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Neuroecology of cyprinids: comparative, quantitative histology reveals diverse brain patterns

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Synopsis

Brain patterns are compared by quantitative histology in 28 native and introduced mid-European cyprinid species, considering 17 primary sensory and higher order brain areas. Cluster analysis (CLA) and principal component analysis (PCA) based on relative volumes of these brain areas indicate that cyprinid brains are diversified into four major groups, basic cyprinid, abramine, octavo-lateralis and chemosensory. PCA recognizes the brain of *Phoxinus phoxinus* as a fifth group. Interspecific differences in brain morphology are mainly caused by variability in relative sizes of the brain stem lobes for external and internal taste (lobus facialis and lobus vagus), as well as of octavo-lateralis and visual areas. Higher order brain areas show little interspecific variation in relative size, and were grouped by PCA according to inter- and intraspecific allometries. Hypotheses on brain functions are based on brain area correlations. We propose that the processing of external taste information in the valvula cerebelli may be particularly important for benthivorous cyprinids, whereas the integration of octavo-lateralis input with visual information via the torus longitudinalis – stratum marginale system may play a key role in the planktivores. Brain patterns suggest two major pathways of cyprinid evolutionary and ecological radiation, one leading from the basic cyprinids towards octavo-lateralis dominated midwater and surface planktivores, the second towards taste-dominated benthivores.

Introduction

Quantitative, comparative brain morphology in specious and closely related vertebrate groups reveals within-group trends of sensory diversification, which can be interpreted ecologically as well as evolutionarily (Bullock 1983, Goldschmid & Kotrschal 1989, Northcutt 1988). With these and related goals, quantitative brain morphology has been applied in ecologically diversified taxa, such as birds, bats and other mammals (Stephan 1967, Stephan & Pirlot 1970, Jolicoeur & Baron 1980, Pirlot & Jolicoeur 1982, Pagel & Harvey 1989).

Teleost fish form the largest of all vertebrate groups and frequently have been the subject of comparative, qualitative brain (eco)morphology (Balon 1968, Davis & Miller 1967, Evans 1931, 1932, 1940, 1952, Khanna & Singh 1966, Kirka 1963a, Kishida 1979, Mayser 1881, Miller & Evans 1965, Northcutt & Wullimann 1988, Schnitzlein 1964, Uchihashi 1953, for comprehensive treatments see Ariens Kappers et al. 1936, Davis &

Northcutt 1983, Northcutt & Davis 1983). However, only few investigations were quantitative (Brandstätter & Kotrschal 1990, Bauchot et al. 1977, 1989, Geiger 1956a, b, Kirka 1963b, Kotrschal & Junger 1988, Kotrschal et al. 1991, Ridet et al. 1977, Snow & Rylander 1982). Only recently, multivariate statistics (Huber & Rylander 1992) has been used to extract information from brain data, allowing for a rigid classification and interpretation.

In the present paper we consider 28 species of common mid-European cyprinids. Included are also a few species introduced from eastern Asia, such as silver carp, grass carp and goldfish. Recently (Kotrschal & Junger 1988), brains in 14 of these species have been examined histologically.

Although cyprinids are the most successful freshwater teleost family in the northern hemisphere (Nelson 1984), comparatively little is known on their biology and evolutionary radiation. Therefore we address the following questions:

(1) What is the morphological radiation of cyprinid brains and which brain areas contribute most to interspecific brain variability?

(2) Does a correlation matrix of brain areas lead to novel ideas concerning brain function and brain area interactions?

(3) Can brain morphology be ecologically interpreted?

(4) Can evolutionary trends be recognized?

Table 1. List of species in alphabetical order, common names according to Maitland (1981), n = number of brains measured, SL = range of standard length, origin, basic habitat requirements (i = indifferent towards currents, r = rheophilic) and feeding styles given. The asterisk (*) indicates that specimens originated from the Stopfenreuther Au, a Danube backwater area, Wall. = Wallersee.

Species	Common name	n	SL, cm	Origin	Habitat/feeder type or food
1 *Abramis ballerus*	blue bream	2	19, 20	*	i, midwater/plankton
2 *A. brama*	common bream	7	13–37	*, Wall.	i, benthos/microzoobenthos + plankton
3. *A. sapa*	whiteye bream	2	17, 17	*	i-r, benthos/benthic + plankton
4 *Alburnoides bipunctatus*	schneider	2	9–9.5	Danube tributary	i-r, midwater/omnivorous
5 *Alburnus alburnus*	bleak	2	11.5–13	*	i, surface/surface + omnivorous
6 *Aspius aspius*	asp	2	22.5–23	*	i-r, midwater/piscivorous
7 *Barbus barbus*	barbel	1	32	*	r, benthic/macrozoobenthos
8 *Blicca bjoercna*	white bream	2	14–17.5	*	i, benthic-midwater/macrozoobenthos
9 *Carassius auratus*	goldfish	3	11–13	local pond	i, benthic/benthos-omnivorous
10 *C. carassius*	crucian carp	2	9.5–11	pond-raised	i, benthic/benthos-omnivorous
11 *Chalcalburnus chalcoides*	shemaya	2	16.5–18	Mondsee	i, pelagic, surface/planktivorous
12 *Chondrostoma nasus*	nase	3	22–41	*	r-i, benthic/benthic grazer
13 *Ctenopharyngodon idella*	grass carp	2	13.5–14	fish farm	i, midwater/macrophytes
14 *Cyprinus carpio*	common carp	3	13–24	fish farm	i, benthic/benthic omnivorous
15 *Gobio gobio*	gudgeon	2	11–12	Mur tributary	r-i, benthic/macrozoobenthos
16 *Hypophthalmichthys molllitrix*	silver carp	1	19	fish farm	i, midwater/phyto-zooplankton
17 *Leucaspius delineatus*	sun bleak	2	5–6	pond-raised	i, midwater/zoophageous
18 *Leuciscus cephalus*	chub	2	16–19	*	i-r, midwater/omnivorous
19 *L. idus*	orfe	3	8–33	*, pond-raised	i, benthic-midwater/omnivorous
20 *L. leuciscus*	dace	2	10–11	Danube tributary	i-r, midwater/omnivore-planktivorous
21 *L. souffia*	streamer	2	12, 12	Mur	r, midwater/omnivorous-drift feeder
22 *Pelecus cultratus*	sabre carp	7	17–35	*, Neusiedlersee	i-r, surface/surface + plankton
23 *Phoxinus phoxinus*	minnow	2	6–9	local creek	r-i, benthic-midwater/zoophageous
24 *Rutilus rutilus*	roach	6	10–24	*, Wallersee	i, midwater/omnivorous
25 *Rhodeus sericeus*	bitterling	2	6, 6	pond-raised	i, benthic/zoophageous
26 *Scardinius erythrophthalmus*	rudd	2	14–20	*	i, midwater/omnivorous
27 *Tinca tinca*	tench	2	17–18	fish farm	i, benthic/benthos-omnivorous
28 *Vimba vimba*	vimba	2	14,14	*	i-r, benthic/macrozoobenthos

Materials and methods

Most fish were gill-netted in the Stopfenreuther Au, a Danube-wetland area in the east of Austria. Additional specimens were obtained by electrofishing in Upper Austrian, Styrian and Salzburg creeks and rivers, or were purchased at a local hatcheries and pet shops (Table 1).

Quantitative histology

Specimens were deeply anaesthetized with MS 222 (1 : 10 000) and fixed by perfusion with 10% buffered formaldehyde solution. Brains were removed from the skull, postfixed for several weeks in the same fixative, embedded in gelatine, incubated overnight in 30% sucrose and cryostat-sectioned at 30 or 40 μm, depending on brain size. Cryostat sections were preferred over paraffin in this quantitative study, because of the possibility of heterogenous shrinkage of brain areas during the paraffin embedding procedure. Alternate sections were mounted in series with gelatine-chromalaun, allowed to dry slowly in a moist environment and stained with cresyl-violet.

For purposes of comparative, qualitative histology, brains of selected species were embedded in paraffin and serial sections were stained with the Bodian silver method.

A total of 82 cryo-sectioned brains from 28 cyprinid species were measured, but only 72 cases were considered in the present study. The remaining, juvenile specimens were excluded to avoid intro-

Table 2. List of measured brain areas and their interspecific mean in % of total brain volume, ranked according to decreasing interspecific coefficients of variation (VR). Major source of input given (cf. McCormick & Braford 1988, Northcutt & Davis 1983, Davis & Northcutt 1983). Crosses code for demarcability, x = closed structure, unambiguously demarcable; xx = some boundaries by definition; xxx = major boundaries by definition, a verbal description of defined boundaries is given. Primary sensory areas coded with 1, higher order and/or multimodal centers with 2. The number of cases was 72 in most variables, except for the stratum marginale (n = 59) and the torus semicircularis (n = 71).

