Behavioral and neural aspects of the spatial processing of conspecific signals in the electrosensory system

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Abstract

Localizing the source of a signal is often as important as deciphering the signal's message. Localization mechanisms must cope with the challenges of representing the spatial information of weak, noisy signals. Comparing these strategies across modalities and model systems allows a broader understanding of the general principles shaping spatial processing. In this review we focus on the electrosensory system of knifefish and provide an overview of our current understanding of spatial processing in this system, in particular, localization of conspecific signals. We argue that many mechanisms observed in other sensory systems, such as the visual or auditory systems, have comparable implementations in the electrosensory system. Our review therefore describes a field of research with unique opportunities to provide new insights into the principles underlying spatial processing.

Keywords: spatial information; localization of conspecifics; neural mechanisms; sensory processing; sensing behavior.

Introduction

The role of sensory systems is to capture information about the environment. Although much of the behaviorally relevant information is contained in the quality and quantity of a signal, its spatial structure is also relevant (Bradbury & Vehrencamp, 2011; McGregor, 1993). Communication and conspecific signals carry much of their meaning in their spectral and temporal modulation: amplitude and frequency modulations in bird songs (Konishi, 1985; Lohr, Wright, & Dooling, 2003 Reid et al., 2005), colors of body ornaments (Doucet, Mennill, & Hill, 2007; Guilford & Dawkins, 1993; Keyser & Hill, 2000), or chirping patterns in weakly electric fish (Dunlap, DiBenedictis, & Banever, 2010; Engler, Fogarty, Banks, & Zupanc, 2000). Even for olfactory signals, the message is represented by the quality (i.e. odor identity) and quantity of the odor (Aragón, 2009; Daly et al., 2016; de Bruyne & Baker, 2008). In most cases, the receiver also tries to determine the location of the signal's source. Seeking out a signaling mate (Arikawa, Wakakuwa, Qiu, Kurasawa, & Stavenga, 2005; Byrne & Keogh, 2007; Mathis, 1990), localizing threats and the alarm calls they trigger in conspecifics (Cäsar, Zuberbühler, Young, & Byrne, 2013) or avoiding a competitor broadcasting its territorial claim (Bee, 2000; Behr, Knörnschild, & Von Helversen, 2009) are a few examples where the spatial aspect of the signal is key in guiding the behavior successfully. When localizing the source of a signal, sensory systems are faced with important challenges as a signal's directionality and strength can be weakened as it propagates through the environment (Bradbury & Vehrencamp, 2011).

Decades of research on the neural and behavioral mechanisms underlying signal localization in various modalities and model systems have led to rich insight into how these challenges are met. As always, comparing solutions across modalities and species can reveal core principles of a mechanism and key adaptation permitting new functions. The study of sensory processing in weakly electric fish has provided important contributions to this comparative approach to understanding neural processing. An extensive literature on the temporal processing of electrosensory signals is matched by a relatively smaller but growing literature focused on the spatial aspects of communication signals. We provide in this review an overview of our current knowledge on the spatial processing of electrocommunication signals but most importantly we point out key challenges faced by this system and commonalities with other sensory systems. We argue that that the difficulty in localizing weak signals, signals in

noise, or simply localizing accurately requires sensitive and efficient mechanisms that share many resemblances across modalities.

The electrosensory system

The ability to sense electric fields is thought to have evolved early in the vertebrate lineage (Bodznick & Northcutt, 1981) and is developmentally derived from lateral line placodes (Modrell, Bemis, Northcutt, Davis, & Baker, 2011). Electroreception was lost in teleost fish but regained at least twice (in Osteoglossomorpha and Ostariophysi) thereby explaining the presence of electroreceptors in a variety of species, including catfish, elephantnose fish and knifefish (see Baker, Modrell, & Gillis, 2013 for a recent review on the topic). In teleosts, electroreceptors are thought to have evolved as a modification of neuromast (Baker et al., 2013). Beyond their detailed evolutionary trajectory, electroreceptor origin is clearly linked to the lateral line and mechanosensory system, similar to the origin of vertebrate auditory receptors (Duncan & Fritzsch, 2012). As a reflection of their similar evolutionary origin, both electroreceptors and auditory receptors travel along the VIIIth cranial nerve (Carr, Maler, & Sas, 1982). Ampullary receptors are the most common type of electroreceptors across species, but in two orders of teleost (Gymnotiformes and Mormyriformes) a second type of electroreceptor evolved - tuberous receptors (Szabo, 1974). Where ampullary receptors are sensitive to low-frequency electric signals, such as the ones produced by contracting muscles, tuberous receptors are sensitive to high frequencies (Bennett, Sandri, & Akert, 1989; Maler, 2009a; Maler, 2009b;Hopkins, 1976) and their evolution accompanies the evolution of electric organs (EO) that generate high-frequency weak electric fields (Fig 1). Derived from a modified muscle or a modified nerve terminal, EO produce pulsatile or continuously oscillating electric fields (Kramer, 1996). Weakly electric fish (Gymnotiformes and Mormyriformes) thereby possess an active electrosense where the electric organ discharges (EOD) (Lissmann, 1958) are perceived by electroreceptors on the skin. Anything in their environment that is more or less resistive than water will cause a distortion of this electric field that will cast an "electric shadow" (Rasnow, 1996) on the sensory surface (we refer to the electrosensory sensorium as the "sensory surface" throughout the review). They rely heavily on this active sense to navigate, localize prey, but also to communicate and interact with conspecifics (Bullock, Hopkins, Popper, & Fay, 1986; Lissmann, 1963). Although Gymnotiformes and Mormyriformes have many similarities in the way they use and process electric signals, the fact that they evolved this active electric sense independently

also leads to significant differences, in particular at the neural level. To facilitate the discussion in this review, we will focus on knifefish (Gymnotiformes), and more specifically the wave type species (e.g. glass knifefish or ghost knifefish) that produce continuous EODs rather than pulsed EODs (Bass 1986; Bennett, 1971); we will simply refer to them as weakly electric fish.

