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Methods for chronic neural recording in the telencephalon of freely behaving fish

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Abstract

We have adapted for use in fish several of the procedures employed for recording single neuron activity in freely behaving rodents. Developing a method for single unit chronic recording in freely behaving fish was motivated by a need for a comparison across taxa of telencephalic neural activity evoked during spatial navigation by animals of their environments. However, the procedures outlined here can be modified easily for underwater recording from most aquatic species and from other brain areas. Under anesthesia, bundles of stereotrodes or tetrodes were implanted into the dorsolateral region of the goldfish or cichlid telencephalon. An infrared light emitting diode (LED) was also fixed to the fish's head at the time of surgery. After recovery from anesthesia, fish were allowed to swim freely within a large aquarium. Single unit activity was analyzed and correlated with stimulus conditions, behavior, and the location and movement of the LED recorded by a camera tracking system. The value of this technique is demonstrated by providing the first evidence in fish for navigation-related neural firing, including "place cells" that display location-specific discharge.

Keywords: Chronic recording; Cichlid; Goldfish; Place cell; Spatial navigation; Telencephalon

1. Introduction

In order to understand the broad principles of nervous system function, it is important not only to describe the processing and interactions of individual brain nuclei within a single species, but it is essential to compare and contrast neural systems across taxa. Thus, we have begun chronic recording studies of the telencephalon of cichlids and goldfish, so that we may compare and contrast neural mechanisms of spatial navigation in fish with what is known for rodents (e.g., Nakazawa et al., 2002; O'Keefe and Dostrovsky, 1971) and pigeons (Siegel et al., 2002). The hypothesis that fish use spatial representations of their environment is based upon behavioral observations of naturally occurring spatial behavior, laboratory testing of spatial navigation, and several lesion studies that suggest telencephalic involvement in spatial navigation (reviewed in Demski and Beaver, 2001).

We present here a summary of the procedures we have used for successful behavioral tracking and neural recordings made from multiple electrodes chronically implanted in freely swimming fish. Methods outlined here are modifications of those previously used by the authors for recording from fish (Canfield and Rose, 1993, 1996) and rats (Cooper and Mizumori, 2001; Leutgeb and Mizumori, 1999; Leutgeb et al., 2000; Mizumori and Williams, 1993; Mizumori et al., 1989). Electrode preparation is simple and economical. Data acquisition from multiple electrodes can range from simply correlating general stimulus or behavioral events with multiunit records, to correlating individual unit firing with unrestrained spontaneous behaviors, including an animal's position in a particular environment. Examples of such data are presented. To date, we have recorded several visual, movement-related, and spatial neural correlates including location-specific single unit firing that is similar to that seen from "place cells" (O'Keefe and Dostrovsky, 1971) found in rodents. The basic methods presented here can be adapted easily to other aquatic species (e.g., some invertebrates, other fish species, amphibians, etc.) and to other brain regions (e.g., auditory nuclei, electrosensory regions, etc.) in order to record other neural-behavioral correlates.

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2. Materials and methods

Similar procedures were used for recording from goldfish (*Carassius auratus*) and cichlids (*Haplochromis burtoni* and *Haplochromis callipterus*). In order to increase the chance that our initial attempts to record chronically from fish would yield navigational correlates, we targeted a specific region of the telencephalon because some authors suggest that there may be homology between regions of the fish and mammalian telencephalon. Northcutt and Davis (1983), based upon anatomical studies of projections and cell morphologies, proposed that the dorsolateral (Dl) region of the fish telencephalon may be homologous with the medial pallium (hippocampus) of mammals, and that the dorsomedial (Dm) region is homologous with the mammalian striatum. Other authors assert that even though there is no firm evidence of homology between these structures, there is a remarkably similar organization that may suggest similar (i.e., homoplastic) types of processing (Nieuwenhuys and Meek, 1990). Bradford (1995) suggests that Dm is homologous to the mammalian amygdala but Dl is similar to nonlimbic pallium. However, the idea that Dl is similar in function to the mammalian hippocampus is supported by evidence of increased transcription in neurons of the Dl but not Dm region in goldfish trained in a spatial task; neither the Dl or Dm region showed increased transcription in nonspatially trained control fish (Vargas et al., 2000). A recent double-dissociation lesion study (Portavella et al., 2002) showed that spatially- or temporally-contingent avoidance learning was impaired by Dl but not Dm lesions, whereas Dm but not Dl lesions impaired emotional learning. This pattern supports an argument for functional similarities between the hippocampus and Dl, and between the amygdala and Dm (Portavella et al., 2002). Based upon the collective evidence for its role in spatial processing, we targeted Dl region recordings for developing the methods outlined below. Fish chronic recording procedures were approved by the University of Washington IACUC.

