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Microhabitat Use, Trophic Patterns, and the Evolution of Brain Structure in African Cichlids[1]

Abstract

The species assemblages of cichlids in the three largest African Great Lakes are among the richest concentrations of vertebrate species on earth. The faunas are broadly similar in terms of trophic diversity, species richness, rates of endemism, and taxonomic composition, yet they are historically independent of each other. Hence, they offer a true and unique evolutionary experiment to test hypotheses concerning the mutual dependencies of ecology and brain morphology. We examined the brains of 189 species of cichlids from the three large lakes: Victoria, Tanganyika, and Malawi. A first paper demonstrated that patterns of evolutionary change in cichlid brain morphology are similar across taxonomic boundaries as well as across the three lakes [van Staaden et al., 1995 ZACS 98: 165–178]. Here we report a close relationship between the relative sizes of various brain structures and variables related to the utilization of habitat and prey. Causality is difficult to assign in this context, nonetheless, prey size and agility, turbidity levels, depth, and substrate complexity are all highly predictive of variation in brain structure. Areas associated with primary sensory functions such as vision and taste relate significantly to differences in feeding habits. Turbidity and depth are closely associated with differences in eye size, and large eyes are associated with species that pick plankton from the water column. Piscivorous taxa and others that utilize motile prey are characterized by a well developed optic tectum and a large cerebellum compared to species that prey on molluscs or plants. Structures relating to taste are well developed in species feeding on benthos over muddy or sandy substrates. The data militated against the existence of compensatory changes in brain structure. Thus enhanced development of a particular function is generally not accompanied by a parallel reduction of structures related to other modalities. Although genetic and environmental influences during ontogeny of the brain cannot be isolated, this study provides a rich source of hypotheses concerning the way the nervous system functions under various environmental conditions and how it has responded to natural selection.

[1] This paper is dedicated to the memory of Humphry Greenwood.

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Introduction

'The essence of evolution is the production of... diversity in brains, its highest achievement' [Bullock, 1993]. The revelation of principles that give rise to diversity of brain function and behavior remains a significant aim of neuroscience, and a variety of methods have been employed to probe the relationships between brain structure and function. The complexity of sensory organs and the perfection with which they are matched to their respective physical constraints provide an important analytical basis for understanding adaptive specializations of the nervous system [Fernald, 1988]. In a complex assemblage of cichlid fishes, we have therefore adopted a comparative approach to investigate the changes in brain morphology that accompany major shifts in feeding mode and microhabitat use, variables with definable close links to fish sensory space. In essence, we try to uncover environmental forces giving rise to brain diversity by searching for behaviorally relevant communalities.

The fish faunas of highly productive, tropical freshwater environments are afforded a rich array of food items ranging from microscopic detritus, algae and plants, to insects, snails, decapods and vertebrates. Search, detection, capture, and ingestion of food place different selective forces on the species' sensory apparatus, depending on the specific type of prey utilized. For instance, food capture in herbivores may consist of nothing more than biting pieces out of plants, scraping algae from a hard substrate, or straining phytoplankton from water as it passes through mouth and gills. Carnivores in contrast, require more elaborate techniques for utilizing prey which exhibit a wide range of behavioral and structural adaptations for avoiding capture. Each food item is associated with a complex set of tactile, optical, acoustic, chemical, and electrical stimuli which fishes perceive through a combination of sensory pathways. Different habitat conditions result in differences in transmission properties of these stimulus modes and should thereby impact the relative biological significance of particular modalities.

Correlates of microhabitat and feeding have been reported for peripheral sense organs, such as the functional design of the eye [Fernald, 1988], eye size [Kotrschal et al., 1990; Huber and Rylander, 1992a; Schellart and Prins, 1993], retinal topography [Levine and MacNichol, 1979; Lythgoe, 1988; Collin and Pettigrew, 1989; Zaunreiter et al., 1991], the spectral properties of visual pigments [Loew and Lythgoe, 1978], the number, arrangement and functioning of cutaneous and internal taste buds [Davis and Miller, 1967; Gomahr et al., 1992], and the anatomy of olfactory sensory structures [Branson, 1979; Yamamoto, 1982] and lateral line systems [Coombs et al., 1988], including the width and placement of the lateral line canals [Kotrschal et al., 1990; Schellart, 1992] and their replacement with superficial neuromasts in low-noise environments [Wilkens, 1977; Coombs et al., 1988; Münz, 1989].

Sensory information received at different peripheral organs also maintains separate channels as it projects into the brain for further processing [Finger, 1988]. As differences in peripheral sense organs closely reflect sensory diversification, the question arises whether subsequent brain regions have responded in similar ways. In fishes, the projections of different modalities into the brain are known in some detail, and the processing is performed in prominent, anatomically distinct lobes. Aspects of ecology are reported to underly differences in central nervous structures in a variety of teleost taxa [Bauchot et al., 1979; Kotrschal and Palzenberger, 1992], from the size of the optic tectum [Davis and Miller, 1967] and its lamination [Kishida, 1979; Kotrschal et al., 1990; Huber and Rylander, 1991; Schellart and Prins, 1993], to the size and histology of gustatory sensory lobes [Davis and Miller, 1967; Odiette, 1984; Kotrschal and Junger, 1988] and the development of the olfactory bulb [Kotrschal and Palzenberger, 1992; Huber and Rylander, 1992a].

One consequence of the close relationship between sensory function and gross structure of fish brains is that the brain constitutes a measurable reflection of the way a species has adapted to any given environmental context or selection regime. For this reason, the parallel radiations of cichlid fish in the Great Lakes of East Africa present an interesting opportunity for the study of brain-environment interactions on an evolutionary time scale.

Cichlid-dominated fish communities are characteristic of lakes in the headwaters of the White Nile, Malagarazi, and Zambezi Systems in East Africa. The larger lakes, Victoria, Malawi, and Tanganyika, contain species 'flocks' of several hundred species, each with rates of endemism approaching 99–100% [Echelle and Kornfield, 1984]. These three faunas are remarkable for their rapid evolution, species richness, and high morphological divergence [Fryer and Iles, 1972], reflecting a diversity of feeding mechanisms and a wealth of morphological and behavioral specializations. As they are the result of largely independent 'explosive speciation' events [Greenwood, 1984; Meyer et al., 1990; Kocher et al., 1993], the East African lacustrine cichlid faunas constitute replicated natural experiments that permit the isolation of certain treatment effects. Morphological, behavioral, or physiological characteristics exhibiting strong convergence and/or parallelism among species in

a variety of habitats can elucidate common patterns underlying adaptive brain changes, just as they do for any other functional domain (e.g., locomotion or reproduction). To this end, first we account for body size, and then we attempt to uncover convergence of brain form with dietary habits and microhabitat use across lakes by posing the following questions: Do species from different microhabitats, or of varied feeding strategies, differ in brain morphology? Given a classification scheme into ecological guilds, which brain characteristics are most useful for distinguishing among these groups? That is, which subsets of ecological variables best predict the size of the different brain regions?

Materials and Methods

The research reported herein largely utilized museum material. These and all live specimens were handled according to guidelines for animal research established at the Museum of Comparative Zoology (Harvard), and the New England Aquarium, Boston MA.