Code	Sensory area	Mean brain vol · % ± sd	VR	Input from	Demarcability, borders
1	lobus facialis	1.34 ± 1.48	110.4%	external taste	x
2	nucleus habenularis	0.11 ± 0.09	81.8%	olfactory/multimodal	x
1	lobus vagus	4.71 ± 3.69	78.3%	internal taste/visceral	x including the motor-layer
1	central acoustic area	0.83 ± 0.65	78.3%	?	x
1	crista cerebellaris	2.18 ± 1.06	48.6%	lateral line/cerebellum	x
1	eminentia granularis	1.88 ± 0.8	42.6%	inner ear/lateral line	x
2	valvula cerebelli	6.59 ± 2.44	37.0%	multimodal	xx: underneath tectum opticum
2	stratum marginale	3.08 ± 1.12	36.4%	t. longitudinalis	x
1	bulbus olfactorius	2.47 ± 0.78	31.6%	olfactory mucosa	x
2	mesencephalic tegmentum	7.47 ± 1.4	31.3%	multimodal	xxx: caudoventral of fasciculus retroflexus to nucleus entopeduncularis
2	torus semicircularis	1.35 ± 0.34	25.2%	octavo-lateralis relays	x
2	corpus cerebelli	13.51 ± 3.16	23.6%	multimodal	xx: cerebellar part free from tectal cover
1/2	tectum opticum	17.22 ± 3.92	22.8%	retina/multimodal	x
2	telencephalon	8.45 ± 1.77	21.0%	multimodal	xx: including commissura anterior, excluding recessus praeopticus and pedunculus cerebri
2	diencephalon	0.96 ± 2.18	19.9%	multimodal	xxx: including recessus praeopticus and nucleus habenularis to rostrodorsal fasciculus retroflexus
2	brain stem caudal to mesencephalic brain stem	22.09 ± 3.53	16.0%	multimodal	xxx: obtained by subtraction of sum-volume of all areas measured from total brain volume

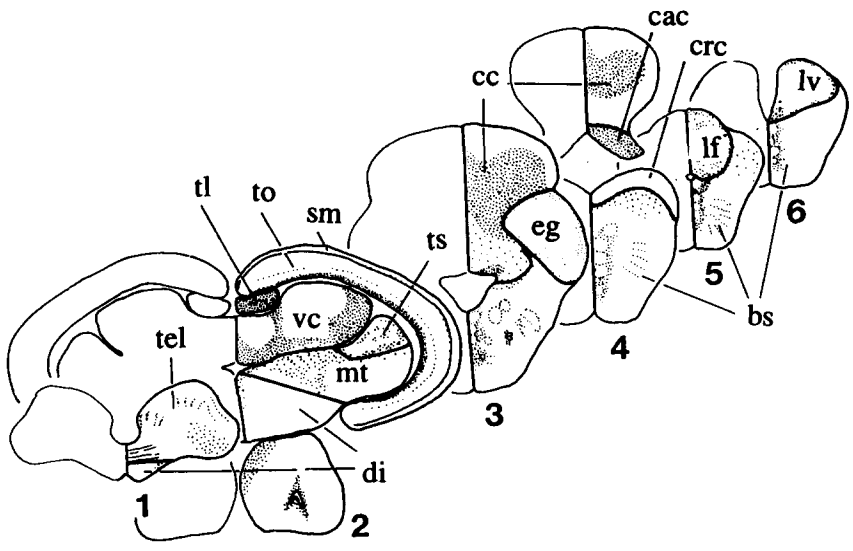

Fig. 1. Demarcation of measured areas exemplified with 6 cross sections through roach brain. 1 = telencephalon at the level of the commissura anterior; 2 = at maximal extension of the tectum opticum; 3 = at maximal cross section areas of the corpus cerebelli and the eminentia granularis; 4 = at the crista cerebellaris; 5 = through the lobus facialis; 6 = through the lobus vagus. Modified after Brandstätter & Kotrschal (1990). Abbreviations: bs = brain stem; cac = central acoustic area (see Materials and methods for comments); cc = corpus cerebelli; crc = crista cerebellaris; di = diencephalon; eg = eminentia granularis; lf = lobus facialis; lv = lobus vagus; mt = mesencephalic tegmentum; sm = stratum marginale; tel = telencephalon; tl = torus longitudinalis; to = tectum opticum; ts = torus semicircularis; vc = valvula cerebelli. Bulbus olfactorius and nucleus habenularis not within section planes 1–6 and therefore not shown.

ducing a major allometric bias (Brandstätter & Kotrschal 1990).

Seventeen areas per brain were measured (Table 2), representing approximately 78% of the total brain volume (of the entire brain from the olfactory bulbs to the caudal end of the lobus vagus). For demarcation of brain areas see Figure 1. Brain areas to be measured were selected according to functional importance and demarcability. The remaining 22% of brain volume consisted mainly of the myelencephalic brain stem, which was not directly measured, but back-calculated by subtracting the sum of all measured brain area volumes from total brain volume (Table 2). Therefore the myelencephalic brain stem was excluded from the multivariate statistical analysis.

By aid of a camera lucida connected to a binocular microscope, cryostat sections were projected to a digitizing tablet and data were fed directly into a computer. Brain areas were measured on 90 (± 15) sections per brain, left and right separately, which resulted in an average of approximately 30 measured planes per brain area. Thus the present study integrates approximately 40000 individual measurements.

In most brain areas considered the number of planes measured exceeded eight. Area volumes were estimated by multiplication of the mean area of the brain structure measured times its length (left and right separately). As no significant (exceeding the measurement error, see below) and consistent lateralization of brain areas could be found, the sums of equivalent bilateral volumes were used for further comparison.

To make volumes of brain areas comparable despite differences in body size between species, area volumes are expressed as % of total brain volume. Although this creates the problem that % volumes are not independent from each other, we feel that this approach is still more valid than standardizing brain volumes with body length or weight, because the cyprinids considered are relatively heterogenous with respect to body shape (Fig. 2) (cf. Stephan 1960).

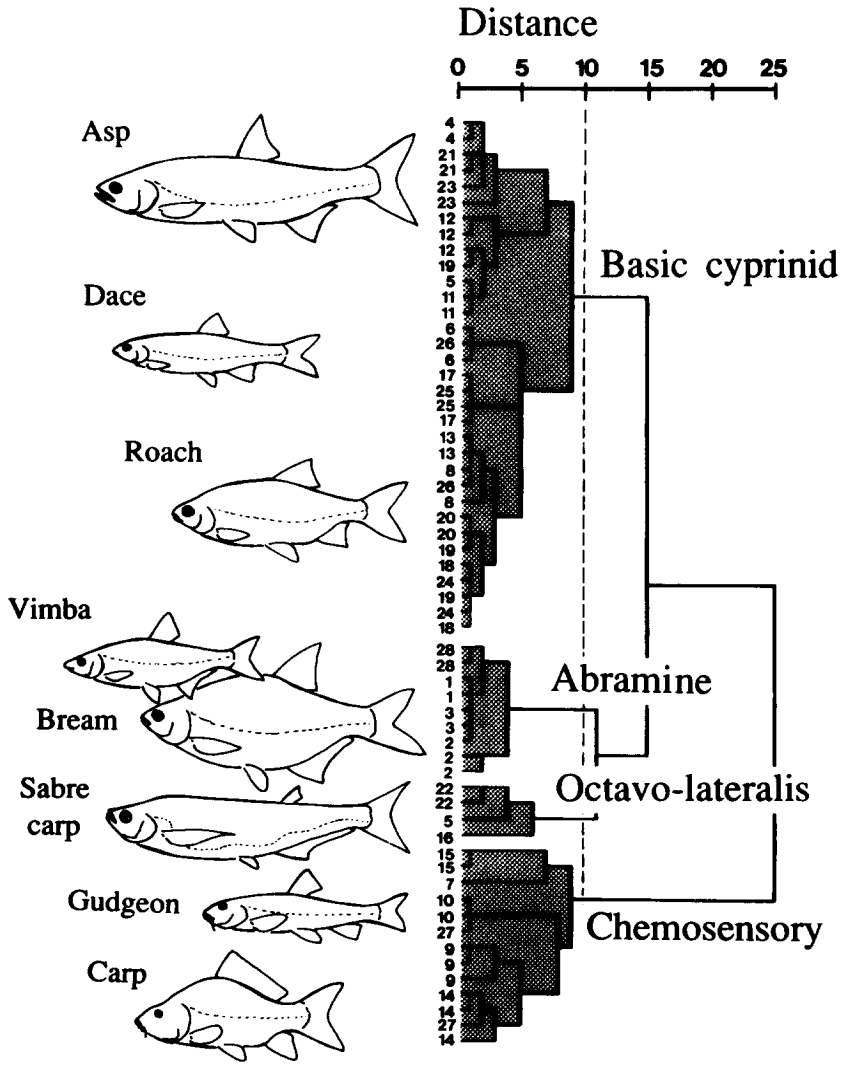

Fig. 2. Dendrogram obtained by cluster analysis (Euclidian distances, Ward's sorting, based on primary sensory brain areas, Table 2) reveals 4 major groups of brain morphologies. Habitus of representative species shown. Numbers at tips of the branches code for species (Table 1).

The measurement error was quantified by tracing 4 differently sized brain structures 5 times successively. The error with respect to area of the structures averaged 4%, the maximal error was 9% in the smallest structure considered, the nucleus habenularis.

Topographic positions of brain areas are given in Kotrschal & Junger (1988) as well as in Figure 1 and Table 2. For information on structure, connectivity and functions of brain areas see Davis & Northcutt (1983), Northcutt & Davis (1983) and Northcutt & Wullimann (1988).

