Long-Term Habituation to Spatial Novelty in Blind Cave Fish (*Astyanax hubbsi*): Role of the Telencephalon and its Subregions

Gernot Riedel¹

Institut für Zoologie
Abteilung III, Johannes Gutenberg Universität
D-55099 Mainz, Germany

Abstract

Blind cave fish, when released into a novel environment, show a typical exploratory behavior characterized by high swim speed along walls shortly after release. This behavior wanes during prolonged exposure and thus may reflect habituation to novelty. As the hippocampus of mammals, which plays a crucial role in spatial learning, is part of the telencephalon, the possible involvement of this brain structure of fish was investigated in exploratory behavior. Ablation of the whole telencephalon or bilateral removal of dorsal parts of the hemispheres reduced activity; in contrast, unilateral lesions of one hemisphere, bilateral lesions of dorsal and dorsoventral parts, and removal of olfactory bulbs increased activity. However, the time course of habituation in a novel environment remained unchanged, except for ablated animals in which there was virtually no habituation in swim speed. These data suggest that the telencephalon of fish may not participate in long-term habituation to spatial novelty but, rather, support the notion of the telencephalon being involved in generation of arousal.

Introduction

Spatial information about the natural environment is important for some fish species. Aronson (1951), for example, observed that when gobies

(*Bathygobius soporator*) were stranded in small tide pools by the receding tide, they jumped from one small pool to the next, which they were unable to see, until they reached the open sea. Spatial knowledge is acquired during exploration of the pools while the tide is in (Aronson 1971). Learning of spatial relationships between objects has also been reported in other fish species such as goldfish (Ingle and Sahagian 1973; Pitcher and Magurran 1983; Warburton 1990; Rodriguez et al. 1994), grunts (Helfman et al. 1982; Helfman and Schultz 1984), and siamese fighting fish (Roitblat et al. 1982). Training procedures, however, were based on various visual cues. Although blind cave fish *Astyanax hubbsi* respond to moving visual stimuli (Teyke and Schaerer 1994), their visual system is greatly reduced (Voneida and Sligar 1976; Voneida and Fish 1984). The major sensory system contributing to spatial information in *A. hubbsi* thus appears to be the lateral line system, by which obstacles and pressure differences are detected (Hassan 1985, 1989; Teyke 1989).

Blind cave fish show a characteristic exploratory behavior when released into unknown surroundings (Teyke 1985, 1989). Shortly after release, fish tend to explore the novel environment with a high swim speed that is accompanied by swimming preferentially along the edges of the tank. The swim speed declines to a minimum within ~6–8 hr, and fish then spend equal amounts of time exploring both center and boundary structures of the tank. Duration of exploration depends on the shape of the tank, with complex tanks (providing more readily discriminable regions) being learned faster (Teyke 1989). Apparently, this performance optimally stimulates lateral line organs, provides maximal information about the environment, and may reflect habituation to novelty.

Lateral line organs are well developed in blind cave fish (Teyke 1990) and consist, as in many

¹Present and corresponding address: Center for Neuroscience, University of Edinburgh, Edinburgh, EH8 9LE, UK.

other teleosts, of numerous freestanding and a limited number of canal-standing neuromasts. There is evidence for a role in object discrimination (von Campenhausen et al. 1981; Weissert and von Campenhausen 1981), but more recent work implicates freestanding neuromasts in the detection of velocity of water movements (Montgomery et al. 1997). Thus, it seems possible that lateral line organs may provide important sensory input for spatial orientation in blind cave fish. What remains to be determined, however, are the brain areas involved in this behavior. One likely candidate is the telencephalon, which may include the fish homolog of the mammalian hippocampus.

Ascending fibers conveying both lateral line sensory and auditory information into the telencephalon have been reported in various fish species (Finger 1980; Boord and McCormick 1984; Ehteler 1985; Bleckmann et al. 1987), and terminals as well as evoked potentials of lateral line afferents have been identified in Dm and Dc of the hemispheres (Finger 1980; Bleckmann et al. 1987).

The function of the telencephalon in fish as studied mainly by lesion and stimulation experiments remains elusive. What is clear, however, is that it plays a role in various forms of behavior, such as avoidance learning (Hainsworth et al. 1967; Overmier and Gross 1974), instrumental conditioning if the reinforcer is temporally or spatially separated from the learned response (Savage 1969; Flood and Overmier 1971), habituation (Peeke et al. 1972; Rooney and Laming 1986), and spatial learning (Warren 1961; Frank et al. 1972). In all these reports, lesions of the telencephalon caused an impairment in learning. However, the spatial tasks needed prolonged training and were difficult. More recently, telencephalic lesions in goldfish have provided evidence for a role in allocentric, but not egocentric, spatial learning and memory (Salas et al. 1996a,b) suggesting that the telencephalon of fish, or at least part of it, may serve similar functions in cognitive mapping as has been proposed for the mammalian hippocampus (O'Keefe and Nadel 1978).

This present report investigates a simple form of naturally occurring spatial learning. Using lesion techniques, the role of the telencephalon and its distinct subregions in long-term exploration to novelty was examined by addressing the following questions: (1) Is the telencephalon of blind cave fish involved in habituation to spatial novelty? (2) What are the behavioral consequences of olfactory bulb lesions? (3) Do distinct regions of the telen-

cephalon have different functions in spatial orientation?