Trophic Classification of Fishes

Variation in dietary habits of cichlids has been reviewed by Fryer and Iles [1972], Lowe-McConnel [1975], and Hyatt [1979] who recognized several recurrent trophic groups among the lakes. Detritivores: Fish with appropriate buccopharyngeal sorting mechanisms use detritus as a valuable source of nutrients. Examples include species feeding on hippopotamus faeces [Fryer and Iles, 1972] or partially digested water lily leaves excreted by herbivores [Hickling, 1961]. Herbivores: Grazers, browsers, and phytoplanktivores utilize a broad range of vegetable matter via mouth, teeth, and pharyngeal apparati adapted for such specialized tasks as scraping algae off rock surfaces or straining and concentrating phytoplankton from the water column. Insectivores: Insects and larvae may be visually located and picked up with forceps-like snouts, or fleshy lips may provide tactile information for subsequent prey capture and increase efficiency of feeding in cracks among rocks. Sand may be picked up and sifted for edible parts using tactile and chemical cues, and in coastal areas trapped terrestrial insects may be obtained from the surface. Molluscivores: Molluscs, which are well protected by their shell, require special strategies for utilization. In some cases the foot of gastropods is grabbed and the animal is wrenched out of its shell. Other species crush the shell with modified buccal teeth or a hypertrophied pharyngeal mill. Zooplanktivores: Zooplankton is taken either by filter feeding with modified gill rakers or, more commonly, by particulate feeding where prey are hunted individually based on visual or mechanosensory cues. Piscivores: Capturing other fish places special demands on the sensory capabilities of a species. Strategies include ambush hunting, stalking, or chasing of prey and may involve largely visual cues, with an additional contribution of chemical, mechanical, and acoustic information. Fin-biters and Scale-eaters: At least nine species of African cichlids have evolved adaptations in the jaw and dentition for feeding on scales and fins of other fish [Keenleyside, 1979]. Paedophages: Several cichlids snatch the eggs or juveniles of other species, often after forcing their release by engulfing the snout or ramming the sides of females [Barel et al., 1989]. Species examined and their ecological classifications are summarized in table 1.

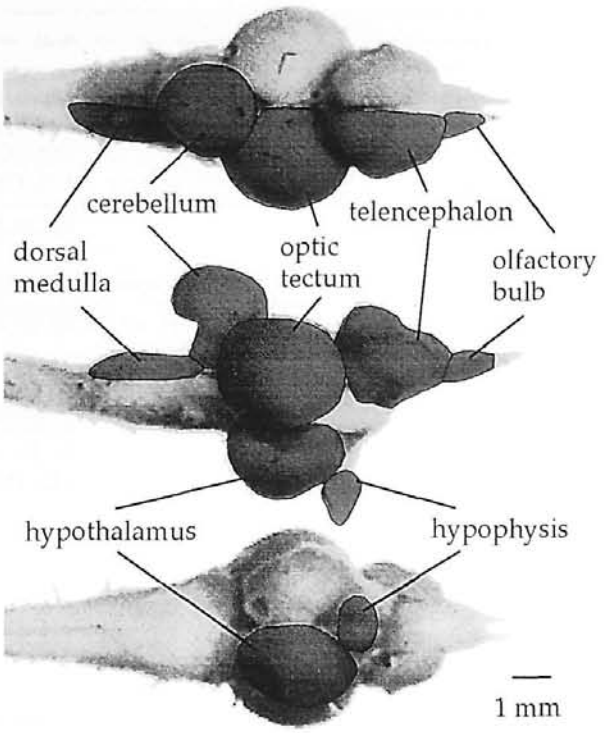

Fig. 1. The brain of *Haemitilapia oxyrhynchus* in dorsal, lateral and ventral view illustrating major brain divisions.

Cichlid Brains

As in other teleosts, the telencephalon consists of paired cerebral hemispheres with olfactory bulbs located at the anterior edge (fig. 1). It appears to be involved in a variety of tasks, such as processing olfactory and, to a lesser extent, visual and gustatory stimuli [Friedlander, 1983; Davis and Kassel, 1983], and in learning, agonistic and courtship behaviors [Demski, 1983; Koyama et al., 1984]. The thalamus, presumably another key feature of brain sensory evolution [Northcutt and Wullimann, 1988], is not discernible from the outside and was not included here. The inferior lobes of the hypothalamus are prominent features of the ventral brain surface. Data from stimulation, lesion, and anatomical studies suggest integrative functions, in some cases related to feeding, aggression, reproduction, and vision [Demski and Knigge, 1971; Demski, 1983; Northcutt and Wullimann, 1988]. The mesencephalon bulges dorsally into a pair of large optic lobes (optic tecta) which receive contralateral projections from the retina [Northcutt, 1983; Vanegas and Ito, 1983]. A central role in proprioception and motor coordination is played by the cerebellum [Demski, 1983]. The dorsal medulla receives both lateral line and taste projections, with rostral components (medial octavolateralis nucleus, crista cerebelli) processing mechanosensory lateral line stimuli and more caudal and medial aspects relating to taste, including the location and evaluation of food items. Precise delineation of these centers in most species would require histological sectioning.

Table 1. Ecological classification for all examined species

	D	M	S–R	S–Sa	S–Mu	S–Veg
Plants			12, 28, 29, 30, 65, 87, 89, 95, 124, 125, 128, 143, 161, 162, 163, 174, 175, 176, 178, 179			43, 76, 115, 123, 169
Molluscs	38		21, 22, 80, 81	16, 23, 24, 27, 33, 34, 36, 37, 39, 40, 41, 96, 140, 186	108	1
Plankton and detritus	8, 10, 56, 91, 92, 93	13, 31, 44, 45, 46, 47, 48, 49, 109, 110, 111, 112, 113, 114, 155	15, 63, 68, 82, 86, 116	71, 73, 78, 85, 149, 152, 156, 177	60, 94	151, 166
Insects	2, 50, 135, 164		4, 20, 32, 66, 70, 77, 79, 83, 84, 90, 107, 126, 127, 142, 154, 171, 185	3, 11, 58, 59, 64, 74, 75, 98, 99, 100, 101, 102, 103, 104, 121, 130, 132, 133, 134, 136, 137, 150, 153, 167, 172, 173, 184, 187, 188, 189	129, 131, 138, 157	7, 159, 160, 168
Fish	17, 62, 141, 182	51, 52, 53, 54, 55, 97, 106, 120, 139, 180, 181	5, 6, 26, 61, 67, 72, 88, 122, 144, 145	9, 14, 18, 19, 35, 42, 57, 69, 105, 118, 148, 158, 165, 170, 183		25, 117, 119, 146, 147

