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Quantitative Histological Studies of the Optic Tectum in Six Species of *Notropis* and *Cyprinella* (Cyprinidae, Teleostei)

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With 3 Figures and 6 Tables

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Abstract: Significant differences in stratification and size of the visual layers of the optic tectum were found between three clear-water minnows *(Notropis amabilis, N. boops, Cyprinella venustas)* and three turbid-water minnows (*N. atherinoides*, *N. bairdi*, and *C. lutrensis)*. Correlations among a variety of neural structures suggested the importance of stratum marginale (SM), stratum opticum (SO), and stratum fibrosum et griseum superficiale (SFGS), stratum griseum centrale (SGC) and stratum periventriculare (SPV) in vision, of stratum album centrale (SAC) and SGC for olfaction, and of SPV for the processing of acoustico-lateral information.

Key words: minnows, neuroanatomy, vision, olfaction

Introduction

The mesencephalon of teleosts is a highly complex region which plays an important role in the integration of a variety of sensory stimuli and in the mediation of many coordinated motor responses (MEYER et al., 1970; SPRINGER et al., 1977). The most prominent feature that develops from the midbrain is the optic tectum; it comprises two symmetrical optic lobes which are divided by a median longitudinal groove. The distinct lamination of this structure has received considerable attention and a variety of nomenclatures have been proposed (RAMÒN, 1899; ARIENS KAPPERS et al., 1936, LEGHISSA, 1955; VANEGAS et al., 1974; MEEK and SCHELLART, 1978; NORTHCUTT 1984). VANEGAS et al. (1974) distinguished six strate (VANEGAS, 1984; MIGUEL HIDALGO, 1986a, b), the most dorsal layer of which, the stratum marginale (SM), comprises numerous unmyelinated fibers that arise from the torus longitudinalis. This paried structure runs as a rostro-caudal ridge along the midline of the brain, below the tectal commissure, and appears to play a role in postural control, detection of luminance levels and monitoring of saccadic movement (ARIENS-KAPPERS et al., 1936; NORTHMORE et al., 1983). Neurons situated in the stratum opticum (SO), stratum fibrosum et griseum superficiale (SFGS), and stratum album centrale (SAC) receive fibers from the contralateral retina as well as the ipsilateral telencephalon (NORTHCUTT and BUTLER, 1976; REPÉRANT and LEMIRE, 1976; VONEIDA and SLIGAR, 1976; LUCKENBILL-EDDS and SHARMA, 1977; EBBESSON and ITO, 1980; REPÉRANT et al., 1981; EKSTRÖM, 1982; FERNALD, 1982). Fibers originating at the stratum griseum centrale (SGC) project to the torus longitudinalis and contralateral tectum (EBBESSON and VANEGAS, 1976; SLIGAR and VONEIDA, 1976). The tori semicirculares, which form a pair of distinct bulges at the dorso-lateral ventricular surface of the mesencephalic tegmentum, appear, in at least some electroceptive teleosts, to be closely related to the tectum (BASTIAN, 1982). The torus semicircularis is considered homologous to the mammalian inferior colliculus and its size varies with the development of the octavo-lateral system (NIEUWENHUYS and POUWELS, 1984). The cerebellum projects a lobe rostrally into the mesencephalic ventricular space, forming the valvula cerebelli, which appears to be responsible for the generation of eye movements and which is intimately connected to the torus longitudinalis and optic tectum (KIDOKORO, 1968; HERMAN 1971; ITO and KISHIDA, 1978; NORTHMORE, 1984).