Knifefish are typically nocturnal species and thus rely heavily on this active electrosense to perceive their environment. The sensory image caused by objects close to them is quite accurate thanks to a relatively high density of receptors over the entire surface of the skin (Carr et al., 1982); allowing them to be efficient hunters of invertebrate prey (Nelson & MacIver, 1999). Similarly, they can locate and identify a conspecific based on the EOD it produces or mediate social interactions via electrocommunication signals such as chirps (Engler & Zupanc, 2001). The sensitivity of their ability to locate each other based on this sense is easily observable both in the field or in the lab (see below). For example, they will chase each other at high speed in a noisy environment with multiple other signal sources or locate each other at such distances that they must base this detection on extremely weak signals.

Localization of conspecifics

The localization of conspecific signals is a different sensory problem to the localization of small objects such as prey items. An object close to the body will cause a local disturbance in the EOD which will be picked up by a limited number of receptors on the corresponding portion of the skin (Rasnow, 1996). The localization strategy in this case is likely to be closer to visual localization or localization in the somatosensory system where exclusive activation of a subset of receptors encodes location in a labeled line code (Cichy & Teng, 2017; Hartmann & Bower, 2001; Krekelberg, Kubischik, Hoffmann, & Bremmer, 2003; Okada & Toh, 2006). Localizing a conspecific based on the EOD it produces cannot rely on this strategy since the sender's EOD will impact the majority of electroreceptors over the entire skin surface (Kelly, Babineau, Longtin, & Lewis, 2008). Therefore, localization of conspecifics probably relies on comparison of the input at the various receptors and location would be computed by the nervous system based on the differences. This task shares similarities with localization in the auditory system, which relies on comparisons of binaural input (Brand, Behrend, Marquardt, McAlpine, & Grothe, 2002; Carr & Konishi, 1990; Jeffress, 1948). Localization in the electrosensory system might therefore be described as a hybrid mechanism that relies on a labeled line strategy for

passive objects (e.g. small prey) that cause a local electrical disturbance, but needs to compute the spatial information about active electro-generating sources (e.g. conspecifics). As such, the electrosensory system is faced with many of the same challenges faced by the auditory or the visual system when localizing signal sources in complex environments. Whether it is a question of localization accuracy (e.g. auditory system), localizing in a noisy environment (cocktail party problem in the auditory system; Cherry, 1953; Liberman, Harris, Hoffman, & Griffith, 1957) or foreground-background separation (visual system; Ölveczky, Baccus, & Meister, 2003), there is a rich literature documenting the various neural and behavioral mechanisms in place to face these challenges.

The electrosensory system has a long history of contribution to our understanding of sensory processing(Bastian & Heiligenberg, 1980). Issues of temporal coding have been particularly well explored in this system (Gabbiani, Metzner, Wessel, & Koch, 1996; Krahe, Bastian, & Chacron, 2008). Understanding localization in the electrosensory system has focused heavily on the spatial aspect of prey capture or the localization of small objects (Babineau, Lewis, & Longtin, 2007; Caputi & Budelli, 2006; Nelson & MacIver, 1999; Rasnow, 1996). Less is known about the spatial processing of conspecific signals, but there are several new studies and a growing interest in the topic (Kelly et al., 2008). Our goal in this review is to provide an overview of what is known about localization of conspecific signals in weakly electric fish, pointing out along the way how this model system can contribute to our general understanding of sensory processing. We will first discuss the behavioral aspects of conspecific localization to provide a good understanding of the tasks that must be carried out by the nervous system. We will then describe the neural mechanisms underlying spatial processing and point out the issues that remain poorly understood. Finally, we compare the electrosensory system with other modalities to highlight the common challenges they face and discuss the similarities and differences in how they accomplish these tasks.

Behavior and signal properties

This electrosense is advantageous for navigating at night or in murky waters. Their ability to navigate and locate prey based on this sense is well documented (Nelson & MacIver, 1999; Postlethwaite, Psemeneki, Selimkhanov, Silber, & MacIver, 2009; Stamper, Roth, Cowan, &

Fortune, 2012; Von Der Emde, Schwarz, Gomez, Budelli, & Grant, 1998). Similarly, they also rely heavily on this electrosense when interacting with conspecifics to identify, communicate and locate each other. Identity can be determined from the EOD pattern (Fig 2a): depending on the species, EOD frequency, shape or pulse pattern can be used to identify conspecifics from individuals of another species (Zupanc, Sîrbulescu, Nichols, & Ilies, 2006) or even differentiate amongst conspecifics (Zakon, Oestreich, Tallarovic, & Triefenbach, 2002). In wave type species, the EOD frequency (and possibly shape; Kolodziejski, Sanford, & Smith, 2007; Petzold, Marsat, & Smith, 2016) is perceived indirectly.

Indeed, when two or more individuals come into close proximity, the electric fields of each fish summate, and the resulting field contains amplitude and phase modulations, collectively known as a "beat" (Fig 2b; Heiligenberg, 1991). The beat frequency is equal to the frequency difference between the EOD of the sender and receiver (note that both fish send and both fish receive but we use this terminology throughout this article to describe the perspective we use (Stamper, Madhav, Cowan, & Fortune, 2012). Furthermore, phase modulations can indicate whether the other fish has an EOD frequency higher or lower than its own (see Carlson & Kawasaki, 2007; Metzner, 1999; Stamper et al., 2012 for more information). Determining beat frequency is important since each fish has a baseline EOD frequency and thus individual discrimination can be based on this signal. In some species, EOD frequency is sexually dimorphic leading beat frequencies to be lower during same-sex interactions and higher for male-female pairs (Engler & Zupanc, 2001). Since beat frequency can indicate species, sex, maturity and even individual identity, many species react differently when exposed to beat signals of various frequencies. For example, the rate of production of certain communication signals in black ghost or brown ghost knifefish depends on the beat frequency (Hupé, Lewis, & Benda, 2008). The most common type of communication signal produced by these fish -chirps- are brief increases in EOD frequency (see Kolodziejski et al., 2007 for more info).