Microhabitat codes indicate deep water species (D), medium depth species (M), shallow over rock (S–R), shallow over sand (S–Sa), shallow over mud (S–Mu), and shallow in vegetation (S–Veg). Species are represented by the following numbers for Victoria (1–49), Tanganyika (50–102), Malawi (103–186), and Madagascar (187–189): *Astatoreochromis alluaudi* (1), *Astatotilapia* 'greenback' (2), *A.* 'red little mouth' sp. nov. (3), *A.* 'thickskin' (4), *A.* 2-striped yellow green (5), *Astatotilapia barbarae* (6), *A. nubila* (7); *A. piceatus* (8); *A.* 'two stripe whitelip' (9), *Enterochromis* 'nigrofasciatus' (10), *Haplochromis* 'spot bar' sp. nov. (11), *H. pseudonigricans* (12), *H. kribensis* (13), *H. diplotenia* (14), *H. nyereri* (15), *Haplotilapia retrodens* (16), *Harpagochromis* 'grey pygmy' (17), *H. guiarti* (18), *H.* red-eye guiarti (19), *Labrochromis* 'rock kribensis' ins. (20), *L.* 'rock kribensis' moll. (21), *L.* 'rock kribensis' Kenya (22), *L.* 'rock kribensis' molariform (23), *L. ishmaeli* (24), *Lipochromis maxillaris* (25), *L. obesus* (26), *Macropleurodus bicolor* (27), *Neochromis* 'velvet black' (28), *N.* Madonna sp. nov. (29), *N. nigricans* (30), *Oreochromis esculentus* (31), *Paralabidochromis chilotes* (32), *P. plagiodon* (33), *Platytaeniodus degeni* (34), *Prognathochromis* sp. (35), *Psammochromis riponianus* (36), *Ptyochromis* Russinga oral sheller (37), *P.* deep xenognathus (38), *P. prodromus* (39), *P. sauvagei* (40), *P. xenognathus* (41), *Pyxichromis orthostoma* (42), *Xystichromis phytophagus* (43), *Yssichromis argens* (44), *Y. coop* (45), *Y. heusinkfeldi* (46), *Y. laparogramma* (47), *Y. pyrrhocephalus* (48), *Y.* 'Fred Astaire' cf. Doublestripe (49), *Aulonocranus dewindti* (50), *Bathybates fasciatus* (51), *B. ferox* (52), *B. graueri* (53), *B. leo* (54), *B. minor* (55), *Benthochromis tricoti* (56), *Boulengerochromis microlepsis* (57), *Callochromis macrops* (58), *C. pleurospilus* (59), *Cardiopharynx schoutedini* (60), *Ctenochromis horii* (61), *Cyphotilapia frontosa* (62), *Cyprichromis leptosoma* (63), *Ectodus descampsii* (64), *Eretmodus cyanostictus* (65), *Julidochromis marlieri* (66), *Lamprologus attenuatus* (67), *L. brichardi* (68), *L. callipterus* (69), *L. compressiceps* (70), *L. hecqui* (71), *L. pleuromaculatus* (72), *Lestredea perspicax* (73), *L. stappersia* (74), *Limnochromis auritus* (75), *Limnotilapia dardenii* (76), *Lobochilotes labiatus* (77), *Neolamprologus calliurus* (78), *N. furcifer* (79), *N. modestus* (80), *N. mondabu* (81), *N. savoryi* (82), *N. sexfasciatus* (83), *N. werneri* (84), *Ophthalmotilapia* sp. (85), *Paracyprichromis nigripinnis* (86), *Petrochromis polyodon* (87), *Plecodus paradoxus* (88), *Simochromis diagramma* (89), *Telmatochromis dhonti* (90), *Trematocara stigmaticum* (91), *T. unimaculata* (92), *T. variabile* (93),*Triglichromis otostigma* (94), *Tropheus moorii* (95), *Tylochromis polylepis* (96), *Xenochromis hecqui* (97), *Xenotilapia longispinis* (98), *X. melanogenys* (99), *X. ochrogenys* (100), *X. ornatipinnis* (101), *X. sima* (102), *Aulonocara ethylwynnae* (103), *A. jacobfreibergi* (104), *Buccochromis atritaeniatus* (105), *Champsochromis caeruleus* (106), *Chilotilapia euchilus* (107), *C. rhodesii* (108), *Copadichromis chrysonotus* (109), *C. flavimanus* (110), *C. mloto* (111), *C. quadrimaculatus* (112), *C. trimaculatus* (113), *C. virginalis* (114), *Cyathochromis obliquidens* (115), *Cynotilapia afra* (116), *Dimidiochromis compressiceps* (117), *D. dimidiatus* (118), *D. strigatus* (119), *Diplotaxodon argenteus* (120), *Fossorochromis rostratus* (121), *Genyochromis mento* (122), *Hemitilapia oxyrhynchus* (123), *Labeotropheus fuelleborni* (124), *L. trewavasae* (125), *Labidochromis chisumulu* (126), *L. textilis* (127), *L. vellicans* (128), *Lethrinops altus* (129), *L. auritus* (130), *L. christyi* (131), *L. furcifer* (132), *L. lethrinus* (133), *L. parvidens* (134), *L. polli* (135), *L.* sp. (136), *Maravichromis guentheri* (137), *M. lateristriga* (138), *M. orthognathus* (139), *M. sphaerodon* (140), *M. spilostichus* (141), *Melanochromis auratus* (142), *M. johanni* (143), *M. vermivorus* (144), *Nimbochromis linni* (145), *N. livingstoni* (146), *N. polystigma* (147), *N. venustus* (148), *Nyassachromis eucinostomus* (149), *N. leuciscus* (150), *Oreochromis shiranus* (151), *Otopharynx argyrosoma* (152), *O. decorus* (153), *O. heterodon* (154), *O. intermedius* (155), *O. nitidus* (156), *O. pictus* (157), *O. speciosus* (158), *O. tetraspilus* (159), *O. tetrastigma* (160), *Petrotilapia genelutea* (161), *P.* sp. (162), *P. tridentiger* (163), *Placidochromis electra* (164), *P.* johnstoni gold (165), *P. longimanus* (166), *Protomelas fenestratus* (167), *P. kirki* (168), *P. similis* (169), *P. spilopterus* (170), *P. taeniolatus* (171), *P. triaenodon* (172), *P. virgatus* (173), *Pseudotropheus aurora* (174), *P. elegans* (175), *P. elongatus* (176), *P. livingstoni* (177), *P. lombardi* (178), *P. zebra* (179), *Rhamphochromis esox/leptosoma* (180), *R.* sp. (181), *Stigmatochromis woodi* (182), *Taeniochromis holotaenia* (183), *Tramitochromis brevis* (184), *T. variabilis* complex (185), *Trematocranus placodon* (186), *Paratilapia polleni* (187), *Paretroplis polyactis* (188), *Ptychochromis oligacanthus* (189).

Table 2. Variables important in sensory ecology of cichlids were derived from the ecological classification of each species based on a review of the literature

Prey speed	
Slow	grazer/picker, rock grazer, epiphyte and plant eater, phytoplanktivore, detritivore, pharyngeal crushing molluscivore, oral crushing – oral shelling molluscivore, sand sifting insectivore
Medium	zooplanktivore, fatlipped insectivore, other insectivore
Fast	piscivore, scale eater, paedophage
Prey size	
Small	phytoplanktivore, zooplanktivore, detritivore
Medium	pharyngeal crushing molluscivore, oral crushing – oral shelling molluscivore, sand sifting insectivore, rock grazer, grazer/picker, fatlipped insectivore, other insectivore, paedophage
Large	piscivore, scale eater, epiphyte and plant eater
Habitat turbidity	
Turbid	all microhabitats in Victoria, shallow mud/vegetation habitats in Malawi and Tanganyika
Medium	shallow sand habitats in Malawi and Tanganyika
Clear	shallow rock habitats in Malawi and Tanganyika
Spatial habitat complexity	
Complex	shallow rock, shallow vegetation
Medium	deep, shallow sand, shallow mud
Simple	medium depth (pelagic)

Measurements

We examined a total of 216 adult specimens (table 1), representing 82 genera and 189 species from Lakes Malawi (n = 100), Tanganyika (n = 58) and Victoria (n = 55), and the island of Madagascar (n = 3). The majority of specimens were obtained from collections at the American Museum of Natural History, the Museum of Comparative Zoology and the Smithsonian Institution [detailed information in van Staaden et al., 1995]. Despite differences in age and method of preservation, most specimens were in good to excellent condition, and we assumed that shrinkage from preservation and subsequent dehydration was similar across tissues. Though suitable for measurement of gross features, preservation methods were inadequate to permit meaningful histological sectioning.