Materials and Methods

SUBJECTS

In this study, 39 blind cave fish (*A. hubbsi*) bought from a local dealer were used. They were 4.5–7.5 cm in size and of both genders. Although raised in groups of 15–20 individuals, the fish were housed individually while in the experiments. The home tanks were 20 × 30 × 30 cm (length × width × height) and filled with tap water maintained at room temperature ($21 \pm 2^\circ\text{C}$), and animals were fed food tablets ad lib every other day.

Fish were randomly assigned to six different groups (for details, see Surgery and Histology): group SL, sham lesioned ($n = 6$); group FBL, telencephalic ($n = 8$); group OB, olfactory bulbectomy ($n = 6$); group DL, lesions of the dorsal part of the hemispheres ($n = 7$); group DVL, lesions of dorsal and dorsoventral parts of the hemispheres ($n = 6$); and group UL, unilateral lesion of either the right or left hemisphere ($n = 6$).

SURGERY AND HISTOLOGY

To immobilize the fish, they were slowly cooled down with ice water (4°C) until they showed no signs of active movements. This approach was used because pilot studies have suggested that animals recover faster from hypothermia compared with conventional anesthesia. Then, the mouth was carefully fixed on a hollow glass tube through which a continuous flow of ice water provided sufficient oxygen for normal opercular activity. The body was kept under water and was further stabilized in a foam holder with the gills free.

Under binocular control, a circular groove was drilled into the skull above the brain; the central flap was then lifted so that it remained attached caudally for later replacement and fixation. Sham-lesioned subjects received no further treatment; the flap of the skull was put back in place and sealed with tissue glue (Histoacryl; Braun Melsungen, Germany). For the lesion groups, the superficial tissue was removed, so that individual brain regions were visible, and lesions were made using

bent, fine ophthalmic scissors and small forceps. Ablations (FBL) were achieved by two vertical cuts, directly behind the telencephalic hemispheres and through the olfactory tract, respectively. The telencephalon was then removed by suction. Similar surgery procedures were used for lesions of the olfactory bulbs (OB) and unilateral ablation of one hemisphere (UL). Careful superficial cuts through the hemispheres resulted in more restricted lesions (DL and DVL).

All operated animals were subsequently returned to their home tanks and were allowed to recover for 10–15 days before further experiments were conducted. The cap formed by the tissue glue remained in place until the bone disc was firmly sealed and fell off shortly thereafter.

Upon termination of the experiments, histological analysis was performed to verify the lesions. Animals were sacrificed by brief immersion in ice water; brains were then quickly removed, fixed in picric acid for 3–5 days, and embedded in paraffin; and sections were cut on a rotary microtome. Coronal sections (20 μ m) were finally stained with cresyl violet acetate, and the lesion size was reconstructed by projecting sections onto corresponding sections of a reference brain.

APPARATUS AND BEHAVIORAL PROCEDURES

Exploratory behavior of blind cave fish in an unfamiliar environment was recorded as described elsewhere (Hassan et al. 1992). In brief, a rectangular tank (19 $\times$ 28 cm, water depth 10 cm, and temperature $\sim$ 21°C) was placed in a room evenly illuminated from below through an opaque glass plate. A video camera monitored the fish, and the signal was transmitted to a computer (Basis 108) that recorded the position of the center of the fish. Coordinates were stored in intervals of 0.5 sec during the first 15 min of each hour for 16 hr. Two main measures were taken: (1) swim speed (V), as an average of the speed in each 15 min period; and (2) location factor (K), which, for data analysis, subdivided the tank into a peripheral and in a central compartment of equal size. The location factor was calculated as

$$K = \frac{\text{time in periphery} - \text{time in center}}{\text{time in periphery} + \text{time in center}}$$

with $K = +1$ reflecting 100% swimming in the periphery and $K = -1$ reflecting 100% swimming in center.

To prevent damage of the cupulae of the lateral line system, fish were transferred to the experimental tank under water in small containers. They were tested twice: First, a control measurement was recorded with the untreated fish. Second, they were recorded again postlesion; this within-subject design allowed the use of the preoperative behavior of each fish as its own control.

STATISTICS

Statistical comparison between groups was performed using analysis of variance (ANOVA). Comparison of the different phases (pre- vs. postoperative) between and within groups was calculated by ANOVA with repeated measures. As an index of habituation, the 16-hr measurement was divided into blocks of 4 hr each, and a statistical analysis was performed comparing the pooled data of the first and last 4-hr of each session.

Results

HISTOLOGY

The general anatomical organization of the telencephalon of teleost fish has been reviewed previously (Nieuwenhuys 1963; Northcutt and Braford 1980; Northcutt and Davis 1983), and the telencephalon of blind cave fish is constructed similarly consisting of two major parts, a dorsal (D) and a ventral (V) one, both having further subdivisions (Riedel 1997).

Upon reconstruction of the lesion sites, our histological material supported a classification of fish into six lesion groups. Sham-lesioned animals showed normal brains and, in particular, an intact telencephalon. Figure 1 summarizes the anatomical data for the other groups and gives typical representatives of lesions for each group. Ablation (FBL) resulted in a complete loss of both olfactory bulbs and telencephalic hemispheres (Fig. 1A). In contrast, removal of the olfactory bulbs (OB) did not damage other telencephalic regions (Fig. 1B). Mainly dorsal aspects of the hemispheres were removed in animals of group DL (Fig. 1C); olfactory bulbs remained intact. Both dorsal and dorsoventral regions were damaged in animals of group DVL (Fig. 1D), but again, olfactory bulbs remained normal. Only one hemisphere (including the olfactory bulb) was removed in animals of group UL (Fig. 1E).