Sensitivity of conspecific detection and localization

In wave type fish, the beat signal results from the presence of a conspecific (see Fig 2), and, therefore, carries information about a conspecific's location. The beat signal will strengthen as the conspecific gets closer and the strength of the signal across the sensory surface (i.e. the body's surface) correlates with its relative position. Both lab and field studies clearly show that

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they monitor this information to detect the presence and position of a conspecific. In an insightful field study, Henninger et al (Henninger, Krahe, Kirschbaum, Grewe, & Benda, 2018) used grids of electrodes placed in river streams and creeks to triangulate and follow individuals in their natural environment during long periods of time. Besides revealing the behavioral and communication dynamic happening during various types of interactions -including courtship or aggression- this study showed the range of detection of conspecifics via this electrosense. Although their data suggests that fish routinely communicate with each other over distances of up to 30 cm, it also shows that two fish can detect and assess a conspecific at distances of 1 meter or more. For example, they showed that a resident fish-initiated attacks on an intruder located as far as 1.7 m away. To emphasize how challenging this task is, they estimated the strength of the sender's signal and showed that a fish 30 cm away creates a signal of 10 µV/cm and that a fish 1.7 m away causes a signal smaller than 1 µV/cm. Note also that this data suggests that these weak signals were not only detected, but also localized since it guided the resident to launch an attack directed at the intruder.

Laboratory studies confirm the sensitivity of this system in detecting and locating a conspecific. Fish adjusted their EOD output (i.e. the response called "envelope tracking") when presented with beats of 10-15% contrast (Metzen, Huang, & Chacron, 2018) which would correspond to a conspecific 20-30 cm away (Fotowat, Harrison, & Krahe, 2013). In another study, fish exposed to a conspecific signal presented from various distances regularly produced chirps only in response to the stimuli located fairly closely (10 cm; Zupanc et al., 2006). However, conditioned responses to weak signals demonstrated that fish could detect signals weaker than 1 µV/cm corresponding to a distance of up to 1.6 m (Knudsen, 1974; Knudsen, 1975). Therefore, despite coming to their conclusion through very different methods, the field and laboratory studies provide very similar estimates and identify a certain range within which fish actively interact with each other (e.g. chirp or envelope tracking) and a wider range delineating the limits of their detection and localization ability.

Conspecific localization and EOD temporal modulation

Information about conspecific location is present in two aspects of the signal: its temporal modulations and its spatial structure (see next section). Temporal modulations are indeed imparted by the relative movement of two fish. As a sender moves closer and further from the

receiver, the beat will proportionally increase and decrease in strength (Fig 2c). The strength of the beat is also called its "contrast" and contrast modulations are called the "envelope signal". The characteristics of these envelope signals have been determined experimentally by recording the signals received by a fish exposed to one or several other moving conspecifics (Fotowat et al., 2013; Yu et al., 2012). Since movement is relatively slow, envelope signals are typically low frequency (<10 Hz). The data also confirmed that the beat elicited by a conspecific nearby can be strong (often above 50% contrast at <10 cm), but decreases quickly with distance (a few % at 30 cm; Fotowat et al., 2013) since these electric fields decrease in strength as a function of the cube of the distance (Caputi, Aguilera, Pereira, & Rodríguez-Cattáneo, 2013). Furthermore, these recordings illustrate another important principle that influences the properties of electric signals. The strength of the signal is not simply related to the distance but also to the relative orientation of the receiver and sender "dipoles" (Rasnow, Assad, & Bower, 1993). To simplify, the EO can be thought of as a stimulus dipole and electroreceptors are sensing dipoles detecting the potential difference across the skin. Electric fields are characterized by isopotential lines and a sensing dipole positioned parallel to an isopotential line would not pick up the signal even if it is close to the stimulus dipole (Fig 1) (Assad & Bower, 1997; Rasnow et al., 1993). Consequently, the strength of the envelope can decrease to zero as the fish moves away or as it rotates 90° making the envelope signal picked up by a given receptor ambiguously related to the location of the sender.

Envelope signals are common in various modalities. In the visual system they are linked to the ability to distinguish contrast based visual contours (Grosof, Shapley, & Hawken, 1993). They are also used by the auditory system for speech perception and sound localization (Lohuis & Fuzessery, 2000; Smith, Delgutte, & Oxenham, 2002). The electrosensory system has provided important insight into how these signals are processed by the nervous system (see next section), but we do not yet know how they are used to gauge the distance of the sender. Furthermore, azimuth and elevation of the sender relative to the receiver is not encoded in this temporal signal, it can only be estimated by comparing the strength of the signal across the sensory surface.

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Electrosensory image

The sensory surface is well suited to capture the spatial aspect of the sensory environment. Most of the body surface of knifefish contains a high density of electroreceptors each capturing the electrical potential within its vicinity (Carr, Maler, & Sas, 1982). Distortion of the fish's own EOD caused by its environment can thus be mapped on this spatially organized sensory array. Distortions experienced by these fish can be categorized as either a passive electric image or an active electric image. The active electric image arises when an object or animal that is more or less conductive than the surrounding water locally influences the strength of the electric field generated by the fish. For example, a conductive prey item near the head (Fig 3) will locally increase the strength of the electric field and cast an "electrical shadow" (or a bright spot in this case) on the skin. A series of seminal studies using modeling, physiological and behavioral approaches have detailed the characterization of the electrosensory image of prey items during hunting behaviors (Nelson & MacIver, 1999; Nelson, MacIver, & Coombs, 2002). The authors measured the 3D relative position of the fish and its prey, modeled the electrosensory image that would result, estimated the activation strength of the various receptors and reconstructed a 3D activation map of the sensory surface. They determined that black ghost knifefish typically detect prey when they are 1-2 cm away that elicit a signal of 1-3 µV and can potentially detect a signal as weak as 0.2 µV. These studies point out once again the extreme sensitivity of this system and provide a clear understanding of how these signals are represented at the periphery. The neural mechanisms underlying prey localization and detection are also a good example of sophisticated neural processing strategies used to accomplish challenging tasks (see next section; Chacron & Bastian, 2008; Clarke, Longtin, & Maler, 2014; Jung, Longtin, & Maler, 2016).