Numerous studies have demonstrated the existence of a relationship between the size of parts of the teleost brain and ecological and behavioral variables (e.g., SCHNITZLEIN, 1964; DAVIS and MILLER, 1967; SAXENA, 1968; KOTRSCHAL and JUNGER, 1988). KISHIDA (1979), in a study of 75 species of 52 teleost families, demonstrated differences in the width and neuronal geometry of various tectal layers that correlate well with the ecology of the species. WINKELMANN and WINKELMANN (1968), comparing the thickness of superficial tectal layers in six teleost

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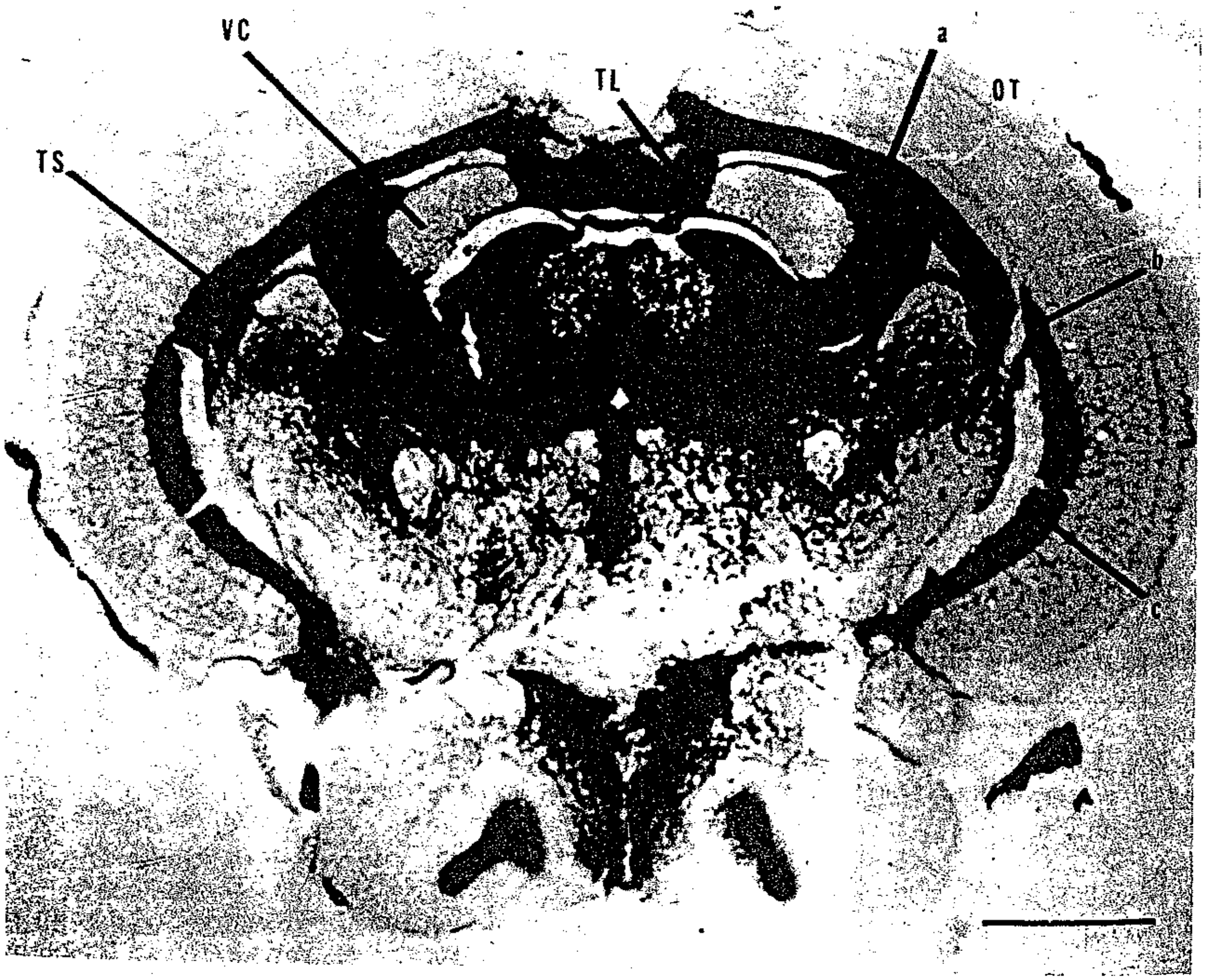
families, reported a well-developed SO and SFGS in visually oriented predators while these layers were thinner in species with other feeding habits.

