

Electrolocation

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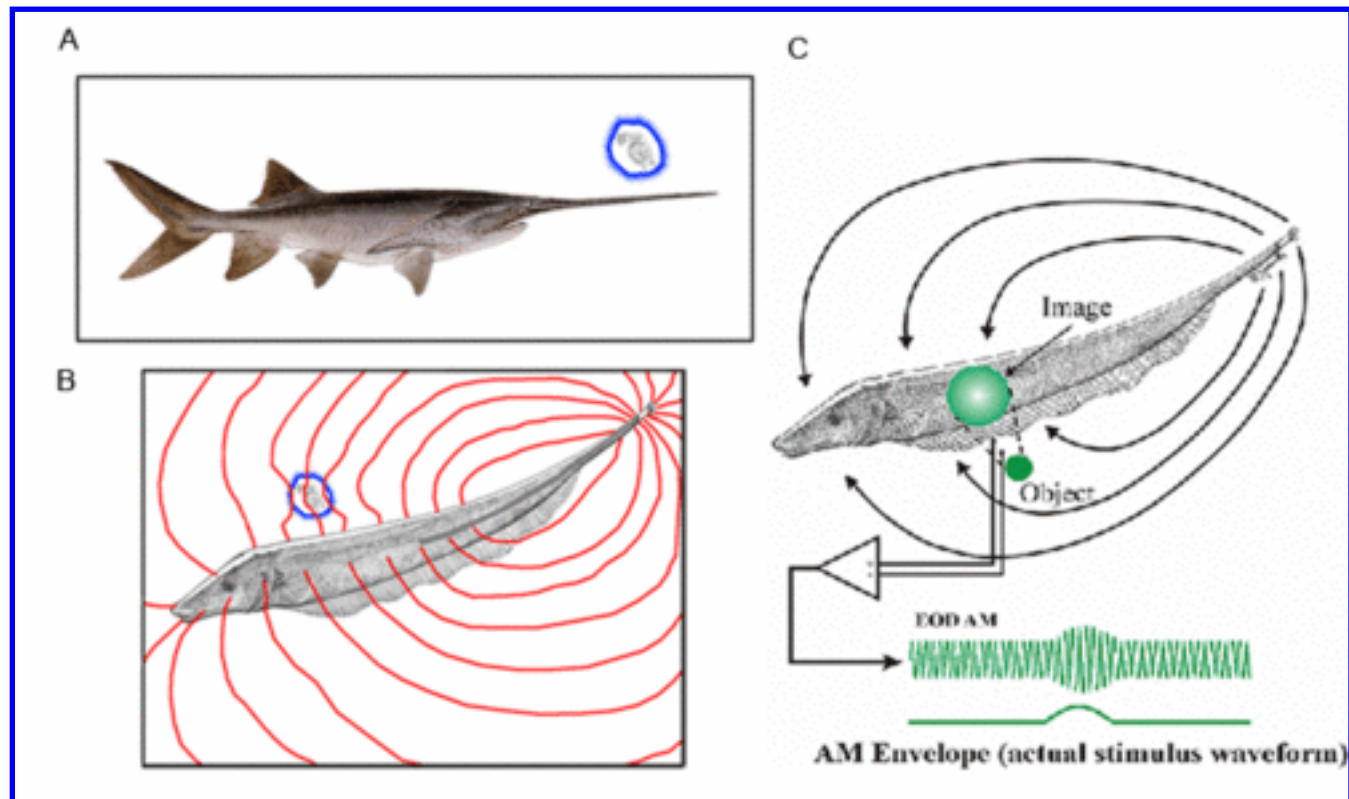


Figure 1: Passive vs. Active electroreception. A: Paddlefish sense electric fields emitted by zooplankton (*Daphnia*) B: The gymnotiform wave-type **weakly electric fish** *Apteronotus Leptorhynchus* emits an electric field, the **electric organ discharge** (EOD), through an electric organ located in its tail. Objects with a conductivity different than that of the surrounding water will cause distortions of this self-generated electric field. Zooplankton has a conductivity greater than that of the surrounding water and will strengthen the electric field locally. C: For active electrolocation, distortions caused by a metal sphere lateral to the animal form an **electric image** on the skin surface. In this case, the metal sphere increases the local amplitude of the EOD. This amplitude modulation is sensed by amplitude coding tuberous electroreceptors on the skin surface.

Electrolocation is a modality of animal [perception](#) through the sensing of electric fields that can be used for:

- object detection
- intraspecies communication
- defensive and offensive [behavior](#) such as prey stinging and warding off predators

Behavioral evidence for the normal sensing of electric fields came from the work of Lissmann (Lissmann, 1958; Lissmann and Machin, 1958; Machin and Lissmann, 1960), thus establishing a new field of research. Electrosensitive [neurons](#) have been found in a wide variety of species including:

- **elasmobranchs** such as rays and skates (Murray, 1960; Kalmijn, 1966)
- **teleost fish** (Lissmann, 1958; Lissmann and Machin, 1958; Machin and Lissmann, 1960)
- **mammals** such as the duck-billed platypus (Scheich et al., 1986)

The study of electrosensory systems is particularly attractive for anatomical, physiological, behavioral, and evolution studies and has already been extensively reviewed (Bullock and Heiligenberg, 1986; Turner et al., 1999; Zakon, 2003; Sawtell et al., 2005; Fortune et al., 2006; Zakon et al., 2006).