A conspecific in close proximity to the receiver will also cast such an active electrosensory image -albeit a bigger one- but few studies have characterized this sensory image. In a recent study combining behavioral recordings and modelling of the electric field and sensory image, Pedraja et al (2016) showed that this active image could guide behavior during aggressive encounters. However, they showed that the passive electrosensory image (see below), rather than the active one, was better correlated with the initiation of attack behavior at close range. This study also indicates that the image of the conspecific is fairly sharp at close range (a small portion of receptors are strongly activated and the others much more weakly) thereby giving a

clear labeled-line representation of conspecific location. In contrast, the image elicited by a conspecific further away (>10 cm) is uniformly weak, thus detection most likely involves pooling all the responses together to average out the noise and localization must rely on comparing the weak responses to determine the even-weaker differences among them. This analysis highlights once again the challenging task that this system must perform. Although it is still not clear to what degree they rely on the passive image versus a combination of passive and active images in close range interactions, the active image cannot underlie the ability to detect and localize conspecifics far away (Knudsen, 1975).

They must thus rely on the passive electrosensory image to detect and localize distant conspecifics. The passive image consists of the spatial pattern of distortion of the receiver EOD caused by the sender EOD. It is important to point out that this terminology, although well defined for prey and for pulse species, is more ambiguous for wave-type species since this passive image is the result of both sender and receiver's active signals (EODs and the resulting beat). Furthermore, the passive and active components will both be perceived through modulations of the receiver's own EOD and thus, are not truly different images but different components of the electrosensory image. We nevertheless use this terminology for consistency with previous studies (e.g. Pedraja, Perrone, Silva, & Budelli, 2016).

The strength of the beat signal at different points on the receiver's skin will vary with position and orientation of the sender. A sender located in front, for example, would cause stronger beats on the rostral than caudal end of the receiver. The detailed activation pattern of the sensory surface also depends on receptor orientation (e.g. dorsal receptors are nearly orthogonal to the nearby receptors on the side of the body). For this reason, the activation pattern of areas like the head will be more complex that for relatively flat area like the side of the mid-body. Several researchers have modelled the electrosensory image caused by a conspecific either fixed (Kelly, Babineau, Longtin, & Lewis, 2008) or approaching (Castelló, Aguilera, Trujillo-Cenóz, & Caputi, 2016; Gómez-Sena, Pedraja, Sanguinetti-Scheck, & Budelli, 2014) the focal fish. Despite being extremely valuable data, the studies typically have simplifications that make evaluating the strength of the input for all electroreceptors more difficult. For example, the models looking at conspecific signals were either limited to 2D or considered receptors only along a line on the side of the fish or did not take into account the various orientation of

receptors. This complexity will be most obvious for regions like the head where receptors very close to one another will have very different orientation and thus very different activation levels. Considering how receptor activation will depend on the relative orientation, in 3D, of the receptor relative to the stimulus, further studies are required to obtain a detailed characterization of the sensory image of conspecifics. An incomplete understanding of the spatial structure of these sensory signals limits our ability to understand how the sensory system extracts this spatial information. Nevertheless, a rich literature on sensory processing in this system documents many of the neural processes relevant to this task.

Sensory system and neural processing

Introduction

Representation of space in sensory systems, for example through topographic mapping, is a key feature in most modalities. In the electrosensory system, the sensory images activate electroreceptors distributed everywhere across the skin. Ampullary receptors (mediating low-frequency passive electrosensation; see Introduction) are less numerous (~700 total in brown ghost knifefish) compared to tuberous receptors (~13,000-17,000 total; Carr et al., 1982). The density of ampullary and tuberous receptors varies across the body surface. Regions of the mouth, face, and head are higher in receptor density, resulting in the formation of an electrosensory fovea. Similar to other sensory systems, this foveal arrangement of receptors permits a higher resolution of sensory input and its location near the mouth is well suited to guide the final stages of prey capture.

There are two kinds of tuberous receptors involved in active electrosensation: T-units and P-units. Time coding units (T-units) are few in number and form a separate channel early in the sensory pathway through spherical cells of the electrosensory lateral line lobe (ELL) and onto a dedicated layer of the Torus semicircularis (Ts) (Maler, Sas, & Rogers, 1981). Most tuberous receptors are amplitude coding (or probability coding units: P-units), providing direct input to ELL pyramidal cells. P-units are solely responsible for encoding the amplitude of the fish's own EOD and the amplitude modulations (AMs) arising from electrolocation and electrocommunication (Nelson, Xu, & Payne, 1997). All tuberous receptors split three ways providing trifurcated input unilaterally to the centromedial segment (CMS), centrolateral

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segment (CLS), and the lateral segment (LS), whereas ampullary receptors project exclusively to the medial segment (MS) of the ELL (Heiligenberg & Dye, 1982). Pyramidal cells across the different maps and different layers of the ELL (deep, intermediate or superficial) vary in their response properties (e.g. low-pass to high pass) or receptive field size and polarity (ON-center or OFF-center cells) (Krahe, Bastian, & Chacron, 2008; Saunders & Bastian, 1984). The three tuberous-driven maps thus have properties adapted for processing different signals. For example, CMS is crucially involved in the jamming avoidance response (JAR), certain stages of prey capture might rely more heavily on CLS, while LS is best at encoding communication signals (Maler, 2009b ; Marsat, Proville, & Maler, 2009; Metzner & Juranek, 1997). ELL neurons project to the Ts in the midbrain and to areas providing feedback to the ELL (see below). Ts has a laminar organization and a complex network of inputs, outputs and connections between layers. Electrosensory input to the Ts is somatotopically conserved and restricted specifically to the dorsal Ts (Carr et al, 1981). The dorsal Ts is divided into twelve laminae, of which layers 3, 5, 6, 7, 8b, and 8d receive electrosensory input. Cells that respond to communication stimuli likely lie within the deeper layers of the Ts. At higher levels the electrosensory pathway splits as Ts projects to the optic tectum (TeO) involved in spatial processing, to the nucleus electrosensorius (nE) processing communication signals, and the preglomerular nucleus (PG) that mediates connectivity with the forebrain (Fig 4) (Giassi, Ellis, & Maler, 2012; Zupanc & Horschke, 1997). As expected, extensive feedback from forebrain areas but also from mid and hindbrain areas interconnect these regions; most are not discussed further here (Bell & Maler, 2005; Giassi et al., 2012).