Species in the genera *Notropis* and *Cyprinella* (Mayden 1990) appear especially useful for a comparative analysis of the optic tectum, as this group comprises a large number of closely related species which occupy virtually every type of freshwater habitat in North America. Moreover, brain morphology in this group is intimately related to the turbidity of the habitat (Huber and Rylander, 1990).

The present study investigates (1) whether the optic tecta of clear-water and turbid-water species of minnows *(Notropis* and *Cyprinella)* differ in the two-dimensional extent and the thickness of its constituent layers, and (2), whether the thickness of tectal layers is correlated with the size of various neural structures, namely the torus longitudinalis, torus semicircularis, valvula cerebelli, corpus cerebelli, telencephalon, and the eye. Such correlations may indicate functional ties.

Materials and Methods

Ten adult, female specimens each of three turbid water species *(Cyprinella lutrensis, Notropis bairdi, N. atherinoides)* and three clear water species *(C. venusta, N. amabilis, N. boops)* were used (for turbidity estimates of these species see Huber and Rylander, 1990). All specimens were collected in the Southwestern U.S. by seigning. They were fixed in 10% phosphate-buffered formalin and total and standard length were measured to the nearest 0.5 mm. The roof of the cranium was removed to facilitate penetration by the fixative. Under a dissecting microscope, the brain was exposed and the length and width of the telencephalon, optic tectum, and corpus cerebelli were measured to the nearest 0.05 mm using 10× magnification and an ocular grid. The diameter of the eye was measured with the same precision along the nasal-temporal axis. The brain was then carefully removed from the skull and stored in 10% buffered



ig. 1. The brain of *N. atherinoides*. Transverse section through the brain of *N. atherinoides* at the level of the caudal ypothalamus. Abbreviations are optic tectum (OT), torus longitudinalis (TL), torus semicircularis (TS), valvula cerebelli C), and three sample areas (a, b, c). Scale bar represents 250 μm.

formalin. The brain was embedded in 25% gelatin, frozen, and sectioned at 50 µm with a freezing microtome. These sections were Nissl-stained using cresyl violet and mounted with Permount. Using a bioscope, sections were projected directly onto a digitizing pad which interfaced with a Macintosh Plus Microcomputer. All measurements were obtained using the morphometric software Microquant (HUBER, unpubl.). Corresponding cross-sections through the caudal hypothalamus (Figure 1) were projected at a final magnification of 980 × and the thickness of the stratum marginale (SM), stratum opticum (SO), stratum fibrosum et griseum superficiale (SFGS), stratum griseum centrale (SGC), stratum album centrale (SAC), stratum periventriculare (SPV) were measured at three locations along the cross-section of the optic tectum (a, b, c in Figure 1, Figure 2). Each measurement was repeated 3 times and an estimate of the thickness of each layer was obtained by averaging these nine measurements. The width of the optic tectum (OTW), the cross-sectional area of the torus longitudinalis (TL), torus semicircularis (TS), and valvula cerebelli (VC) were measured at a magnification of 310 ×. Optic tectum length (OTL) was determined as the product of the number of sections containing the optic tectum and section thickness. The tectal area (OT) was calculated as the product of length and width of the optic tectum.

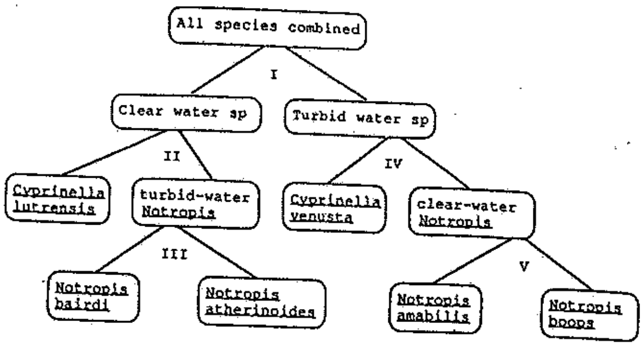


Fig. 3. A set of orthogonal comparisons was used to compare the size of the optic tectum and its stratification in three turbid-water species (*C. lutrensis, N. bairdi, N. atherinoides*) and three clear-water species (*C. venusta, N. amabilis, N. boops*) of minnows. First, all clear water species were compared to all turbid species (I); the species of *Cyprinella* was compared to the two species of *Notropis* within clear-water (II; and turbid-water species (IV); and, finally, in each turbidity group the two species of *Notropis* were compared to each other (III, V).