Standard length, head length, maximum body depth and maximum body width were measured to the nearest 0.01 mm using digital calipers. The diameter of the eye was measured along the nasal-temporal axis to the nearest 0.01 mm. The skull was opened dorsally under a dissecting microscope and the entire brain removed. Dorsal, ventral and lateral views of the brains were videotaped, the images digitized (Data Translation DT2255-60Hz or MacVision) and 35 different measurements taken from each brain using morphometric software [Microquant, R. Huber unpubl.]. Measurements for length, width, height and shape of olfactory bulb, telencephalon, optic tectum, hypothalamus, hypophysis, cerebellum, and dorsal medulla (combined octavolateralis nuclear complex, facial and vagal lobes) are detailed in van Staaden et al. [1995].

Linear measurements of the length, width and depth of the various structures were translated into volumetric measures (V) using an ellipsoid model:

$$V = \frac{1}{6} \pi abc$$

where a represents the length, b the width, and c the depth of the respective structure. Eye volume was estimated as a half sphere of the measured eye diameter (ED)

$$V = \frac{1}{12} \pi ED^3$$

A large proportion of our specimens were rare, and they were often part of small collections, due to the severe environmental threats brought upon many of these species in the wild. Considerable damage is done to these specimens during brain removal, and it was therefore not possible to use multiple individuals for every species. In a previous paper we judged intraspecific differences minor compared to interspecific variation [van Staaden et al., 1995], and individual data were averaged for nine species where more than one specimen was available.

Analysis

Extensive use has been made of multivariate statistical techniques, as any study investigating the complex relationships between brain morphology and ecological variables is necessarily constrained by many significant variables with unknown mutual dependencies.

Removal of Body Size. Considerable controversy exists over the effects of body size and allometries and methods for their adequate removal [see Sneath and Sokal, 1973]. To detect and control for these effects our null hypothesis is one of size-correlated constancy of shape [Strauss, 1984]. There is little consensus regarding the optimal methods for removing size effects, and the application of several common techniques yielded virtually identical results in this study [van Staaden et al., 1995]. Our method of choice used Principal Components Analysis (PCA) to estimate a combined size/shape variable from individual body length, width and height measures. The PCA extracted one main axis, explaining in excess of 92% of the variance contained in these size measures and presumably representing body size. Linear regression analysis was then performed for the volumes of log-transformed brain regions onto this size/shape estimate, and their residuals were used in all further analyses.

Brain Morphology Differences Among Microhabitats, of Varied Feeding Styles, and Lakes. Multivariate Analysis of Variance

(MANOVA) was used to test hypotheses concerning the effects of lake and ecology on brain morphology. Two-way complete model MANOVAs were performed for the size corrected volumes of all structures with (1) lake and microhabitat and (2) lake and feeding type as treatment factors. In all univariate tests we performed a priori orthogonal contrasts comparing Victoria to the rift lakes (Malawi and Tanganyika) and the rift lakes to each other. A priori orthogonal contrasts of different microhabitats were also used to compare deep-water species with all others, species of medium depth with shallow-water species, shallow rocky substrates with other shallow substrates, and species living over mud and in vegetation to those living over sand. A third set of a priori orthogonal contrasts analyzed feeding types with species capturing mobile prey (fish, insects, plankton) compared to those feeding on relatively immobile food items (molluscs, plants), species feeding on large mobile items (fish) vs. small mobile food (insects, plankton), insect vs. plankton feeders, and plant vs. mollusc feeders. The lack of independence between the individual treatment factors and the fact that some overlap between feeding and microhabitat was unavoidable during species selection means that it is difficult to estimate the exact contribution of each single variable. Hence we assigned brain differences to those variables producing the best fit.

Brain Characteristics of Species with Different Ecological Backgrounds. Discriminant Function Analysis (DFA) was used to identify those brain structures that best distinguish among species differing in feeding type or microhabitat. Performing this analysis on size-corrected measures, rather than using body size as a predictor, gains little [Baron and Jolicoer, 1980] but is used here to facilitate direct comparison with results obtained from other methods.

Sensory Ecology as a Force in Brain Evolution. A set of variables with presumed importance for sensory ecology, such as habitat turbidity, prey size and prey agility, and spatial habitat complexity, was derived from the ecological classification of the species (table 2). Based on information from the literature, each species was further classified as utilizing either a narrow or a broad spectrum of food items. For each particular brain region, Multiple Linear Regression Analysis [Procedure REGRESSION, SPSS Inc., 1988] identified those variables that best explained these differences.

Results

Morphological variation in African cichlid brains is extensive, and a few selected examples are featured in figure 2. The three lakes, differences in feeding strategy, and variation in microhabitat use all related significantly to patterns in brain structure (table 3). The most prominent effects were contributed by feeding type, microhabitat use, and their interactions with lake, while lake-specific patterns alone reached significance by only a narrow margin. Univariate analyses of each separate structure, with a priori contrasts, indicated that the smaller eyes of the Victoria species, compared to those of the two rift lakes, were largely responsible for these differences. Fishes of different feeding types (table 4) were characterized by size differences in several brain structures: piscivores had larger olfactory bulbs and optic tecta than insectivores and zooplanktivores; increased eye size was characteristic of piscivores, planktivores, and insectivores compared to molluscivores and plant eaters. The inclusion of microhabitat use (table 5) accounted for several differences: the telencephalon increased in size from deep to shallow water; eye size was larger in medium depth compared to shallow species, where eye size was smallest over rocky substrates and largest over sand; the optic tectum was smallest in species from deep habitats and largest in medium depth species; the cerebellum was largest in medium depth (pelagic) species; and the size of the gustatory sensory lobe increased from rocky to sandy substrates, with species over mud being intermediate.

Multiple Discriminant Function Analysis (DFA) was used to further characterize these patterns in brain structure with respect to ecological function. The DFA for feeding type identified two significant sources of brain differentiation (table 6) cumulatively accounting for 86% of the variance. The first axis (DF1) summarized predominantly visual structures and featured a prominent negative association between eye size and optic tectum. Inspection of the canonical centroid plot (fig. 3a) demonstrated a separation of large-eyed insect and plankton feeders from piscivores, who have enlarged optic tecta. A second significant separation was accomplished along an axis (DF2) characterized by an inverse size relationship between eyes on the one

Table 3. The effects of lake, feeding type, and microhabitat use on overall brain morphology were estimated using separate two-way MANOVAs with lake and feeding type or lake and microhabitat as treatment factors

Source	df	F	P
Lake and feeding type			
Model	91,944	3.187	0.000***
Lake	14,300	1.741	0.047*
Feeding type	28,542	2.563	0.000***
Lake × feeding type	56,813	2.260	0.000***
Lake and microhabitat			
Model	91,775	2.843	0.000***
Lake	14,246	1.861	0.031*
Microhabitat	28,445	4.818	0.000***
Lake × microhabitat	56,668	1.904	0.000***

As not all feeding types were present within each microhabitat, data precluded the use of a complete model three way analysis of Variance. Univariate tests for each brain structure separately are reported in tables 4 and 5. Abbreviations are degrees of freedom (df), Wilk's Lambda (F), level of significance (P). *$0.01 < p \leq 0.05$, ***$p < 0.001$.