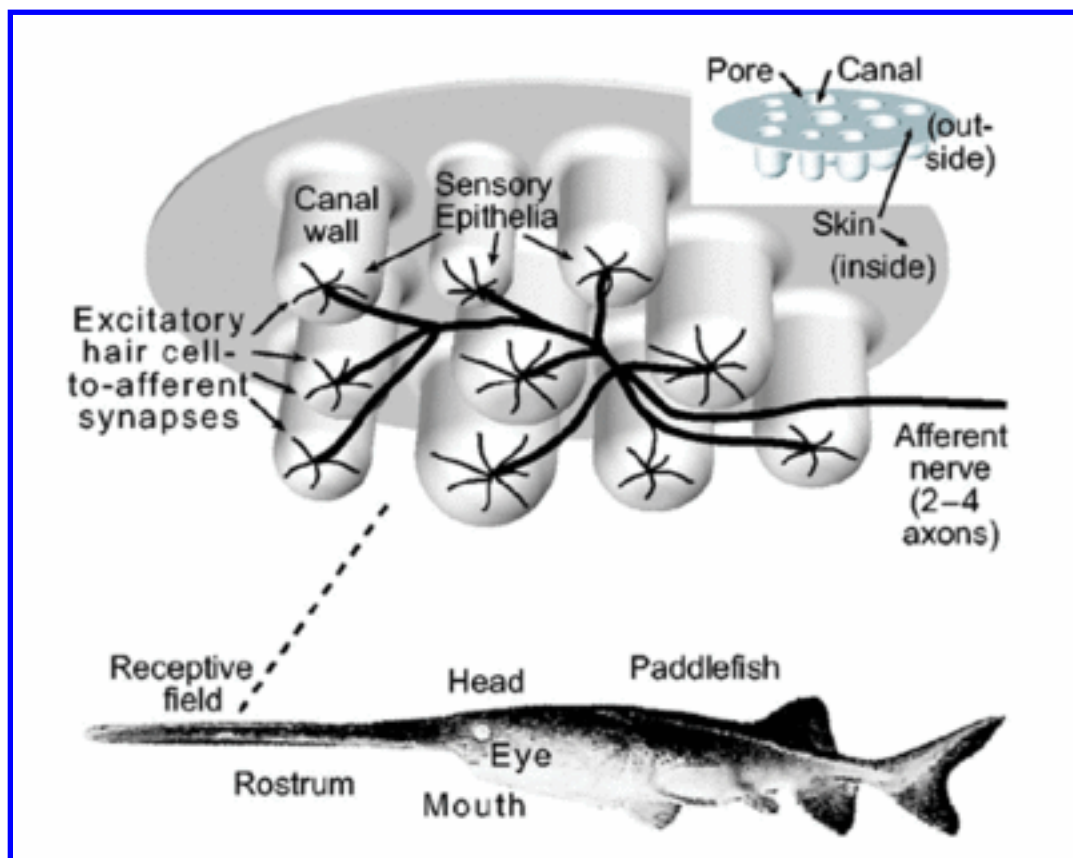


Figure 2: Electroreception in the paddlefish. Electroreceptors form pores on the animal's rostrum. Epithelial hair cells at the bottom of the pore sense changes in the transmembrane potential and increase their probability of releasing neurotransmitter with increasing depolarization. The post-synaptic depolarization summate and lead to the generation of action potentials within the afferent nerve. This

information is transmitted to higher order neurons in the [brain](#). Figure reprinted, with permission, from Neiman and Russell (2001).

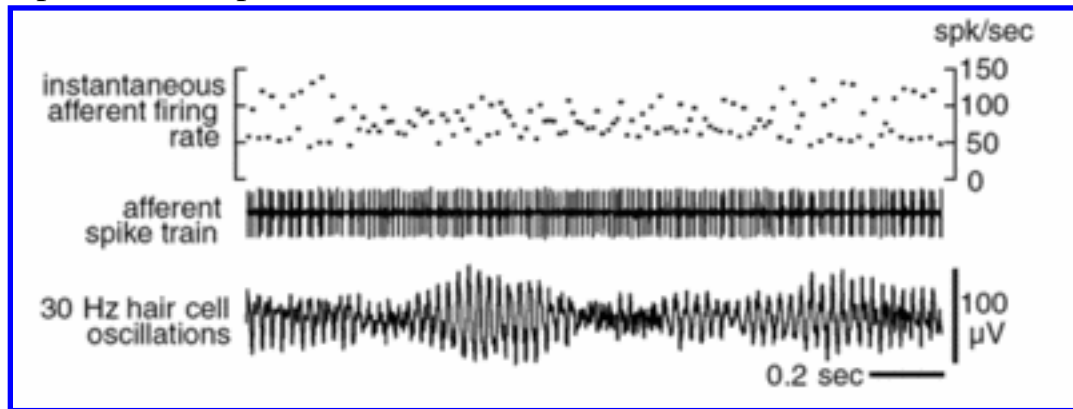


Figure 3: Top panel, instantaneous firing of a paddlefish ampullary electroreceptor afferent. Middle panel, quasi-periodic [spike](#) train of the afferent nerve. Bottom panel, oscillating transmembrane potential recorded in the pore. Figure reprinted, with permission, from Neiman and Russell (2001).