2.1. Electrode preparation

We found that 20 μm diameter HML-insulated tungsten wire (California Fine Wire) worked well for recording from fish telencephalic neurons as it does in rodents (e.g., Mizumori et al., 1989); up to six electrode wires were implanted per hemisphere (see below). Wires were configured into pairs (“stereotrodes”) or groups of four (“tetrodes”) by bonding the wires together with Epoxylite (6001-M, Epoxylite Corp.), and baking at 350 °F degrees for 60 min. These bundles were then inserted and superglued into 1 cm long, 30 gauge stainless steel guide cannula so that the recording tips extended 1–1.5 mm past the cannula end. Guide cannulae were cut from stainless steel hypodermic tubing (Small Parts, Inc.) using a Dremel rotary tool and fine cut off wheel; the internal edges of the ends were de-burred using an 25 gauge syringe needle. Using superglue, two guide cannulae were first glued together. Then, as a unit, these were glued to a separate length of 30 gauge tubing which extended several centimeters past the back of the guide cannulae. This “post” cannula, removed after implantation (see below), served as a means to hold the electrode assemblies in an electrode holder mounted to a manipulator. The upper end of each tungsten wire electrode wire was stripped of insulation and then nickel-printed (GC Electronics) to one of the three-stranded stainless steel wires that comprised the tether cable (see below). All connections were then coated with 5 min epoxy for insulation and glued to the back end of the guide cannula to relieve the strain on the connections. Immediately prior to surgery the electrode tips were cut to length (which could vary between electrode bundles) and each electrode was gold plated to about 50 kΩ impedance.

2.2. Tether cable

The electrical connection between the fish and the headstage/commutator assembly is a compromise between being stiff enough to prevent coiling and to turn the commutator as the fish swims, but not so stiff as to impede the fish’s swimming. Also, unlike most chronic single unit recordings of terrestrial animals, the unity gain headstage was not attached to or near the animal’s head. Rather, making the headstage integral with the commutator (about one meter distant from the recording electrodes) reduced the drag on the fish. To further reduce weight and drag, no connectors were placed in the tether cable between the nickel print connections to the recording electrodes and the terminal connector attached to the headstage. The tether cable was made with multiple Teflon coated, three-strand stainless steel wires (#7934, 150 μm insulated, A-M Systems, Inc.), one wire per each of the six recording electrodes, one for the reference electrode, plus two wires for light emitting diode (LED) power. One nine wire tether cable was about the maximum for the size of fish used here, but smaller gauge wire could be used to accommodate additional recording channels. We used both unilateral and bilateral placements of the six recording electrodes, but with larger fish, up to six electrodes were implanted in each hemisphere and each bundle of nine wires was terminated with a separate McIntyre miniature nine pin connector (Scientific Technology Centre, Carleton University, Ottawa, Canada) so that each hemisphere could be monitored alternately.

Each bundle of nine stainless steel tether wires was coated with silicone sealant and inserted into 1/16 in. diameter shrink tubing. While the sealant was still wet, the shrink tubing was heated from one end toward the other and as the tubing shrank the excess sealant was wiped from the cable. This created a cable with ideal flexibility for these experiments. About 3–4 cm of stainless steel wire was left uncovered by the shrink tubing to allow for connecting to the electrodes.

