Matched Filtering in African Weakly Electric Fish: Two Senses with Complementary Filters

9

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Contents

Abstract

African weakly electric fish live nocturnally in tropical freshwater streams. To sense their surroundings, they have developed a highly specialized system of two senses, which allows them to perceive nearby objects at high precision with an active electric sense and to detect large, fast-moving objects with their visual sense at greater distances. Both senses are highly specialized and are equipped with matched filters for efficient detection and analysis of relevant object features and for neglecting unimportant items. Active electrolocation in the near field involves the production of an electric signal, which serves as a carrier for sensory information. This signal and the resulting electric field around the fish are shaped by the fish's body and its internal structure. The electric skin

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properties and the accessory structures of the electroreceptor organs further filter the signal and form two electroreceptive foveae. In contrast, the visual system is adapted for detecting large objects at longer distances. A grouped retina forms a visual matched filter, which filters out small, nearby objects but efficiently detects fast-moving distant objects even under noisy and dim light conditions.

9.1   Electroreception

Many aquatic animals are able to detect naturally occurring electric signals coming from the environment. Electroreception is an ancient sensory modality which was present already in early fishlike vertebrates (Bullock et al. 1983). The fact that electroreception is still present in most fish taxa, with the notable exception of many teleosts, shows that the perception of electric signals offers an advantage in the aquatic habitat. The majority of electroreceptive animals use *passive* electrolocation, during which they can detect and analyze electric signals from the environment (Bodznick and Montgomery 2005; Wilkens and Hofmann 2005). Besides fish, only a few vertebrates and maybe some invertebrates possess this sense, i.e., several aquatic urodele amphibians, the platypus (*Ornithorhynchus anatinus*), the short-beaked echidna (*Tachyglossus aculeatus*) (Pettigrew 1999; Proske et al. 1998; Scheich et al. 1986), and the Guiana dolphin (*Sotalia guianensis*) (Czech-Damal et al. 2012). All these animals probably detect environmental electric fields for orientation and for prey detection, i.e., to find and identify benthic prey animals by the electric fields they unintentionally emit. Passively electrolocating animals have developed matched filters for these types of signals, which, however, will not be reviewed in this chapter (for additional information, see, e.g., Hofmann et al. 2005).

9.2   Weakly Electric Fish

In addition to being able to passively perceive environmental electric signals, weakly electric fish can actively produce electric signals for the purpose of *active* electrolocation (Lissmann and Machin 1958) and for electrocommunication (Szabo and Moller 1984). African (Mormyriformes) and South American (Gymnotiformes) weakly electric fish use specialized electric organs to produce their high frequency electric signals (i.e., with significant energy up to about 5 kHz or more), which are therefore called electric organ discharges (EOD). There are two main types of EODs: (1) brief, pulse-like signals and (2) continuous wave-type discharges. Pulse-type EODs have a duration that is much shorter than the inter-pulse intervals, which means they can be shorter than 200 μs in some mormyrids, while other species generate EODs with durations of several milliseconds. In the case of mormyrids, inter-pulse intervals of single individuals are highly variable

and depend on the behavioral context. Most pulse-type EODs have extremely constant waveforms, which depends on the species, the sex, and the hormonal state of the sender animal. Since the animals cannot vary the EOD waveform on a short-term basis, they have to rely on other means such as modulating the inter-pulse intervals to change the information content during electrocommunication.

Since weakly electric fish produce their own signals for environmental sensing and for electrocommunication, they have to invest stimulus – energy. Even though there are no experimental studies on the costs of electric signaling in mormyrids, it has been found that in the gymnotiform pulse-fish *Brachyhypopomus gauderio* females allocate only a small fraction (3 %) of their daily energy budget to electrogenesis. In contrast, males of this species invest daily 11–22 %, on average 15 %, of their energy into the production of their sexually dimorphic signals (Salazar and Stoddard 2008; Stoddard and Salazar 2011). This discrepancy originates from males producing EODs of higher amplitude and longer duration than females in order to signal territory ownership and attract females. Their high energy allocation therefore serves communicative functions during female sexual selection, while EODs in females are used for navigational purposes only. Males may respond to these high energetic costs by showing a daily plasticity in EOD production with EOD duration and amplitude being reduced during daytime, when the fish are inactive and resting. In a recent article, the energetics of electric organ discharge generation in gymnotiform weakly electric fish was investigated in a theoretical analysis (Salazar et al. 2013). This study showed that performance-related costs of EOD generation in Gymnotiformes can be surprisingly high, up to 30 % of the routine energy consumption, but it depends very much on the species, the sex, and the behavioral situation of the animal. Similar studies on the mormyrid *G. petersii* are missing, but it can be assumed that for mormyrids, energy costs for EOD production may be similar to those measured for female Gymnotiformes, indicating that in general production of navigational signals in African electric fish may represent only a relatively small fraction of their total energy budget (Stoddard and Salazar 2011), similar to a bat's navigational sonar (Speakman and Ravey 1991). In contrast, the processing of electrosensory input in mormyrids may be much more costly. In one study, it was shown that the huge brain of *G. petersii* is responsible for 60 % of the resting energy consumption (Nilsson 1996).

Weakly electric fish are usually active at night, and in the absence of light, they use their EODs for active electrolocation and electrocommunication. An advantage of the use of electric signals for these tasks in contrast to acoustic or visual signals is that EOD waveform is only little distorted by the environment (Hopkins 2009). Whereas acoustic signals are often distorted by the medium and objects within it in various and often frequency-dependent ways (reflection, refraction, scattering, attenuation), electric signals are only attenuated (but not in a frequency-dependent way) and their waveforms pass almost unaffected through the medium, even if this is turbid and noisy. As a consequence, the shape of the received signals varies only slightly from the emitted signals. Weakly electric fish exploit this fact by using

temporal and waveform cues during both electrocommunication and active electrolocation (von der Emde 2011).

All electroreceptive animals possess specialized electroreceptor organs, which are located in their skins (Hopkins 2009). In weakly electric fish, three types of special receptor organs are used for passive electrolocation, for active electrolocation, and for electrocommunication. During active electrolocation, a weakly electric fish discharges its electric organ and thus builds up an electric field around its body that is perceived by an array of cutaneous electroreceptor organs that are distributed over almost the entire body surface of the fish (Hollmann et al. 2008). Objects differing in electric impedance from the surrounding water are detected because they interact with the electric field and modulate the EOD amplitude and waveform, which is detected by the animal's electroreceptor organs (von der Emde and Engelmann 2011).

9.3   The Elephant Nose Fish *Gnathonemus petersii* as a Model System in Sensory Ecology

In this chapter, we will concentrate on the weakly electric fish *Gnathonemus petersii*, the elephantnose fish, which is a well-studied example for sensory adaptations and matched filtering in several sensory modalities. *Gnathonemus* is well known for its movable chin appendix, the Schnauzenorgan, a characteristic fingerlike sense organ covered densely by electroreceptor organs (Amey-Özel et al. 2015). Since we know a lot not only about *G. petersii's* electric sense but also about its visual sense, this species is a perfect example of how animal senses adapt to environmental conditions and how different sensing tasks are allocated to different sensory modalities.

G. petersii lives in small creeks and rivers of Central and West Africa, where – at least seasonally – floods might cause a high turbidity of the water (Moller 1995). The major freshwater environments inhabited by *G. petersii* are moist forest rivers, but they were also found in savanna/dry forest rivers as well as in floodplains, swamps and lakes, and large river deltas (Moritz 2010). Common features of all these habitats are relative low light levels because of shade provided by tree or bush cover, a reddish color of the water, and often rather fast-flowing currents (Fig. 9.1). The water is of low electric conductivity, usually below 100 μs/cm, and has temperatures above 25° C. *G. petersii* was regularly observed within fast-flowing parts of the river (e.g., under roots and driftwood), in holes in the embankment, or at sites of dense vegetation, always close to current (Moritz 2010). The turbidity of the water was found to be relatively high, with turbidity values between 45 and 1,670.5 FTU (Ogbeibu and Ezeunara 2005; Francke et al. 2014). In such an environment, active electrolocation offers clear advantages, because electric signals in contrast to visual or acoustic signals are better suited to pass unaffected through the turbid and noisy water environment (Hopkins 2009).