The authors are aware of possible oversimplifications when associating brain areas with sensory functions. The tectum opticum for example, although the primary brain area for most of the visual input, is a multimodal center. The term 'central acoustic area' (Evans 1931, based on the co-occurrence of well developed auxilliary auditory structures with a well developed CAC) lacks experimental confirmation. As this area, including the

present study, shows strong correlations with other octavo-lateralis areas, the term central acoustic area is tentatively used as a working hypothesis, although no primary octavo-lateralis terminals were found there (McCormick & Braford 1988).

Multivariate statistics

Data were analyzed by multivariate statistics, cluster analysis (CLA) and principal component analysis (PCA), employing SPSSx (Brosius 1989) and CLUSTAN-software. Each individual brain was treated as a single case. The relative volumetric data matrix (% of areas of total brain volumes) was arc-sine transformed prior to analysis (Sokal & Rohlf 1981) to correct for compressed variances at either ends of the %-scale. Only basic statistical procedures (Table 2) were performed on the original %-matrix.

CLA is an ordination technique which is based on finding similarities or dissimilarities between cases. Squared Euclidian distances in combination with Ward's sorting were employed to generate a dendrogram (Fig. 2). Only the primary sensory brain areas and those showing strong correlations with the latter were used (see PCA for reason, Tables 2, 4), although the classification was found to be relatively robust even when applied with the entire set of variables (not shown).

PCA is a standard ordination and data reduction method, different from CLA. PCA finds a small number of new variables (principal components [PCs], or factors), based on the correlations between original variables. Factor loadings (0–1, Table 4) describe the contribution of the original variables to the newly found PCs. The number of significant PCs (those which explain a high % of the total variance in the data set) was determined by the scree-test (plotting the Eigenvalues in decreasing order). This revealed only 2 PCs in the primary sensory area subset and 3 PCs in the higher order brain area subset (see below, Table 4). The cases factor scores were calculated with the Bartlett-method (for Fig. 3, 4). A reasonable coherence of variables within a data set is a prerequisite for PCA. Communality was estimated by the Kaiser-Meyer-Olkin (KMO) measure for sample adequacy (Brosius 1989, Kaiser 1974). Generally, the KMO was higher in the primary sensory areas as compared to the higher order brain areas. KMO was low (< 0.7) when applied to the entire set of variables. When variables were divided into two groups, primary sensory and higher order, the KMO was within suitable ranges for both data subsets (0.75, 0.72). The tectum opticum is both a primary sensory and higher order brain structure, showing reasonable communalities with both subsets and was therefore included in both. The stratum marginale and the valvula cerebelli were included in the primary sensory subset, because of their strong correlations and high communalities with the latter (Table 3). The correlation matrix was produced with the undivided set of variables.

Results

Brain area variability

The highest interspecific variation (VR) of all brain areas is shown by primary sensory areas, particularly the brain stem taste lobes (Table 2). The nucleus habenularis is also highly variable in size, although part of this variability may be due to a relatively high measurement error in this small structure (see Materials and methods). The octavo-lateralis associated brain areas are next in variability. Still relatively high in interspecific variability are certain higher-order multimodal areas, such as the valvula cerebelli, the stratum marginale of the optic tectum and the torus longitudinalis, all of which show strong correlations with primary sensory areas (Table 3). Two primary sensory areas are relatively low in interspecific variability, the bulbus olfactorius and the tectum opticum. All basal brain areas, such as the myelencephalic, rhombencephalic and mesencephalic tegmentum as well as the diencephalon and telencephalon are at the lower range of interspecific variability.

Brain area correlations

Table 3 presents a matrix of all significant correlations found among the present variables (= brain areas, Table 2), which serves as a base for PCA and functional hypotheses.

External and internal taste lobes are positively correlated (Table 3), as are the octavo-lateralis areas as well as the visual areas among themselves. A highly significant negative correlation exists between the lobus facialis (external taste) and all octavo-lateralis areas, but not between the lobus vagus (internal taste) and the octavo-lateralis areas. There are also highly significant negative correlations between taste and visual areas. Although there is no correlation between the tectum opticum as a whole and octavo-lateralis areas, the stratum marginale of the tectum is significantly correlated with all three, as is the torus longitudinalis, the source of origin of unmyelinated parallel stratum marginale fibers (Vanegas 1983).

There is a highly significant positive correlation of the valvula cerebelli with the lobus facialis. Negative correlations exist between the valvula and one octavo-lateralis area, as well as between valvula and visual areas (Table 3). There is no correlation between the torus semicircularis and octavo-lateralis areas, but the correlation between the torus and the tectum opticum is highly significant.

Aside from being significantly correlated with all octavo-lateralis areas and the stratum marginale, the torus longitudinalis correlates negatively with the lobus facialis.

Positive correlations of the corpus cerebelli were found with two octavo-lateralis areas (Table 3), as well as with the valvula cerebelli and with the torus longitudinalis.

The bulbus olfactorius shows no correlation with any other primary sensory area. The telencephalon is positively correlated with the bulbus olfactorius only, negatively with the valvula cerebelli (Table 3).

Correlations of the bulbus olfactorius, the telencephalon, the diencephalon and mesencephalon (Table 3) seem to a lesser degree be determined by sensory interactions than by intra- and interspecific allometries (see below, Fig. 3).

Cluster analysis

Cluster analysis (CLA) found four major groups of brain morphologies (Fig. 2). Most species show a basic cyprinid brain, which is characterized by fairly well developed visual centers, but only moderately sized octavo-lateralis and brain stem chemo-

Table 3. Matrix of significant, positive and negative correlations between brain areas, based on relative volumes of all specimens considered. *: ≥ 0.01; **: ≥ 0.001; ns = not significant. All except for correlations with the myelencephalic brain stem listed. Brain areas associated with 5 functional groups, taste, octavo-lateralis, vision, multimodal areas with strong correlations to sensory areas, and multimodal. For abbreviations see Figure 1.

taste	lf	−	lv													
	lv	+**	−	eg												
	eg	−**	ns	−	cac											
oct.-l.	cac	−**	ns	+**	−	crc										
	crc	−**	ns	+**	+**	−	to									
vision	to	−**	−**	ns	ns	ns	−	sm								
	sm	−**	n.s.	+*	+*	+**	+**	−	vc							
sens.-	vc	+**	ns	−*	ns	ns	−**	−*	−	ts						
multimod.	ts	ns	ns	ns	ns	ns	+**	ns	ns	−	tl					
	tl	−**	ns	+**	+**	+**	ns	+**	ns	ns	−	cc				
	cc	ns	ns	ns	+*	+**	−*	ns	+*	ns	+**	−	bo			
multimodal	bo	ns	ns	ns	ns	ns	ns	ns	ns	−*	ns	ns	−	tel		
	tel	ns	ns	ns	ns	ns	ns	ns	−*	ns	ns	ns	+*	−	di	
	di	ns	ns	−*	−*	−**	+*	ns	−**	ns	−*	−**	ns	+*	−	mt
	mt	−*	−**	ns	ns	ns	+**	ns	−**	+*	ns	−**	ns	ns	+*	−

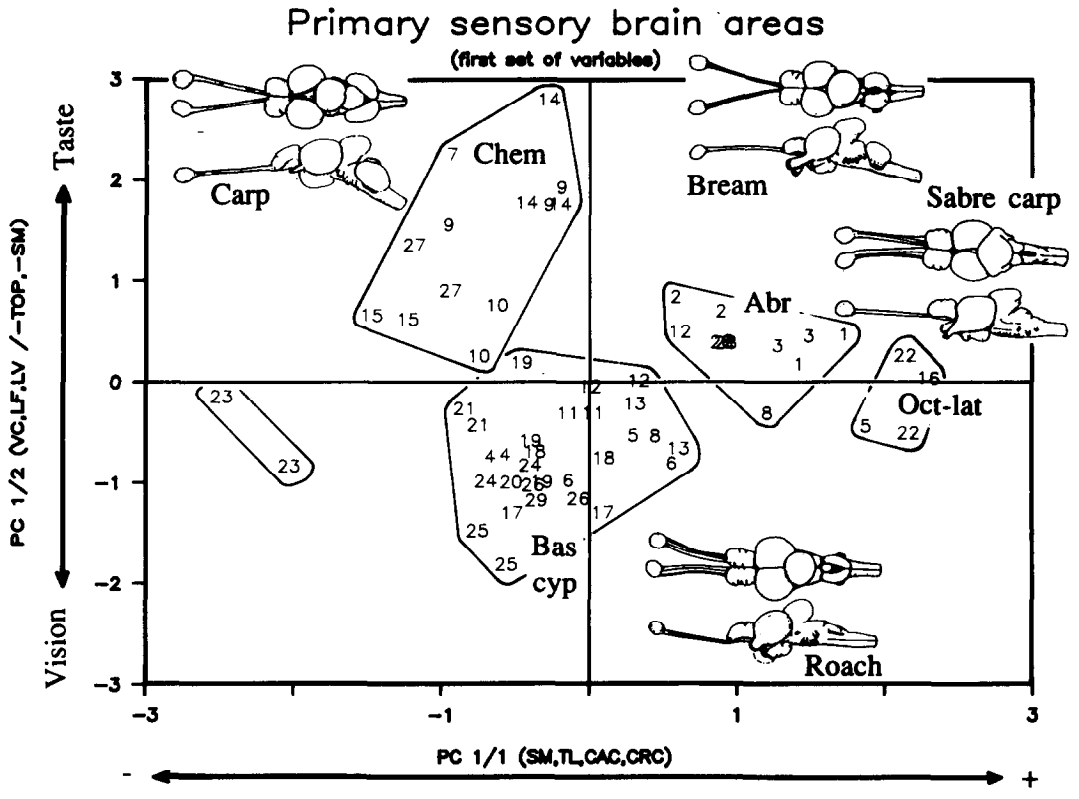

Fig. 3. Principal component (PC) plot of PC scores of individual brains, based on primary sensory brain areas (Table 2). Numbers code for species (Table 1). PC1/1 represents an octavo-lateralis and torus longitudinalis-stratum marginale axis. PC1/2 represents a visual (−) versus brain stem taste (+) axis. For factor loadings see Table 4a. Groups, basic cyprinid (Bas cyp), abramine (Abr), octavo-lateralis (Oct-lat), chemosensory (Chem) and *Phoxinus phoxinus* (23) surrounded by polygons. External morphologies of representative brains shown in dorsal and lateral view.

centers (e.g. roach brain; for representative examples of external brain morphologies from the different groups see Fig. 3). Although appropriate from a purely morphological viewpoint, the potentially misleading term 'generalized' was avoided for this brain group, as it contains also ecologically specialized species, such as the piscivorous *Aspius aspius*.