2.3. Implantation

Initially, fish (about 12 cm standard length) were deeply anesthetized by immersion in 0.03% MS-222 (Sigma) in buffered aquarium water until active respiration ceased, whereupon the fish was transferred to a surgical holder and respired with a continuous flow (20–60 ml/min) of 0.01–0.02% MS-222 (cichlids are more aerobic and sometimes required the higher flow rates and dosage). The fish was positioned so that only the top of the head was above the water bath; all other surfaces were submerged or covered with a tissue paper that wicked water from the bath. Under general anesthesia, 20% benzocaine in a gel (Zottoli et al., 1999) was applied to the skin surface where the skin was cut and removed. After 10 min the skin and muscle tissue overlying the anterior cranium was removed and the cut edges of tissue were again coated with benzocaine. After another 10 min, excess benzocaine was removed and the tissue edges were coated with Vetbond (3M) to reduce fluid seepage and to form a barrier from the electrode glue.

The exposed cranium was dried to increase the anchor strength for subsequent gluing. A rotary burr (Fine Science Tools #19007-07) was used to drill two-four holes through the cranium (away from the electrode site) for insertion of self-tapping anchor screws (FST # 19010-10). Screws were held with fine forceps (bent to accommodate the thread diameter) and screwed in with a jeweler's screwdriver; a gap of about one millimeter was left between the bottom of the screw head and the skull. An additional small, remote hole was drilled to accommodate a reference electrode (125 μm, Teflon insulated stainless steel; Medwire). Bilateral craniostomies (1–2 mm diameter) were drilled over the telencephalic hemispheres for electrode placement. After aspirating the fatty tissue from within the cranium and visualizing the each hemisphere, the craniostomies were sometimes elongated to better accommodate visually-guided electrode placement.

At this point a small amount of 5 min epoxy gel (the gel form does not flow as readily as regular epoxy) was used to coat the skull surface and anchor screws in the areas away from the craniostomies and reference electrode hole; the epoxy was allowed to dry for at least 10 min. Application of this thin coating generates little heat buildup, providing a bonding surface for subsequent small applications of epoxy. This critical bone-glue bond can cure throughout the duration of the electrode implantation. The application of Vetbond to all exposed tissues prevents any toxic effect of the epoxy on the surrounding skin or muscle.

Electrode assemblies, each held in a manipulator by the 30 gauge post cannula, were positioned over the Dl region and lowered 100–800 μm into the brain. Once the electrodes were positioned, a small amount of epoxy gel was used to bridge the electrode assembly to the skull and allowed to dry; subsequent small applications of epoxy gel gradually sealed the craniostomies. Using forceps, the reference electrode was bent and inserted into the cranium. One to three coats of regular epoxy were applied and allowed to flow over all components of the implant in order to ensure that the ends of the Teflon insulated tether wires are well glued and sealed. As the epoxy was beginning to set, the infrared LED (LD242-3 Osram/Infineon) also was positioned at the front of the implant and held in place until the glue hardened. After releasing the post cannulae from the manipulators, the tether cables were positioned caudally parallel to the back of the fish. The exposed posts were carefully removed with fine wire cutters, and a final application of glue sealed the post cannulae, further insulated the LED and its connections, and held the tether cables in position.

2.4. Recovery

Once the final epoxy coat had hardened, the fish with tether attached was removed from the surgical holder and moved to a container of aged aquarium water and supported by hand. When handling the tether and its attached connector, care was taken to avoid any static discharge that might be conducted to the brain. Aged, anesthetic-free aquarium water was allowed to flow over the fish's gills through a gravity-fed tube placed in the mouth. After about 15 min the tube was removed from the mouth to see if the fish would begin spontaneous respiratory movements; during this phase of recovery, gilling began only after the tube was removed and often decreased when the tube with flowing water was reinserted. It is important to repeatedly test in this way for the strength of gilling and to be sensitive to muscle tone while holding the fish. After sufficient respiration had returned and the fish had shown some trunk movements, the fish was transferred to the test arena and the tether cables were connected to the headstage. The square test arena (a large Rubbermaid wreath box) was supported on an isolation table to reduce floor-transmitted vibrations and surrounded by black curtains to reduce visual cues (particularly from the experimenters). Also, because of the one meter distance between the fish and headstage, aluminum screen shielding was installed above and outside of the black curtain to reduce electrical noise. Fish were fed remotely with live blackworms by injecting the worms with water into the arena through small vinyl tubing; four feeder tubes were set up, one near each arena corner to test for cells that might respond to food locations.