Like most mormyrids, *G. petersii* hides during the day, becomes active at dusk, and stays so throughout the night (Moller et al. 1979; Okedi 1965). It is a bottom

Fig. 9.1 Typical habitat of *Gnathonemus petersii*, the Iguidi river in Benin, a relatively fast-moving creek during daytime. *G. petersii* (*inset*) lives in red-colored forest streams shaded by vegetation (Photo by Vivica von Vietinghoff. *Inset* photo by Maik Dobiey taken in the lab of the authors)

feeder, searching for small insect larvae, mainly chironomids (Diptera), which are buried in the soil. *G. petersii* digs them out, using its Schnauzenorgan. This is also indicated by the large amount of sand and organic matter found in their stomachs (Nwani et al. 2011). For detecting its prey on the ground, the active electric sense (active electrolocation) plays a dominant role, accompanied by the chemical senses (von der Emde and Bleckmann 1998). To do so, the fish have evolved a special matched filter for electric prey detection (see below). The presence of light does not improve prey detection, suggesting that vision is not used for prey identification. The prey items are rather small and thus probably not visually detectable by the fish, since *G. petersii* cannot see objects spanning less than about 3° of visual angle (see below, Schuster and Amtsfeld 2002; Landsberger et al. 2008; Kreysing et al. 2012).

Generally, the dominant sense for object detection and identification in *G. petersii* is the active electric sense. It is very difficult to train the fish to react to the presence of an object which they only can see but not electrolocate (Schuster and Amtsfeld 2002; Landsberger et al. 2008). In contrast, several studies have shown that *G. petersii* can quickly and easily learn to discriminate electrically between two objects differing in shape, size, material composition, or distance (von der Emde et al. 2010; von der Emde and Fetz 2007). These studies also showed that the fish usually do not use vision to discriminate between stationary objects (even large objects of several centimeter size).

Nevertheless, the eyes of *G. petersii* are large and well developed, and the fish obviously respond to visual signals, which can be noticed easily when keeping the fish in an aquarium. So, what is the function of the visual sense in these animals? Below, we will argue that these fish have a division of labor between the active electric and the visual senses: Since the electric sense takes over the tasks of prey detection and close-up object inspection, the visual sense has evolved a matched filter for the detection of large moving objects and the detection of self-movement in fast water currents. In addition, the fish have developed a unique anti-noise filter, which allows them to see through turbid ("noisy") waters carrying lots of small particles.

9.4   The Electric Sense in the Weakly Electric Fish *Gnathonemus petersii*

9.4.1   Prey Detection

As mentioned above, *G. petersii* employs active electrolocation for navigating in its environment and for detecting prey (mosquito larvae) during its nocturnal activity period. Detecting a partially buried, tiny insect larva on the ground of a tropical river is not an easy task, considering the abundance of many similarly shaped nearby objects, which may have similar electric resistances as the prey. One might think that prey detection and especially prey identification is like finding a "needle in the haystack" and requires complex and thus "costly" neural machinery with a lot of signal processing power. However, as shown below, this is not the case. The solution to the problem is the exploitation of characteristic sensory features of living prey items and the use of matched filters for their detection.

Finding prey might be easier for an electric fish if the prey item has unique properties, which are absent in the multitude of other objects surrounding the prey. It was suggested that such a unique mark might be the *capacitive properties*, which only living objects (water plants, other fishes, and insect larvae) possess in addition to resistive components (Schwan 1963; Heiligenberg 1973). To test whether mormyrids can perceive capacitive object properties, behavioral experiments were conducted. It turned out that indeed *G. petersii* (von der Emde 1990) and other mormyrids (von der Emde and Ringer 1992) can unambiguously discriminate between resistive and capacitive objects. They can distinguish a capacitor from a resistor, and thus a living prey item from a dead object, by measuring the capacitive-induced *waveform distortions* of the locally perceived EOD (von der Emde and Bleckmann 1992a). Waveform distortions only occur in the presence of capacitive, i.e., living, objects. They depend on the capacitive value of the object (as well as on its size and shape) and are thus unique indicators of certain prey items. Using active electrolocation, mormyrids are able to measure quantitatively even very small EOD waveform distortions caused by a living object and thus identify their prey (von der Emde and Ronacher 1994). Because of this, it was suggested that capacitive properties of prey items are like colors of visually
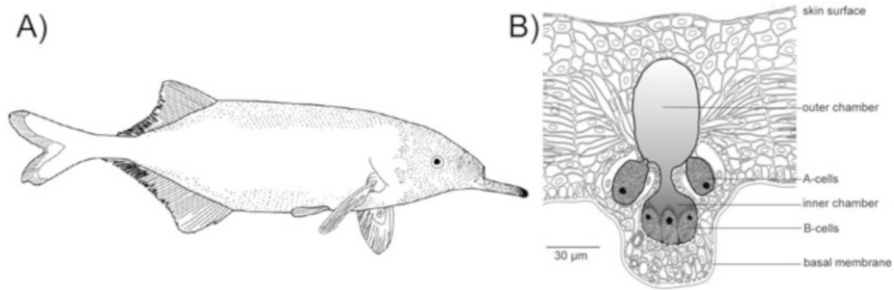
Fig. 9.2 (**a**) Density of mormyromast electroreceptors over the body surface of *G. petersii* (Modified after Hollmann et al. 2008), showing highest numbers of electroreceptor organs at the tip of the Schnauzenorgan. (**b**) Drawing of a section through the skin of *G. petersii* with a mormyromast organ (Modified after von der Emde et al. 2008)

perceived objects, and in analogy, capacitance detection was called "electric color perception" in weakly electric fish (von der Emde 1993; von der Emde and Schwarz 2002). A living insect larva on the ground of the river thus stands out of the surrounding inanimate objects by having an "electric color" and is thus quickly detected and identified by foraging *G. petersii*.

9.4.1.1 Matched Filters for Prey Identification

According to Wehner's definition (1987), a matched filter is an arrangement of specialized sensory elements in such a way that it is matched to the sensory stimuli to be received. As a consequence, the sensors respond optimally only to those stimuli that the animal aims to detect, while other stimuli are discarded. Because the unwanted stimuli do not even reach the brain, the nervous system is freed of dealing with them and can concentrate on the relevant aspects of sensory input. The periphery takes over the task of filtering the sensory input, which results in a fast and effective recognition of relevant sensory information.

The relevant stimuli for prey identification are the waveform distortions of the local EOD, which are caused by the capacitive properties of the prey items. How are they detected? The local EOD has a duration of only about 500 μs, and to detect minute distortions of such a short signal might require an extremely fast receptor unit with a sampling rate in the nanosecond range, which a biological receptor cell cannot achieve. The solution to this problem is matched filtering realized by pre-receptor mechanisms of the electroreceptor organs.