To compare the stratification of the optic tectum in different species, a set of *a priori* orthogonal comparisons in a multivariate analysis of covariance design (MANCOVA; Procedure MANOVA, SPSSX Inc., 1988) was performed (Figure 3) with thickness of SM, SO, SFGS, SGC, SAC and SPV as dependent variables and standard length as a covariate. In these orthogonal contrasts all clear-water species were compared to all turbid-water species (I); both within clear-water and within turbid-water species, the species of *Cyprinella* was compared to the two species of *Notropis* (II, IV); and, finally, the two species of *Notropis* were compared to each other within each turbidity group (III, V). In addition, identical *a-priori* contrasts were performed on each dependent variable separately as univariate analyses of covariance (ANCOVAs). In a further analysis, the area of the optic tectum was compared in such *a-priori* contrasts.

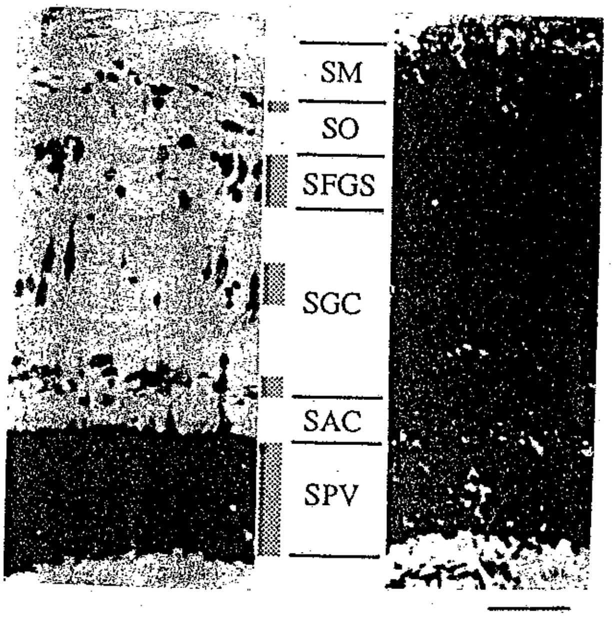


Fig. 2. Laminar structure of the optic tectum in *N. atherinoides*. Nissl-stained frontal section (left) reveals five cell layers, indicated by stippled areas. Nauta silver stain as modified by Vogt (Heimer and Robards, 1981) demonstrates some of the fiber patterns (right). Abbreviations are stratum marginale (SM), stratum opticum (SO), stratum fibrosum et griseum superficiale (SFGS), stratum griseum centrale (SGC), stratum album centrale (SAC), and stratum periventriculare (SPV). Scale bar represents 30 µm.

Sets of interrelated structures were determined based on variation in size. First, a matrix of PEARSON's correlation coefficients (Procedure CORRELATION, SPSSX Inc., 1988) was calculated using the size of the optic tectum, width of all its constituent layers, the torus longitudinalis, torus semicircularis, valvula cerebelli, corpus cerebelli, telencephalon, and eye as variables. Additionally, a principal components analysis (PCA) (Procedure FACTOR, SPSSX Inc., 1988) was performed to identify the main factors subsuming the variation in brain morphology. In this test, variables that are correlated with a certain axis, i.e., have high loadings on this axis, are considered to be interrelated.

Although species were similar in size, as a precaution, all analyses were performed on the residuals from a linear regression on standard length either directly, or by the use of Analyses of Covariance (ANCOVAs). Standard length, rather than body weight, was chosen to represent body size, as it is less influenced by physiological and nutritional factors. Regressions of the variables on standard length proved significant in all cases ($P < 0.001$).