Relatively close to the basic cyprinid brains are the abramine brains, including *Vimba vimba* and *Blicca bjoerkna* being intermediate between the basic cyprinid and abramine brains. These breams are characterized by a relatively distinct development of brain areas representing all three major sensory faculties, vision, octavo-lateralis and brain stem chemosense (e.g. bream, Fig. 3).

The octavo-lateralis brains of sabre carp, silver carp and bleak show relatively large octavo-lateralis and visual centers, but only very small brain stem chemosensory lobes (e.g. sabre carp, Fig. 3).

The chemosensory brains were most distantly placed by CLA from the basic cyprinid brains. The latter contain mainly benthivorous, often barbed murky water species, such as the barbel, common carp, crucian carp, tench and gudgeon (Fig. 2). Chemosensory brains are characterized by large brain stem taste lobes and a large valvula cerebelli, but small octavo-lateralis and visual centers (e.g. common carp, Fig. 3).

Within the dendrogram the majority of individuals within species are grouped together. Interspecific brain variation is greater than intraspecific variation and brain patterns are indeed species-specific.

Principal component analysis

Principal component analysis (PCA) with the primary sensory subset of variables (see Materials and methods) confirms the robustness of the classification found by CLA (Fig. 2). Two significant principal components (PCs) were extracted. As indicated by factor loadings, PC1/1 is an octavo-lateralis axis, whereas PC1/2 is a taste-visual axis (Table 4a). By plotting the cases factor scores, the groups found by PCA are essentially the same as those found by CLA (Fig. 2, 3).

Due to its outlier position, *Phoxinus phoxinus* has to be recognized as a fifth group. *P. phoxinus* brains are characterized by a relatively large tectum opticum, a small vagal, but well developed facial lobe and small octavo-lateralis centers. A large tectum opticum, but only moderate brain stem taste lobes are shared by all small-sized species present, thus body size influences the PC1/2 axis (Fig. 5). On the other hand, small sized species are distributed over the entire range of PC1/1.

Distributions of two tribes, the leuciscines and the abramines, are restricted to small areas of the PC1/1-PC1/2 morphospace (Fig. 3).

No particular grouping was found by PCA within the second subset of variables, representing mainly the multimodal brain areas (Fig. 4, Tables 2, 4b). In this subset, PCA extracted 3 significant PCs. PC2/1 represents an axis of tegmentum versus cerebellum. PC2/2 may be interpreted as an olfactory axis (Table 4b, Fig. 4) and PC2/3 only loads with the negatively allometric nucleus habenularis.

Within the PC2/1-PC2/2 morphospace cases are separated according to size. Thus, the vertical position of species polygons (Fig. 4) indicates that PC2/2 is an axis determined by intraspecific allometry, with small individuals at the + range of PC2/2. Also, it seemed that PC2/1 represents a grade from large (negative range of PC2/1) to small (positive range of PC2/2) species. To test this hypothesis, the PC scores of all four PCs (1/1-2/2) were plotted versus standard body length (SL, from tip of the snout to tail fin base). Only the plot of PC1/2 versus SL (Fig. 5) resulted in a significant negative correlation, which confirmed that PC2/1 is indeed mainly determined by interspecific allometry. Large fish (within and between species) have a relatively large cerebellum, but small tectum opticum and vice versa in small fish (Fig. 4, Table 4b, Brandstätter & Kotrschal 1990).

Table 4. Factor loadings of principal components (PC) for the 2 subsets of data: (a) primary sensory including stratum marginale, torus longitudinalis and valvula cerebelli, (b) higher order, multimodal areas including the bulbus olfactorius and the tectum opticum. Areas ranked according to decreasing coefficients of variation. Only loadings > 0.5 shown.

(a)	PC1/1	PC1/2	
lobus facialis		+0.72	
lobus vagus		+0.79	
central acoustic area	+0.80		
crista cerebellaris	+0.92		
eminentia granularis	+0.55		
valvula cerebelli		+0.76	
stratum marginale	+0.65	−0.56	
torus longitudinalis	+0.78		
tectum opticum		−0.92	
(b)	PC2/1	PC2/2	PC2/3
nucleus habenularis			+0.94
bulbus olfactorius		+0.70	
mesencephalic tegmentum			+0.80
torus semicircularis	+0.52		
corpus cerebelli	−0.73		
tectum opticum	+0.75		
telencephalon		+0.79	
diencephalon	+0.65	+0.51	

Discussion

Most studies on functional brain morphology focus on fiber connections and input-output characteristics of areas (Northcutt & Davis 1983, Davis & Northcutt 1983), but offer little explanation of the patterns of morphological variation and their biological basis. In the following we attempt to scratch the surface of these issues.

Two assumptions have to be met to be able to draw meaningful conclusions from a quantitative interspecific comparison of brain areas, when relative size is the only parameter considered:

1. The species in question need to be sufficiently

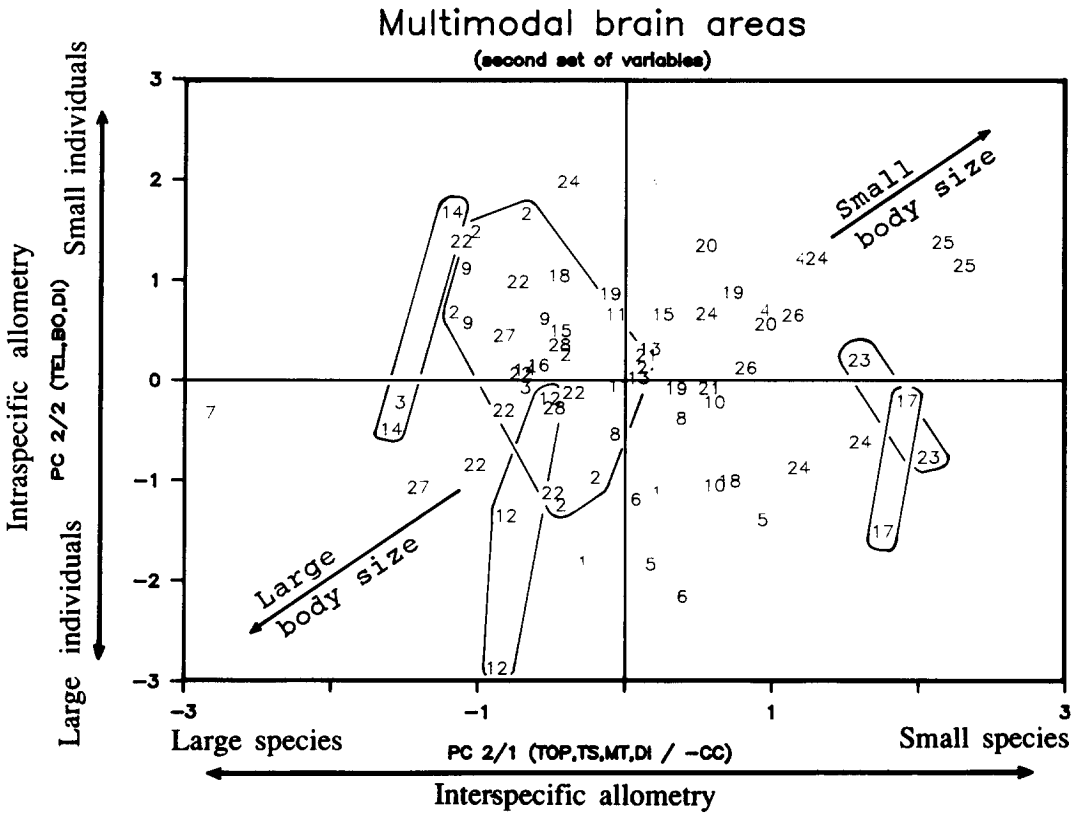

Fig. 4. Plot of PC scores of individuals based on multimodal brain areas (Table 2). Numbers code for species (Table 1). PC2/1 represents an axis of corpus cerebelli (−) versus mesencephalic and diencephalic areas (+). PC2/2 represents an olfactory-telencephalic-diencephalic axis. Examples of vertical orientation of species groups highlighted by polygons. Body size distribution indicates that PC2/1 sorts specimens according to interspecific allometry (cf. Fig. 4), PC2/2 separates according to intraspecific allometry.

closely related to ensure a high probability that the compared brain areas fulfill comparable functional roles (Goldschmid & Kotrschal 1989, Northcutt 1988). If this is the case, then relative sizes of major sensory brain lobes may indicate the 'relative importance of sensory faculties within and between species'. Clearly, questions as to whether this means different spatio-temporal fidelity, sensitivity or differences in filter properties (e.g. degree of color vision, Blaxter 1988, Lythgoe 1988), demand a closer look at the sensory systems in question (Gomahr et al. 1992, Junger & Kotrschal 1989, Kotrschal et al. 1991, Zaunreiter et al. 1991) and cannot be addressed by quantitative brain morphology.