The processing of conspecific signals has been most extensively studied at the receptor and ELL levels and so we focus on the early sensory processing in the next sections of this review. Conspecific stimuli cause both phase and amplitude modulations in the input signal (Stamper, Fortune, & Chacron, 2013; Stamper et al., 2012; Yu et al., 2012). While phase information relayed by the T-unit receptors is essential to generate the JAR behavioral response, the bulk of the processing at this early stage focuses on the AM. Most notably, the beat AM present during conspecific interactions must be detected, localized and its frequency determined. As is typical with early stages of sensory processing, receptors encode the AM fairly linearly and ELL pyramidal cells -although possessing important non-linearities- still represent the shape of a broad range of AM signals in modulations of their firing rate. Various response properties and

coding mechanisms have been described at this level such as interspike interval (ISI) correlations to reduce noise (Ratnam & Nelson, 2000), bursting to improve feature detection (Gabbiani, Metzner, Wessel, & Koch, 1996) or decorrelation to enhance information bandwidth and coding accuracy (Marsat & Maler, 2010). We also have a detailed understanding of how communication signals, chirps more specifically, are encoded in the early sensory pathway. Chirp coding crucially depends on the frequency of the beat that is present in the background of these interactions (Marsat, Longtin, & Maler, 2012; Walz, Grewe, & Benda, 2014). For example, the receptors can synchronize or de-synchronize in response to a chirp depending on whether the beat is low or high frequency (Benda, Longtin, & Maler, 2006) and ELL neurons might respond with bursts only for some chirp-beat combinations (Allen & Marsat, 2018; Benda et al., 2006). For both chirp and beat coding, Ts neurons respond more sparsely and selectively (Vonderschen & Chacron, 2011) although some neurons still encode the signal AM in detail. Although the coding properties alluded to above could influence the conspecific localization mechanism, we will focus below on two mechanisms that play a large role in this process, namely envelope coding and beat cancellation.

We described in the behavior section how the movements of interacting fish would cause an envelope modulation - a signal that could serve to gage distance between individuals. Several recent publications have clarified the neural mechanisms underlying envelope coding (Huang, Metzen, & Chacron, 2018; Metzen & Chacron, 2014; Savard, Krahe, & Chacron, 2011; Thomas, Metzen, & Chacron, 2018). For firing rate to reflect the envelope strength, a non-linear transformation must happen. To illustrate this point, consider an envelope signal that decreases as if the conspecific was moving away. During this decrease in envelope (beat contrast), the mean EOD strength that reaches the receptors does not change, it still varies around the same amplitude of the fish's own EOD. Therefore, if mean firing rate is to change, even though mean EOD strength does not change, the nervous system must implement a non-linear transformation. Several mechanisms might contribute to the envelope coding mechanism. At weaker intensities, ovoid cells can perform this task (Middleton, Longtin, Benda, & Maler, 2006) and direct feedback can enhance the sensitivity of the envelope responses (Huang et al., 2018). At higher intensities, the receptors provide the main mechanism implementing this non-linear transformation. Due to the threshold and saturation of receptors, the incoming signal is half-rectified and then low-pass filtered at the synapse with the pyramidal cells (Savard et al., 2011).

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These mechanisms extracting the envelope strength could therefore contribute to evaluating conspecific distance.

The ELL receives both direct feedback from the nucleus praeminentialis (nP; see Figs 4, 5) and indirect feedback from cerebellar granular cells (EGp, Figs 4, 5).The encoding of beats in the ELL is also influenced by indirect feedback inputs (Joseph Bastian, 1986a, 1986b). The role of the latter in cancelling the response to beats has been extensively documented (Bol, Marsat, Harvey-Girard, Longtin, & Maler, 2011; Chacron, Doiron, Maler, Longtin, & Bastian, 2003). A subset of pyramidal cells, the superficial and to some degree the intermediate cells, receive massive parallel fibers inputs onto their apical dendrites. Plasticity at these synapses adjusts the relative contribution of each fiber so that the overall input is in antiphase to the feedforward input from the receptors thereby reducing the strength of the response in these cells (Bol et al., 2011; Harvey-Girard, Lewis, & Maler, 2010). This mechanism operates for relatively low frequency beats but does not cancel the responses to beat frequencies higher than 15-20 Hz (Chacron, Maler, & Bastian, 2005). This feedback only affects a subset of cells; it does not influence the response of deep pyramidal cells and cancellation in the CMS and LS segments is less pronounced. Nevertheless, since it affects the coding of the beat, and because beat strength can mediate the localization of conspecifics, this feedback can potentially influence the localization mechanism (see below).

Topographic representation and spatial information

Each receptor on the skin captures the strength of the electric signal at a given point on the skin and thus the pattern of activation of the array of electroreceptors covering the body will reflect the spatial structure of the electrosensory image elicited by the presence of a conspecific. This spatial pattern of activation of receptors is conserved through the topographic projection into the ELL. Thereby each of the four segments of the ELL (from medial to lateral) is organized as a topographic map of the sensory surface (Lannoo, Maler, & Tinner, 1989). The three maps sensitive to EOD (CMS, CLS and LS) differ in size and in the shape of their topographic representation (see Krahe & Maler, 2014). CMS is the largest map containing ~2800 pyramidal cells (in brown ghost knifefish) and the head representation is disproportionately big compare to the trunk. At the other extreme, LS is the smallest segment (~900 pyramidal cells on each side) and the head representation occupies a smaller portion of the maps compared to CMS. Pyramidal

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cells are organized in columnar functional units where three ON cells and three OFF cells located at various depths (deep, superficial or intermediate) have receptive fields with similar centers. Each of the six pyramidal cells within a column has different response properties and connectivity thus representing complementary channels of information. Taking digital images as an illustration, each column would represent a pixel and the spatial resolution of the sensory image on one side of the body would thus be of 150, 235 or 470 total pixels (i.e. columns) for LS, CLS and CMS segments respectively (Maler, 2009b).