For the period from recovery until the end of recording, it is important to minimize the number of startle responses evoked from the fish as a C-start can cause the electrodes to be displaced and unit recordings to change abruptly.

2.5. Recordings

The tether from the electrode assemblies was connected to a unity-gain headstage (each channel including reference passed through a SK9149 FET) that was hardwired to a nine channel commutator (Biela Idea Development, Anaheim, CA; Crist Instrument Co.). Because the commutator we

used had nine channels, this limited the number of channels recorded simultaneously to six (two channels are used to provide electrical power to the headstage and infrared LED and one was used for the reference electrode). We have implanted up to six electrodes per hemisphere by using separate nine-pin connectors for each hemisphere array (plus LED power). Some critical considerations for the number of electrodes that can be implanted include: size of the fish, size and weight of the implant with epoxy, stiffness of the tether cable as a function of the number of wires incorporated into it, mass of the headstage, and the number of channels through the commutator (since rotational inertia increases with number of channels).

After passing through the headstage and commutator, signals were relayed through a shielded cable to a patch panel that could allow for different electrode combinations to be compared. From here, signals were bandpass filtered between 300 Hz and 6 kHz, amplified 15,000 times using a software controlled amplifier (Neuralynx 8), and acquired by computer using Discovery Software (Datawave Technologies). The fish's LED position was simultaneously monitored by video camera and recorded. Single unit data from each electrode channel and position data were time stamped and stored on the hard drive for later offline analysis. Recordings were made up to several times per day (depending upon the stability of the electrode and the relative activity of the individual fish) over a 5-day period. At the end of the recordings the fish were euthanized, perfused with formalin, and the brains were prepared for histology.

Untrained fish were allowed to swim freely about the test arena. A hexagonally shaped piece of clear Plexiglas (constructed to be as wide as the arena) was inserted into the arena. This prevented the fish from "hiding" in the corners of the square arena and prevented the fish from entangling the tether on a corner air filter. For most studies, a clay pot (cut and placed on its side) was positioned in the arena to provide a shelter for the fish (Fig. 1). While developing these chronic recording techniques, the main goal was to determine if neural correlates of spatial navigation could be recorded in the fish telencephalon. Ongoing work is examining specific spatial correlates including whether directional heading is also coded by fish telencephalic neurons as in rodents (e.g., Blair and Sharp, 2002; Taube, 1998). Thus, an additional, smaller Plexiglas octagon can be inserted into the