The electroreceptor organs used for active electrolocation are the so-called mormyromasts (Szabo and Wersäll 1970). There are about 2,500 mormyromasts in the skin of a *G. petersii*, and they are distributed over large parts of the body surface except for an area at the flanks of the animal (Fig. 9.2a). Like all electroreceptor organs, mormyromasts are located in the epidermis and contain several electroreceptor cells and supporting structures. Each mormyromast houses two types of receptor cells that are tuned to different aspects of the signal carrier, i.e.,

one channel for amplitude and one for waveform coding. A-cells are found at the basal part of the outer chamber, while B-cells are located inside of an inner chamber (Fig. 9.2b). Both are innervated by separate nerve fibers, which project to the brain, where type A and B afferents terminate in separate areas (Bell 1990). The most important difference between A- and B-type afferent fibers is the sensitivity of only the B-cells to waveform distortions of the EOD, such as those which are caused by capacitive objects (von der Emde and Bleckmann 1992a). Type B cells are exquisitely sensitive to such distortions, whereas type A cells are not. Both are similarly sensitive to changes in EOD amplitude. It follows that in the presence of a capacitive object, B-cells but not A-cells will respond by firing more action potentials because of the waveform distortions caused by the object. These findings suggest that the fish sense the capacitive properties of objects independently of the resistive properties, by centrally comparing the responses of A- and B-cells.

How does the waveform sensitivity of the B-cells come about? A "normal" electroreceptor cell would not respond to waveform distortions at all, but would require other signal properties such as higher signal amplitudes to increase firing. The B-cells are located inside an inner chamber of the mormyromast, which is connected to an outer chamber through a small canal. The outer chamber houses the A-cells and is connected by another canal to the surface of the skin, where the mormyromast forms a small pore (Fig. 9.2b) (Amey-Özel et al. 2012). The chambers and the canals of the whole organ are loosely filled with epidermal cells, and the walls are made by supporting cells, which form a tight barrier between the surrounding tissue and the inside of the chambers. This arrangement of the mormyromast is crucial for the sensory properties of the electroreceptor organ and for the waveform sensitivity of the B-cells, in particular. The building blocks of the mormyromasts shape, or filter, the sensory signal (the locally occurring EOD) in such a way that even minor waveform distortions of the local EOD caused by living prey items will depolarize the membrane of B-cells and cause it to fire action potentials (von der Emde and Bleckmann 1992b). This filtering is exactly matched to those waveform distortions, which are caused by living objects. Other, unnatural types of waveform distortions are not affective and will either not work at all or even inhibit the receptor cell (von der Emde and Bleckmann 1997).

As mentioned above, A-cells do not respond to waveform distortions and therefore should not change their firing activity in the presence of a capacitive object that does not change signal amplitude. To our surprise, however, when recording from A-cell afferents, we found that A-cells responded negatively, i.e., with a reduced firing activity, when a capacitive object approached the receptor pore (von der Emde and Bleckmann 1992a). The reason for this is that A-cells are tuned to much lower frequencies than those at the peak of the spectrum of a single EOD. Capacitive objects not only distort the EOD waveform but in addition they shift the peak power spectral frequency to higher values, even further away from the optimal frequency of the A-cell's tuning curve. A frequency shift to higher values thus causes A-cells to fire less when a capacitive object is present. As a result, capacitive objects evoke an opposite response in A- and B-cells, which increases the contrast in firing behavior between the two cell types. All this is achieved by the

peripheral filtering apparatus of the receptor organ, only, and without any neural processing.

The described matched filter for capacitive object properties is located in the periphery of the electrosensory system and makes complex neural machinery for signal analysis unnecessary. Instead of involving a multitude of downstream neurons in the brain, the job is done in the periphery by the membrane properties of the receptor cells and by a certain arrangement of supporting non-sensory structures of simple and "cheap" epidermal cells.

9.4.2 The Electric Fovea Hypothesis

Mormyrid fish possess three types of epidermal electroreceptor organs, each containing at least one type of electroreceptor cell. In addition to the mormyromasts, which are exquisitely employed for active electrolocation, African electric pulse fish also have so-called ampullary receptor organs (used for passive electrolocation) and Knollenorgan receptor organs (used for electrocommunication). Electroreceptor organs form arrays on the skin of weakly electric fish and the spatial arrangement of the organs affects the functional properties of the whole array during environmental imaging. A certain arrangement can therefore be regarded as a kind of filter that can extract certain stimulus parameters and dismiss others. This principle can be shown for the array of mormyromast receptor organs, which are used for imaging of the environment during active electrolocation. In most mormyrids, mormyromasts are distributed unevenly over the body surface and generally occur at highest density at the head, especially at the Schnauzenorgan, while the tail and the lateral sides of the trunk are free of electroreceptor organs (Harder 1968). Hollmann et al. (2008) divided the fish's electrosensitive skin into three regions: the Schnauzenorgan, where a continuous decrease from extremely high concentration of mormyromasts at the tip toward moderate density at the base was found; the nasal region above the mouth, where a moderate yet still about three-times higher density occurred compared with the third region, which is the rest of the body (Fig. 9.2a). A similar concentration of receptor organs employed for active electrolocation around the snout was observed in some South American electric fish leading to the idea that this arrangement bears some resemblance to the visual fovea in the retina of vertebrate eyes. Castello et al. (2000) suggested that Gymnotiformes have an electric fovea and a "parafovea" around their mouth and von der Emde and Schwarz (2001b, 2002) described two electric foveae in *G. petersii*, at the Schnauzenorgan and at the nasal region.

G. petersii has two areas of high receptor organ densities, one at the Schnauzenorgan and the second one at the nasal region. Both of these regions can be regarded as electric foveae, because besides a high receptor density, they have additional specializations that turn them into specialized matched filters (von der Emde et al. 2008). The receptor organs in the foveal regions are smaller and have fewer receptor cells than those outside the foveae (Amey-Özel et al. 2012). As in the visual fovea, both foveal regions of *G. petersii* are overrepresented in the brain,
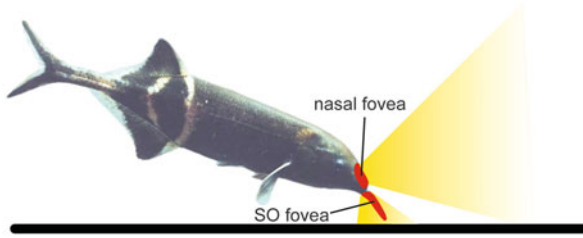
Fig. 9.3 Swimming posture of *G. petersii* when searching for prey on the ground. The two electric foveae at the nasal region and the Schnauzenorgan (*SO*) are highlighted in *red*, and their regions of sensory input are indicated by *yellow* areas

which means that more nerve cells process the information from a single receptor organ (Bacelo et al. 2008). Finally, there are behavioral adaptations for focusing an object of interest onto the fovea for detailed analysis. Because the nasal region has a circumferential view of the surroundings, by placing it at an angle of ca. 50° relative to the ground, it is brought into a position to optimally inspect the space in front of and at the side of the animal during foraging (Fig. 9.3). In contrast, the Schnauzenorgan performs rhythmic left-right movements. This ensures that during foraging it performs sweeping movements over the ground in order to detect possible prey items with its sensible tip (Fig. 9.3). When an object of interest is encountered, the Schnauzenorgan interrupts its left and right rhythm and moves over the object, following its outline in a certain "fixation pattern."

The two foveae serve different functions: the nasal region is a long-range guidance system that is used to detect obstacles or other large objects during foraging. Because of the properties of the skin and the internal tissue of the fish (see below) and because of the arrangement of the mormyromast receptor organs, the nasal fovea responds best to larger objects in front of and at the side of the animal. The Schnauzenorgan, on the other hand, is short-range movable (prey) detection system that is used to find and identify prey on the ground or inspect details of objects. The anatomical structure of the Schnauzenorgan fovea and the special arrangement of mormyromasts turn this area into an effective prey detection device, i.e., a matched filter for living chironomid larvae in and on the ground (see above). Even without neural processing by specialized brain areas, the electroreceptors at the two electric foveae respond only to the relevant stimuli they are specialized for.