Figure 1: Histological reconstruction of telencephalic lesions in blind cave fish. Typical examples of lesion sites were given. (A,B) Lateral view of the brain of blind cave fish. The hatched area shows the lesion site consisting of either telencephalon and olfactory bulbs (A) or olfactory bulbs (B). (C–E) Coronal sections through the telencephalon of lesioned animals (extent of lesion, in black, was evaluated comparing the brain of the lesioned fish to the matching control brains). In group DL (C), only dorsal parts (black) of the telencephalon were damaged bilaterally. Both dorsal and dorsoventral regions of the telencephalon were lesioned in group DVL (D). Unilateral ablation of one hemisphere, here the left one, also resulted in removal of one olfactory bulb (E).

BEHAVIOR

When fish were released into their home tanks after surgery, they would slowly sink to the ground, where they lay for ~15 min. Then, they slowly started swimming, in small circles and later along the walls, often bumping into the walls. Within a day, they fully recovered and swam normally in their home environment. In a separate study, it has been shown that fish with telencephalic ablation can normally discriminate between the frequency of two spheres vibrating at different frequency (Platt 1991). These results support the notion that telencephalon-lesioned fish can swim and learn a discrimination task not differently to

controls.

The results of behavioral measurements of this study are summarized for all groups in Figures 2 and 3 for swim speed (V) and location factor (K), respectively. Because the preoperative data were not different between groups, I explored the effects by comparing the pre- and postoperative performance in the first and last 4 hr of testing for each group. The results are shown in Figure 4.

PREOPERATIVE PERFORMANCE

Released into the test tank, all animals showed normal exploration as described previously (Teyke

Figure 2: Comparison between pre- and postoperative swim speed (V) for all groups as a function of time after release into the experimental tank. Only means are shown for the sake of clarity. (A) Preoperative data. Shortly after release, V is high and declines over time. This behavioral pattern is similar in all groups, and statistical analysis revealed no differences. (B) Postoperative data. Whereas sham-lesioned (SL) animals showed no difference compared with the preoperative phase, lesions of the whole telencephalon, or parts of it, caused differences in exploration. Note that telencephalic (FBL, ●) fish showed reduced and nearly no change in swim speed during the recording time. Partial lesions, on the other hand, induced hyperactivity. (OB, ◇) Olfactory bulbectomy; (DL, △) lesion of dorsal parts; (DVL, ○) lesions of dorsal and dorsoventral parts; (UL, ▽) unilateral lesion.

Figure 3: Comparison between pre- and postoperative location factor (K) for all groups as a function of time after release into the experimental tank. Only means are shown for the sake of clarity. (A) Preoperative data. Shortly after release, K is high and declines over time. This behavioral pattern is similar in all groups, and statistical analysis revealed no differences. (B) Postoperative data. Sham-operated (SL) animals showed no difference compared with the preoperative phase, but lesions caused subtle differences in exploration. (For abbreviations and symbol designation, see legend to Fig. 2).

1989; Hassan et al. 1992). The results for V are summarized in Figure 2A indicating a similar swimming pattern in all groups. Blind cave fish started with a high V immediately after release into the experimental tank, which declined throughout the measurement.

To calculate habituation, the swimming pattern in the first 4 hr was pooled and compared with the last 4 hr. For V, an overall ANOVA with group and time (first vs. last 4 hr) as factors revealed no main effect of group [$F(5,33) = 1.4$, $P > 0.05$] and no group-by-time interaction [$F(5,33) = 2.2$, $P > 0.05$]. There was, however, a significant main effect of time [$F(1,33) = 50.5$, $P < 0.0001$] confirming that habituation had occurred.

Similar results were obtained for K, which is high shortly after release and continuously declines during recording (Fig. 3A). That the groups did not differ was confirmed statistically with no main effect of group ($F < 1$) and no interaction between group and time ($F < 1$). Habituation, however, was observed as indicated by a main effect of time [$F(1,33) = 26.4$, $P < 0.0001$].

POSTOPERATIVE PERFORMANCE

After recovery, animals were again released into the test tank. Figure 2B summarizes the results for V for all groups recorded after surgery. As is obvious, substantial differences in exploration between groups were found. This impression was confirmed statistically. An overall ANOVA for the postoperative V with group and time as factors revealed significant main effects of group [$F(5,33) = 5.2$, $P < 0.01$] and of time

Figure 4: Effect of lesions on habituation to novelty. Summarized are the results for all lesion groups comparing pre- and postoperative data pooled for the first (hr 1–4) and last (hr 13–16) 4 hr of recording. Mean and S.E.M. not shown for sake of clarity. Each graph represents one group and combines the results for swim speed, V [V preoperative (■) and postoperative (●)]; and location factor, K [K preoperative (□) and postoperative (○)]. (A) Sham lesions; (B) forebrainless group; (C) olfactory bulb lesions; (D) dorsal hemisphere lesioned; (E) dorsal plus dorsoventral hemisphere lesioned; (F) unilateral ablation.

[$F(1,33) = 42.5$, $P < 0.0001$] confirming habituation but no interaction [$F(5,33) = 1.7$, $P > 0.05$]. Likewise, K (Fig. 3B) was significantly different postoperatively between groups [$F(5,33) = 8.4$, $P < 0.0001$] and time [$F(1,33) = 34.4$, $P > 0.0001$]. Again, no interaction was found [$F(5,33) = 1.7$, $P < 0.05$]. These data suggest that complete or partial forebrain lesions cause severe alterations in exploratory activity. These differences occurred in swimming velocity and location factor and also, although not significantly, affected the rate of decline of the swim speed.