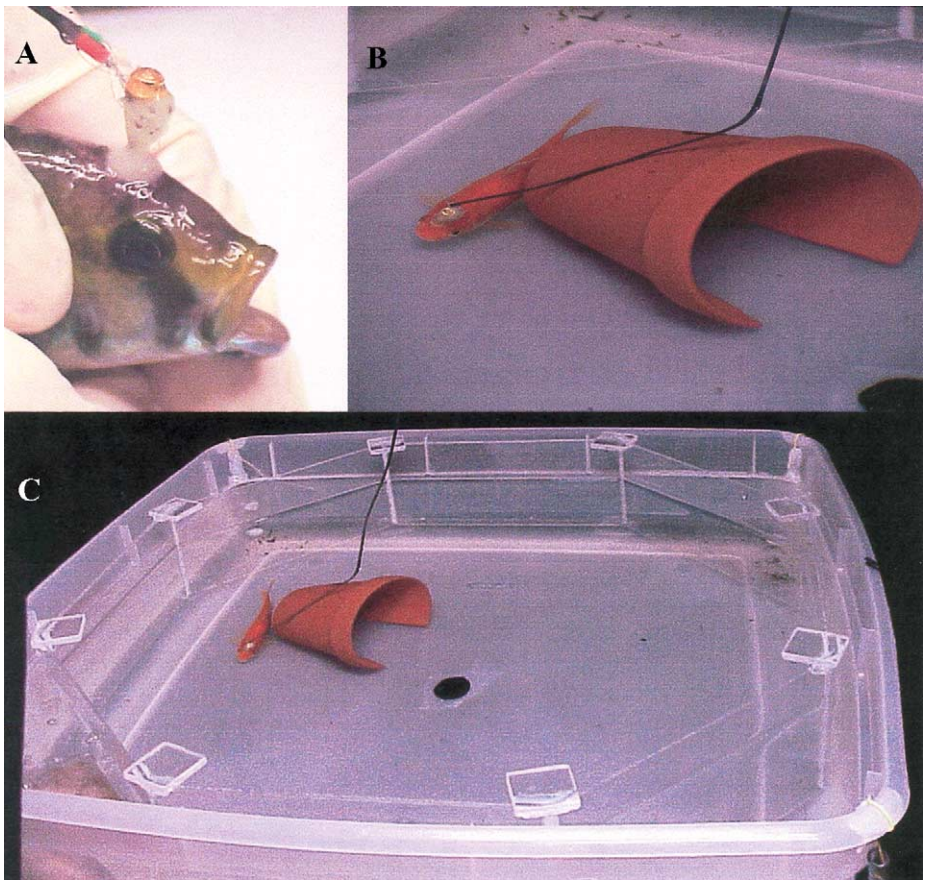

Fig. 1. (A) A cichlid is shown immediately after the implantation procedure before recovery from anesthesia. This is an early style implant in which the LED was mounted on top of the cannulae where the tether cable was connected. Large fish had no trouble with this style but the high tether connection caused significant rotational torque (roll) on smaller fish. (B) A goldfish is shown swimming near the clay pot in the test arena. This fish has the more compact style implant where the cannulae are shorter (accomplished by using the post cannula) and the LED is positioned to the front of the cannulae. (C) The recording arena with the goldfish and clay pot are shown.

arena to form a narrow octagonal track that facilitated directional swimming. Also, a narrow linear Plexiglas track can be inserted to facilitate bidirectional swimming (the ends of the track were enlarged to allow the fish to turn around). Placing either insert into the arena does not require handling the fish.

3. Results

Adult goldfish and cichlids were successfully implanted (three and four fish, respectively; 10–12 cm standard length), and multiunit and single unit activity were recorded. Photographs of implanted fish are shown in Fig. 1. Fig. 1A shows an early version of the implant, depicting a relatively large final product. Later implants were reduced in height, with the LED placed in front of, rather than on top of, the glue-covered cannulae. Cannulae length was also shortened. These small modifications helped to reduce the rotational torque (roll) on the fish from the weight of the implant. Fig. 1B and C shows a goldfish with the smaller implant swimming within the arena.

Multiunit activity (recorded without using the Discovery software to isolate individual units) in the fish telencephalon showed visual, movement, and spatial correlates. Visual responses by telencephalic units were fairly common, and some units were particularly sensitive to movements made by the experimenters. Fig. 2 depicts unit activity that was correlated with the room lights being turned off and on (Fig. 2A and B), and with the movement of a flashlight in the darkened room (Fig. 2C). Some cells also appeared to have a movement correlate, firing when the fish moved in either the illuminated or darkened arena. Fig. 3 shows the activity of a cichlid neuron that was heightened when the fish resided within the clay pot, irrespective of the location of the pot within the arena. The activity was not correlated with a change in the amount of visual stimulation because the spike rate was heightened even when the fish's body was mostly inside the pot but his head was outside the entry. Other units displayed phasic activity wherever the fish swam about its environment but not when the fish was stationary (Fig. 4).