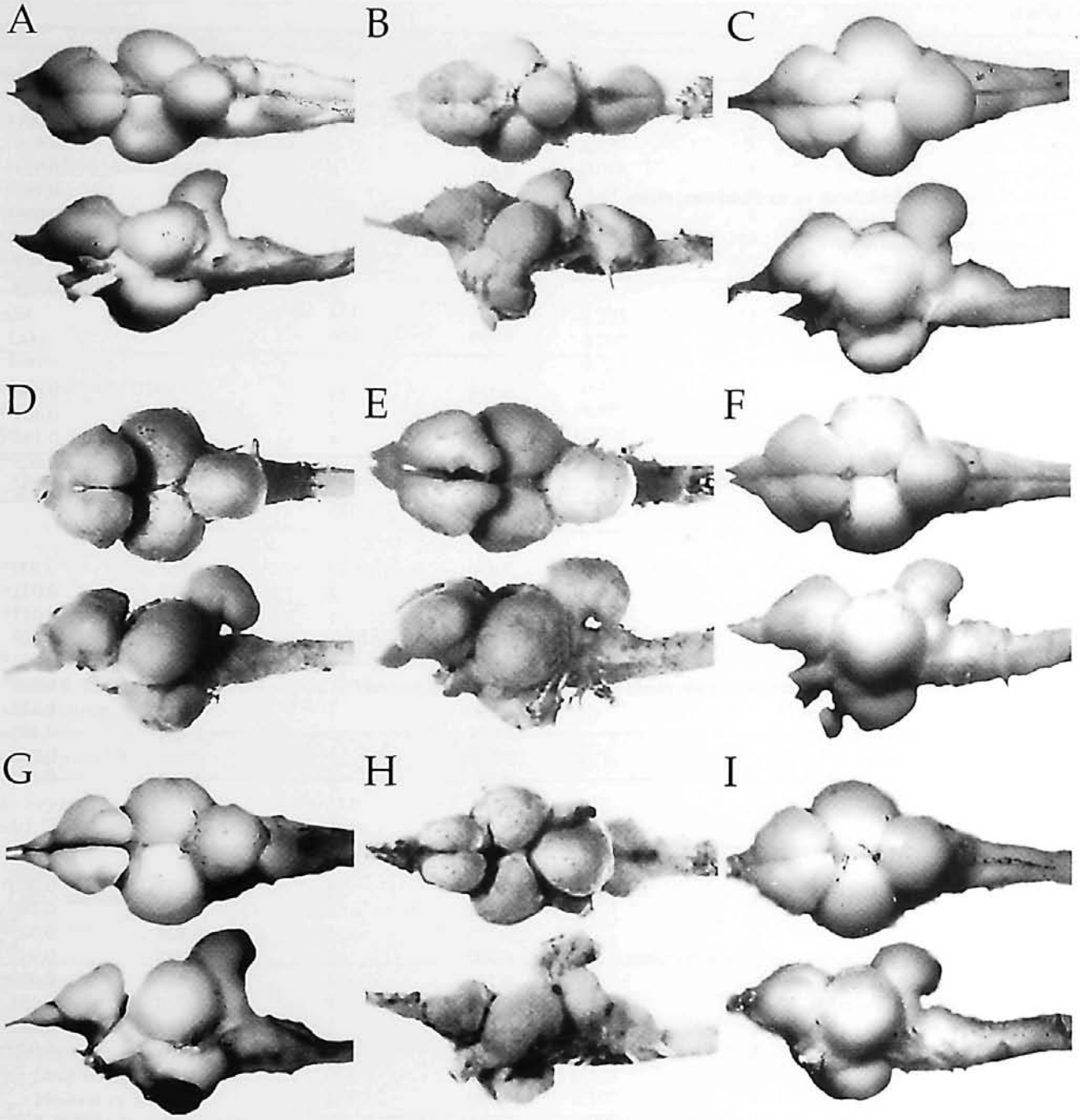

Fig. 2. Digitized brain images of representative cichlids differ in the relative size of most structures: **A** *Xenotilapia ornatipinnis* (shallow sand, sand-sifting insectivore) with enlarged taste lobes; **B** *Maravichromis lateristriga* (shallow vegetation, sand-sifting insectivore) where lateral line and taste centers form separate bulges in the dorsal medulla; **C** *Chilotilapia rhodesii* (shallow mud, oral-crushing molluscivore); **D** *Simichromis diagramma* (shallow rock, grazer/picker) exhibits enlarged telencephalic lobes similar to those of **E**, **F** and **I**; **E** *Labeotropheus fuelleborni* (shallow rock, grazer); **F** *Protomelas similis* (shallow vegetation, feeding on higher plants); **G** *Maravichromis orthognathus* (medium depth, paedophage), **H** *Bathybates minor* (medium depth, piscivore) with prominent lateral line centers; **I** *Haplochromis nyereri* (shallow rock, zooplanktivore).

Table 4. Results of univariate Analyses of Variance (ANOVAs) with a priori contrasts and lake, feeding type, and their interaction as treatment effects

Source of variation	SS	df	F or t	P
Olfactory bulb				
Model	1.628	14	2.167	0.011*
Lake	0.069	2	0.645	0.526
Feeding type	0.641	4	2.985	0.021*
Fish, insectivore, planktivore vs. molluscivore, plants	0.065	1	–1.103	0.282
Fish vs. insectivore, planktivore	0.432	1	2.838	0.005**
Insectivore vs. planktivore	0.129	1	1.549	0.124
Molluscivore vs. plants	0.002	1	0.165	0.869
Lake × feeding type	0.725	8	1.690	0.105
Error	8.156	152		
Total	9.784	166		
Telencephalon				
Model	0.719	14	2.336	0.006**
Lake	0.040	2	0.918	0.401
Feeding type	0.137	4	1.556	0.188
Lake × feeding type	0.512	8	2.915	0.005**
Error	3.758	171		
Total	4.476	185		
Eye				
Model	2.496	14	4.557	0.000***
Lake	0.311	2	3.973	0.021*
Malawi, Tanganyika vs. Victoria	0.229	1	2.419	0.017*
Malawi vs. Tanganyika	0.105	1	–1.639	0.103
Feeding type	0.663	4	4.237	0.003**
Fish, insectivore, planktivore vs. molluscivore, plants	0.363	1	3.045	0.003**
Fish vs. insectivore, planktivore	0.090	1	–1.517	0.131
Insectivore vs. planktivore	0.041	1	–1.028	0.305
Molluscivore vs. plants	0.115	1	1.714	0.088
Lake × feeding type	0.587	8	1.874	0.067
Error	6.691	171		
Total	9.188	185		
Optic tectum				
Model	0.703	14	2.967	0.000***
Lake	0.047	2	1.401	0.249
Feeding type	0.258	4	3.808	0.005**
Fish, insectivore, planktivore vs. molluscivore, plants	0.000	1	–0.072	0.943
Fish vs. insectivore, planktivore	0.206	1	3.487	0.000***
Insectivore vs. planktivore	0.050	1	–1.726	0.051
Molluscivore vs. plants	0.001	1	–0.199	0.842
Lake × feeding type	0.398	8	2.886	0.005**
Error	2.877	170		
Total	3.580	184		
Hypothalamus				
Model	0.489	14	1.563	0.095
Lake	0.028	2	0.635	0.531
Feeding type	0.183	4	2.042	0.091
Lake × feeding type	0.304	8	1.700	0.102
Error	3.556	159		
Total	4.045	173		

Table 4. *(cont.)*

Source of variation	SS	df	F or t	P
Cerebellum				
Model	0.854	14	2.289	0.007**
Lake	0.178	2	3.343	0.038*
Malawi, Tanganyika vs. Victoria	0.159	1	2.445	0.016*
Malawi vs. Tanganyika	0.028	1	–1.031	0.430
Feeding type	0.197	4	1.846	0.122
Lake × feeding type	0.512	8	2.400	0.018*
Error	4.505	169		
Total	5.359	183		
Dorsal medulla				
Model	1.373	14	1.338	0.192
Lake	0.207	2	0.247	0.247
Feeding type	0.254	4	0.868	0.485
Lake × feeding type	0.438	8	0.747	0.650
Error	10.921	149		
Total	12.294	163		

Abbreviations are degrees of freedom (df), level of significance (P); *$0.01 < p \leq 0.05$; **$0.001 < p \leq 0.01$; ***$p \leq 0.001$.