Results

Comparison of the optic tectum

When the thickness of all tectal layers was compared simultaneously among species, an orthogonal set of MANCOVAs (Table 1) indicated that this structure differed significantly between turbid-water and clear-water species ($P < 0.001$), between *C. lutrensis* and the two turbid water species of *Notropis* ($P < 0.001$), and between *N. bairdi* and *N. atherinoides* ($P < 0.001$). No significant differences were detected among the three clear-water species. Results of univariate tests comparing each layer separately in identical orthogonal sets are reported in Table 2. Clear and turbid-water species differed in the thickness of SM, SO and SAC. *C. lutrensis* differed from the two turbid-water species of *Notropis* in the width of the SFGS and SPV. *N. bairdi* and *N. atherinoides* differed in the thickness of all layers, except the SAC. In the comparisons of clear-water species only the SM was different among *C. venusta* and the species of *Notropis*, which differed from each other only in the width of the SFGS. An analysis of the size of the optic tectum in orthogonal ANCOVAs (Table 3) demonstrated that clear-water species were characterized by having larger tecta than turbid-water species ($P < 0.001$). Within turbid water species *C. lutrensis* had larger tecta than did the two species of *Notropis* ($P < 0.001$). None of the remaining comparisons were significant. Means and standard deviations of all examined structures are shown in Table 4.

Table 1. Results of an orthogonal set of MANCOVAS comparing the optic tectum in turbid-water and clear-water species of *Notropis* and *Cyprinella* with standard length as covariate. The thickness of SM, SO, SFGS, SGC, SAC, and SPV were compared between clear-water and turbid-water minnows (I), between the species of *Cyprinella* and the two species of *Notropis* within turbid-water (II) and clear-water species (IV), between the two turbid-water (III) and the two clear-water species (V) of *Notropis*. *Pillais'*, *Hotellings'*, and *Wilks'* criteria yielded in all instances identical F-values and significance (P).

Source	df	Wilks' Lambda	F	P
I	52	0.537	7.484	***
II	22	0.367	6.337	***
III	12	0.192	8.417	***
IV	22	0.706	1.525	ns
V	12	0.511	1.916	ns

ns, non-significant; ***, $P < 0.001$

Table 2. Results of orthogonal *a-priori* sets of univariate tests for the thickness of each tectal layer separately comparing turbid-water and clear-water species of *Notropis* and *Cyprinella* with standard length as covariate. Roman numerals represent the same contrasts as described in Table 1. Abbreviations are stratum marginale (SM), stratum opticum (SO), stratum fibrosum et griseum superficiale (SFGS), stratum griseum centrale (SGC), stratum album centrale (SAC), and stratum periventriculare (SPV).

Source	SM	SO	SFGS	SGC	SAC	SPV
I	***	***	ns	ns	**	ns
II	ns	ns	*	ns	ns	*
III	***	*	***	*	ns	***
IV	*	ns	ns	ns	ns	ns
V	ns	ns	*	ns	ns	ns

ns, non-significant; *, $0.01 \leqq P < 0.05$; **, $0.001 \leqq P < 0.01$; ***, $P < 0.001$

Table 3. Results of an orthogonal *a-priori* set of t-tests comparing the size of the optic tectum in turbid-water and clear-water species of *Notropis* and *Cyprinella* using standard length as a covariate. Roman numerals represent the same contrasts as described in Table 1.

Source	df	t	P
I	52	−5.160	***
II	52	−3.730	***
III	52	0.055	ns
IV	52	1.389	ns
V	52	−1.991	ns

ns, non-significant; ***, $P < 0.001$

Relationships among neural structures

The matrix of Pearson's Correlations Coefficients between a variety of neural structures is given in Table 5. All significant correlations were positive, except the size of the optic tectum and the thickness of the SAC, which proved significantly negative. A variety of positive correlations were detected among structures which are considered functionally related, such as the size of the optic tectum, eye, valvula, torus longitudinalis, and the thickness of the SM, SO and SFGS. The SPV was correlated with virtually every other quantified neural structure except the size of the telencephalon, the corpus cerebellum, and the thickness of the SAC. The telencephalon showed significant correlation only with the size of the corpus cerebelli.