2. As a further prerequisite, contributions of brain-internal allometries to inter- and intraspecific brain variability should be minor and detectable, if the goal of the investigation is to identify those brain areas which account for the sensory interspecific variation. This is evidently important in vertebrates with non-terminal growth such as fish (Geiger 1956a, Brandstätter & Kotrschal 1989). In an ontogenetic study on four major cyprinid brain morphologies (Kotrschal & Junger 1988), Brandstätter & Kotrschal (1990) found substantial brain-internal allometries, which decreased in dynamics with growth. For this reason, only adults or large juveniles were considered in the present study. Still, size effects remained and were recognized by principal component analysis (see below).

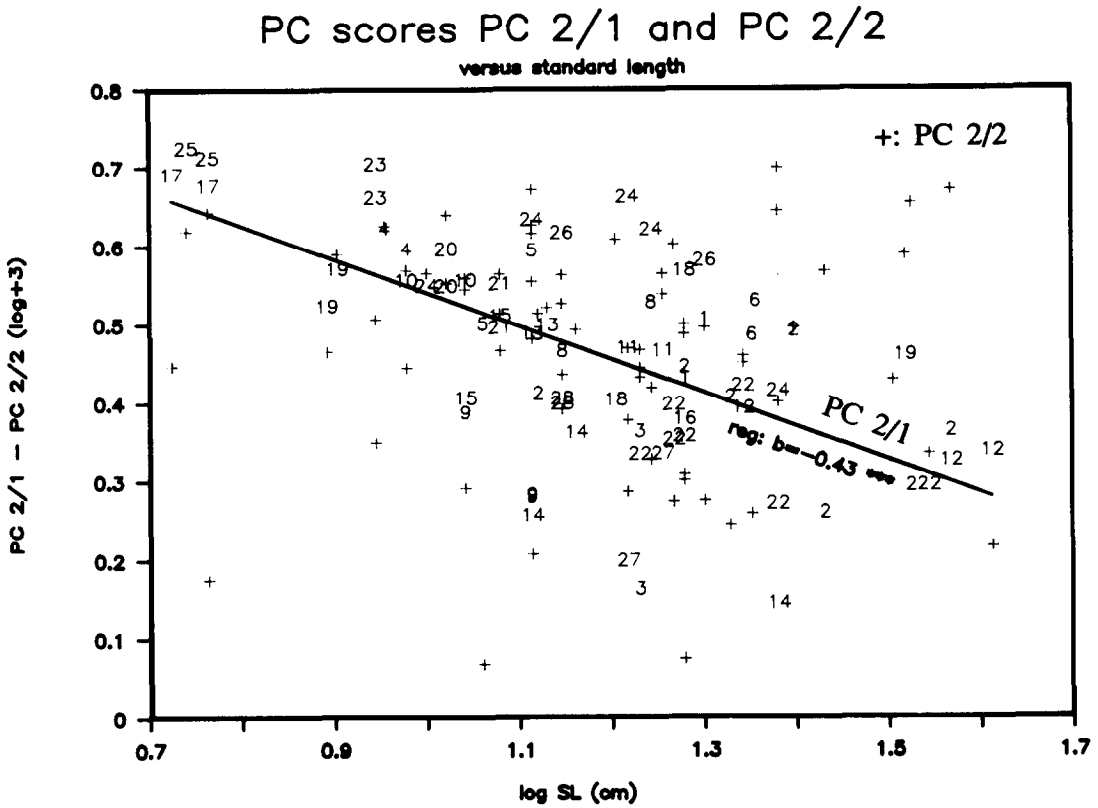

Fig. 5. Regression (log/log scale) of the PC scores PC2/1 (data points coded by species numbers, Table 1) and PC2/2 (crosses) versus standard body length (SL) of individuals. Only the regression of PC2/1 with SL is significant ($\alpha < 0.001$, $b = -0.43$).

Brain area correlations as a source for functional hypotheses

Correlations between brain areas may or may not indicate causal relationships and if they do, it is appropriate to invoke a nested set of explanations from different causal levels, allometric, evolutionary-adaptive and functional (the lack of correlations, however, does not indicate the lack of functional relationships).

One category of correlations is caused by allometries and thus growth, rather than by functional interactions between brain areas. This is the case with the negative correlation between the tectum opticum and the cerebellum and between other multimodal areas.

The evolutionary-adaptive history of cyprinids may generate the 'construction rules' for their brains as discussed below, whereas functional interactions between brain areas are defined by the nature of present information exchange. Secondary and higher order brain areas may or may not covary with primary sensory areas from which they receive information.To preserve and process spatio-temporal information at higher system levels, synaptic connectivity has to be elaborated, causing higher order centers of a labelled pathway to covary in size with their primary centers, as is the case between brain stem taste lobes and the secondary gustatory nucleus (Finger 1988).

Sensory information may diverge widely within the brain, or travel along modality-specific pathways through a series of brain areas, as is the case with lemniscal pathways for taste (Finger 1983a, 1987, 1988, Herrick 1905, Morita & Masai 1980) and octavo-lateralis (Echteler 1985, McCormick & Braford 1988). Input, processing and output may even be mainly localized within a single brain lobe, as is the case with the vagal oropharyngeal reflex pathways (Morita & Finger 1985a, b, 1987). Strik-

ing differences in relative sizes and structural organization of the cyprinid vagal lobes (Kotrschal & Junger 1988, Mayser 1881) may therefore, indicate interspecific differences in oropharyngeal sorting capabilities (Sibbing 1988).

Multimodal convergence onto higher order areas may make it difficult to define their major tasks merely on the basis of their fiber connections, as obtained in tracing experiments. One of the strengths of comparative quantitative morphology is to generate functional hypotheses based on covariation of brain areas, even if fiber connections between the areas involved are still insufficiently known. Within the present correlation matrix (Table 3) surprising examples for such relationships emerged: the clear positive correlation between the facial lobe and the valvula cerebelli suggests that the valvula may play an important role in the processing of external taste information. The function of the valvula is still unclear (Finger 1983b); the valvula seems to receive no direct, afferent fibers from the brain stem taste centers (Wullimann & Northcutt 1989).

The second, even more striking example is provided by correlations between the octavo-lateralis associated lobes and the torus longitudinalis-stratum marginale system (Table 3). This suggests integration of lateral line (highly significant correlation with the crista cerebellaris) with visual information within the stratum marginale of the tectum opticum. This hypothesis is backed by physiological and ecological evidence. Torus longitudinalis unit activity is related to eye movements (Northmore et al. 1983, Northmore 1984) and superficial stimulation of the frontal tectum opticum elicits eye convergence and food search behavior (Vanegas 1983). Plankton feeders show the greatest development of the octavo-lateralis areas as well as the stratum marginale system within the cyprinids (Kotrschal & Junger 1988) and within the teleosts in general (Kishida 1979, Winkelmann & Winkelmann 1968). It was shown, that lateral line input may be used for localizing plankton prey (Bleckmann 1988, Montgomery & Macdonald 1987). We therefore suggest that lateral line information may be used to attract visual attention, may prime and guide vision for focussing at, and discriminating small-sized prey.

Although the major source of input into the torus longitudinalis in common carp was found to be the valvula cerebelli, the torus longitudinalis also has afferent connections with the torus semicircularis and other areas (Ito & Kishida 1978). It seems reasonable to assume that the quantity of afferents from different sources varies according to relative importance of sensory systems in different species and that the outcome of Ito & Kishida's (1978) study, had it been conducted with breams or sabre carps, would have been different than in the taste-oriented carp.

Brain diversification in cyprinids

Virtually identical associations of species with brain morphology groups were found by both CLA and PCA. If the major cause of interspecific size variation of primary sensory areas is quantitative, variation in afferent nerve endings, as well as degree of intra-lobe processing (Gomahr et al. 1992, Kotrschal & Junger 1988, Kotrschal et al. 1990), the present four major groups indicate sensory diversification.

Brain area correlations and patterns of cyprinid brain diversification (the PC1/1-PC1/2 morphospace, Fig. 2, 3) allow us to formulate a set of 'construction rules' for cyprinid brains. Some of these rules apply for all cyprinids investigated, irrespective of body size: brains with relatively large visual centers may or may not show large octavolateralis centers, but brains with large octavo-lateralis centers always show a relatively large tectum opticum and a thick stratum marginale in particular. Taste lobe-determined brains always show relatively small visual and octavo-lateralis centers. Similar brain area relationships in cyprinids were recognized by earlier workers and sight feeders, mouth and skin tasters were distinguished (Evans 1940, Evans 1952).