Table 5. Results of univariate Analyses of Variance (ANOVAs) with a priori contrasts and lake, microhabitat use, and their interaction as treatment effects

Source of variation	SS	df	F or t	P
Olfactory bulb				
Model	0.533	14	0.626	0.626
Lake	0.014	2	0.114	0.892
Microhabitat	0.318	4	1.306	0.270
Lake × microhabitat	0.185	8	0.380	0.930
Error	9.250	152		
Total	9.784	166		
Telencephalon				
Model	2.649	14	2.071	0.016*
Lake	0.002	2	0.040	0.961
Microhabitat	0.259	4	2.890	0.024
Deep vs. medium, shallow	0.129	1	–2.405	0.017*
Medium vs. shallow	0.102	1	–2.132	0.035*
S. rock vs. S. mud, vegetation, sand	0.002	1	0.325	0.745
S. sand vs. S. mud, vegetation	0.011	1	0.714	0.476
Lake × microhabitat	0.336	8	1.878	0.067
Error	3.827	171		
Total	4.476	185		
Eye				
Model	3.667	14	8.113	0.000***
Lake	0.992	2	15.363	0.000***
Malawi, Tanganyika vs. Victoria	0.747	1	4.811	0.000***
Malawi vs. Tanganyika	0.382	1	–3.438	0.001***

Table 5. *(cont.)*

Source of variation	SS	df	F or t	P
Microhabitat	1.435	4	11.114	0.000***
Deep vs. medium, shallow	0.082	1	1.596	0.112
Medium vs. shallow	0.503	1	3.948	0.000***
S. rock vs. S. mud, vegetation, sand	0.317	1	3.133	0.002**
S. sand vs. S. mud, vegetation	0.213	1	–2.570	0.011*
Lake × microhabitat	1.128	8	4.369	0.000***
Error	5.521	171		
Total	9.188	185		
Optic tectum				
Model	0.466	14	1.818	0.040
Lake	0.064	2	1.738	0.179
Microhabitat	0.294	4	4.013	0.004**
Deep vs. medium, shallow	0.110	1	–2.450	0.015*
Medium vs. shallow	0.155	1	2.913	0.004**
S. rock vs. S. mud, vegetation, sand	0.019	1	–1.027	0.306
S. sand vs. S. mud, vegetation	0.036	1	–1.408	0.161
Lake × microhabitat	0.164	8	1.117	0.354
Error	3.114	170		
Total	3.580	184		
Hypothalamus				
Model	0.200	14	0.589	0.871
Lake	0.029	2	0.598	0.551
Microhabitat	0.022	4	0.231	0.921
Lake × microhabitat	0.182	8	0.939	0.486
Error	3.846	159		
Total	4.045	173		
Cerebellum				
Model	0.749	14	1.961	0.024
Lake	0.112	2	2.061	0.131
Microhabitat	0.370	4	3.389	0.011*
Deep vs. medium, shallow	0.035	1	–1.131	0.260
Medium vs. shallow	0.293	1	3.276	0.001***
S. rock vs. S. mud, vegetation, sand	0.082	1	–1.728	0.086
S. sand vs. S mud, vegetation	0.050	1	–1.348	0.179
Lake × microhabitat	0.350	8	1.605	0.127
Error	4.610	169		
Total	5.359	183		
Dorsal medulla				
Model	4.042	14	5.213	0.000***
Lake	0.209	2	1.890	0.155
Microhabitat	2.657	4	11.992	0.000***
Deep vs. medium, shallow	0.000	1	–0.006	0.995
Medium vs. shallow	0.041	1	0.863	0.390
S. rock vs. S. mud, vegetation, sand	1.453	1	5.123	0.000***
S. sand vs. S. mud, vegetation	0.218	1	–1.982	0.049*
Lake × microhabitat	1.093	8	2.467	0.015*
Error	8.252	171		
Total	12.294	185		

Due to small sample sizes, species living in shallow water over mud or in vegetation were lumped. Abbreviations are degrees of freedom (df), level of significance (P); *$0.01 < p \leq 0.05$; **$0.001 < p \leq 0.01$; ***$p \leq 0.001$.

Table 6. Canonical discriminant functions and standardized function coefficients for brain measures grouped according to feeding type

	DFA 1	DFA 2	DFA 3	DFA 4
χ^2	85.183***	37.011**	13.164	5.140
df	28	18	10	4
Eigenvalue	0.425	0.192	0.061	0.039
% variance explained	59.36	26.77	8.49	5.38
Olfactory bulb	–0.371	0.054	0.306	0.353
Telencephalon	0.440	**–0.553**	**–0.692**	0.147
Eye	**0.652**	**0.773**	–0.163	–0.040
Optic tectum	**–0.885**	**0.465**	**0.610**	–0.411
Hypothalamus	0.281	–0.045	–0.330	**0.707**
Cerebellum	–0.221	0.315	–0.254	0.262
Dorsal medulla	0.268	**–0.616**	**0.733**	0.344

Values above 0.45 were considered large and are highlighted. In addition, a centroid plot of this analysis is shown in figure 3a. Abbreviations are degrees of freedom (df), discriminant function axis (DFA); $^{**}0.001 < p \leq 0.01$; $^{***}p \leq 0.001$.

Table 7. Canonical discriminant functions and standardized function coefficients for brain measures grouped according to microhabitat

	DFA 1	DFA 2	DFA 3	DFA 4
χ^2	104.912***	59.696***	21.299*	3.667
df	28	18	10	4
Eigenvalue	0.394	0.326	0.138	0.027
% variance explained	44.50	36.80	15.62	3.08
Olfactory bulb	0.401	–0.133	**0.563**	**0.642**
Telencephalon	**0.472**	**–1.054**	0.219	**–0.483**
Eye	0.213	0.383	–0.138	0.046
Optic tectum	0.189	**0.943**	**0.792**	0.113
Hypothalamus	–0.165	–0.166	**–0.942**	**0.653**
Cerebellum	**–0.875**	0.233	0.155	**–0.654**
Dorsal medulla	**0.894**	0.046	–0.089	–0.306

Values above 0.45 were considered large and are highlighted. In addition, a centroid plot of this analysis is shown in figure 3b. Abbreviations are degrees of freedom (df), discriminant function axis (DFA); $^{*}0.01 < p \leq 0.05$; $^{***}p \leq 0.001$.