PCA of the regression residuals extracted 12 PC-axes, of which four had an eigenvalue $\geqq 1$ and cumulatively accounted for 67.5% of the total variation among individuals. The loadings of different structures on each PC-axes following varimax rotation are listed in Table 6. Functional relationships among the optic tectum, torus longitudinalis, eye, SM, and SO were suggested by the component loadings on PC1. The optic tectum, the torus longitudinalis, and the valvula cerebelli represent a set of interrelated structures indicated by loading together on PC2 and PC10. A relationship of torus longitudinalis and SM, SO, and SFGS was suggested from PC3.

Discussion

The differences in stratification and size of the optic tectum among clear-water and turbid-water minnows are in accordance with previous studies that report relationships between brain anatomy and ecological

Table 4. Means and standard deviations for structures measured in this study. Abbreviations are length (LEN), eye diameter (ED), optic tectum (OT), corpus cerebelli (CC), telencephalon (TEL), thickness of the optic tectum (TT), stratum marginale (SM), stratum opticum (SO), stratum fibrosum et griseum superficiale (SFGS), stratum griseum centrale (SGC), stratum album centrale (SAC), stratum periventriculare (SPV), torus longitudinalis (TL), torus semicircularis (TS), and valvula cerebelli (VC). Measurements are in mm (LEN, ED), mm^2 (OT, CC, TEL), μm (TT, SM, SO, SFGS, SGC, SAC, SPV), and μm^2 (TL, TS, VC).

Species	LEN	OT	CC	TEL	ED	TT
C. lutrensis	68.1 ± 6.15	5.30 ± 0.63	4.47 ± 0.56	2.28 ± 0.29	3.74 ± 0.33	257.4 ± 20.00
N. bairdi	54.0 ± 4.92	2.85 ± 0.36	3.61 ± 0.44	1.81 ± 0.26	3.08 ± 0.18	195.8 ± 15.20
N. atherinoides	58.1 ± 7.06	3.32 ± 0.64	3.59 ± 0.80	1.64 ± 0.44	3.38 ± 0.34	243.6 ± 25.85
C. venustus	70.1 ± 5.09	5.53 ± 0.97	4.39 ± 0.83	2.35 ± 0.37	4.04 ± 0.32	234.1 ± 20.15
N. amabilis	56.5 ± 2.92	4.61 ± 0.69	3.87 ± 0.56	1.70 ± 0.26	4.26 ± 0.35	244.8 ± 14.39
N. boops	60.2 ± 5.65	4.48 ± 0.72	3.53 ± 0.36	1.83 ± 0.39	4.30 ± 0.53	246.9 ± 14.82

Species	SM	SO	SFGS	SGC	SAC	SPV
C. lutrensis	35.83 ± 8.03	13.21 ± 3.35	60.38 ± 11.5	77.32 ± 12.0	31.36 ± 7.31	38.94 ± 7.52
N. bairdi	26.23 ± 7.75	11.79 ± 3.71	39.27 ± 4.49	58.52 ± 9.98	28.83 ± 6.96	31.10 ± 5.27
N. atherinoides	39.91 ± 7.43	15.23 ± 4.66	50.56 ± 10.3	69.24 ± 13.5	32.35 ± 9.05	37.08 ± 5.64
C. venustus	35.13 ± 9.12	16.44 ± 4.19	50.23 ± 8.94	69.19 ± 12.6	27.95 ± 5.61	36.00 ± 5.62
N. amabilis	45.86 ± 12.1	17.16 ± 3.68	53.36 ± 9.18	66.31 ± 11.6	26.88 ± 4.70	36.89 ± 7.29
N. boops	43.76 ± 7.96	17.06 ± 4.14	49.35 ± 8.81	70.50 ± 11.7	28.89 ± 5.53	38.48 ± 6.24