As suggested by the anatomy, the receptive fields of ELL cells vary from segment to segment with smaller receptive fields in CMS (6–14 mm^2 corresponding to the area covered by 25–50 P-units), than CLS (26–60 mm^2/100–240 P-units), and much larger receptive fields in LS (160–360 mm^2/640–1400 P-units; (Bastian, Chacron, & Maler, 2002; Shumway, 1989a; Shumway, 1989b). The segments also vary in amount of overlap between the receptive fields of neighboring cells (larger in LS than CMS). Pyramidal cells have a classical center receptive field and a surround receptive field with an ON-center/OFF-surround (or vice versa) pattern similar to the well-known phenomenon in the visual system. The size of the surround relative to the center also varies across maps with LS maps having proportionally smaller surrounds and CMS having larger surrounds.

These differences in feedforward convergence and receptive field sizes could lead to differences in spatial representation and sensitivity. The small receptive fields are often associated with high spatial resolution, but lower sensitivity and might thus be geared towards detecting nearby small objects such as prey. Larger receptive fields are typically thought to mediate lower spatial resolution but higher sensitivity, since the input from many receptors are pooled and the noise can be averaged out. They would be best at responding to weak, distant signals that cast spatially extended (diffuse) images such as a distant conspecific. The use of smaller receptive fields and higher density of receptors for higher spatial accuracy might be the simplest scenario, but it is not the only possible processing strategy. For example, it was shown that accurate localization can be achieved with a broad receptive field if the neurons responded with high signal-to-noise ratio (Snippe & Koenderink, 1992). No matter what strategy is used, differences in spatial mapping across the ELL should support the efficient processing of spatial information from a variety of signals.

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The topographic representation is preserved in the Ts where many of the layers contain a map of the body surface (Carr, Maler, Heiligenberg, & Sas, 1981). Similarly, the tectum is topographically organized but the other targets of Ts (nE and PG) are not (Fig 4). In non-electrosensory fish species, the tectum is largely driven by visual inputs and directs visually guided behaviors. It is thus no surprise that this structure receives electrosensory inputs in species that rely heavily on this sense to guide motor behavior. While the tectum projects to locomotive motor areas, the nE projects to electromotor areas to control EOD and communication signal generation. Note that nE and tectum are interconnected through feedback loops therefore; a communication signal from a conspecific processed in nE can influence the spatial processing of the conspecific location in tectum or the spatially directed behavior it generates.

The role of spatial differences in receptor activation has been highlighted in studies of the jamming avoidance response (Carlson & Kawasaki, 2007). However, spatial representation and coding of an active conspecific signal has not been detailed explicitly at any level of the nervous system. In contrast, spatial coding of passive objects has been the focus of several behavioral and neurophysiological studies (e.g. Caputi & Budelli, 2006; Nelson & MacIver, 1999; Sicardi et al., 2000). The electrosensory image of a daphnia at the time of detection can be as weak as 0.2 µV and covers a small (2-3 cm diameter) diffuse area of the body surface (Chen, House, Krahe, & Nelson, 2005). This very weak signal barely causes any increase in the firing rate of electroreceptors or ELL pyramidal cells and researchers have investigated the mechanism that permits such a sensitive detection. For example, it was suggested that a 0.2 µV prey signal would elicit an increase in firing rate of 0.2 spikes corresponding to about 1/10th the SD of baseline firing rate (i.e. noise).

The most obvious way to solve this problem is to pool and average the information over many receptors. Theoretical calculations based on the strength and size of these signals and the convergence of electroreceptors onto pyramidal cells of various maps determined that, given certain assumptions, the LS could achieve reliable detection of 0.2 µV prey signals but those assumptions remain to be tested (Maler, 2009b). Coding accuracy could also be optimized and a noise-reducing mechanism to do so has been identified. The spiking pattern of electroreceptors at baseline is not random and displays negative serial correlation in interspike intervals (i.e. short

interval followed by long and vice-versa) due to an adaptation process (Ratnam & Nelson, 2000). This pattern reduces the low-frequency content of baseline noise, thus enhancing the ability to detect the low-frequency signals typical of prey stimuli (Chacron, Lindner, Maler, Longtin, & Bastian, 2005; Chacron, Longtin, & Maler, 2001).

It was further suggested that prey signals would cause a slight disruption in this patterned receptor spike train and that pyramidal cells could extract this change in pattern (Jung et al., 2016; Nesse, Marsat, Longtin, & Maler, 2012). Although these mechanisms were revealed by focusing on prey capture mechanisms, they are also relevant to the detection of distant conspecific signals and we expect that these concepts will be explored when investigating the mechanisms permitting sensitive conspecific detection and localization.

Network dynamic and spatial processing

Localization of a passive object like prey differs from localizing the active signal of a conspecific for several reasons. The sensing volume for prey or small passive objects is limited to a few cm around the body and even large objects, such as a tank wall, do not significantly affect the strength of the EOD signal when it is more than 10 cm away (Chen et al., 2005; Fotowat et al., 2013). Passive objects that are detected cause a disturbance of the EOD over a limited area of the skin (a spot for a prey, one side of the body for a wall, etc.). In contrast, a conspecific at distances of more than 10 cm causes a very diffuse image where the signal strength at most points on the receiver's body differs only by small amounts (Pedraja et al., 2016). Furthermore, active conspecific signals will cause a complex activation pattern of the sensory surface because of the relative orientation of the sender fish EO and cutaneous receptor orientation. Consequently, two receptors situated equally far from the sender could perceive signals of very different strengths if they are oriented differently (e.g. along the ventral-dorsal axis for receptors on the back and medial-lateral for receptors on the side). In other words, the activation of the receptor array is not simply related to the xyz position of the conspecific but also to its orientation.