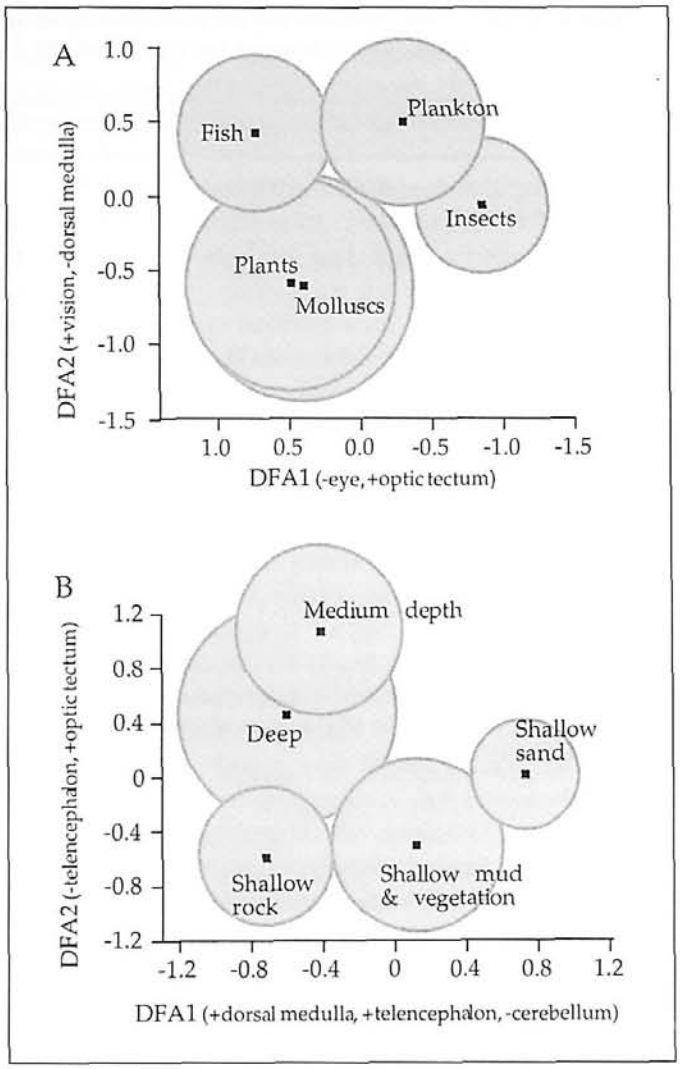

Fig. 3. Results of discriminant function analyses summarized as canonical centroid plots with centroids for ecological groups and respective 95% confidence intervals. Euclidan distances separating centroids and the overlap of confidence limits depicts differentiation in multivariate space. **A** Feeding type analysis separated insectivore brains with a moderate development of most structures, planktivores with enlarged eyes, piscivores with large optic tecta, and species feeding on plants and molluscs with a similar increase in taste components. **B** Microhabitat separated shallow-water species with large telencephala from pelagic and deep-water cichlids. Moreover, species on sand exhibited characteristically large taste centers. Interpretation of discriminant function axes (DFA1, DFA2) is based on data presented in tables 6 and 7.

Table 8. Multiple linear regression analysis of individual brain regions with independent variables relating to microhabitat (depth, turbidity, spatial complexity) and feeding strategies (prey speed and size, feeding specificity) was performed on a restricted data set containing only haplochromine cichlids

Structure	R^2	df	F	Variables in equation	p. reg.	Beta	t
Olfactory bulb	0.089	1,135	13.103***	prey size	0.105	0.297	3.620***
Telencephalon	0.097	2,146	7.829***	depth	−0.073	−0.309	−3.811***
				prey speed	0.030	0.157	1.944
Eye	0.177	3,145	10.402***	habitat turbidity	−0.072	−0.282	−3.596***
				spatial habitat complexity	−0.061	−0.189	−2.375*
				prey size	−0.050	−0.159	−2.066*
Optic tectum	0.105	3,144	5.644**	prey speed	0.043	0.246	2.979**
				depth	−0.042	−0.197	−2.299*
				habitat turbidity	−0.031	−0.184	−2.155*
Hypothalamus				no significant variables			
Cerebellum	0.150	3,144	8.498***	habitat turbidity	−0.074	−0.365	−4.380***
				depth	−0.048	−0.188	−2.250*
				prey speed	0.043	0.222	2.713**
Gustatory sensory lobe	0.213	4,130	8.809***	prey speed	−0.116	−0.356	−4.369***
				habitat turbidity	−0.010	−0.312	−3.565***
				depth	−0.096	−0.247	−2.672**
				spatial habitat complexity	−0.061	−0.156	−1.715

Backward elimination was used to identify subsets of variables that serve as predictors of the respective brain region volume. Abbreviations are coefficient of determination (R^2), degrees of freedom (df), partial regression coefficient (p. reg.), Beta coefficient (Beta), $*0.01 < p \leq 0.05$; $**0.001 < p \leq 0.01$; $*** p \leq 0.001$.

hand and telencephalon and dorsal medulla on the other. Plankton feeders and piscivores, for whom vision presumably plays an important role during prey capture, scored highly positive, while species feeding on molluscs and plants were highly negative, indicating a relative reduction in visual structures and relative enlargement of those associated with taste (fig. 3a).

When species were grouped according to preferred microhabitat, size differences in individual brain structures revealed three significant discriminant axes (table 7), explaining virtually all of the variation (97%). A size reduction of the cerebellum, paralleled by an increase in the size of the telencephalon and dorsal medulla, accounts for the first axis (DF1). This axis (fig. 3b), presumably representing swimming ability, separated the species associated with mud and sand (highly negative scores) from those with a more pelagic or rock-bound existence (positive values). The second axis (DF2) was dominated by an inverse size relationship of telencephalon and optic tectum, with species living in complex habitats created by shallow rock and vegetation featuring a large telencephalon, whereas pelagic and deep-dwelling species possessed large optic tecta. Hypothalamus, optic tectum, and olfactory bulb all contribute to DF3, which separates predominantly deep-water species from all others.

Multiple linear regression equations for individual brain structures were constructed with independent variables related to microhabitat (depth, habitat turbidity, spatial complexity) and feeding strategies (prey speed and size, feeding specificity). In a restricted data set of haplochromine cichlids only, the ecological variables accounted for significant amounts of size variation in all structures except the hypothalamus (table 8) ranging from 21.3% for sensory areas of the dorsal medulla to 8.9% for the olfactory bulbs. Prey maneuverability proved significant for the cerebellum, optic tectum, telencephalon, and lateral line/taste centers; the size of the prey related to eye size, and olfactory bulb; depth contributed to eyes, telencephalon, cerebellum and dorsal medulla; habitat turbidity accounted for eyes, optic tectum, cerebellum, and medulla; and habitat complexity influenced eyes and medulla.

Discussion

African Great Lake cichlids are characterized by differences in size and shape of their component brain structures that cannot be explained by simple allometric relationships or developmental constraints [Finlay and Darlington,

1995]. Ecological and behavioral parameters accounted for significant amounts of variation in virtually every part of these cichlid brains and provided clear evidence for the existence of a close link between brain morphology and fine-scale ecological functionality of the species, such as feeding strategy or preference for a particular microhabitat. Such multivariate trends in brain structure relating to ecology are in accord with a series of recent studies using similar approaches on other teleost taxa [Kotrschal et al., 1990; Huber and Rylander, 1992a; Schellart and Prins, 1993]. Diversification of basic cyprinid brain morphology, with moderately developed visual centers, involves either an enlargement of areas for chemosensation (taste brains) in benthivorous or turbid water species, or an enlargement of areas for octavolateralis reception (lateral line brains) which is predictive of plankton or surface-feeeding [Kotrschal and Palzenberger, 1992]. Parallel changes in the size of specific brain parts related to ecological adaptations have also been observed in a variety of terrestrial vertebrates, including birds [Healy and Guilford, 1990; Krebs, 1990], and several mammalian families [Armstrong et al., 1987; Gittleman, 1991; Barton and Dean, 1993].