Species	TL	TS	VC
C. lutrensis	36.197 ± 10.791	37.947 ± 7.969	225.749 ± 56.603
N. bairdi	16.072 ± 3.172	28.701 ± 4.993	132.284 ± 31.936
N. atherinoides	23.615 ± 3.708	33.444 ± 6.273	149.692 ± 20.427
C. venustus	34.170 ± 8.561	33.163 ± 9.280	229.709 ± 46.594
N. amabilis	33.788 ± 3.347	29.743 ± 5.912	186.043 ± 32.772
N. boops	38.996 ± 6.143	31.622 ± 7.347	169.871 ± 42.698

Table 5. Pearson's correlation coefficients for correlations between the optic tectum (OT), torus longitudinalis (TL), torus semicircularis (TS), valvula cerebelli (VC), corpus cerebelli (CC), telencephalon (TEL), eye (ED), stratum marginale (SM), stratum opticum (SO), stratum fibrosum et griseum superficiale (SFGS), stratum griseum centrale (SGC), stratum album centrale (SAC), and stratum periventriculare (SPV) are reported in the lower left triangle. The residuals from a regression on standard length were used instead of the original variables. Levels of significance (ns, non-significant; *, $0.01 \leqq P < 0.05$; **, $0.001 \leqq P < 0.01$; ***, $P < 0.001$) are listed in the upper right.

	OT	TL	TS	VC	CC	TEL	ED	SM	SO	SFGS	SGC	SAC	SPV
OT	—	***	ns	***	ns	ns	***	**	***	**	ns	*	**
TL	0.550	—	ns	***	ns	ns	***	***	***	ns	*	ns	***
TS	0.173	0.051	—	**	*	ns	ns	ns	ns	ns	ns	ns	*
VC	0.502	0.523	0.327	—	ns	ns	ns	ns	ns	ns	ns	ns	*
CC	0.168	−0.105	0.260	0.171	—	**	ns	ns	ns	**	ns	*	ns
TEL	0.578	−0.102	0.173	0.087	0.341	—	ns	ns	ns	ns	ns	ns	ns
ED	0.457	0.584	−0.023	0.150	0.103	0.019	—	***	***	*	ns	ns	*
SM	0.361	0.482	0.013	0.073	0.026	−0.165	0.658	—	***	***	**	ns	***
SO	0.382	0.469	0.034	0.172	0.098	0.000	0.475	0.624	—	***	ns	ns	***
SFGS	0.346	0.210	0.126	0.049	0.302	0.039	0.236	0.492	0.457	—	***	**	***
SGC	0.205	0.236	0.145	0.019	0.132	0.185	0.153	0.375	0.172	0.493	—	**	***
SAC	−0.217	−0.208	0.190	−0.195	0.297	0.097	−0.154	0.079	0.042	0.355	0.281	—	ns
SPV	0.321	0.395	0.266	0.231	−0.003	−0.050	0.235	0.441	0.317	0.401	0.403	0.039	—

Table 6. Matrix of component loadings on PC1 through PC12 and variance explained by each axis. Loadings less than 0.20 have been replaced by zero. Abbreviations are Eigenvalue (EV), % variation explained (V), optic tectum (OT), torus longitudinalis (TL), torus semicircularis (TS), valvula cerebelli (VC), corpus cerebelli (CC), telencephalon (TEL), eye (ED), stratum marginale (SM), stratum opticum (SO), stratum fibrosum et griseum superficiale (SFGS), stratum griseum centrale (SGC), stratum album centrale (SAC), stratum periventriculare (SPV).