To show the power of correlating neural activity and location, single units were isolated and their activity was

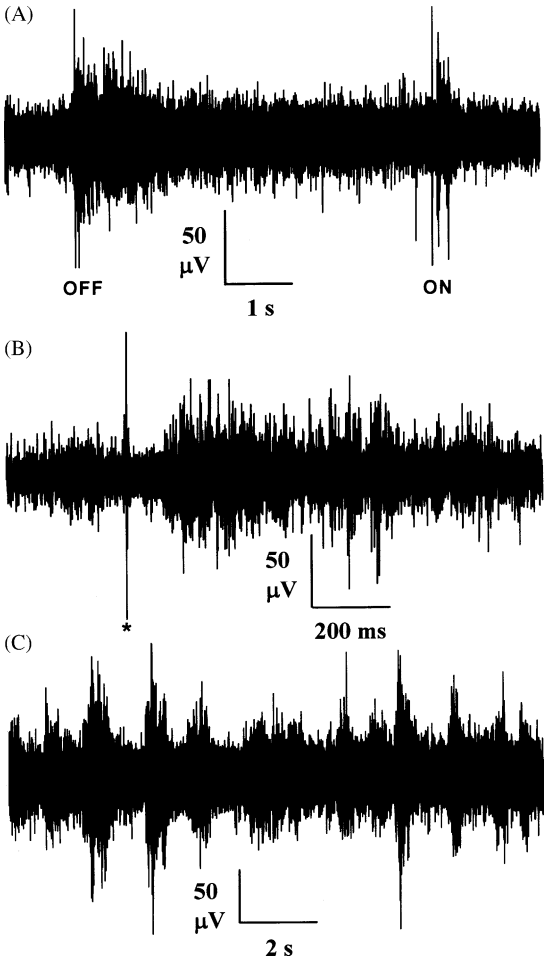

Fig. 2. Examples are shown of multiunit records that display visual responses in freely swimming cichlid. (A) Bursts of activity were evoked by turning the room lights off and back on. (B) A time expanded recording of the "on response". Note the suppression of baseline activity immediately following the light onset (*) and the subsequent burst. (C) Back and forth movement of a light spot projected onto the black curtain evoked repeated bursts of activity.

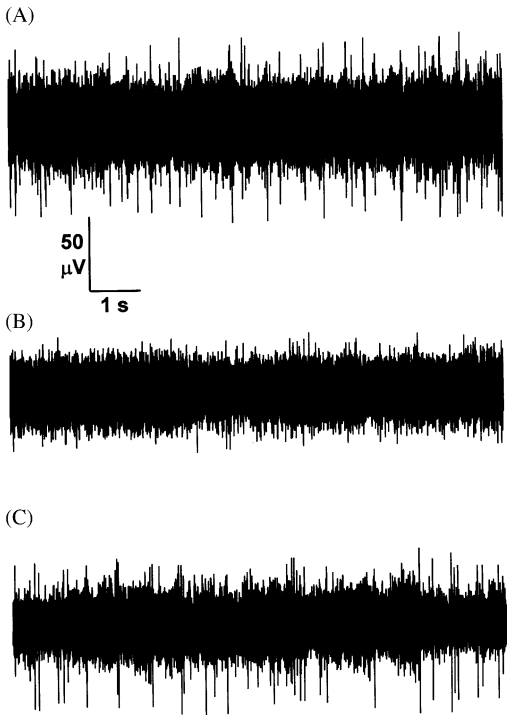

Fig. 3. A multiunit record that depicts a "pot cell" is presented. The recording shows heightened activity (A) as the fish was hovering inside the clay pot (with its head outside) and the pot was located in the northwest area of the arena. When the fish was swimming outside of the pot (B), neural activity was diminished. After the clay pot was moved to the southwest part of the arena and the fish again hovered inside (C), neural activity returned to its heightened level.