Sensory capacities in combination with species-specific search procedures have responded over evolutionary time to the identity, characteristics, distribution, and abundance of prey for any given habitat [Hyatt, 1979]. Ancestral cichlids were presumably riverine insectivores, most closely approximated in the present data set by the Madagascar specimens. Our data suggest that two distinct forces have shaped the evolution of vision in East African cichlids, each leading to a characteristic brain morphology. Visual performance is optimized towards either increased resolving power or superior motion perception. Planktivore and detritivore species displayed a prominent hypertrophy of the eyes. This is in agreement with some previous observations [Kotrschal et al., 1990] but contrary to Dullemeijer and Barel [1977] who concluded that relative eye size is a character that remains stable among species. All else being equal, large eyes carry a higher number of receptor cells per visual angle, and psychophysical experiments confirm an increased resolving power [van der Meere, 1986; Fernald, 1988; Schellart, 1992]. The alternative strategy of superior motion detection was shown in piscivores, who hunt fast moving prey. Motion processing is largely the domain of the optic tectum, where many of the cells are direction sensitive [Guthrie, 1990]. Piscivorous cichlids were characterized by particularly large optic tecta, in contrast to the much smaller tecta of cichlids feeding on stationary or slow-moving food items. These tectal differences were closely paralleled by variation in cerebellum size, hinting that the ability to detect fast moving prey is combined with the facility to pursue and capture them. Such contrasting morphologies, with presumed differences in sensory performance, are the proximal manifestations of the evolution of trophic specialization [Hyatt, 1979].

Visual conditions of the habitat explain large amounts of variation in the structure of cichlid brains. Our data show that both water turbidity and depth significantly impact brain morphology, particularly the size of visual structures. Linear relationships between water clarity or depth and the development of eyes, tectum, cerebellum, and several other structures were evident. Previous authors had concluded that at least some of these aspects do not impact brain structures and eye size [Branson, 1979; Schellart and Prins, 1993], but our findings are concordant with studies on North American cyprinids in which several correlations of turbidity and gross brain structure were detailed [Huber and Rylander, 1992a]. Our results are also consistent with corresponding knowledge of the histology of the optic tectum [Huber and Rylander, 1991] and ultrastructure of the optic nerve [Huber and Rylander, 1992b].

Visual structures exhibited enhanced development in Tanganyika and Malawi, both highly transparent rift lakes with lower water column productivity, compared to those from more turbid Victoria. We postulate that visual capabilities have been proportionately favored in the evolution of rift lake cichlids, with greater relative eyes compared to their counterparts in Victoria. Also, the age of the species flocks of Tanganyika and Malawi compared to that of monophyletic and relatively young Victoria may explain an abundance of 'extreme' morphotypes [Mayr, 1984]. A detailed analysis of lake effects on cichlid brain evolution is to be found in van Staaden et al. [1995]. Investigations of the ecological and evolutionary significance of mammalian brain size [e.g., Jerison, 1973; Pagel and Harvey, 1988; Harvey and Krebs, 1990] have shown associations with many behavioral, ecological and life-history factors, including diet, social behavior, locomotion, home range size, and activity cycles (e.g., Eisenberg and Wilson, 1978; Clutton-Brock and Harvey, 1980; Mace et al., 1981]. Residence in complex habitats appears to favor the development of large brains in mammals [Mace et al., 1981] and fish [Bauchot et al., 1977, 1989]. In this context, it is singularly interesting that cichlids living among reeds and within rocky crevices (constrained in three spatial dimensions) exhibited large brains, whereas species over sand and mud (two dimensions) were intermediate, and pelagic species proved relatively small-brained (1-way ANOVA, $F=5.992^{**}$). The only component structure closely matching this pattern was the telencephalon, suggesting that this structure may, at

least in part, contribute to the ability to subsist in a spatially structured environment. Although the forebrain had proven the most variable brain region in this cichlid data set [van Staaden et al., 1995], few ecological or biogeographical variables proved of explanatory value. A relationship between this multi-modal association center and the challenges of spatial complexity in the environment is rational in the context of brain development in birds or mammals. We predict that a dedicated analysis of structural patterns in cichlid telencephala, incorporating behavioral criteria such as territoriality, pair formation, and communication abilities, will provide new and interesting experimental models for aspects of higher brain function.

Although this study successfully associated several ecological conditions with specific patterns in brain structure, additional insight may have accrued had other factors that impact the sensory space of the species been included. For example, cichlids are remarkable, not only in terms of the level of trophic specialization achieved but also with regard to the degree of flexibility and adaptability with which single species utilize a variety of different foods. It is perhaps more accurate to think of trophic specialization in any one species of fish as a locus of exceptional talent in an otherwise broad spectrum of competencies. Indeed, over their lifetimes most fish change the main components of their diet as they themselves increase in size and are able to handle new forms of prey [Keenleyside, 1979; Fernald, 1988; Kotrschal et al., 1990]. Further complexities in trophic patterns stem from the fact that many species are highly opportunistic, varying their diets quickly to capitalize on ephemeral prey. Species usually considered food specialists have, on closer examination, been found to routinely incorporate into their diets items from several trophic levels [Fishelson, 1977], consistent with theories of adaptations in other fish systems [Kotrschal, 1988, 1989]. Moreover, the need to perform a variety of social decisions, such as with whom to mate, and how to minimize one's own vulnerability during feeding [Kamil, 1988], may greatly impact the sensory space of a species. A further difficulty might involve brain regions that are heterogeneous with respect to function, as it is difficult to separate evolutionary progressions and regressions of multiple neighboring functions which may mask each other [Jolicoeur et al., 1984].

It is likely that structural variability in fish brains is determined by local environmental conditions, as well as by mechanisms that are genetically fixed [Davis and Miller, 1967], but the exact contribution of each is not known and most likely not constant. Rearing some species of cichlids under extreme environmental conditions changed ultrastructural and functional variables but had little effect on the gross morphological development of brain structures [Zeutzius et al., 1984] or some peripheral sense organs [Münz, 1986]. In contrast, relative eye size in cyprinids has been shown to be largely dependent on habitat conditions during development [A. Peschel and K. Kotrschal, personal communication].

The presence of prominent morphological differences in gross brain structure among cichlids of different ecological backgrounds suggests that this anatomical pattern extends also to a functional level. The need to elucidate the rules that translate into differences in actual performance cannot be overstated [Davis and Miller, 1967]. Psychophysical determination of sensory performance in animals raised under controlled environmental conditions should contribute valuable insights concerning the relationship between form and function, as well as the significance of ontogenetic influences. We need to determine whether these size differences represent different spatial-temporal fidelity, sensitivity, or filter properties, and to confirm the biological role of various structures in field and laboratory experiments. Ecomorphologists frequently ask if the form-function complex is optimized with respect to its biological roles. If significant associations between form and function are weak or lacking, it would be worth identifying the relevant contraints on function and their biological consequences. Ultimately, variability in multiple levels of brain structure and the associated potential for behavioral plasticity, may, even in fish, prove more interesting than linear structure-function correlations.

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