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Passive Electrolocation

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Passive electrolocation was first discovered through observations that receptors in **elasmobranchs**, **Ampullae of Lorenzini**, were sensitive to changes in weak electric fields (Murray, 1960). Since then, another category of electroreceptors called ampullary receptors have been discovered in teleost fish that evolved independently from those found in **elasmobranchs** (Bennett, 1971).

Active Electrolocation

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Some fish, called **weakly electric fish**, actively generate electric fields through electric organs and possess specialized neural circuitry to detect distortions of that field caused by objects. Unlike strongly electric fish (e.g. electric eels), electric fields produced by weakly electric fish are low in amplitude (~1 mV/cm) and are used for electrolocation and electrocommunication rather than electro-offense or defense (Bullock and Heiligenberg, 1986). Active electrolocation has evolved independently in both African Mormyriiform and south American Gymnotiform weakly electric fish that comprise hundreds of species (Bennett, 1971). Active electroreception requires specialized electroreceptors called **tuberos receptors**. It should also be noted that the spatiotemporal characteristics of the **electric organ discharge** (EOD) vary widely: some species have wavetype EODs whereas other species have pulse-type EODs (Bennett et al., 1961; Bennett, 1971; Hopkins and Heiligenberg, 1978; Bass, 1986). For wavetype species, the EOD is highly [periodic](#) with frequencies ranging from 60 Hz to 2000 Hz depending on the species. For pulse-type species, the pulse frequency is much lower and does not exceed 90 Hz (Bass, 1986). Pulse-type fish often display a novelty response characterized by a transient increase in EOD frequency upon encountering a novel object in the environment (Toerring and Moller, 1984; Schwarz and Von der Emde, 2000).

Electroreceptor Categories

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Electroreceptor afferents typically form canals at the skin surface. Epithelial hair cells are found at the bottom of each canal and form excitatory synapses with the afferent nerve containing a spike initiation zone. The afferent nerve then transmits action potentials to the brain (figure 2). Some receptors are sensitive to external electric fields while others are sensitive to distortions of the self-produced EOD.

Ampullary receptors

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Ampullary receptors detect very weak low frequency electric fields and are used to detect prey (Parker and Van Heusen, 1917; Kalmijn, 1974; Zakon, 1986). Recent work has used computational data analysis and modeling to understand how the [dynamics](#) present in the ampullary electroreceptors of the paddlefish contribute to information processing. Recordings from epithelial hair cells located in the pore

have revealed a tendency for these to oscillate ~ 30 Hz. As well, the spike initiation zone of the afferent nerve located in the Ganglia tends to fire action potentials in a quasi-periodic manner ~ 75 Hz (figure 3). A modeling study was successful in explaining interactions between the hair cell as well as the spike initiation zone (Neiman and Russell, 2001; Neiman and Russell, 2004). These interactions manifest themselves as peaks in the power spectrum as frequencies related to the difference and sum of the frequencies of the hair cell oscillation and the afferent nerve firing.

Behavioral [stochastic resonance](#) has been demonstrated in the paddlefish. Thus, increased environmental noise caused for example by a daphnia swarm, actually facilitates single daphnia capture by juvenile paddlefish (Russell et al. 1999). It is thought that hair cell oscillations might mediate this effect by increasing receptor sensitivity to values near threshold (Neiman and Russell, 2004). Alternatively, the internal noise generated from epithelial oscillations may serve to randomize the timing of spikes from different afferents. This would decrease the probability of coincident firing in the absence of external stimuli and thus lower the probability of false alarms.

Ampullary electroreceptors of paddlefish also display [bursting](#) when driven by an external stimuli. Multiunit recordings have shown that such receptors tend to fire [synchronous bursts](#) in response to a common stimulus (Neiman and Russell, 2002). Higher order neurons may possess specialized circuitry to detect these synchronous bursts. Further work is however necessary in order to elucidate the mechanisms by which higher order neurons in paddlefish decode information from electroreceptor afferents.

Tuberous receptors

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Tuberous receptors are found only in two groups of teleost fish: Mormyriforms and Gymnotiforms (Bullock 1982). In both groups, tuberous receptors can be distinguished into two categories. Phase coders are sensitive to changes in EOD frequency while amplitude coders are sensitive to changes in EOD amplitude. We will briefly examine the role of phase coders and focus on the role of amplitude coders in this review.

Phase coding in pulse-type fish

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Knollenorgans in mormyrid fish have high sensitivities and can respond to both the animal's own pulse-type EOD as well as the discharges of other fish (Bennett 1965; 1971; Bell, 1986). These afferents typically respond to stimuli with a single action potential (Bennett 1965). They are generally insensitive to stimulus intensity. As such, it was proposed that these afferents are used exclusively to detect and measure the discharges of other fish (Bell, 1986).