9.4.3   Production of Electric Signals and the Self-Produced Field of *G. petersii*

As shown above, weakly electric fish developed matched filters that delegate certain tasks of signal analysis into the periphery. Because *G. petersii* uses an *active* electrosensory system, matched filtering in these animals also involves the production of the appropriate EODs, which function as the carriers of
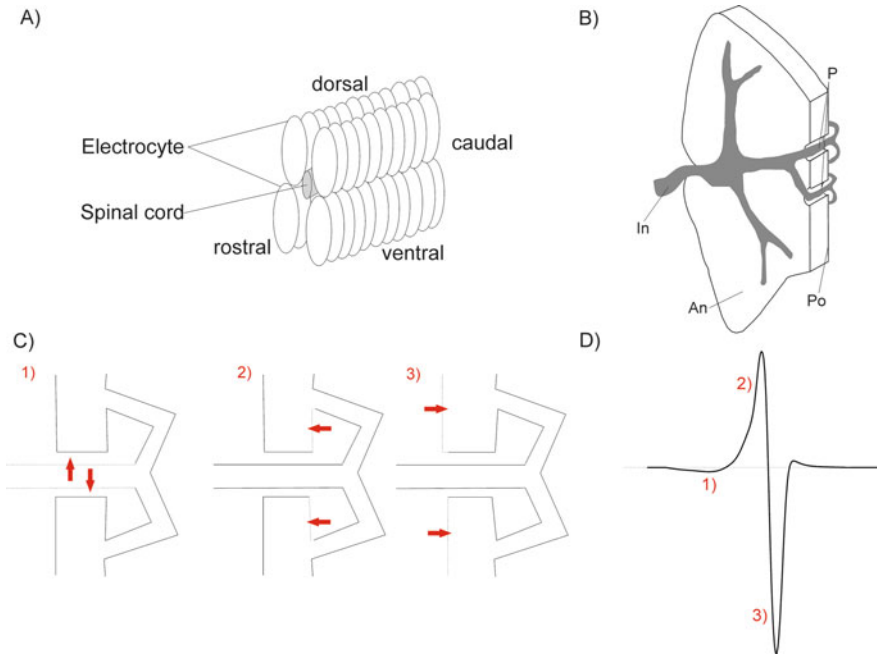
Fig. 9.4 (**a**) Simplified organization of *G. petersii*'s electric organ located in the caudal peduncle of the tail (Modified after Carlson and Gallant 2013). (**b**) PA-type electrocyte; **P**enetrating with **a**nterior innervation of stalk (*In* innervation, *An* anterior, *Po* posterior, *P* penetration) (Modified after Cheng 2012) (**c**) Depolarizing current flow through electrocyte, which determines EOD polarity and number of phases (Modified after Carlson and Gallant 2013). (**d**) *Gnathonemus* EOD with references to phases of (**c**)

electrosensory information. Especially at the two foveal regions, the electric field is conditioned by pre-receptor mechanisms to provide a suitable carrier for the respective filtering task.

In mormyrids, the electric organ which emits the EOD is localized in the caudal peduncle of the fish (Fig. 9.4a, b). Electric organs of mormyrids evolved out of the skeletal musculature which used to move the tail of the animals. Tail movement now is achieved through tendons connecting the tail fin to muscles in the trunk anterior to the caudal peduncle. The electric organ consists of hundreds of electrocytes arranged in four columns, which all fire synchronously and thus emit an extremely constant and precise electric signal that builds up an electric field around the animal and ultimately stimulates the epidermal electroreceptor organs (Fig. 9.5a).

Mormyrids produce a short multiphasic electric signal, which has a species-specific (and sometimes sex specific) extremely constant waveform and frequency composition. This constancy is important for active electrolocation, because the electroreceptors respond to even minute changes in signal amplitude and waveform caused by nearby objects. The waveform of the EOD needs to be constant and
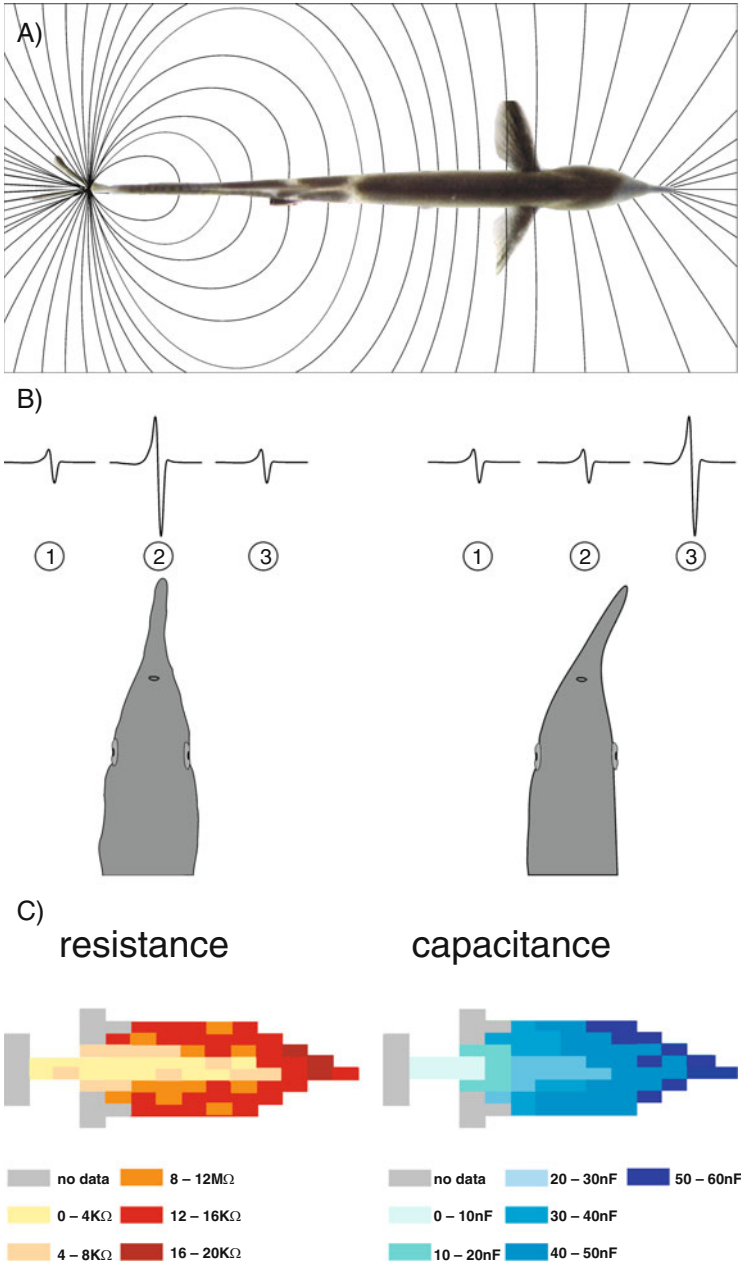
Fig. 9.5 (**a**) Electric field lines around *Gnathonemus*' body during an EOD. (**b**) Effect of movement of the Schnauzenorgan on the amplitude of the local EOD. The *circles* indicate the positions of the recording electrodes with the local EOD recorded at that position shown *above*. On the *left*, the electrode at *circle 2* records the EOD directly at the tip of the Schnauzenorgan. The amplitudes measured at *circles 1* and *3* are much lower. When the Schnauzenorgan is bent to the *right* by about 62°, the EOD amplitude remains high at the tip (electrode 3) and decreases at electrode 2 (After Pusch et al. 2008). (**c**) Resistive (*left*) and capacitive (*right*) skin properties of

reliable especially for capacitance detection, which is achieved by measuring waveform distortions of the local signal (see above).