The cause for these rules may be some sort of constructional constraint (Maynard Smith et al. 1985). More likely these sensory patterns are due to

adaptation, because certain sensory combinations are more useful than others to cope with certain sets of habitat variables and thus were selected for. Therefore, the brain groups found may represent occupied peaks in the adaptive landscape (Bock 1980, Simpson 1944). Under relatively clear midwater conditions a combination of lateral line and vision may be more adaptive than an elaborate chemosensory apparatus, whereas for benthic and benthivorous species, often dwelling in turbid water, the focus of sensory selection is evidently on external taste (cf. Huber & Rylander 1992). Also in the blind cave fish (*Astyanax* spp.), the loss of vision was evidently compensated by hypertrophy of the external taste, but not the lateral line (Schemmel 1967).

Adaptation is both, a state of being and a process (Bock 1980). Therefore the present adaptive interpretation of cyprinid brain diversification also implies our present evolutionary hypothesis. The scenario is summarized by two arrows in the sensory PCA morphospace. After attaining the cyprinid brain synapomorphies, such as a distinctive brain stem (Fig. 3), both, the octavo-lateralis as well as the chemosensory brains evolved out of the pool of basic cyprinid brain morphologies. The two arrows are not intended as a statement concerning the number of evolutionary pathways, but simply indicate the direction of morphological change. We have to assume multiple and parallel evolution has occurred, as not all species (but some, see position of abramines and leuciscines, Fig. 3, cf. Pagel & Harvey 1989) within the chemosensory and octavolateralis groups are closely related.

This evolutionary hypothesis is backed by ontogeny. Abramine and chemosensory brains at least, diversify lifelong into their specific morphologies during juvenile and adult growth (Brandstätter & Kotrschal 1990) and brains of small juveniles are relatively similar to the basic cyprinid brains.

Some construction rules are size related. This applies to a changing relationship in relative sizes of the tectum opticum and the cerebellum with growth and in differently sized species (Fig. 4, 5; Brandstätter & Kotrschal 1989, 1990). In the case of the tectum opticum this allometry probably reflects release from size constraints at the level of the retina during postlarval growth (Kotrschal et al. 1990). The reason for the positive allometry of the corpus cerebelli is less clear (Brandstätter & Kotrschal 1990), but may be related to its late development in vertebrates (Finger personal communication).

Within the second set of variables, including mainly the multimodal brain areas, only a few correlations, such as between the bulbus olfactorius and the telencephalon merit functional interpretation (Table 3). The majority of correlations within this group seems to result from within brain allometries (F2/1-F2/2, Fig. 4, 5). Allometry is therefore a major source of intra- and interspecific fish brain variability.

A recent study (Brandstätter & Kotrschal 1989) on adult brain growth patterns in representatives of the four major cyprinid brain morphologies (the same as shown in Fig. 3) revealed two types of brain-internal allometries: Type 1 allometries, either positive or negative, are common to all species and affect the cerebellum and tectum opticum (Geiger 1956a), but also the telencephalon, the bulbus olfactorius and the nucleus habenularis. Type 2 allometries are species specific and affect different primary sensory areas. In roach for example, the facial lobe decreases in relative size during juvenile to adult growth, whereas the facial and vagal lobes in carp increase steadily in size.

In the present study, type 1 allometry is not only found within specific size ranges of particular species, but is also valid in terms of absolute size: as a rule of thumb, small species show a relatively large tectum opticum, but a small cerebellum and vice versa in the large species. In this respect, the brains of small species match the juvenile brains of large species.

To a lesser extent, absolute body size may also affect taste areas and thus type 2 allometries, as indicated by the restricted position of small species (bitterling, bleak, dace, minnow, schneider, streamer, sun bleak) in the sensory PCA morphospace (PC1/1-PC1/2, Fig. 3, 6). Within the chemosensory group, the small gudgeon occupies a position close to the basic cyprinid brain type (Fig. 2, 3). This

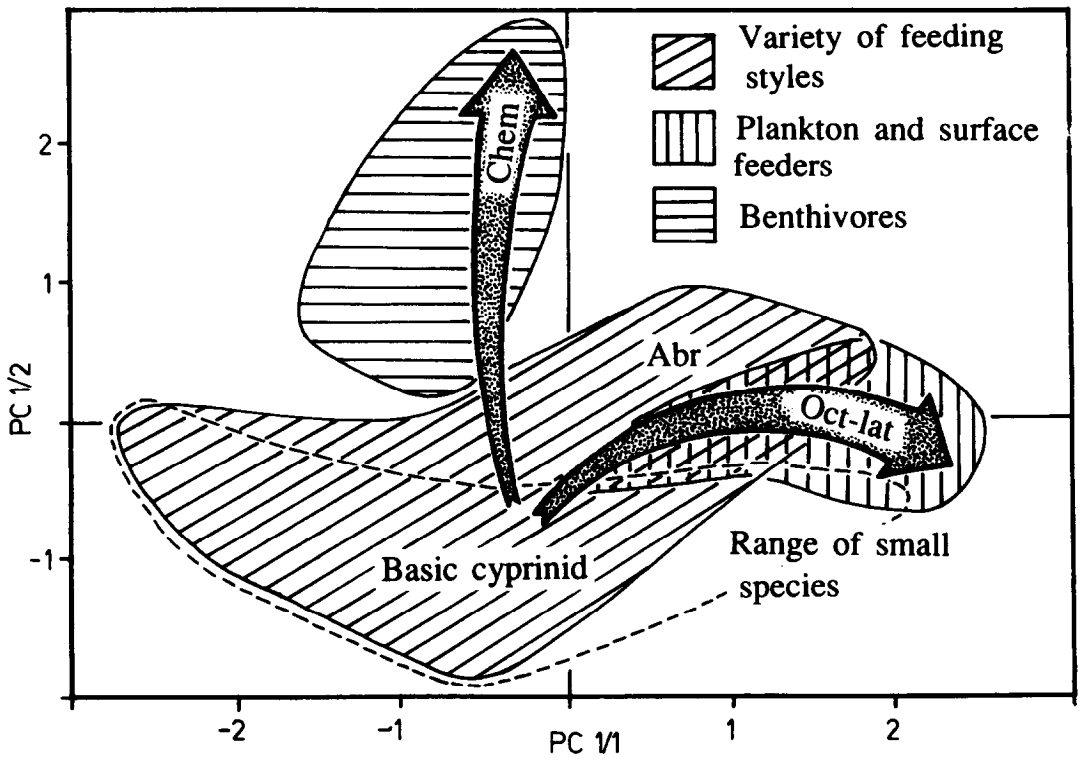

Fig. 6. Ecological (habitat and feeding style) and evolutionary interpretation superimposed over the sensory brain area PCA plot (identical with Fig. 3). Distribution of small species shown by broken lines. Arrows indicate proposed directions of ecological shifts with changing morphology from basic cyprinid brains to chemosensory (Chem) and octavo-lateralis (Oct-lat) brains. Therefore these arrows also represent our hypothesis on cyprinid neuroecological evolutionary diversification. Finally, arrows indicate the direction of brain differentiation during growth (Brandstätter & Kotrschal 1990).

suggests, that absolute body size is a major constraint for potential taste specialization.

This lack of small, taste-orientated species in temperate European freshwater may be caused by brain internal or size constraints as is the case with the retina (Kotrschal et al. 1990). However, the latter hypothesis is rendered implausible by the existence of small, taste-orientated cyprinids, such as the genus *Barbus* or *Labeo* in the Old World tropics. Geological and evolutionary histories as well as differences in the distribution of ecological factors (such as temperature, food, habitat complexity, etc.) may account for the scarcity of small, taste-oriented species in central Europe.

Ecomorphology: is brain morphology related to the life style?

Distinct relationships between brain morphologies and life styles have been found (Bauchot et al. 1989, Davis & Miller 1967, Evans 1931, 1932, 1935, 1940, Evans 1952, Kirka 1963b, Miller & Evans 1965, Peter 1979, Uchihashi 1953). However, in these qualitative studies interpretations mellowed at coarse levels and it was unclear how reliable brain structures were as predictors of ecology.

When superimposing cyprinid life styles (Balon et al. 1986, Ladiges & Vogt 1965, Maitland 1981, Schiemer 1985, 1988) on the sensory morphospace (Fig. 3, 6) consistent trends can be recognized only at the more specialized ranges of brain morphology. Octavo-lateralis brains are associated with plankton or surface feeding, whereas chemosenso-

ry brains are found in benthic and benthivorous species. Particularly the octavo-lateralis brain stem areas in combination with very small chemosensory brain stem lobes as well as the relative thickness of the stratum marginale seem excellent predictors for planktivorous or surface-feeding life styles. In the benthivores, particularly diagnostic brain areas are large brain stem taste centers and a large valvula cerebelli.

No definite correlation between life style and brain morphology is evident within the bulk of species with a basic cyprinid brain. This group contains very different ecotypes, such as the generalized roach and the piscivorous asp. Sensory specializations, e.g. the elaborate visual system in asp only become apparent at a closer inspection of sensory systems (Gomahr et al. 1992, Junger & Kotrschal 1989, Kotrschal et al. 1990, Zaunreiter & Kotrschal 1990).

Species with basic cyprinid brains, such as roach and chub may be prone to a high degree of ecological flexibility (Schiemer 1985, 1988). Generalized sensory and motor patterns may allow for flexible reactions to environmental change (Brabrand 1985, Lammens et al. 1987) and may be a major component of their success.