GROUP SL

Figure 4A shows the performance in a novel environment of fish that underwent sham operations. Sham operations did not alter the exploratory behavior, and the reduction in activity between the first and the last 4 hr of measurement was not different compared with prelesion controls. Statistical comparison revealed no significant main effect of treatment [V: $F(1,5) = 1.7$, $P > 0.05$; K: $F < 1$], and no interaction between time of recording and treatment (V: $F < 1$; K: $F < 1$). There was, however, a significant main effect of time [V: $F(1,5) = 15.4$, $P < 0.05$; K: $F(1,5) = 17.1$, $P < 0.01$], confirming the appearance of habituation pre- and postoperatively. Thus, sham operations did not alter exploration in blind cave fish.

GROUP FBL

Complete bilateral removal of the telencephalon including olfactory bulbs had severe effects on performance. As compared with preoperative control data, FBL animals reduced both V and K (Fig. 4B) after the operation. ANOVA with repeated measures and treatment and time as factors confirmed significant main effects of pre- and postcomparison [V: $F(1,7) = 35.4$, $P < 0.001$; K: $F(1,7) = 43.8$, $P < 0.001$] and of time [V: $F(1,7) = 27.7$, $P < 0.01$; K: $F(1,7) = 28$, $P < 0.01$], but no interaction [V: $F(1,7) = 5.25$, $P > 0.05$; K: $F < 1$]. These data indicate that, although FBL animals drastically reduce V, there is some habituation, but V may be so low that a floor effect has occurred.

GROUP OB

In contrast to FBL fish, bilateral ablation of

olfactory bulbs, and thereby deprivation of olfactory input, had opposite effects. Immediately after release into the test tank, postoperative performance of OB individuals was characterized by a more pronounced enhancement in V than in K (Fig. 4C). This enhancement was statistically significant only for V [$F(1,5) = 9.9$, $P < 0.05$], but not K [$F(1,5) = 4.6$, $P > 0.05$]. Likewise, there was a main effect of time for V [$F(1,5) = 7.6$, $P < 0.05$] but not K [$F(1,5) = 4.2$, $P > 0.05$], and no interaction [V: $F < 1$; K: $F < 1$]. Thus, OB animals increase V postoperatively without significantly changing K.

GROUP DL

Bilateral damage of dorsal aspects of telencephalic hemispheres had opposite effects on postoperative behavior in a novel environment compared with the OB group. Compared with their preoperative performance, DL animals postoperatively swam with reduced V, but K remained unchanged (Fig. 4D). This was confirmed statistically, because there was a main effect of treatment for V [$F(1,6) = 8.8$, $P < 0.05$] but not for K [$F < 1$]. Although a main effect of time was observed for both measures [V: $F(1,6) = 67.3$, $P < 0.001$; K: $F(1,6) = 11.6$, $P < 0.05$], no interaction between these two factors was obtained [V: $F(1,6) = 1.6$, $P > 0.05$; K: $F(1,6) = 2.9$, $P > 0.05$], suggesting that habituation did not differ comparing pre- and postlesion data.

GROUP DVL

Compared with preoperative control data, animals with more extensive damage of especially dorsoventral aspects of the telencephalon showed a significant postoperative increase in V [$F(1,5) = 27.6$, $P < 0.01$] and K [$F(1,5) = 6$, $P < 0.05$], as depicted in Figure 4E. The appearance of habituation was confirmed for both measures [V: $F(1,5) = 119$, $P < 0.001$; K: $F(1,5) = 9.7$, $P < 0.05$], but no interaction between treatment and time point of recording was obtained [V: $F(1,5) = 1.5$, $P > 0.05$; K: $F < 1$]. These results suggest that postoperative habituation is similar compared with preoperative control measurements, but general levels of activity are increased.

GROUP UL

Because no behavioral differences between

animals with right or left hemispheric lesions were observed, they are considered together in one group. Lesions of one hemisphere caused a pronounced postoperative increase in both V and K (Fig. 4F), which was significantly different compared with prelesion data [V: $F(1,5) = 20.8$, $P < 0.01$; K: $F(1,5) = 13.3$, $P < 0.05$]. There was also a significant main effect of time for each measure [V: $F(1,5) = 7.1$, $P < 0.05$; K: $F(1,5) = 4.9$, $P < 0.05$], but no interaction [V: $F(1,5) = 2.9$, $P > 0.05$; K: $F < 1$]. Thus, UL animals do not alter exploration to novelty but, as shown for other lesions before, increase activity.

Discussion

Results of this lesion study are summarized in Table 1. It is surprising that partial lesions that include the major olfactory centers of the telencephalon (groups OB, DVL, and UL) lead to increases in both swim speed and location factor. In contrast, complete removal of the telencephalon including olfactory bulbs significantly reduced behavioral activity. However, these alterations did not affect the ability of habituation to the novel environment in any group, as confirmed by statistical analysis. It was only after telencephalic ablation that a reduced, although not significantly, rate of decline in swim speed was obtained (Fig. 4B).

THE ROLE OF THE TELENCEPHALON IN HABITUATION

Habituation of nonspatial responding in telencephalic fish has been studied with mixed results. Ten minutes of exposure of goldfish to live brine shrimps confined in a clear plastic tube caused predatory responses, and these bites waned during the test session. Ablation of the telencephalon resulted in normal within-session habituation but virtually no savings between days (Peeke et al. 1972), suggesting deficits in long-term rather than short-term habituation to feeding responses. However, if repeatedly exposed to startle stimuli, telencephalic goldfish also showed impaired within-session habituation (Laming and McKee 1981; Laming and Emis 1982). Similarly, when presented with the mirror image of a conspecific, telencephalon-ablated male Siamese fighting fish (*Betta splendens*) showed less habituation compared with controls (Shapiro et al. 1974; de Bruin 1980), suggesting deficits in short-term habituation.