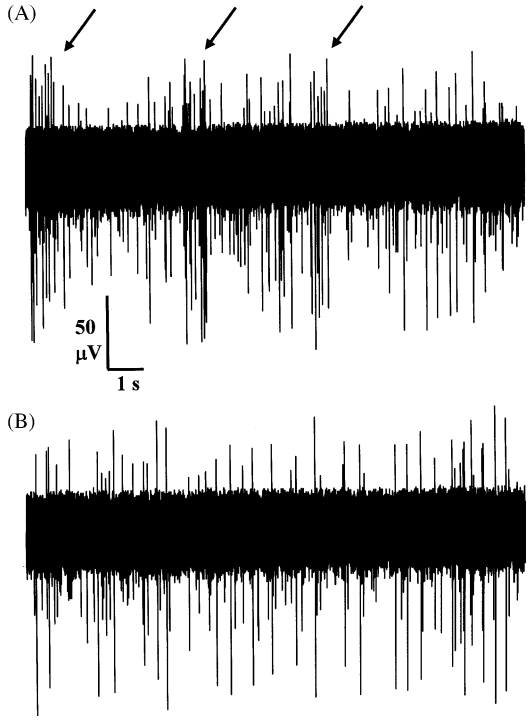

Fig. 4. Movement-related phasic activity (arrows) is shown in (A) when a fish was swimming about the arena, but the activity was diminished and nonphasic when the fish remained stationary while occupying its clay pot refuge (B).

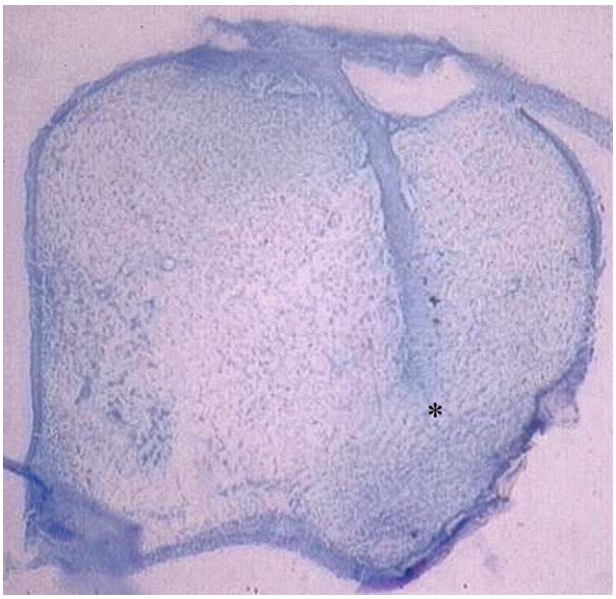

Fig. 6. A 70 mm thick, cresyl violet stained section of the right telencephalon of a goldfish shows an electrode tract terminating at the asterisk, approximately at the border of the Dl.

correlated with the fish's location in the arena. The unit depicted in Fig. 5A showed a strong velocity correlate and was active whenever the fish swam about the maze irrespective of the fish's location in the maze. Perhaps the most