The discharge of the electric organ builds up an electric field around the fish, which is shaped by the electric properties of the fish's skin and its internal tissue. For optimal filtering at the two foveal regions at the front of the fish, the field has to be strong enough also at the anterior body parts. This is achieved by an increase in skin resistance and capacitance along the fish's body (Fig. 9.5c) and a low electric resistance of the internal body tissue (von der Emde and Schwarz 2001a; Castello et al. 2000). This ensures that the electric current is funneled through the fish's body to the head region; a mechanism called "funneling effect." Currents are additionally channeled by the constantly open mouth, which leads to a homogenous voltage distribution at the nasal region. The vectorial components of the local EOD are out of phase at the trunk of the fish, resulting in a loss of signal intensity. In contrast, at the two foveal regions, these EOD components are highly in phase, which is called "collimation effect." As a result, the EOD amplitude is almost uniform at the nasal region and the direction toward the sensory surface is constant (Pusch et al. 2008; Castello et al. 2000). This makes the signal carrier equally sensitive to objects located in all three axial spatial dimensions in front of the fish. *G. petersii* can thus detect and analyze objects that are located in front and at the sides of the fish turning the nasal fovea into a specialized all-round detection device.

Funneling of currents together with the so-called tip effect ensures high-amplitude EODs also at the tip of the Schnauzenorgan, the region with the highest density of receptor organs. The angle of the electric field vector at the Schnauzenorgan is approximately 45° and thus different from that at other body regions, where it is about 90°. To affect the signal carrier at the Schnauzenorgan, an object has to be placed right in front of the animal. Interestingly, the high EOD amplitude at the tip of the Schnauzenorgan is not affected by movements of the chin appendix (Fig. 9.5b). During exploratory and foraging behaviors, *Gnathonemus* can move its Schnauzenorgan at high velocity of up to 800°/s. These regular scanning movements are often associated with EOD frequencies of 60–80 Hz. Thus, *Gnathonemus* scans the direct surrounding of the Schnauzenorgan at a rate of up to 10°/EOD (von der Emde et al. 2008). Because of the funneling, collimation, and tip effects, the electric field at the Schnauzenorgan's tip is very stable and persistent. As a consequence, the receptors at the Schnauzenorgan perceive a constant electric field, which is not altered by self-generated motions.

Alterations of the electric field by body movements and thus a change in electroreceptor input can pose a problem for signal processing in weakly electric fish. In order to detect an object, the fish have to detect even minute object-caused amplitude changes, which are often much weaker than those caused by movements of the fish's body. In order to perceive object-induced amplitude changes, the brain

Fig. 9.5 (continued) G. petersii. Electric properties are color coded onto the contour of a fish (*lateral view*) with *darker colors* indicating higher values (Modified after von der Emde and Schwarz 2001b)

of the animal has to filter out the self-induced EOD alterations, which requires a complex neuronal machinery and a lot of brain power. The fact that in *G. petersii* EOD amplitude remains constant even during strong Schnauzenorgan movements thus relieves the nervous system of the task to calculate the exact amount of movement-induced amplitude change and makes the sensory system much more sensitive.

9.5   The Visual Sense in the Weakly Electric Fish *Gnathonemus petersii*

Because of their nocturnal activity and their turbid and noisy blackwater habitats, mormyrids were thought to have only a poor sense of vision (Moller et al. 1979). In addition, the structures of the mormyrid visual brain areas in the mes- and diencephalon appear to be highly reduced (Wullimann and Northcutt 1990; Lazar et al. 1984). However, many mormyrids have rather large eyes and also respond sensitively to visual stimuli when held in captivity. In early anatomical work on the eyes of mormyrid fish, which was done even before their active electrosensory system was discovered, it was found by Franz (1921) and then later described in detail by McEwan (1938) that the retina of mormyrids contains large bundles of photoreceptor cells which are collectively ensheathed by large retinal pigment epithelial cells forming cuplike structures. In this section, we argue that the function of the retina in *G. petersii* is not to transmit information about the point-to-point pattern of the distribution of light and dark in a visual image but to analyze visual stimuli for the detection of fast-moving, low-contrast objects under "noisy" conditions.

9.5.1   Anatomy, Morphology, and Cytoarchitecture of the *Gnathonemus* Retina

On the one hand, the retina of *G. petersii* shows the typical five-layered structure of a vertebrate retina (Kreysing et al. 2012; Landsberger et al. 2008), while on the other hand, it reveals some gross anatomical specializations, which make it very special when compared to other teleosts (Francke et al. 2014) (Fig. 9.6). As in most teleosts, the inner retina consists of the retinal ganglion cells (RGCs) separated by a peculiarly thin inner plexiform layer (IPL) from the inner nuclear layer (INL). The very thin outer plexiform layer (OPL) separates the inner retina from the outer retina. The latter is composed of the photoreceptor nuclei, representing the outer nuclear layer (ONL), and the photoreceptor inner and photosensitive outer segments. In *G. petersii*, the ONL is formed by two layers of outer segments (Fig. 9.6a). Therrod outer segments (ROS) are aligned at the distal sclerad side of the ONL, and the cone outer segments (COS) are more proximal at the vitread side (Kreysing et al. 2012). The two plexiform layers are the main site for synaptic contacts between the retinal cells. Amacrine, bipolar, and horizontal cells in the
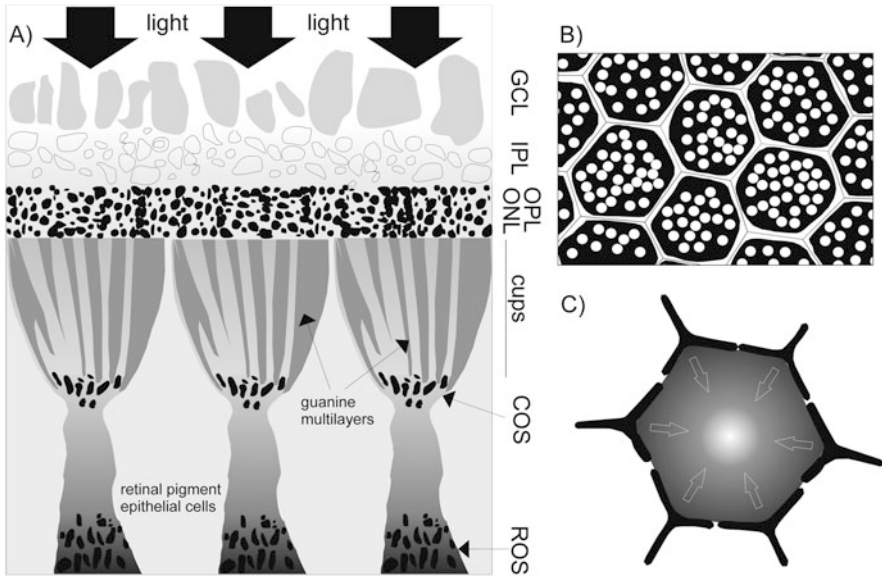
Fig. 9.6 (**a**) General morphology of the retina of *G. petersii* (light-adapted state). Light has to pass through the cellular layers of the retina, ganglion cell layer (*GCL*), inner plexiform layer (*IPL*), outer plexiform layer (*OPL*), and outer nuclear layer (*ONL*), before reaching the cups outlined by highly reflective guanine multilayers. (**b**) *Top view* onto the cups of the grouped retina slightly above the level of the COS (*white circles*). (**c**) Indication of light reflection by the walls of six retinal pigment epithelial cells forming the cuplike structure

INL mediate the intraretinal visual transfer properties (Wagner 2007; Dowling 2012).