Habituation of exploration in blind cave fish

Table 1: Summary diagram of lesion effects on swim speed (V) and location factor (K) in blind cave fish

Lesion site	Change pre- vs. postablation	
	V	K
SL	no change	no change
FBL	↓	↓
OB	↑	↑
DL	↓	no change
DVL	↑	↑
UL	↑	↑

Summary of the behavioral changes of complete or partial lesions of the telencephalon on both swim speed and location factor monitored in a novel environment for 16 hr. Arrows indicate either an increase (↑) or a decrease (↓). For abbreviations, see Materials and Methods.

has been studied previously (Teyke 1985, 1988, 1989). It is different from the traditional spatial habituation of rats in that it lasts for an extended time period that may preclude a direct comparison. Moreover, this long-term habituation is not fatigue, because transfer of the animal into another environment after 4–5 hr resulted in normal exploration (Teyke 1989). However, effects of telencephalon lesions have not been investigated. Although various parts of the telencephalon were lesioned, no differences in habituation, that is, waning of exploratory activity, were obtained. Ablation of the telencephalon in blind cave fish significantly reduced swim speed compared with preoperative control measurements, but statistical analysis of the data did not give a significant treatment by time interaction, indicating that some habituation has occurred after the ablation. Although normal habituation was found for the location factor, ablated fish tended to remain more in the center of the tank than in its periphery. The data, however, strongly suggest a reduction in general activity in *A. hubbsi* after complete, but not partial, lesion of the forebrain.

The observation that telencephalic fish are less active in novel environments is in accordance with data from Davis et al. (1978) showing similar effects in paradise fish (*Macropodus opercularis*). In *Macropodus*, surfacing for air was recorded as an index of activity. Telencephalon-ablated fish showed significant suppression of surfacing, but exploration was not recorded in paradise fish. Moreover, experimental tanks have been rather simple and could easily be investigated visually by

Macropodus, and selective lesions of the dorsal part of the telencephalon in paradise fish had no effect. In contrast, blind cave fish of the DL group showed a reduction in activity, suggesting that dorsal parts of the hemisphere may be differently involved in various forms of behavior.

In contrast to visual orientation in paradise fish, information about the environment is acquired predominantly by activation of the lateral line system in *A. hubbsi* (Teyke 1988; Hassan 1992a,b, 1993). By increasing swim speed, the hydrodynamic stimulus at freestanding neuromasts is supposed to increase (Hassan 1985), and this may improve the perception of environmental features. Behavioral activity in unfamiliar surroundings, that is, high activity after release progressively decreasing to lower levels, has been cited as evidence for the flow-field hypothesis (Teyke 1988).

Partial lesions of the telencephalon, which included Dm and Dc (group DL), led to a marginal reduction in swim speed but did not cause an impairment in long-term habituation. It is thus possible that flow-field perception per se and habituation might be related but are two different processes: one dealing with the actual perception and the other one dealing with memory formation.

Similarly, bilateral ablation of the olfactory bulbs, which did not disrupt ascending lateral line input, did not alter habituation. The data, however, provide evidence for a potential role of smell in the modulation of activity in blind cave fish. Selective lesions of dorsal and dorsoventral parts of the telencephalon (group DVL) had similar effects. Because these areas in *A. hubbsi* receive massive input from the olfactory bulbs (Riedel and Krug 1997), this is further evidence for the importance of olfactory input in general activity, rather than in habituation. Finally, habituation to various startle stimuli in goldfish also does not require olfactory input (Rooney and Laming 1984).

ON THE ROLE OF THE TELENCEPHALON IN FISH

Various learning paradigms have been applied to elucidate the possible role of the telencephalon in fish, but habituation and spatial learning have received little attention. Telencephalon-ablated blind cave fish showed reduced exploratory behavior in the experimental tank. Similar deficits in motivation have been reported previously in goldfish (Janzen 1933), minnows (Hosch 1936), green sunfish (Hale 1956a,b), and cichlids (Ribbink 1972).

The nature of this deficit can most easily be explained in terms of the hypothesis that the telencephalon of fish may serve as an “activator” or “energizer” of lower brain centers (Aronson 1948; Kaplan and Aronson 1967). It is thus conceivable that the telencephalon determines the level of arousal of the animals. Telencephalic fish should show reduced motivation, which would result in reduced exploration of the tank.

A variety of investigations have confirmed that telencephalon-ablated fish exhibit exaggerated defensive reactions (for review, see Davis and Kassel 1983), which may also be responsible for decreases in aggressive behavior (de Bruin 1980; Davis and Kassel 1983). Hyperdefensiveness can be long lasting and may result in extreme flight reactions to pursuit by the investigator's hand (Hosch 1936). In their home tanks, telencephalic blind cave fish showed prolonged violent zig-zag swimming when startled by the experimenter knocking on the front glass of the tank. Hyperdefensiveness could result in enhanced suppression of behavior, induced by placement into a novel environment for example (Shapiro et al. 1974; Davis et al. 1978). This would mean that telencephalon-ablated blind cave fish should show reduced activity, and this is in agreement with the hypothesis that the forebrain regulates the balance between excitatory and inhibitory neural circuits (Segaar 1965; Ribbink 1972).