Two distinct tribes, the abramines including the closely related white bream and vimba and the leuciscines occupy relatively restricted areas of morphospace (Fig. 3). High within-group similarity in brain morphology may indicate relatively recent speciation. Still, lifestyles vary within these groups, spanning the range from different types of benthivory to planktivory. Thus, in contradiction to most of the recent work on fish brain ecomorphology quoted above, it has to be concluded that brain structure is not necessarily a close predictor of ecology. As is the case with fish jaws (Kotrschal 1989), and in other animal taxa (Haslett 1989), it seems that morphology at least at the present level of consideration is more conservative than behavior and ecology. It is necessary to recognize the patterns of diversification within a taxon to deduct ecological predictions at least in the morphologically more 'specialized' ranges.

In conclusion, quantitative comparative brain morphology is a powerful tool to generate novel hypotheses on brain area interactions and to investigate sensory diversification within groups of closely related fish such as the cyprinids.

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References cited

Ariens Kappers, C.U., G.C. Huber & E.C. Crosby. 1936. The comparative anatomy of the nervous system of vertebrates, including man. Vol. 1–3. Macmillan, New York. 1350 pp.

Balon, E. 1968. Beitrag zur Systematik, Ökologie, Morphologie, Alter, Wachstum und Eizahl der Eier der Ziege [*Pelecus cultratus* (L.)] aus der Donau bei Medevedov. Biologické práce (Bratislava) 13: 63–88.

Balon, E.K., S.S. Crawford & A. Lelek. 1986. Fish communities of the upper Danube River (Germany, Austria) prior to the new Rhein-Main-Donau connection. Env. Biol. Fish. 15: 243–271.

Bauchot, R., M.L. Bauchot, R. Platel & J.M. Ridet. 1977. Brains of Hawaiian tropical fishes: brain size and evolution. Copeia 1977: 42–46.

Bauchot, R., J.M. Ridet & M.L. Bauchot. 1989. The brain organization of butterflyfishes. Env. Biol. Fish. 25: 205–219.

Blaxter, J.H.S. 1988. Sensory performance, behavior and ecology of fish. pp. 203–232. *In:* J. Atema, R.R. Fay, A.N.

Popper & W.N. Tavolga (ed.) Sensory Biology of Aquatic Animals, Springer Verlag, New York.

Bleckmann, H. 1988. Prey identification and prey localization in surface-feeding fish and fishing spiders. pp. 619–641. *In:* J. Atema, R.R. Fay, A.N. Popper & W.N. Tavolga (ed.) Sensory Biology of Aquatic Animals, Springer Verlag, New York.

Bock, W.J. 1980. The definition and recognition of biological adaptation. Amer. Zool. 20: 217–227.

Brabrand, A. 1985. Food of roach (*Rutilus rutilus*) and ide (*Leuciscus idus*): significance of diet shifts for interspecific competition in omnivorous fishes. Oecologia 66: 461–467.

Brandstätter, R. & K. Kotrschal. 1989. Life history of roach, *Rutilus rutilus* (Cyprinidae, Teleostei): a qualitative and quantitative study on the development of sensory brain areas. Brain, Behav. Evol. 34: 35–42.

Brandstätter, R. & K. Kotrschal. 1990. Brain growth patterns in four European cyprinid fish species (Cyprinidae, Teleostei): roach (*Rutilus rutilus*), bream (*Abramis brama*), common carp (*Cyprinus carpio*) and sabre carp (*Pelecus cultratus*). Brain, Behav. Evol. 35: 195–211.

Brosius, G. 1989. Spss/pc. Advanced statistics and tables. McGraw Hill, Hamburg. 350 pp.

Bullock, T.H. 1983. Why study fish brains? pp. 361–368. *In:* R.E. Davis & R.G. Northcutt (ed.) Fish Neurobiology, The University of Michigan Press, Ann Arbor.

Davis, B.J. & R.J. Miller. 1967. Brain patterns in minnows of the genus *Hybopsis* in relation to their feeding habits. Copeia 1987: 1–39.

Davis, R.E. & R.G. Northcutt (ed.). 1983. Fish neurobiology. Vol. 2. The University of Michigan Press, Ann Arbor. 370 pp.

Echteler, S. 1985. Organization of central auditory pathways in a teleost fish, *Cyprinus carpio*. J. Comp. Physiol. A. 156: 267–280.

Evans, H.M. 1931. A comparative study of the brains in British cyprinoids in relation to their habits of feeding, with special reference to the anatomy of the medulla oblongata. Proc. R. Soc. Lond. B 108: 233–257.

Evans, H.M. 1932. Further observations on the medulla oblongata in cyprinoids; and a comparative study of the medulla of clupeoids and cyprinoids with special reference to the acoustic tubercles. Proc. R. Soc. Lond. B 111: 247–280.

Evans, H.M. 1935. The brain of *Gadus*, with special reference to the medulla oblongata and its variation according to feeding habits of different Gadidae-I. Proc. R. Soc. B. 117: 56–68.

Evans, H.M. 1940. Brain and body of fish. A study of brain pattern in relation to hunting and feeding in fish. Technical Press, London. 224 pp.

Evans, H.E. 1952. The correlation of brain patterns and feeding in four species of cyprinid fishes. J. Comp. Neurol. 97: 133–142.

Finger, T.E. 1978. Gustatory pathways in the bullhead catfish. II. Facial lobe connections. J. Comp. Neurol. 180: 691–706.

Finger, T.E. 1983a. The gustatory system in teleost fish. pp. 285–311. *In:* R.G. Northcutt & R.E. Davis (ed.) Fish Neurobiology, Vol. 1, The University of Michigan Press, Ann Arbor.

Finger, T.E. 1983b. Organization of the teleost cerebellum. pp. 261–284. *In:* R.G. Northcutt & R.E. Davis (ed.) Fish Neurobiology, Vol. 1, The University of Michigan Press, Ann Arbor.

Finger, T.E. 1987. Gustatory nuclei and pathways in the central nervous system. pp. 331–354. *In:* T.E. Finger & W.L. Silver (ed.) Neurobiology of Taste and Smell, J. Wiley Publishers, New York.

Finger, T.E. 1988. Organization of the chemosensory systems within the brains of bony fishes. pp. 339–363. *In:* J. Atema, R.R. Fay, A.N. Popper & W.N. Tavolga (ed.) Sensory Biology of Aquatic Animals, Springer Verlag, New York.

Geiger, W. 1956a. Quantitative Untersuchungen über das Gehirn der Knochenfische mit besonderer Berücksichtigung seines relativen Wachstums. I. Acta anat. 26: 121–163.

Geiger, W. 1956b. Quantitative Untersuchungen über das Gehirn der Knochenfische mit besonderer Berücksichtigung seines relativen Wachstums. II. Acta anat. 27: 324–350.

Goldschmid, A. & K. Kotrschal. 1989. Ecomorphology: developments and concepts. Progr. Zool. 35: 501–512.

Gomahr, A., M. Palzenberger & K. Kotrschal. 1992. Density and distribution of external taste buds in cyprinids. Env. Biol. Fish. 33: 125–134.

Haslett, J.R. 1989. Adult feeding by holometabolous insects: pollen and nectar as complementary nutrient sources for *Rhingia campestris* (Diptera: Syrphidae). Oecologia 81: 361–363.

Huber, R. & M.K. Rylander. 1992. Brain morphology and turbidity preference in *Notropis* and related genera (Cyprinidae, Teleostei). Env. Biol. Fish. 33: 153–165.

Herrick, C.J. 1905. The central gustatory paths in the brains of bony fishes. J. Comp. Neurol. Psychol. 15: 375–456.

Ito, H. & R. Kishida. 1978. Afferent and efferent fiber connections of the carp torus longitudinalis. J. Comp. Neurol. 181: 465–476.

Jolicoeur, P. & G. Baron. 1980. Brain center correlations among Chiroptera. Brain, Behav. Evol. 17: 419–431.

Junger, H. & K. Kotrschal. 1989. Developmental changes in the optic tracts of cyprinids (Cyprinidae, Teleostei). p. 191. *In:* N. Elsner & W. Singer (ed.) Dynamics and Plasticity in Neuronal Systems, Proceedings of the 17th Göttingen Neurobiology Conference, Georg Thieme Verlag, Stuttgart.

Kaiser, H.F. 1974. An index of factorial simplicity. Psychometrica 39: 31–36.

Khanna, S.S. & H.R. Singh. 1966. Morphology of the teleostean brain in relation to feeding habits. Proc. Nat. Acad. Sci. India 336: 306–316.

Kirka, A. 1963a. Brain structures in the Danube representatives of perciformes and the role of brain study for the systematic and ecology of fishes. Zool. Zhurnal 42: 400–407 (in Russian).

Kirka, A. 1963b. Die äußere Gehirnform des Donaunerflings (*Rutilus pigus virgo* He.) und ein Vergleich seines Gehirns mit der Donauplötze (*Rutilus rutilus carpathorossicus* Vladykov) und der Elbeplötze (*Rutilus rutilus frici* Misik). Zeit-

schrift für Fischerei und deren Hilfswissenschaften 11: 129–141.

Kishida, R. 1979. Comparative study on the teleostean optic tectum. J. Hirnforsch. 20: 57–67.

Kotrschal, K. 1989. Trophic ecomorphology in eastern Pacific blennioid fishes: character transformation of oral jaws and associated change of their biological roles. Env. Biol. Fish. 24: 199–218.