The most striking difference to a "normal" fish retina is the observation that the photoreceptors in the *Gnathonemus* retina are grouped together in bundles consisting of about 330 rods located below about 25 cones. Each bundle of rods and cones lies in a hexagonal cuplike structure, which is formed by six large retinal pigment epithelial (RPE) cells (Landsberger et al. 2008; Kreysing et al. 2012) (Fig. 9.6b). A retina composed of such cups is called a grouped retina (Locket 1977) and similar assemblies are found only in a few other teleostean fish groups, many of which are deep-sea fish (Francke et al. 2014). Each cup forms a macroreceptor unit and has a diameter of around 50 μm, giving rise to an angle of aperture of 2.5° (Francke et al. 2014). Thus, the spatial resolution of the *Gnathonemus* eye is very low compared to most other teleosts. *Gnathonemus* cannot separate objects less than about 3° apart (Kreysing et al. 2012). For comparison, the goldfish (which has no grouped retina) is known to visually resolve details at angles more than 15 times smaller, i.e., down to 0.14° (Land and Nilsson 2002).

The inner surface of the *Gnathonemus* retinal cups acts as a mirror, formed by the reflecting multilayers of guanine crystals, while a mirror surface below the cup is missing (Fig. 9.6). At the bottom of each cup, the cone outer segments (COS) are

located. They are thus exposed to the light, which is focused onto the cone outer segments with an increase of the incident light intensity by more than 500 %. In contrast, the rod outer segments (ROS) lie below the cup in a medium filled with light-scattering, submicron-sized guanine crystals and melanin granules, protecting them from the incoming light. Thus, the ROS receive a reduced level of illumination. While light levels for the cones at the bottom of the cup are amplified, the disordered phase of guanine crystallites underneath the cup attenuates the light leaking through the bottom of the cup and only a very small fraction of light reaches the ROS. The combined effect of this arrangement is that both the less sensitive cones and the very sensitive rods receive appropriate amounts of light to allow their simultaneous operation at mesopic light levels, which prevail in the dim habitat of the fish (Francke et al. 2014; Kreysing et al. 2012).

In *Gnathonemus*, the absorption maximum of the rod pigments is at 536 nm (green), while the single type of cone is most sensitive to 615 nm (red light) (Kreysing et al. 2012). In response to the daily changes of light and darkness, rods change their position to regulate light sensitivity or visual acuity via a process called retinomotor movement (Burnside and Nagle 1983). Under photopic daytime conditions, the bottoms of the cups are almost closed forming a small bottleneck through which the rods protrude into the light-protected area below. Thus, COS and ROS are separated from each other during daytime with the ROS being shielded from the light, while COS are fully light exposed. In contrast during dark adaptation, the bottleneck opens and the cups form a cylinder, in which the ROS are drawn inside the cup toward the inner retina. These movements are induced by rod myoid contractions.

The inner plexiform layer of the retina is rather thin, with about half the thickness as that of most other teleosts. Furthermore, the retina of *Gnathonemus* appears to lack local specializations such as a visual streak or a fovea centralis. All this suggests that information processing in the grouped retina is less complex than elsewhere. However, the presence of ten types of retinal ganglion cells suggests that like in other retinae, the visual stimuli are processed in several parallel pathways. In particular, fast and dynamic visual stimuli may be mediated by certain ganglion cells, while the amacrine cells may provide for direction and movement sensitivity (Francke et al. 2014). Interestingly, the information provided by rods and cones may be pooled already at the bipolar cell level such that color information is unlikely to be extracted by the brain.

In summary, the retina of *G. petersii* is a highly specialized and complex structure shaped by specialized epithelial cells. However, its spatial resolution is very low and there is only one type of cone, and also some retinal layers are rather thin and reduced. Information leaving the retina is colorblind but appears to be specialized for the processing of movement. The arrangement into reflecting cups by RPE cells reflects to a high degree the functional properties of the *Gnathonemus* retina. The apparent disadvantages this retinal arrangement imposes on the fish, however, might actually be advantageous when considering the habitat of the fish. In particular, we argue that the grouped retina forms a matched filter for certain

signal properties, namely, for the detection of large, fast-moving objects under dim and noisy light conditions.

9.5.2   Anatomy of Visual Brain Areas

The optic nerve (ON) consists of the bundled axons of retinal ganglion cells. In *G. petersii*, the ON is rather thin compared with the size of the eye or the brain, due to the relatively small numbers of retinal ganglion cells of each eye. Before entering the brain, the ON crosses the midline beneath the diencephalon at the optic chiasm and terminates as optic tract in the mesencephalic tectum and tegmentum and in the rostral diencephalon (thalamus, hypothalamus) (Lazar et al. 1984).

A detailed analysis of the retinal projections of *G. petersii* reveals that many well-established retinofugal connections into the teleost diencephalon are extremely reduced or even absent, while other primary visual regions receive only limited visual input but participate in active electrolocation, instead (Wullimann and Northcutt 1990; Northcutt and Wullimann 1988). In teleosts, retinal projections usually terminate in the suprachiasmatic nucleus (SCN) of the hypothalamus, driving the circadian rhythm. Large retinal terminal fields are also present in the thalamus and in the pretectal complex (central pretectal nucleus (CPN), periventricular pretectal nucleus (PPN), superficial pretectal nucleus (SPN)). The latter structure is further reciprocally connected to the optic tectum (OT) and by this probably involved in the detection of moving objects. In addition, the dorsal and ventral accessory optic nuclei located in the pretectal region receive direct retinal input and are involved in optokinetic oculomotor reflexes (Northcutt and Wullimann 1988; Rupp et al. 1996; Vanegas and Ito 1983).

In *G. petersii*, this general pattern is modified: retinal efferents terminate in the SCN, the thalamus, the PPN, as well as the OT. CPN receives reduced visual input, while an SPN and accessory visual nuclei are absent (Lazar et al. 1984; Wullimann and Northcutt 1990). The OT forms a relatively minor part of the whole brain, and it is differently located and shaped when compared to other teleosts (Fig. 9.7a). The very large, mostly electrosensory torus semicircularis pushes the two tecta rostrally and laterally, and the huge cerebellum covers the complete dorsal surface of the brain. The right and left tecta are interconnected by the intertectal commissure only at their rostralmost parts. The tectum is stratified as in other teleosteans into seven laminae (Fig. 9.7b) (Pusch et al. 2013b; Meek 1983). The visual input to the OT is only poorly developed, as retinal fibers terminate exclusively in a narrow strip in the stratum fibrosum et griseum (Lazar et al. 1984), whereas in the majority of teleostean species, retinal fibers terminate in three or four deeper layers of the tectum (Fig. 9.7b) (Wullimann 1998; Stürmer and Easter 1984).