Nevertheless, no matter what the relationship is between the spatio-temporal pattern of activation of the array of receptors and conspecific location, it carries the spatial information necessary for localization. As described above, the feedforward circuit preserves a spatially accurate representation of the sensory image due to its localized receptive field. The ELL

network contains a variety of elements that can influence spatial representation, each driven by more or less localized receptive fields (Fig 5). Most notably, two types of feedback inputs are known to influence pyramidal cell responses. While the feedback pathway through bipolar cells of the nP is poorly understood, the inputs from stellate cells are well characterized. It is driven by a receptive field slightly larger than the pyramidal cell it projects to. This feedback has been proposed to function as a "searchlight" (Berman & Maler, 1999) and recent papers by (Clarke et al., 2014; Clarke & Maler, 2017) demonstrated how this feedback enhances the response to moving prey-like stimuli. This mechanism could also play a role in shaping the response to conspecifics in close proximity, but it is unlikely that it will affect responses to more distant individuals since its modus operandi relies on the activation of relatively small receptive fields. The feedback through nP's stellate cells has also been shown to enhance the response to envelope signals elicited by moving conspecifics (Metzen et al., 2018). The authors of this study showed that the sensitivity of a specific electromotor reaction to the envelope signals of medium to low strength (10-15% contrast) required this input. A 10-15% contrast corresponds to a fish 20-25 cm away (Fotowat et al., 2013) and it is unclear how this feedback affects the processing of signals from more distant individuals. Nevertheless, it would be interesting to determine whether this feedback pathway shapes the spatial representation of conspecific signals, particularly for a conspecific at short to medium distances.

The indirect feedback through the EGp is described in the section above as mediating a cancellation of the response to beats, and thus could also affect the spatial representation of conspecific signals. The precise extent of the receptive field driving this feedback has been shown to be very large and thus is well suited to provide an input that reflects the activation pattern over a large area of the sensory surface. As described in the next section, this type of spatially diffuse input has been shown in other systems to shape spatial processing through background suppression and contrast enhancement, so we suggest it could influence spatial representation in this system too.

Discussion

We have outlined some of the challenges faced by weakly electric fish when trying to detect and locate a conspecific and presented some of the mechanisms involved in spatial

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processing in this system. We have argued in the introduction that the electrosensory system can compare in some ways with the visual system but in others with the auditory system. We hope that some of the insight presented along the way has reinforced this statement. For example, we pointed out that topographic mapping from the periphery all the way to the optic tectum that can guide locomotion is a featured shared with the visual system. On the other hand, the auditory system must "compute space" by comparing the signal at the two ears. For conspecific signals that are not in the immediate vicinity, this same process must happen and considering the shared developmental and evolutionary origins we speculate that solutions to this common problem could share some features. To stress further the potential for insight we can obtain from comparing these sensory systems, we point out below a few important mechanisms that the auditory or visual system utilizes to perform challenging tasks and explain how they can relate to the electrosensory system.

Sound localization has been thoroughly studied in a variety of systems but research on the barn owl, with its exquisite accuracy in sound localization, has a particularly rich history of insightful studies (Grothe, 2018). Research by Konishi, Knudsen, Carr and others have unraveled how the interaural time differences (ITD) of sound arrival at each ear, and interaural level differences (i.e. amplitude; ILD) enhanced, combined and how they support localization accuracy of just a few degrees (Carr & Konishi, 1990; Knudsen, 1981; Konishi, 1973). This corresponds to ITDs of a few µs and champions the sensitivity of most vertebrates' auditory systems. Electrolocation of conspecific fish cannot rely on timing differences since the speed of light would not give rise to significant differences. However, the electrosensory signal will cause differences in amplitude similar to the ILD used by the owl auditory system. In this system, localization on the vertical plane (elevation) relies heavily on ILD and sensitivity to these cues first arises in the posterior nucleus of the ventral lateral lemniscus where neurons receive excitation from one ear and inhibition from the other (Takahashi & Keller, 1992). In mammals, ILD sensitivity contributes to the localization on the horizontal plane (at least for high frequency sounds) and a binaural comparison occurs in the lateral superior olive. There, excitatory inhibitory inputs combine with contralateral inhibitory inputs driven indirectly by globular bushy cells driven by a large number of auditory receptors (Grothe & Pecka, 2014). Contralateral inhibition enhancing binaural contrast is common in auditory systems and can interact with the temporal processing of the signals (Koch & Grothe, 2000) to enhance sound localization

specifically for behaviorally relevant signal patterns (Marsat & Pollack, 2005). The neural circuitry to perform a similar operation is present in the ELL of knifefish (Fig 6). The indirect feedback is driven by spatially diffuse inputs and can attenuate the response to conspecific signals particularly relevant in some interactions (i.e. low frequency beats). For a pyramidal cell that is only weakly excited by the conspecific signal because it is not ideally located relative to the conspecific location, the feedback might draw its inputs from a region that is maximally stimulated by the conspecific and thus the beat would be effectively cancelled in these pyramidal cells. For cells strongly excited by the feedforward stimulation from the conspecific, the feedback might not completely cancel the beat response. Although this mechanism is simply a hypothesis and remains to be tested, the elements to implement it seem to be present.

Beyond localizing a single signal, the auditory system might be faced with the "cocktail party problem" where it must attend to one signal among many (Cherry, 1953). The mechanisms allowing the resolution of this issue have also been thoroughly investigated (e.g. Middlebrooks et al., 2017) and still lead to new discoveries regularly (e.g. Popham, Boebinger, Ellis, Kawahara, & McDermott, 2018). Listening to a communication signal with only one ear in a noisy environment makes extracting the message more difficult than if binaural hearing is used. It is suggested that sound location allows to segregate elements from one stream and top-down feedback inputs allow the enhanced coding of this signal stream (for a review on the topics see Haykin & Chen, 2005). Although most of the mechanisms suggested to contribute to solving the cocktail party problem focused on cortical network, mechanisms present as early as the dorsal cochlear nucleus have been suggested (Pressnitzer, Sayles, Micheyl, & Winter, 2008). It is common to see electric fish locate and chase one another in cluttered environments even when other conspecifics are present (e.g. Henninger fig 2; Henninger et al., 2018). Thus, we argue that they are likely faced with a similar "cocktail party problem". This suggestion naturally leads to the question of how this issue is solved in the electrosensory system. Considering the proposed role of the direct feedback input from nP as a "searchlight" mechanism (a sort of low-level spatial attention mechanism) we suggest that it could contribute to segregating competing signals by enhancing the response (as in Metzen et al., 2018) to the most salient one.