Phase coding in wave-type fish

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In gymnotiforms, T-type electroreceptors display 1:1 phase-locking with respect to the EOD (i.e. 1

action potential per EOD cycle) at a fixed phase. Earlier studies have shown that measurements of phase were essential for a behavior known as the jamming avoidance response (JAR) which has been extensively reviewed elsewhere (Heiligenberg, 1991). However, it is likely that they serve other functions as not all wave-type fish display a JAR. Comparative studies of electric fish species that do and do not display a JAR have revealed important anatomical, physiological, and morphological differences (Matsubara, 1981; Losier and Matsubara, 1990). Further, a recent computational study has shown that phase coders might have other functions even in species that display the JAR. Specifically, T-units can actually encode amplitude modulations quite well (Carlson and Kawasaki 2006). Further studies are necessary to verify whether information about amplitude modulations contained in T-unit spike trains is actually decoded in higher centers and, if so, by which mechanisms.

Amplitude coding in pulse-type fish

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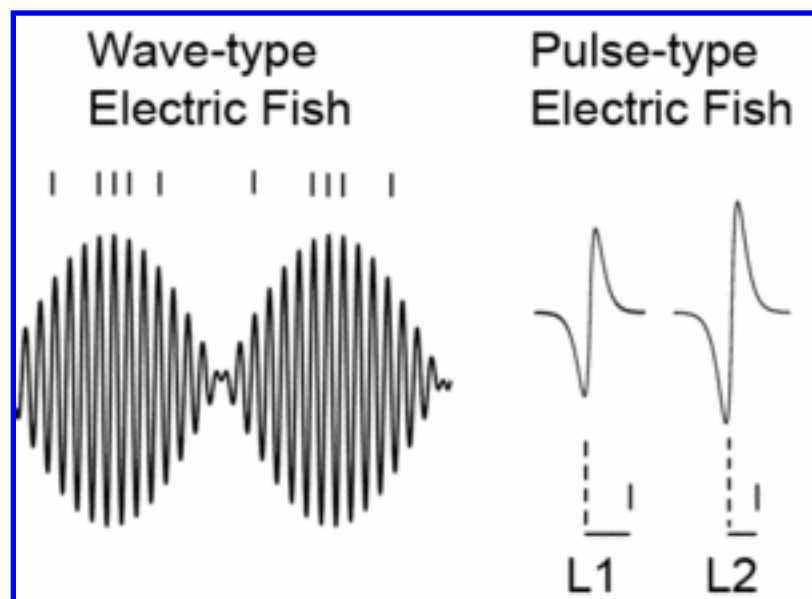


Figure 4: Amplitude coding by electroreceptor afferents in wave-type vs. pulse-type weakly electric fish. In wave-type fish, P-units are phase locked to the EOD and increase their probability of firing with increasing amplitude. In pulse-type mormyrid fish, mormyromasts will fire one action potential per EOD pulse. However, the latency to firing depends on the EOD amplitude: large amplitudes will lead to shorter latencies (L2) than lower amplitudes (L1).

Mormyromast organs in Mormyriiform weakly electric fish use a [temporal code](#) to represent changes in EOD amplitude. It was found that there was a very precise relationship between amplitude and the latency to first afferent spike after the EOD pulse: larger EOD amplitudes will give rise to smaller latencies and vice-versa (Szabo and Hagiwara, 1967; Bell, 1990; Sawtell et al., 2006). A recent study has used information theory to quantitatively characterize the latency code used by mormyromast electroreceptors in mormyriiform electric fish (Sawtell et al., 2006). This study has found that the first

spike latency in mormyromast electroreceptors did not solely depend on the EOD amplitude but also depended on the recent history of EOD amplitudes and interpulse intervals. It was found that mormyromast electroreceptor spike trains contained significant information about EOD amplitude and that over 80% of this information could be recovered by a linear stimulus reconstruction (Sawtell et al., 2006).

Amplitude coding in wave-type fish

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P-type electroreceptors in wave-type fish respond to changes in EOD amplitude with changes in firing rate (figure 4). While initial studies of these receptors used simple stimuli such as step increases or sinewaves, more recent studies have used information theory to characterize P-unit responses to noise stimuli (Gabbiani et al., 1996; Wessel et al., 1996; Metzner et al., 1998; Gabbiani and Metzner, 1999; Kreiman et al., 2000; Chacron et al., 2005c; Carlson and Kawasaki, 2006; Chacron, 2006). P-units follow changes in EOD amplitude with great fidelity (Wessel et al., 1996) and linear decoding algorithms can often recover in excess of 80% of the information contained in their spike trains (Chacron, 2006). Spike trains from P-units are furthermore largely insensitive to addition or deletion of spike timing jitter, implying that most, if not all, the information is contained in their time dependent firing rate (Kreiman et al., 2000; Chacron, 2006). As such, there are large differences between the neural codes used by wave-type electric fish, [rate codes](#), and those used by pulse-type electric fish, [temporal codes](#).