The midbrain optic tectum integrates multisensory input and is the main visual center in teleosts. In *G. petersii*, tectal efferents project reciprocally into PPN, CPN, and the thalamus, while only restricted tectal terminations were detected in the preglomerular region (PG), which in most teleosts serves as a relay station for ascending visual information (Wullimann and Northcutt 1990). Because of limited
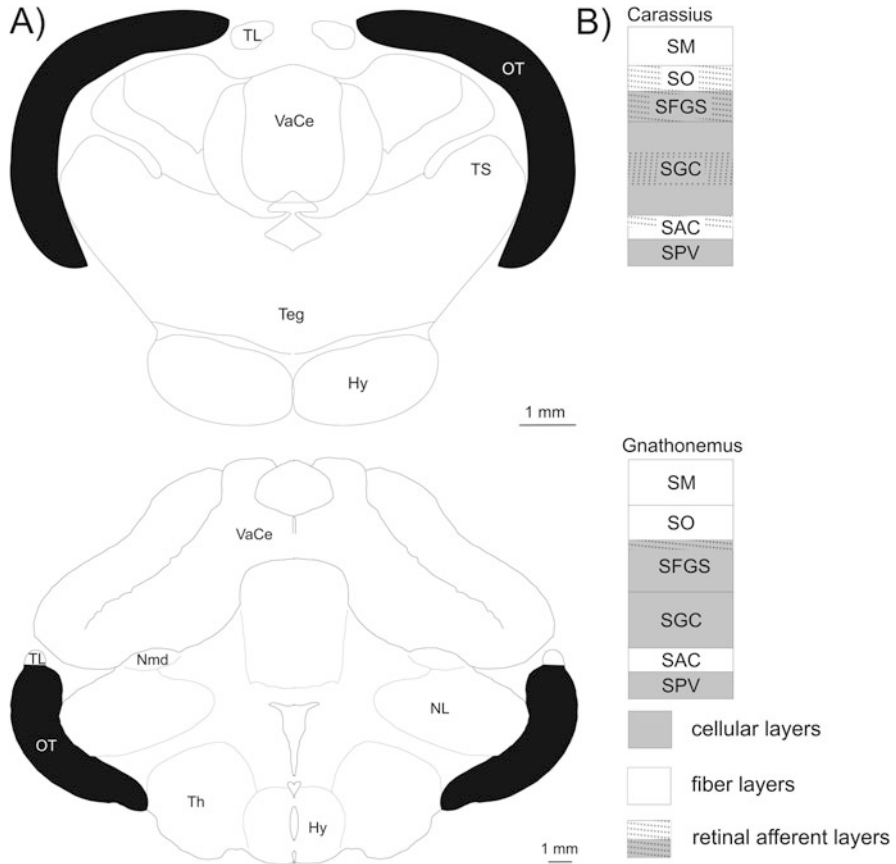
Fig. 9.7 (**a**) Brain sections on the level of the mesencephalon of *Carassius* and *Gnathonemus*. (**b**) General overview of layers of the OT in *Carassius* and *Gnathonemus*. For further explanation, see text. *Abbreviations*: *Hy* hypothalamus, *Nmd* mediodorsal mesencephalic nucleus, *NL* nucleus lateralis of the torus semicircularis, *OT* optic tectum, *SAC* stratum album central, *SFGC* stratum fibrosum et griseum, *SGC* stratum griseum central, *SO* stratum opticum, *SPV* stratum periventriculare, *SM* stratum marginale, *Teg* tegmentum, *Th* thalamus, *TL* torus longitudinalis, *TS* torus semicircularis, *VaCe* valvula cerebelli

tectofugal projections in the PG, it might be speculated that visual projections ascending to the dorsal telencephalon have to be provided by another route (Prechtl et al. 1998), maybe involving the torus semicircularis. Even though the tectum is thought to act as a multisensory neural processing area, which is essential for behavioral reactions, anatomical investigations in *Gnathonemus* showed only very weak electrosensory projections into the tectum (Ruhl et al. 2011; von der Emde unpublished data). However, there are tectal projections into the lateral nucleus of the torus semicircularis, representing the midbrain center for electrosensory processing (Wullimann and Northcutt 1990). Different parts of the

electrosensitive torus semicircularis project to the PG area in *Gnathonemus* (Bell 1981; Finger et al. 1981), suggesting that PG might be more involved in electroreception than in vision and thus might have different functions than those described for other teleosts (Braford et al. 1983).

In summary, even though the retina is highly specialized, the whole visual system in the *Gnathonemus* brain is clearly reduced. Anatomical findings suggest that during evolution, electrosensation took over some visual regions, e.g., CPN, PG, SPN, and accessory visual nuclei. This suggests that in *Gnathonemus* vision might be subordinate to the active electric sense. However, it also could mean that the two senses are used for separate tasks. Here, we argue that there is a division of labor between vision and the active electric sense, which led to the development of separate and complementary matched filters in the visual and electric sensory systems. Anatomical and physiological findings indicate that the visual system evolved a matched filter for the detection of fast-moving, large objects and purposely filters out most other visual stimuli.

9.5.3   Functional Aspects of the Visual System

9.5.3.1 Detection of Visual Stimuli

In contrast to training *G. petersii* with electrosensory stimuli, pure visual training is quite difficult and time consuming. When the animals are trained for long enough, they can learn, however, to approach a black square projected onto a screen (Schuster and Amtsfeld 2002; Landsberger et al. 2008). These experiments confirmed that the spatial resolution is so poor that *Gnathonemus* cannot see objects smaller than about $3°$ of visual angle, no matter whether these objects are stationary or moving (Kreysing et al. 2012). *G. petersii* can also learn to discriminate between large, differently shaped visual patterns indicating that visual pattern recognition involves template matching (Schuster and Amtsfeld 2002).

Since the fish cannot see small particles, the involvement of the visual sense in finding their prey (small insect larvae) during foraging is negligible (von der Emde and Bleckmann 1998). In other behaviors, for example, during certain startle responses, it is much stronger. When presenting visual stimuli that rapidly expand in size mimicking the silhouette of an approaching predator, *G. petersii* consistently responds with a quick flight reaction away from the stimulus. Especially under dim light conditions, this response is much more reliable in *Gnathonemus* than in the goldfish (*Carassius auratus*), whereas under bright light, the two species show no differences (Kreysing et al. 2012). Startle experiments like this also showed the advantage of color blindness for *G. petersii*. The animals were significantly better than goldfish (which can see colors) at detecting an expanding virtual circle which was dynamically defined by the random exchange of equiluminant red and green floating particles. *Gnathonemus* detected such color-camouflaged stimuli significantly better than the goldfish, showing the advantage of missing color discrimination (i.e., "color pooling") (Kreysing et al. 2012).
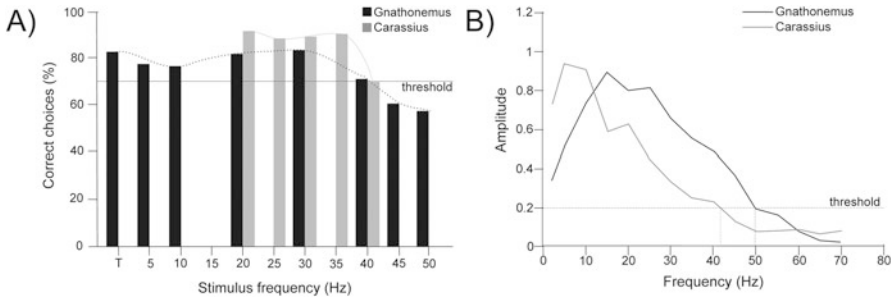
Fig. 9.8 (**a**) Behaviorally determined critical flicker fusion frequency in *G. petersii* (*black*) and *Carassius* (*gray*). The behavioral response to flickering light was tested in a two-alternative forced-choice procedure (Modified after Mora-Ferrer and Gangluff 2002; Pusch et al. 2013a). (**b**) Normalized amplitudes of visually evoked field potentials in the OT for the different flicker frequencies in *Gnathonemus* (*dark gray*) and *Carassius* (*light gray*) (Modified after Pusch et al. 2013a)

Another study described that *G. petersii* performs an optomotor response (OMR) when a moving stripe pattern was projected onto the bottom of the tank. Interestingly, the OMR of *G. petersii* is a very robust behavior, which does not adapt even after longer stimulus periods. The OMR is remarkably resistant to reduced light intensity with a constant gain over more than four orders of magnitude (Landsberger et al. 2008).

When trained in a two-alternative forced-choice paradigm to discriminate between a constant and a flickering light source, the flicker fusion frequency (FFF) of *G. petersii* was found to lie between 40 and 45 Hz (Fig. 9.8a) (Pusch et al. 2013a). In a similar experiment, the FFF of *Carassius* was measured at 35–40 Hz (Mora-Ferrer and Gangluff 2002). Behavioral measurements of the animals' FFF were substantiated by electrophysiological recordings (Fig. 9.8b), showing that in *G. petersii* the FFF thresholds of neurons in the tectum opticum were at about 50 Hz, while for *Carassius* it were at about 40 Hz (Pusch et al. 2013a). It follows that *G. petersii*'s visual system shows a higher temporal resolution than that of the goldfish (Fig. 9.8). In addition, *G. petersii*'s visual system is less sensitive to a reduction in contrast. In conclusion, both the retinal specializations and the brain circuits of the visual system of *G. petersii* enable the fish to be extremely effective in detecting fast-moving objects such as approaching predators under dim light conditions.

