose the chemical identity of the transmitter content of these MA-neurons and their connectivity and function.

Acknowledgements

Supported by the Deutsche Forschungsgemeinschaft (SFB4/H1). We wish to thank Prof. J. Boeckh and Prof. H. Altner for their kind loan of histological equipment and a freeze-drying machine. We also wish to thank Prof. H. Grobecker and Dr. F. Kees (Pharmacology Department) who performed the HPLC-measurements in their laboratory. Ernst Leitz GmbH kindly allowed us the use of their computer-controlled MSF equipment at Wetzlar. We are grateful also to Dr. T. Szabo, C.N.R.S.–Gif sur Yvette (France), for his most valuable criticism of the manuscript.

Abbreviations

CA: catecholamines; DA: dopamine; D.C.: direct current; EOD: electric organ discharge; HPLC: high performance liquid chromatography; MA: monoamines; MAO: monoamine-oxidase; MSF: microspectrofluorometry; NA: noradrenaline; S.E.: standard error; 5-HT: 5-hydroxy-tryptamine (serotonin); 5-HTP: 5-hydroxytryptophane.

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