P-unit activity is phase-locked to the EOD since the probability of firing is greatest close to EOD local maxima (Bastian, 1981; Xu et al., 1996; Nelson et al., 1997). Initial studies have found that P-unit tuning curves were high-pass (Bastian, 1981) and an ad-hoc model was developed that accounted for these high-pass characteristics (Nelson et al., 1997). However, it was later observed that intrinsic dynamics in P-units gave rise to lower variability than expected at low frequencies (Ratnam and Nelson, 2000). A phenomenological leaky [integrate-and-fire](#) with threshold fatigue was found to reproduce experimental data (Chacron et al., 2000; Chacron et al., 2001b, a, 2003a; Chacron et al., 2003b; Chacron et al., 2004a), including the low variability at low frequencies (Chacron et al., 2001a). Further understanding of the actual mechanism by which intrinsic threshold dynamics in the model gave rise to lower variability was obtained through theoretical studies showing that negative correlations between subsequent interspike intervals gave rise to noise shaping (Chacron et al., 2004b, c; Lindner et al., 2005b): the total noise power is conserved but noise power is redistributed. In particular, negative ISI correlations give rise to reduced noise power at low frequencies, thereby improving signal transmission at these frequencies. Subsequent experimental studies have verified that P-type electroreceptors indeed displayed noise shaping as predicted from theory (Chacron et al., 2005c). Calcium-activated potassium currents found in electroreceptors (Bennett and Obara, 1986) most likely underlie this noise shaping.

More recent studies have focused on responses of P-units to natural communication signals in weakly electric fish: chirps. Chirps are brief interruptions in the EOD signal used by males to communicate during agonistic encounters (small chirps) and during courtship behaviour (large chirps). It was found that small chirps led to a phase resetting of the ongoing sinusoidal amplitude modulation that occurs

during agonistic situations (Benda et al., 2005) whereas large chirps lead to transient [desynchronization](#) of P-type electroreceptor activity (Benda et al., 2006).

A recent computational study has shown that P-type electroreceptors could also encode phase-modulations of the EOD (Carlson and Kawasaki 2006). These results suggest that information about amplitude and phase modulation of the EOD are not completely segregated between P and T-units in wave-type gymnotiform fish.

Second order sensory neurons

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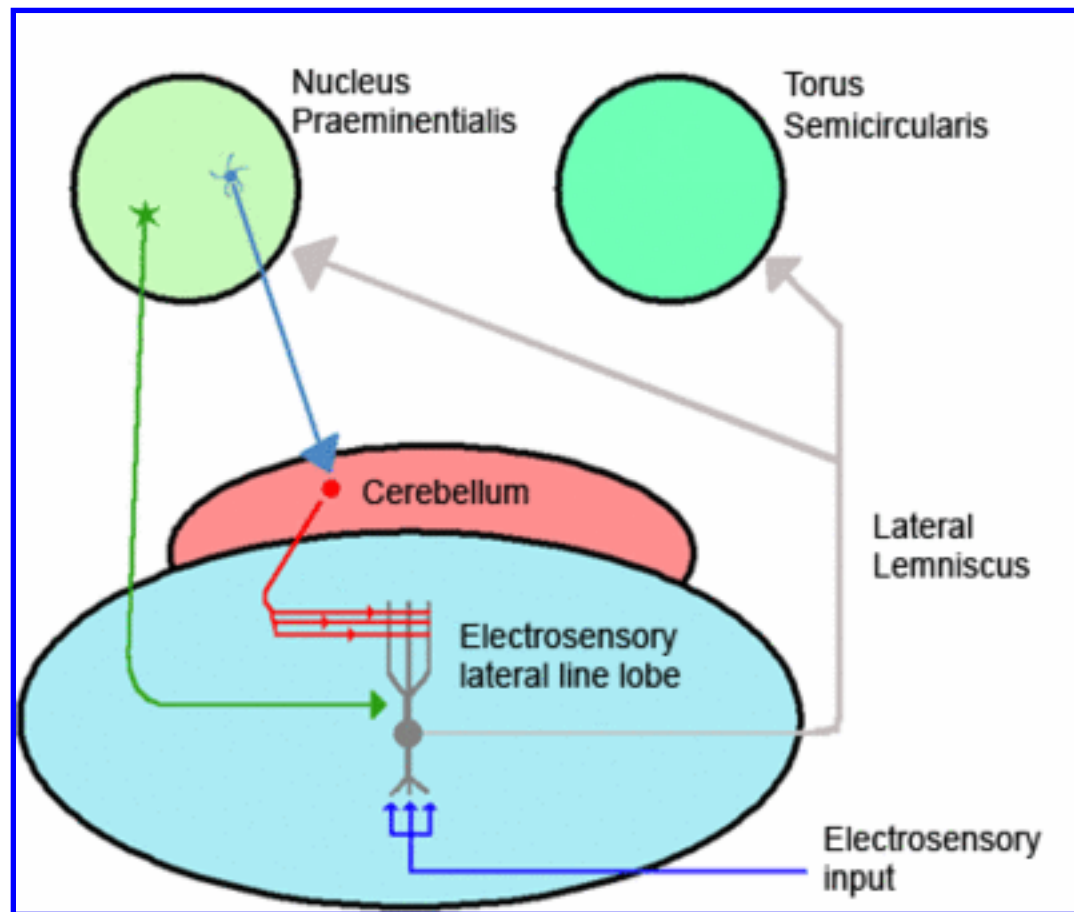



Figure 5: Anatomy of mormyriiform and gymnotiform electric fish. 