9.5.3.2 Noise Tolerance of the Visual System

Considering one macroreceptor of *G. petersii* with its wide spacing of 50 μm as being the smallest functional unit of the retina, visual spatial resolution is rather low. The bad spatial resolution of the *Gnathonemus* retina works like a low-pass filter and prevents the animals from seeing small objects and high spatial frequencies. When the fish were trained to respond to a sharp-edged square, *G. petersii* was easily outperformed by the sunfish (*Lepomis gibbosus*), a visual
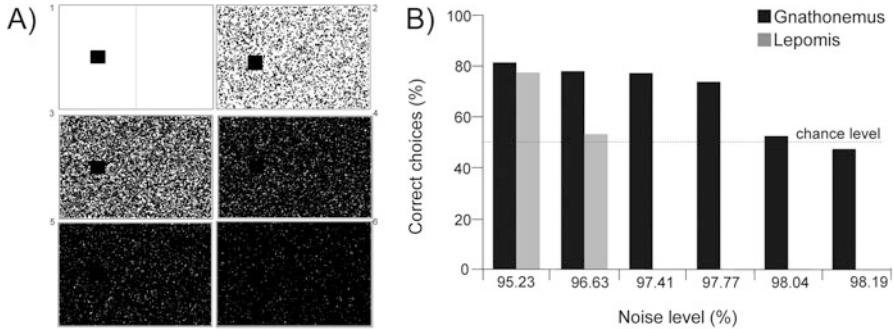
Fig. 9.9 (**a**) Different noise levels for disguising a square object during visual object detection: *1 – 0 %, 2 – 25.9 %, 3 – 62.4 %, 4 – 93.3 %, 5 – 96.6 %, 6 – 97.8 %.* While *Gnathonemus* still could perceive the *large square* in *5* and *6*, *Lepomis* was unable to do so. (**b**) In a noise suppression experiment with *Gnathonemus* (*black*) and *Lepomis* (*gray*) in a two-alternative forced-choice procedure, the fish had to swim toward that side of a screen which contained a *large black square*. The choice of the side with the *square* was rewarded. When different levels of visual noise were added, *Gnathonemus* could detect the *square* even with 97.8 % of noise, while *Lepomis* failed to do so at 96.6 %

specialist taken for comparison. However, if the stimuli were low-passed filtered, which removed all sharp edges, *G. petersii* could detect these objects better than *Lepomis* (Landsberger et al. 2008).

As mentioned above, *G. petersii* lives in blackwater streams carrying dissolved matter and many small particles making these waters very "noisy" (Moritz 2010). In a behavioral experiment, this effect was mimicked by adding small particles to a stripe pattern projected on the bottom of an aquarium, showing that the OMR of *G. petersii* is remarkably noise tolerant (Landsberger et al. 2008). Similar noise particles were also added to the stimuli in the abovementioned experiments with expanding circles eliciting a startle response in *G. petersii* and *Carassius*. The flight responses of both species declined when the threatening stimulus was disguised by dynamic gray noise particles. *Gnathonemus*, however, was less affected than *Carassius* (Kreysing et al. 2012). In a two-alternative forced-choice task, *Gnathonemus* and *Lepomis* were tested to recognize a black square moving over a screen. More and more dynamic noise particles were added, which concealed the object (Fig. 9.9a). It turned out that *Gnathonemus* was able to detect the object under higher noise levels than the sunfish, which does not have a grouped retina (Fig. 9.9b) (Petruschke and von der Emde unpublished data).

The abovementioned findings show that the fact that *G. petersii* cannot see high spatial frequencies and small objects can offer an advantage to these animals when the water is filled with small particles. Such visual noise is filtered out and the fish are able to see the larger objects behind the noise. This allows detection of approaching larger objects, e.g., a predator, which is additionally supported by the high temporal resolution of the visual system. In addition, when swept away by

the current, fish might be able to see the ground or approaching obstacles even under noisy conditions.

9.6   Partitioning of Environmental Sensing

In conclusion, weakly electric mormyrid fish possess an elaborated electrosensory system, which consists of peripheral matched filters and a large brain for processing of electrosensory information. The functions of the electric sense are clearly defined: it works very sensitively in a three-dimensional area around the fish up to a distance of about one fish length. It is very effective in detecting and recognizing small objects, mainly prey items, in a very complex environment containing many similar types of objects ("finding the needle in the haystack"). In addition, it can analyze the spatial and material properties of larger objects during close-up inspection very precisely. However, the electrosensory system does not work at larger distances: object detecting fails at distances larger than about 15 cm and object analysis ends even at a distance longer than 4–5 cm in a fish with a standard length of about 12 cm (von der Emde et al. 2010; Fechler and von der Emde 2013).

As shown above, these exceptional electric sensing abilities are made possible by the production of an optimal electric carrier signal, the EOD, and an elaborated processing of electrosensory information by the nervous system. Both EOD production and sensory processing depend to a high degree of peripheral structures, which take over certain aspects of processing and electromotor production and thus free the nervous system of processing duties. In the periphery, the fish have developed several matched filters, which tune the electric carrier by shaping the electric signals (tip effect, funneling effect, electric skin properties). On the sensory side, the fish have evolved two peripheral sensory foveae, one at the tip of the Schnauzenorgan (for prey detection and close-range object analysis) and one in the nasal region (for obstacle detection and short-range navigation). These areas contain specialized electroreceptor organs that due to their accessory structures form matched filters by responding primarily to certain types of electric stimuli. These electrosensory matched filters delegate several aspects of electrosensory processing to the periphery and thus make the system very fast and efficient. Nevertheless, the brain areas of *G. petersii* that are involved in signal production and perception of electrosensory stimuli are numerous and extremely large. *Gnathonemus* has a huge brain, which uses up to 60 % of the oxygen consumption of the fish (Nilsson 1996).

Like all mormyrids, *G. petersii* has highly evolved eyes of a very peculiar structure. Its grouped retina consists of retinal cups with a light-reflecting surface that focuses the light onto the outer segments of the cones and attenuates the light that reaches the rods. This leads to an alignment of the working ranges of rods and cones and enables simultaneous activity of both receptor types during daylight. As a consequence, *Gnathonemus* shows a superior response to visual stimuli in the mesopic range of illumination compared with fish without a grouped retina. In addition, the grouped retina of *G. petersii* filters out visual noise and responds extremely well to fast-moving stimuli.

The *Gnathonemus* retina thus forms a peripheral matched filter turning it into a highly specialized predator detector. Large objects moving at a distance from the fish are especially well detected. If a predator starts an attack against the fish by darting toward it, the grouped retina of *G. petersii* allows its detection even under unfavorable, "noisy" conditions. The peripheral matched filter frees the nervous system of processing tasks, which in other fishes are performed by the visual centers of the brain. In *G. petersii* visual brain structures are reduced and partly taken over by the electrosensory system. This "freeing up" of processing power in the brain leads to significant energy savings in the visual system and allows at least parts of the available computational capacity to be redirected to other tasks, e.g., to active electrolocation.

G. petersii has evolved a clear partitioning of sensing: in the near field, they employ active electrolocation and are thus able to find and identify their small prey items within a lot of background clutter in the absence of light during their nocturnal activity period. In addition, they can inspect nearby objects and detect their material and spatial properties. In the far field, the visual sense takes over, which, thanks to its matched filter in the retina, is well adapted to see fast-moving, large objects in dim light even under noisy conditions.

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