Whether olfactory input to the forebrain modulates activity requires further investigations. However, if such input would inhibit activity, one would predict that the availability of olfactory cues reduces levels of activity and, possibly as a by-product, may lead to faster habituation. In fact, preliminary findings support this notion. Blind cave fish ($n = 3$), released into a test tank, in which an odor was provided on one side, started with reduced swim speed and habituated within 2–3 hr. No lesions have been tested so far, and it would be interesting to see how distinct lesions of telencephalon regions affect exploration with olfactory cues present.

COMPARISON TO THE MAMMALIAN HIPPOCAMPUS

Although there is no conclusive anatomical evidence for which part of the fish telencephalon may correspond to the hippocampus, the present study was conducted to examine whether the telencephalon, or parts of it, may be a hippocampal

analog according to its behavioral role. Hippocampal lesions in rodents have been shown to induce behavioral deficits in habituation to novelty. When subjected to an open field, lesioned animals normally show increased activity, which is maintained for hours; hippocampal animals do not habituate compared with controls (for review, see O'Keefe and Nadel 1978). Because the time course between habituation in rats and blind cave fish is very different, a direct comparison may be rather inconclusive.

However, the role of the mammalian hippocampus has also been assessed in various other paradigms, and impairments in spatial tasks have been reported consistently (Morris et al. 1982). Deficits were reported mainly for allocentric spatial learning, and recent work on goldfish shows similar impairments after removal of the telencephalon (Salas et al. 1996a,b). Egocentric spatial learning, however, remains unaffected by ablations, and the time to find the reward was only marginally altered. Thus, it seems possible that, provided blind cave fish have established a spatial cognitive map, this map may be based on egocentric rather than allocentric information. Memory stored in terms of egocentric spatial relationships would not be affected by telencephalic ablation (Salas et al. 1996a,b). This requires further testing.

CONCLUSION

This is the first study that has used a naturally occurring behavior to determine the function of the telencephalon in fish. Aspiration lesions have caused behavioral alterations when animals were tested for habituation to a novel environment. Data fail, however, to support any role of the forebrain of blind cave fish in long-term habituation to spatial novelty, that is, waning of exploratory activity over hours. The reason why the telencephalon might not participate in this form of learning remains to be investigated; as a mere speculation, I would imagine that knowledge about surroundings is essential information for *A. hubbsi* that is processed in lower brain centers such as the tectum or tegmentum, for example.

On the other hand, the data provide clear evidence for a role of the fish forebrain in the modulation of general activity. Smell may be important in the case of *A. hubbsi*, because selective lesions of either the olfactory bulbs or the projection areas of olfactory fibers within the telencephalon re-

sulted in hyperactivity. In contrast, telencephalic animals showed reduced activity.

Acknowledgments

This work was performed under the guidance of Prof. C. von Campenhausen. His help, continuous encouragement, and constructive criticism was very much appreciated. I also wish to thank Mrs. M. Grosz, Mr. W. Hoch, and Mr. J. Altmeier for expert technical assistance, as well as the Drs. B. Platt and E.M. Macphail for helpful critical comments on an earlier version of this manuscript. This research was supported in part by scholarships from the Landes-Graduerten-Foerderung-Gesetz (LGFG) (Rheinland Pfalz, Germany) and the University of Mainz to G.R.

The publication costs of this article were defrayed in part by payment of page charges. This article must therefore be hereby marked "advertisement" in accordance with 18 USC section 1734 solely to indicate this fact.

References

- Aronson, L.R. 1948. Problems in the behavior and physiology of a species of African mouthbreeding fish. *Trans. N.Y. Acad. Sci.* **11**: 33–42.
- . 1951. Orientation and jumping behavior in the gobiid fish *Bathygobius soporator*. *Amer. Mus. Nov.* **1486**: 1–22.
- . 1971. Further studies on orientation and jumping behavior in the gobiid fish, *Bathygobius soporator*. *Ann. N.Y. Acad. Sci.* **188**: 378–392.
- Bleckmann, H., T.H. Bullock, and J. M. Jorgensen. 1987. The lateral line mechanoreceptive mesencephalic, diencephalic and telencephalic regions in the thornback ray, *Platyrrhinoidis triseriata*. *J. Comp. Physiol. A* **161**: 67–84.
- Boord, R.L. and C.A. McCormick. 1984. Central lateral line and auditory pathways: A phylogenetic perspective. *Am. Zool.* **24**: 765–774.
- Davis, R.E. and J. Kassel. 1983. Behavioral functions of the telencephalon. In *Fish neurobiology* (ed. R.G. Northcutt and R.E. Davis), pp. 237–263. University of Michigan Press, Ann Arbor, MI.
- Davis, R.E., R. Reynolds, and A. Ricks. 1978. Suppression behavior increased by telencephalic lesions in the teleost, *Macropodus opercularis*. *Behav. Biol.* **18**: 165–177.
- de Bruin, J.P.C. 1980. Telencephalon and behavior in teleost fish: A neuroethological approach. In *Comparative neurology of the telencephalon* (ed. S.O.E. Ebbesson), pp. 175–202. Plenum Press, New York, NY.
- Echteler, S.M. 1985. Organization of central auditory pathways in a teleost fish, *Cyprinus carpio*. *J. Comp. Physiol. A* **156**: 267–280.