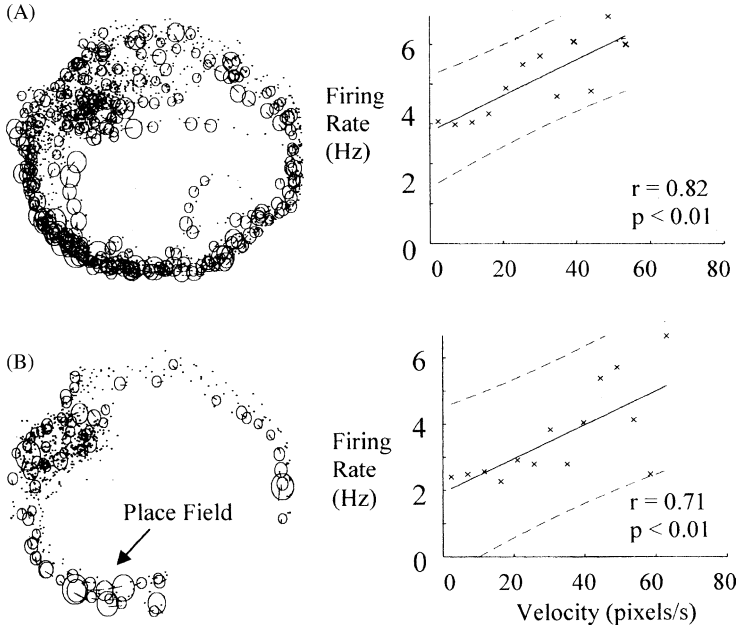

Fig. 5. When individual units are isolated from the multiunit record with the Discovery software, and the activity is correlated with the position of the fish (LED), the spike rate can be correlated with certain movement or position characteristics. In the position plots shown in the left panels of (A) and (B), the diameter of each circle is correlated with spike rate and the line associated with each circle depicts the direction of movement. The individual cells depicted in (A) and (B) were recorded simultaneously. (A) A movement-related cell showed no location preference for any region in the arena as depicted by its relatively constant rate of activity throughout (left panel). However, analysis of spike activity and movement parameters showed a significant velocity correlate (right panel). (B) This unit displayed a relatively elevated spike rate in the southwest region of the arena (left panel) suggesting a place preference (a "place field"). For this neuron, the infield and outfield spike rates were 12.45 and 2.46 Hz, respectively. This cell also showed a significant velocity correlate (right panel).

intriguing correlate is shown in Fig. 5B, where the neural activity of an isolated unit shows a heightened activity in a relatively discrete location within the arena. This "place cell" showed greater activity in the southwest region of the arena (the larger circles depict higher rate firing) despite the fish's preference to swim close to the clay pot (the "halo" of activity in the northwest region of the arena). This neuron was recorded in a goldfish telencephalon, near the medial border of the Dl, as determined histologically from the electrode tract (Fig. 6). To date we have not detected a feeding-related neural correlate.

4. Discussion

The results presented above demonstrate that chronic recording methods commonly used in rodent navigational studies can be readily adapted for use in aquatic species. Perhaps the major difference between terrestrial and aquatic chronic recordings is the duration of recording from a specific single unit. Some individual neurons can be recorded for weeks in rodents, during which a number of behavioral manipulations can be performed to test for unit activity related correlates. In fish, we have recorded well isolated units for up to about a day, including units where behavioral manipulations were performed. Part of the difficulty in maintaining a recording of a specific neuron's activity is that, in adult fish, the brain is considerably smaller than the cranium, allowing for potentially large movements of the brain relative to the skull-fixed electrode (we have not yet implanted juvenile fish which may display less brain movement and perhaps more stable recordings). Still, it has been possible to demonstrate several navigationally relevant neural correlates. It may be possible to stabilize the telencephalon by refilling the cranium, but we have not yet tried this method as the replacement material may cause the displacement of the location of the electrode penetration. A possible alternative is to use finer, more flexible electrode wire.

Another difference in rodent verses fish recordings is that we have not yet incorporated a movable drive on which electrodes can be mounted. It may be possible to adapt a movable electrode design (e.g., Demski and Picker, 1973) for the stereotrodes or tetrodes used here. Future work will address this possibility keeping in mind that added implant weight can affect normal fish behavior and any adjustment in electrode depth may necessitate handling the fish which in turn may cause the electrode to be displaced further than the micrometer adjustment.

Despite these current differences in rodent and fish telencephalic recordings, with just seven implanted fish, the methods outlined here have demonstrated initial success when used to search for neural correlates of navigational behavior. While recording multiple Dl neurons on single electrodes, we have observed units that display visual responses to the investigator's hand movements or lights on and off (Fig. 3), visual-motion cells (these tend to fire as the fish swims about the test aquarium), and cells that fire a burst of activity when the fish quickly accelerates (data not shown). These correlates are consistent with the multisensory nature of the afferents to Dl (Demski and Beaver, 2001) and with the movement representations found in mammalian hippocampus (e.g., Ranck, 1973). Also, of particular interest was a neuron that fired primarily when the fish sought refuge in a clay pot (Fig. 3), and may be similar to box- and goal-related cells recorded in rat hippocampus (Gothard et al., 1996a,b). Some units show movement-related correlates that are not location dependent (Figs. 4 and 5A). Lastly, we now have the first evidence for place cell coding in the fish telencephalon (Fig. 5B), a spatial representation correlate that may be common across a phylogeny that includes fish, birds, and rodents.

In this paper, we have delineated the procedures involved in adapting chronic recording methods used commonly in rodents for use in recording from the telencephalon of goldfish and cichlids. Only small changes in these procedures should make chronic recording a viable option in other brain areas (perhaps regions that are more stable like midbrain and hindbrain structures), and in other aquatic species.

Acknowledgements

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