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12
OT	0.247	0.284	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.872	0.0	0.0
TL	0.448	0.462	0.239	0.0	0.0	0.0	0.0	0.0	0.0	0.216	0.0	0.596
TS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.964	0.0	0.0	0.0
VC	0.0	0.937	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.204	0.0	0.0
CC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.951	0.0	0.0	0.0	0.0
TEL	0.0	0.0	0.0	0.0	0.0	0.976	0.0	0.0	0.0	0.0	0.0	0.0
ED	0.910	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SM	0.751	0.0	0.386	0.250	0.217	0.0	0.0	0.0	0.0	0.0	0.212	0.216
SO	0.303	0.0	0.907	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SFGS	0.0	0.0	0.216	0.242	0.0	0.0	0.0	0.0	0.0	0.0	0.870	0.0
SGC	0.0	0.0	0.0	0.933	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SAC	0.0	0.0	0.0	0.0	0.0	0.0	0.948	0.0	0.0	0.0	0.0	0.0
SPV	0.0	0.0	0.0	0.0	0.928	0.0	0.0	0.0	0.0	0.0	0.0	0.0
EV	3.977	2.042	1.634	1.116	0.859	0.681	0.579	0.570	0.461	0.371	0.288	0.267
V	30.6%	15.2%	12.6%	8.6%	6.6%	5.2%	4.5%	4.4%	3.5%	2.9%	2.2%	2.1%

parameters (KISHIDA, 1979; KOTRSCHAL and JUNGER, 1988). However, the present study is unique in detecting such a relationship among closely related species.

Unexpectedly, significant differences in the thickness of tectal lamina were also detected among species within turdidity groups. The optic tecta of turbid water species were found to be especially heterogeneous. In clear water, vision is assumed to be superior to all other sensory modalities. However, species inhabiting turbid habitats may rely on a variety of sensory stimuli and the detected differences may represent adoptations to different sensory strategies.

The close relationship between functional and anatomical characteristics was also supported by high correlations in the size of structures known to be functionally related (e.g. all visual structures). These correlations, while not providing conclusive evidence concerning functional relationships, may be used to generate testable hypotheses for physiological experiments.

Tectal layers were generally highly correlated with each other. Moreover, the highest correlations were detected between neighboring layers in the optic tectum. Similarity in thickness among these layers may be related to the way the optic tectum processes information.

The role of the superficial tectal layers in integrating visual stimuli is supported by the high correlation demonstrated between these layers and eye size. Two additional findings support this hypothesis: (1) in the PCA the optic tectum, torus longitudinalis, SM and SO loaded together with eye size, and (2) univariate tests demonstrated that differences between clear and turbid water species were largely due to differences in the thickness of SM, and SO. These findings agree with studies that report a high density of retinofugal terminals in these layers in a variety of cyprinids (NEALE et al., 1972; SHARMA, 1972; REPÉRANT et al., 1976; REPERANT and LEMIRE, 1976; PEYRICHOUX et al., 1977; SCHMIDT, 1979; SPRINGER and GAFFNEY, 1981).

The SAC was correlated with only one visual structure, the optic tectum, where the relationship was significantly negative. This finding was unexpected, as this layer has previously been reported to receive a low density of retinal terminals (LANDRETH et al., 1975). However, the development of this layer may vary in accordance with the development of the olfactory apparatus. KISHIDA (1979) reported a particularly large SAC in eels (Anguilliformes), which rely strongly on olfactory stimuli (UCHIHASHI, 1953; TUGE et al., 1968). Moreover, telencephalic neurons projecting to the SAC are located in the central zone of the area dorsalis (ITO and KISHIDA, 1977), an area which is known to receive prominent olfactory projections in sunfish and trout (Northcutt and Davis, 1984). Therefore, it is hypothesized that the negative correlation reflects an increase of the importance of olfaction in species with poor eye sight.

The SGC is correlated with the SAC and receives similar telencephalic input. The SGC is also correlated with the superficial 'visual' layers, suggesting a possibile function in olfacto-visual integration.

The high correlation of the SPV with visual structures as well as with the torus semicircularis may indicate a role in the integration of visual and acoustico-lateral stimuli. Shepherd (1974) postulated an internuncial function for this layer. Positive correlations between visual structures and the SPV contradict the findings of Kishida (1979), who reported a large SPV in species with a poorly developed tectum.

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