Riedel

- Finger, T.E. 1980. Nonolfactory sensory pathways to the telencephalon in a teleost fish. *Science* **210**: 671–673.
- Flood, N.B. and J.B. Overmier. 1971. Effects of telencephalic and olfactory lesions on appetitive learning in goldfish. *Physiol. Behav.* **6**: 35–40.
- Frank, A.H., N.B. Flood, and J. B. Overmier. 1972. Reversal learning in telencephalon ablated and olfactory tract sectioned teleosts, *Carassius auratus*. *Psychonom. Sci.* **26**: 149–151.
- Hainsworth, F.R., J.B. Overmier, and C.T. Snowdon. 1967. Specific and permanent deficits in instrumental avoidance responding following telencephalon ablation in the goldfish. *J. Comp. Physiol. Psychol.* **63**: 111–116.
- Hale, E.B. 1956a. Social facilitation and telencephalon function in maze performance of green sunfish, *Lepomis cyanellus*. *Physiol. Zool.* **29**: 93–106.
- . 1956b. Effects of telencephalon lesions on the aggressive behavior of green sunfish, *Lepomis cyanellus*. *Physiol. Zool.* **29**: 107–127.
- Hassan, E.-S. 1985. Mathematical analysis of the stimulus for the lateral line organ. *Biol. Cybern.* **52**: 23–36.
- . 1989. Hydrodynamic imaging of the surroundings by the lateral line of the blind cave fish *Anoptichthys jordani*. In *The mechanosensory lateral line: Neurobiology and evolution* (ed. S. Coombs, P. Görner, and H. Münz), pp. 217–227. Springer, New York, NY.
- . 1992a. Mathematical description of the stimuli to the lateral line system of fish derived from a 3 dimensional flow field analysis: 1. The cases of moving in open water and of gliding towards a plane surface. *Biol. Cybern.* **66**: 443–452.
- . 1992b. Mathematical description of the stimuli to the lateral line system of fish derived from a 3 dimensional flow field analysis: 2. The case of gliding alongside or above a plane surface. *Biol. Cybern.* **66**: 453–461.
- . 1993. Mathematical description of the stimuli to the lateral line system of fish derived from a 3 dimensional flow field analysis: 3. The case of an oscillating sphere near the fish. *Biol. Cybern.* **69**: 525–538.
- Hassan, E.-S., H. Abdel-Latif, and R. Biebricher. 1992. Studies on the effects of Ca^{++} and Co^{++} on the swimming behavior of the blind mexican cave fish. *J. Comp. Physiol. A* **171**: 413–419.
- Helfman, G.S. and E.T. Schultz. 1984. Social transmission of behavioral traditions in a coral reef fish. *Anim. Behav.* **32**: 379–384.
- Helfman, G.S., J.L. Meyer, and W.N. McFarland. 1982. The ontogeny of twilight migration patterns in grunts (Pisces: Haemulidae). *Anim. Behav.* **30**: 317–326.
- Hosch, L. 1936. Untersuchungen über Grosshirnfunktionen der Elritze (*Phoxinus laevis*) und des Gründlings (*Gobio fluviatilis*). *Zool. Jahrb. Abt. Allg. Zool. Physiol.* **57**: 57–98.
- Ingle, D.J. and D. Sahagian. 1973. Solution of a spatial constancy problem by goldfish. *Physiol. Psychol.* **1**: 83–84.
- Janzen, W. 1933. Untersuchungen über Grosshirnfunktionen des Goldfisches (*Carassius auratus*). *Zool. Jahrb. Abt. Allg. Zool. Physiol.* **52**: 591–628.
- Kaplan, H. and L.R. Aronson. 1967. Effect of telencephalon ablation on the performance of a conditioned avoidance response in the teleost fish, *Tilapia macrocephala*. *Anim. Behav.* **15**: 438–448.
- Laming, P.R. and M. McKee. 1981. Deficits in habituation of cardiac arousal responses incurred by telencephalic ablation in goldfish, *Carassius auratus*, and their relation to other telencephalic functions. *J. Comp. Physiol. Psychol.* **95**: 460–467.
- Laming, P.R. and P. Emis. 1982. Habituation of fright and arousal responses in the teleosts, *Carassius auratus* and *Rutilus rutilus*. *J. Comp. Physiol. Psychol.* **96**: 460–466.
- Montgomery, J.C., C.F. Baker, and A.G. Carton. 1997. The lateral line can mediate rheotaxis in fish. *Nature* **389**: 960–963.
- Morris, R.G.M., P. Garrud, J.N.P. Rawlins, and J. O'Keefe. 1982. Place navigation impaired in rats with hippocampal lesions. *Nature* **297**: 681–683.
- Nieuwenhuys, R. 1963. The comparative anatomy of the actinopterygian telencephalon. *J. Hirnf.* **6**: 171–196.
- Northcutt, R.G. and M.R. Braford Jr. 1980. New observation on the organization and evolution of the telencephalon of actinopterygian fishes. In *Comparative neurology of the telencephalon* (ed. S.O.E. Ebbesson), pp. 41–98. Plenum Press, New York, NY.
- Northcutt, R.G. and R.E. Davis. 1983. Telencephalic organization in ray-finned fishes. In *Fish neurobiology* (ed. R.G. Northcutt and R.E. Davis), pp. 203–236. University of Michigan Press, Ann Arbor, MI.
- O'Keefe, J. and L. Nadel. 1978. *The hippocampus as a cognitive map*. Clarendon Press, Oxford, UK.
- Overmier, J.B. and D. Gross. 1974. Effects of telencephalic ablation upon nest-building and avoidance behavior in East African mouthbreeding fish, *Tilapia mossambica*. *Behav. Biol.* **12**: 211–222.
- Peeke, H.V.S., S.C. Peeke, and J.S. Williston. 1972. Long-term memory deficits for habituation of the predatory behavior in the telencephalon ablated goldfish, *Carassius auratus*. *Exp. Neurol.* **36**: 288–294.
- Pitcher, T.J. and A.E. Magurran. 1983. Shoal size, patch probability and information exchange in foraging goldfish. *Anim. Behav.* **31**: 546–555.