In both groups, electrosensory input arrives at the principle efferent neurons of the electrosensory lateral line lobe. These neurons contact higher centers such as the Torus Semicircularis as well as the Nucleus Praeminentialis. Different cell types within the Nucleus Praeminentialis feedback unto principle efferent neurons. One cell type makes direct contact. The other cell type contacts granule cells within the caudal lobe of the cerebellum. These cerebellar granule cells make contact unto principle efferent neurons via parallel fibers.

P-type electroreceptor afferents in Gymnotiform fish [synapse](#) unto pyramidal cells whereas

mormyromast afferents in Mormyriiform fish contact large fusiform and large ganglion cells within the electrosensory lateral line lobe (figure 5). In both groups, the efferent cells also receive large amounts of feedback from higher centers (Maler, 1979; Maler et al., 1981; Bell et al., 1997c; Sawtell et al., 2005) and several studies have focused on functional roles for this input.

Cancellation of redundant stimuli

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As weakly electric fish generate an active electric field, changes in posture that routinely occur during behaviour can give rise to large changes in EOD strength on the body surface which could mask other behaviourally relevant stimuli. It was initially found that, while electroreceptor afferents were strongly driven by such changes, second order sensory neurons were largely insensitive (Bell, 1981, 1982; Bastian, 1995, 1996a, b; Bell et al., 1997b; Bastian, 1998; Bastian, 1999). It should be noted that similar mechanisms are also found in elasmobranchs where proprioceptive input cancels electrical distortions caused by gill or fin movements (Montgomery and Bodznick, 1994; Hjelmstad et al., 1996). A recent review also highlights similarities with other systems (Cullen, 2004).

The circuitry underlying the cancellation of reafferent stimuli in weakly electric fish is similar in both mormyriiform and gymnotiform fish (figure 5). In both instances, electrosensory reafferent signals from electroreceptor afferents are cancelled by a “negative image” provided by feedback input. Subsequent studies have shown that this cancellation is highly plastic: changes in the strength of the reafferent stimulus lead to appropriate changes in the strength of the negative image through plasticity (Bastian, 1995, 1996b, a; Bell et al., 1997b; Bell et al., 1997a; Bell et al., 1997c; Bastian, 1998; Bastian, 1999; Mohr et al., 2003). We now concentrate on the differences between mormyriiform and gymnotiform electric fish.

In mormyriiform pulse-type electric fish, large ganglion and fusiform cells receive a direct corollary discharge signal through feedback pathways. An anti-Hebbian form of spike timing dependent plasticity has been shown to mediate adaptive cancellation of predictable sensory input caused by EOD pulses (Bell et al., 1997a). Further theoretical studies have investigated the computational consequences of these asymmetric [learning](#) rules (Roberts, 1999; Roberts and Bell, 2000, 2002; Williams et al., 2003).

In gymnotiform wave-type fish, pyramidal cells do not receive any direct corollary discharge signal. Hence, cancellation of purely electrosensory stimuli must make use of the sensory reafferent input provided by electroreceptors. Previous studies have documented large heterogeneities in pyramidal cell morphology (Bastian and Courtright, 1991; Bastian and Nguyenkim, 2001), receptor density (Zupanc et al., 1992; Berman et al., 1995), and responses to sensory input (Bastian et al., 2002). A recent study has shown that pyramidal cells also displayed differential levels of adaptive cancellation of electrosensory stimuli: cells with large apical dendrites showed the most plasticity whereas cells with small apical dendrites showed almost no plasticity (Bastian et al., 2004). A network model predicted that, in order to maximize the efficiency of cancellation, only non-plastic pyramidal cells should project to higher centers involved in generating the negative image and this prediction was then verified anatomically (Bastian et al., 2004).

It should be noted that cancellation of reafferent stimuli is not necessarily adaptive. An example of this is found in neurons of the rhombencephalic nucleus of the lateral line lobe (nLLL) in mormyrid fish. These neurons receive direct input from knollenorgans through [gap junction](#) synapses as well as GABAergic inhibitory corollary discharge input from the pacemaker cells (Maler and Mugnaini, 1987). Physiological experiments have shown that, when stimulated by the animal's own EOD, neurons of the nLLL received precise inhibition that blocked their response to the knollenorgan input (Szabo et al. 1979). In contrast with the precise [spike-timing dependent plasticity](#) described in ganglion cells, the inhibitory input unto nLLL neurons does not seem to be plastic (Bell, 1986). It has been hypothesized that the animal's own EOD and the lack of sensitivity of Knollenorgan afferents to stimulus intensity might explain this lack of plasticity.