Kotrschal, K. & H. Junger. 1988. Patterns of brain morphology in mid-European Cyprinidae (Pisces, Teleostei): a quantitative histological study. J. Hirnforsch. 29: 341–352.

Kotrschal, K., H. Adam, R. Brandstätter, H. Junger, M. Zaunreiter & A. Goldschmid. 1990. Larval size constraints determine directional ontogenetic shifts in the visual system of teleosts. A mini-review. Z. Zool. Syst. Evolutionsforsch. 28: 166–182.

Kotrschal, K., R. Brandstätter, A. Gomahr, H. Junger, M. Palzenberger & M. Zaunreiter. 1991. Brain and sensory systems. *In:* I.J. Winfield & J.S. Nelson (ed.) Cyprinid Fishes, Systematics, Biology and Exploitation, Chapman and Hall, London.

Ladiges, W. & D. Vogt. 1965. Die Süßwasserfische Europas. Paul Parey, Hamburg. 299 pp.

Lammens, E.H.R.R., J. Geursen & P.J. McGillavry. 1987. Diet shifts, feeding efficiency and coexistence of bream (*Abramis brama*), roach (*Rutilus rutilus*) and white bream (*Blicca bjoercna*) in hypertrophic lakes. pp. 153–162. *In:* S. Kullander & B. Fernholm (ed.) Proceedings of the V Congress of European Ichthyologists, Stockholm.

Lythgoe, J.N. 1988. Light and vision in the aquatic environment. pp. 57–82. *In:* J. Atema, R.R. Fay, A.N. Popper & W.N. Tavolga (ed.) Sensory Biology of Aquatic Animals, Springer Verlag, New York.

Maitland, P.S. 1981. Freshwater fishes of Britain and Europe. Hamlyn, London. 256 pp.

Maynard Smith, J., R. Burian, S. Kauffman, P. Alberch, J. Campbell, B. Goodwin, R. Lande, D. Raup & L. Wolpert. 1985. Developmental constraints and evolution. Quart. Rev. Biol. 60: 260–287.

Mayser, P. 1881. Vergleichend anatomische Studien über das Gehirn der Knochenfische mit besonderer Berücksichtigung der Cyprinoiden. Arch. wiss. Zool. 36: 259–366.

McCormick, C.A. & M.R. Braford, Jr. 1988. Central connections of the octavolateralis system: evolutionary considerations. pp. 733–756. *In:* J. Atema, R.R. Fay, A.N. Popper & W.N. Tavolga (ed.) Sensory Biology of Aquatic Animals, Springer Verlag, New York.

Miller, R.J. & H.E. Evans. 1965. External morphology of the brains and lips in catastomid fishes. Copeia 1965: 467–487.

Montgomery, J.C. & J.A. Macdonald. 1987. Sensory tuning of lateral line receptors in Antarctic fish to the movement of planktonic prey. Science 235: 195–196.

Morita, Y. & T.E. Finger. 1985a. Topography and laminar organization of the vagal gustatory system in the goldfish, *Carassius auratus*. J. Comp. Neurol. 238: 187–201.

Morita, Y. & T.E. Finger. 1985b. Reflex connections of the facial and vagal gustatory systems in the brain stem of the bullhead catfish, *Ictalurus nebulosus*. J. Comp. Neurol. 231: 547–558.

Morita, Y. & T.E. Finger. 1987. Topographic representation of the sensory and motor roots of the vagus nerve in the medulla of goldfish, *Carassius auratus*. J. Comp. Neurol. 264: 231–249.

Morita, Y. & H. Masai. 1980. Central gustatory paths in the crucian carp, *Carassius carassius*. J. Comp. Neurol. 191: 119–132.

Nelson, J.S. 1984. Fishes of the world. J. Wiley & Sons, New York. 523 pp.

Northcutt, R.G. 1988. Sensory and other neural traits and the adaptationist program: mackerels of San Marco? pp. 869–883. *In:* J. Atema, R.R. Fay, A.N. Popper & W.N. Tavolga (ed.) Sensory Biology of Aquatic Animals, Springer Verlag, New York.

Northcutt, R.G. & R.E. Davis (ed.). 1983. Fish neurobiology, Vol. 1. The Michigan University Press, Ann Arbor. 345 pp.

Northcutt, R.G. & M.F. Wullimann. 1988. The visual system in teleost fishes: morphological patterns and trends. pp. 515–552. *In:* J. Atema, R.R. Fay, A.N. Popper & W.N. Tavolga (ed.) Sensory Biology of Aquatic Animals, Springer Verlag, New York.

Northmore, D.P.M. 1984. Visual and saccadic activity in the goldfish torus longitudinalis. J. Comp. Physiol. A 155: 333–340.

Northmore, D.P.M., B. Williams & H. Vanegas. 1983. The teleostean torus longitudinalis: responses related to eye movements, visuotopic mapping, and functional relations with the optic tectum. J. Comp. Physiol. A 150: 39–50.

Pagel, M.D. & P.H. Harvey. 1989. Taxonomic differences in the scaling of brain on body weight among mammals. Science 244: 1589–1593.

Peter, R.E. 1979. The brain and feeding behavior. pp. 121–159. *In:* Hoar & Randall (ed.) Fish Physiology, Vol. 8, Academic Press, New York.

Pirlot, P. & P. Jolicoeur. 1982. Correlations between major brain regions in Chiroptera. Brain. Behav. Evol. 20: 172–181.

Ridet, J.M., R. Bauchot, M. Diagne & R. Platel. 1977. Croissance ontogenetique et phylogenetique de l'encephale des Teleosteens. Cahiers Biol. Marine 18: 163–176.

Schemmel, C. 1967. Vergleichende Untersuchungen an den Hautsinnesorganen ober- und unterirdisch lebender *Astyanax*-Formen. Z. Morph. Tiere 61: 255–305.

Schiemer, F. 1985. Die Bedeutung der Augewässer als Schutzzonen für die Fischfauna. Österr. Wasserwirtschaft 37: 239–245.

Schiemer, F. 1988. Gefährdete Cypriniden – Indikatoren für die ökologische Intaktheit von Flußsystemen. Natur und Landschaft 63: 370–373.

Schnitzlein, H.N. 1964. Correlation of habit and structure in the fish brain. Amer. Zool. 4: 21–32.

Sibbing, F.A. 1988. Specializations and limitations in the utilization of food resources by the carp, *Cyprinus carpio:* a study of oral food processing. Env. Biol. Fish. 22: 161–178.

Simpson, G.G. 1944. Tempo and mode in evolution. Columbia University Press, New York. 420 pp.

Snow, J.L. & M.K. Rylander. 1982. A quantitative study of the optic system of butterflyfishes (family Chaetodontidae). J. Hirnforsch. 23: 121–125.

Sokal, R.R. & F.J. Rohlf. 1981. Biometry, 2nd ed. Freeman, San Francisco. 859 pp.

Stephan, H. 1960. Methodische Studien über den quantitativen Vergleich architektonischer Struktureinheiten des Gehirns. A. wiss. Zool. 164: 143–172.

Stephan, H. 1967. Quantitative Vergleiche zur phylogenetischen Entwicklung des Gehirns der Primaten mit Hilfe der Progressionsindices. Mitt. Max-Planck Ges. 2: 63–68.

Stephan, H. & P. Pirlot. 1970. Volumetric comparison of brain structures in bats (an attempt to a phylogenetic interpretation). Bijdr. Dierkunde 40: 95–98.

Uchihashi, K. 1953. Ecological study of Japanese teleosts in relation to brain morphology. Bull. Jap. Sea Regional Fish. Res. Lab. 2: 1–166.

Vanegas, H. 1983. Organization and physiology of the teleostean optic tectum. pp. 43–87. *In:* R.E. Davis & R.G. Northcutt (ed.) Fish Neurobiology, The University of Michigan Press, Ann Arbor.

Werner, E.E. 1984. The mechanisms of species interactions and community organization in fishes. pp. 360–383. *In:* D.R. Strong, D. Simberloff, L.G. Abele & A.B. Thistle (ed.) Ecological Communities, Conceptual Issues and Evidence, Princeton University Press, Princeton.

Wieser, W. 1986. Die Ökophysiologie der Cyprinidenfauna österreichischer Gewässer. Ein Forschungsschwerpunkt des Fonds zur Förderung der wissenschaftlichen Forschung. Österreichs Fischerei 36: 88–93.

Winkelmann, E. & L. Winkelmann. 1968. Vergleichend histologische Untersuchungen zur funktionellen Morphologie des Tectum opticum verschiedener Teleostier. J. Hirnforsch. 10: 1–16.

Wullimann, M.F. & R.G. Northcutt. 1989. Afferent connections of the valvula cerebelli in two teleosts, the common goldfish and the green sunfish. J. Comp. Neurol. 289: 554–567.

Zaunreiter, M. & K. Kotrschal. 1989. Shifting retinal parameters during growth in roach (*Rutilus rutilus,* Cyprinidae, Teleostei). p. 192. *In:* N. Elsner & W. Singer (ed.) Dynamics and Plasticity in Neuronal Systems, Proceedings of the 17th Göttingen Neurobiology Conference, Georg Thieme Verlag, Stuttgart.

Zaunreiter, M., H. Junger & K. Kotrschal. 1991. Ecomorphology of the cyprinid retina: a quantitative histological study on ontogenetic shifts and interspecific variation. Vision. Res. 31: 383–394.