- Platt, B. 1991. "Die Rolle des Telencephalon beim Lernverhalten." Ph.D. thesis, Mainz, Germany.
- Ribbink, A.J. 1972. The behavior and brain function of the cichlid fish, *Hemihaplochromis philander*. *Zool. Africanis* **7**: 21–41.
- Riedel, G. 1997. The telencephalon of the blind cave fish *Astyanax hubbsi* (Characidae): I. General anatomy of the telencephalon. *Brain Behav. Evol.* **49**: 20–38.
- Riedel, G. and L. Krug. 1997. The telencephalon of the blind cave fish *Astyanax hubbsi* (Characidae): II. Projections of the olfactory bulb. *Brain Behav. Evol.* **49**: 39–52.
- Rodriguez, F., E. Duran, J.P. Vargas, B. Torres, and C. Salas. 1994. Performance of goldfish trained in allocentric and egocentric maze procedures suggests the presence of a cognitive mapping system in fishes. *Anim. Learn. Behav.* **22**: 409–420.
- Roitblat, H.L., W. Tham, and L. Golub. 1982. Performance of *Betta splendens* in a radial maze. *Anim. Learn. Behav.* **10**: 108–114.
- Rooney, D.J. and P.R. Laming. 1984. Effects of olfactory bulb ablation on cardiac and ventilatory arousal responses and their habituation in the goldfish. *Behav. Neural Biol.* **42**: 120–126.
- . 1986. Localization of telencephalic regions concerned with habituation of cardiac and ventilatory responses associated with arousal in the goldfish. *Behav. Neurosci.* **100**: 45–50.
- Salas, C., C. Broglio, F. Rodriguez, J.C. Lopez, M. Portavella, and B. Torres. 1996a. Telencephalic ablation in goldfish impairs performance in a spatial constancy problem but not in a cue one. *Behav. Brain Res.* **79**: 193–200.
- Salas, C., F. Rodriguez, J.P. Vargas, E. Duran, and B. Torres. 1996b. Spatial learning and memory deficits after telencephalic ablation in goldfish trained in place and turn maze procedures. *Behav. Neurosci.* **110**: 965–980.
- Savage, G.E. 1969. Some preliminary observations on the role of the telencephalon in food-reinforced behavior in the goldfish, *Carassius auratus*. *Anim. Behav.* **17**: 362–373.
- Segaar, J. 1965. Behavioral aspects of degeneration and regeneration in fish brain: A comparison with higher vertebrates. *Prog. Brain Res.* **14**: 143–231.
- Shapiro, S., H. Schuckman, D. Sussman, and A.M. Tucker. 1974. Effects of telencephalic lesions on the gill cover response in Siamese fighting fish. *Physiol. Behav.* **13**: 749–755.
- Teyke, T. 1985. Collision with and avoidance of obstacles by blind cave fish *Anoptichthys jordani* (Characidae). *J. Comp. Physiol. A* **157**: 837–843.
- . 1988. Flow field, swimming velocity and boundary layer: Parameters which affect the stimulus for the lateral line organ in blind fish. *J. Comp. Physiol. A* **163**: 53–61.
- . 1989. Learning and remembering the environment in the blind cave fish. *J. Comp. Physiol. A* **164**: 655–662.
- . 1990. Morphological differences in neuromasts of the blind cave fish *Astyanax hubbsi* and the sighted river fish *Astyanax mexicanus*. *Brain Behav. Evol.* **35**: 23–30.
- Teyke, T. and S. Schaerer. 1994. Blind mexican cave fish (*Astyanax hubbsi*) respond to moving stimuli. *J. Exp. Biol.* **188**: 89–101.
- von Campenhausen, C., I. Riess, and R. Weissert. 1981. Detection of stationary objects by the blind cave fish (*Anoptichthys jordani*). *J. Comp. Physiol. A* **143**: 369–374.
- Voneida, T.J. and C.M. Sligar. 1976. A comparative neuroanatomic study of retinal projections in two fishes: *Astyanax hubbsi* and *Astyanax mexicanus*. *J. Comp. Neurol.* **165**: 89–106.
- Voneida, T.J. and S.E. Fish. 1984. Central nervous system changes related to the reduction of visual input in a naturally blind fish (*Astyanax hubbsi*). *Am. Zool.* **24**: 775–782.
- Warburton, K. 1990. The use of local landmarks by foraging goldfish. *Anim. Behav.* **40**: 500–505.
- Warren, J.M. 1961. The effects of telencephalic injuries on learning paradise fish, *Macropodus opercularis*. *J. Comp. Physiol. Psychol.* **54**: 130–132.
- Weissert, R. and C. von Campenhausen. 1981. Discrimination between stationary objects by the blind cave fish *Anoptichthys jordani*. *J. Comp. Physiol. A* **143**: 375–381.

Received June 5, 1997; accepted in revised form February 27, 1998.

Long-term habituation to spatial novelty in blind cave fish (*Astyanax hubbsi*): role of the telencephalon and its subregions.

G Riedel

Learn. Mem. 1998, 4:

Access the most recent version at doi:[10.1101/lm.4.6.451](https://doi.org/10.1101/lm.4.6.451)

References

This article cites 55 articles, 2 of which can be accessed free at:
<http://learnmem.cshlp.org/content/4/6/451.full.html#ref-list-1>

License

Email Alerting Service

Receive free email alerts when new articles cite this article - sign up in the box at the top right corner of the article or [click here](#).