Bursting

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[Bursting](#) is prominent in the central nervous system and has been extensively characterized in the pyramidal cells of gymnotiform wave-type fish both in vitro and in vivo. In vitro studies have extensively characterized the [burst](#) discharge of pyramidal cells (Turner et al., 1994; Lemon and Turner, 2000; Doiron et al., 2003a; Noonan et al., 2003; Fernandez et al., 2005). Burst firing occurs intrinsically and is mediated by a somato-dendritic interaction: somatic action potentials backpropagate through the dendritic tree and can activate dendritic sodium channels, thereby causing dendritic action potentials. These dendritic action potentials then invade the soma, causing a depolarising after potential (DAP) that can thus cause another somatic spike. This “ping-pong” mechanism continues and the time interval between successive somatic spikes is shortened until the dendritic refractory period is reached. At this point, backpropagation fails to elicit a dendritic spike, thus terminating the burst (figure 5). A detailed compartmental model reproducing this burst pattern was developed (Doiron et al., 2001). Subsequently, a reduced two-compartmental version known as the “ghostburster” was obtained (Doiron et al., 2002). Detailed nonlinear dynamical analysis using a separation into fast-slow subsystems showed that the ghostburster did not fit into the same category as other burst models (Izhikevich, 2000) as the burst termination is connected with a [bifurcation](#) from a period 1 to a period 2 limit cycle.

Recent studies have also looked at the functional implications of burst firing in vivo. Pyramidal cell bursts were initially found to reliably detect particular features of the stimulus (Gabbiani et al., 1996; Metzner et al., 1998; Gabbiani and Metzner, 1999; Krahe et al., 2002). More recently, it was shown that bursts and isolated spikes within a pyramidal cell’s spike train formed two separate information channels (Oswald et al., 2004): bursts selectively encoded the low frequency components of the stimulus while single spikes selectively encoded the high frequency components of the stimulus. Furthermore, it appears that the pyramidal cell bursting seen in vivo is related to the bursting seen in vitro as dendritic failures can be seen in vivo (Oswald et al., 2004). However, further studies are needed in order to understand how bursting seen in vitro is affected by in vivo conditions.

Contextual coding

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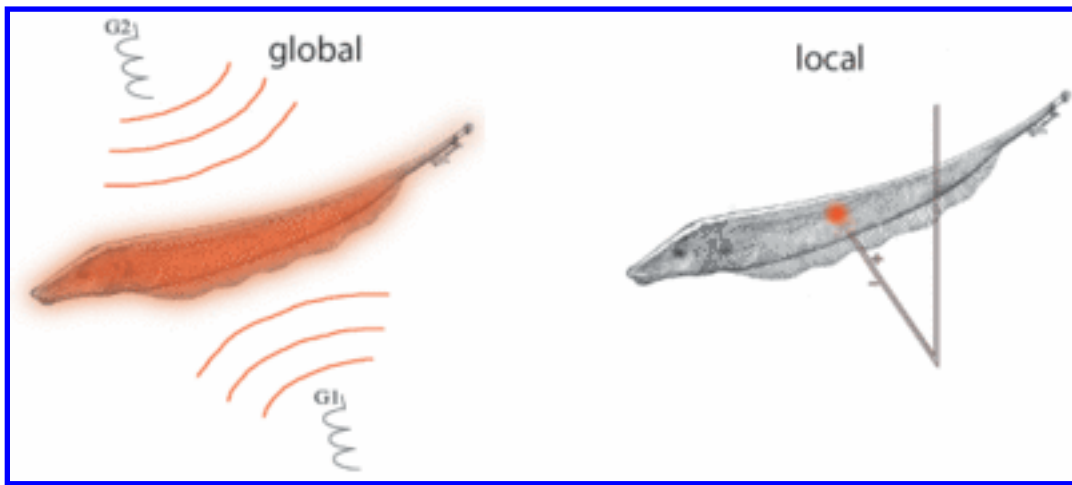


Figure 6: Global (left) and local (right) stimulation geometries. [\[edit\]](#)
 With global stimulation, the electric image covers most of the animal's skin surface. With local stimulation, the electric image covers only a small patch of skin.

Like every animal, weakly electric fish must detect stimuli with vastly different spatiotemporal characteristics in order to survive in their environment. In particular, these fish must detect electrosensory signals caused by prey as well as those caused by conspecifics. Behavioral studies in gymnotiform wave-type fish have shown that the stimuli spatially localized caused by prey contained low frequencies and peaked at 10 Hz (Nelson and MacIver, 1999). In contrast, spatially diffuse stimuli used during communication can contain high frequencies between 50 and 100 Hz (Zupanc and Maler, 1993). Recent studies have used stimulation geometries to mimic prey and communication stimuli and will be henceforth referred to as local and global stimulation, respectively (figure 6).

Network Oscillations

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Recent work has focused on pyramidal cell oscillatory dynamics under local and global stimulation in gymnotiform weakly electric fish. It was found that pyramidal cells tended to display oscillatory dynamics under global but not local stimulation (Doiron et al., 2003b). A network model using diffuse delayed inhibitory feedback could reproduce these results with surprising accuracy and predicted that activation of diffuse inhibitory feedback unto pyramidal cells by diffuse global stimuli caused the oscillation. This prediction was verified experimentally through reversible pharmacological blockade of inhibitory feedback, thereby blocking the oscillation. Further studies then showed that spatial correlations in the stimulus were required to give rise to the oscillation (Doiron et al., 2004; Lindner et al., 2005a).

Tuning shift

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Other studies have focused on correlating pyramidal cell activity with the stimulus under local and global geometry. It was initially found that pyramidal cells gave vastly different responses to stimuli

delivered both locally (mimicking prey) and globally (mimicking communication): whereas responses to local stimuli are tonic in general, responses to global stimuli are more phasic (Bastian et al., 2002). It was then shown that pyramidal cell tuning was geometry dependent: pyramidal cells switch their preferred frequency range from low (<10 Hz) to high (>25 Hz) frequencies contingent on switching the stimulus geometry from local to global (Chacron et al., 2003c). The close match between the preferred frequency tuning of pyramidal cells under local and global geometry and the frequency content of prey and communication stimuli, respectively, suggests that this switch is behaviourally relevant. Further studies have elucidated the origins of this switch in tuning: activation of diffuse feedback input in the form of a negative image by global stimuli has been shown to attenuate the low-frequency response of pyramidal cells both experimentally and in models (Bastian et al., 2004; Chacron et al., 2005a; Chacron et al., 2005b; Chacron, 2006) whereas spatial saturation of the receptive field center by global stimulation will increase pyramidal cell responses to high frequency stimuli (Chacron et al., 2003c; Chacron, 2006).

Higher Order Processing

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In mormyriiform as well as gymnotiform weakly electric fish, efferent projections from the electrosensory lateral line lobe contact neurons within the torus semicircularis (figure 3). Recent work on gymnotiform fish has focused on understanding the cellular mechanisms by which Toral neurons integrate information from pyramidal cells. In vivo patch clamp studies (Rose and Fortune, 1996) have established that Toral neurons possess subthreshold activated sodium conductances that lead to nonlinear amplification of coincident synaptic input (Fortune and Rose, 1997; Fortune and Rose, 2003).

Burst Selective cells in Torus

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Fortune and Rose (1997) showed that some Toral neurons were selectively responsive to frequencies typically associated with prey stimuli (<10 Hz). Interestingly, these same cells showed marked paired pulse facilitation to direct stimulation of the pyramidal cell axon bundle with 10 msec interpulse interval (Fortune and Rose, 2000; Fortune and Rose, 2001), which corresponds to pyramidal cell bursts. This suggests that synaptic facilitation enhances the transmission of pyramidal cell bursts in the Torus. Furthermore, as pyramidal cell bursts selectively encode low frequencies (Oswald et al., 2004), this suggests that burst firing is primarily involved in the coding of prey stimuli in gymnotiform weakly electric fish. Furthermore, the presence of subthreshold sodium conductances (Fortune and Rose, 1997; Fortune and Rose, 2003) suggests that Toral neurons will maximally respond to synchronous bursts from pyramidal cells.

Origins of [directional selectivity](#)

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While pyramidal cells are largely insensitive to the direction of moving objects, a recent study has shown that directional selectivity to moving objects could be induced by gamma-range (20-50 Hz) oscillatory stimuli (Ramcharitar et al., 2006). These oscillations furthermore occur naturally when

groups of fish are in proximity (Tan et al., 2005). These results further show that this selectivity is correlated with the magnitude of short-term synaptic depression caused by these oscillatory stimuli (Ramcharitar et al., 2006). Previous models of synaptic depression have shown mechanisms by which such depression could lead to directional selectivity (Chance et al., 1998) but further studies are needed to see if these mechanisms are indeed responsible for enhanced directional selectivity in the Torus.

Future Directions

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- While information theory and other computational analyses have been used to characterize coding in both the p-type electroreceptors and pyramidal cell of wavetype weakly electric fish, these techniques are only beginning to be used for pulse-type fish (Sawtell et al., 2006). Further studies are needed to understand information processing by neurons within the electrosensory lateral line lobe in these fish.
- In wavetype fish, we are starting to understand the principles by which information is encoded by single pyramidal cells. Further studies are however needed to understand how populations of pyramidal cells encode sensory information. Moreover, the mechanisms by which this information is being decoded by neurons within the Torus semicircularis are just starting to be elucidated.
- In wavetype fish, burst firing in pyramidal cells seems to encode prey but not communication stimuli. As such, there must be mechanisms to control pyramidal cells burst firing. Pyramidal cells receive massive amounts of feedback as well as cholinergic and serotonergic input. Further experimental studies complemented by modeling are needed to understand the functional roles of such inputs and their effects on pyramidal cells burst firing.

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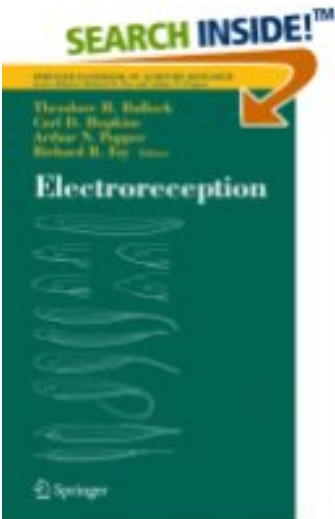
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