Mechanisms of scene analysis, such as the ones involved in solving the cocktail party problem, are also central issues in visual processing. In particular, foreground-background

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separation is required when trying to attend to an object – when fixating a moving object for example. Background suppression is largely influenced by the activity of wide field, polyaxonal amacrine cells. These polyaxonal amacrine cells mediate retinal ganglion cell (RGC) selectivity of an object over the background (Ölveczky et al., 2003). This background suppression mechanism relies on the amacrine cells receiving input from a wide receptive field surround and suppressing RGC activity (Baccus, Olveczky, Manu, & Meister, 2008). As in the auditory mechanism described above, or the electrosensory mechanisms hypothesized, this visual mechanism enhancing spatial processing relies on inhibition with a different receptive field as its target, emphasizing that this contrast enhancement procedure is a common strategy in scene analysis (see Fig 6).

The remarkable sensitivity of sensory systems has been the focus of a variety of studies in the auditory system (Fettiplace & Hackney, 2006; Hill & Boyan, 1977; Knudsen & Konishi, 1979), visual system (Jacobs et al., 2009), olfactory system (Daly, Carrell, & Mwilaria, 2007) and others. Mechanisms underlying the ability to detect extremely weak prey stimuli have been identified in weakly electric fish and are likely relevant to the detection of similarly weak conspecific signals. One of the mechanisms identified by Jung et al (2016) relies on a finely balanced inhibition and excitation from feedforward inputs. Balanced inhibition and excitation is a staple feature of many neural networks (e.g. cortex; Haider, 2006) and is involved in shaping sensory tuning in various systems (e.g. Anderson, Carandini, & Ferster, 2000). We also described how the presence of ISI correlation in receptors spike train enhances coding accuracy by decreasing variability, a process observed in a variety of neurons (e.g. Farkhooi, Strube-Bloss, & Nawrot, 2009). Several other mechanisms enhance the sensitivity of this system but have not been discussed here (e.g. bursting serving the same function in this system as in others; (Krahe & Gabbiani, 2004) for lack of space or because they are less obviously relevant to processing the spatial aspect of conspecific signals.

Finally, it should be noted that behavioral strategies can contribute to the localization process. A good example of this phenomenon is calling song localization in crickets. Females will approach a song source in zig-zag patterns but the angle of each turn is much greater than the angular resolution of localization in the frontal field (Schöneich & Hedwig, 2010). This suggest that the cricket lateralizes the sound, turns coarsely in that direction and after a few steps

re-evaluates whether the sound is still coming from that side or not. This zig-zag behavioral strategy can thus be explained by the reliance on accurate lateralization rather than all around accurate localization. In elephantnose (mormyrid) electric fish, behavioral strategies might also hint at the sensory mechanism in place. An individual moving towards a conspecific will tend to follow electric field lines rather than moving straight towards it (Schluger & Hopkins, 1987). This pattern arises presumably from the fish aiming to balance the strength of the electric field on each side of the body. Various active sampling strategies are also used in different organisms to enhance a sensory signal (Schroeder, Wilson, Radman, Scharfman, & Lakatos, 2010). A well described example is the microsaccades used in the visual system to prevent firing rate adaptation, thereby preventing the fading of visual images representations (Schroeder et al., 2010). Similarly, knifefish use the motions of their body to enhance the localization of nearby objects (Stamper, et al., 2012). Furthermore, Heiligenberg (Heiligenberg, 1975) found that tail bending enhances the electric image/shadow that the object of interest casts on the fish's body (see also Sim & Kim, 2011). A variety of object localization and detection mechanisms involving movement have been suggested (Hofmann, Sanguinetti-Scheck, Gómez-Sena, & Engelmann, 2017; Pedraja et al., 2018; Pourziaei, Lewis, Huang, & Lewis, 2019; Sim & Kim, 2011) and should be discussed in a separate dedicated review .

Behavioral tests in knifefish have not yet identified behavioral strategies that are used during conspecific localization specifically (rather than simply object localization) and could be the topic of future experiments. In particular, it would be useful to test explicitly whether the fish can accurately localize other distant individuals at any azimuth or if they simply rely on a lateralization of the signals.

In conclusion, we would like to reiterate that weakly electric fish accomplish difficult tasks when detecting and localizing conspecifics. Many of these challenges resemble those faced by most modalities but the particularities of the electrosense allows us to probe the generality versus specificity of mechanisms observed across these sensory systems. Researchers studying weakly electric fish are continuing to build on a rich history of contribution to our understanding of behavior and its neural basis. Spatial processing in this system is one of the lines of research that has many unanswered questions and the potential for insightful discoveries.

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Figures and Legends
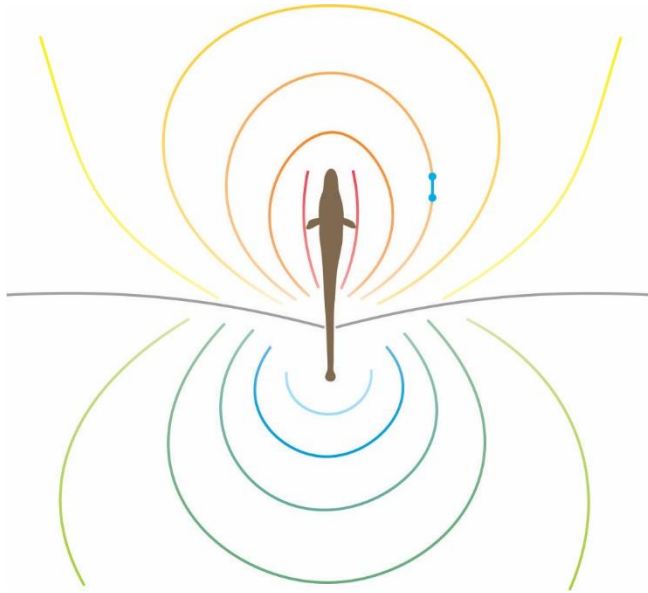
Figure 1. Spatial structure of an *Apteronotus leptorhynchus'* weakly electric field.

Illustration of an *Apteronotus leptorhynchus*, brown ghost knifefish, (center) surrounded by its electric field. Multicolored isopotential lines project outward from the fish. A small receiving dipole (blue) is shown measuring along an isopotential line (orange). The electric field potential is highest close to the fish and decreases as a function of distance. The grey line depicts the zero-potential plane of the fish's electric field.
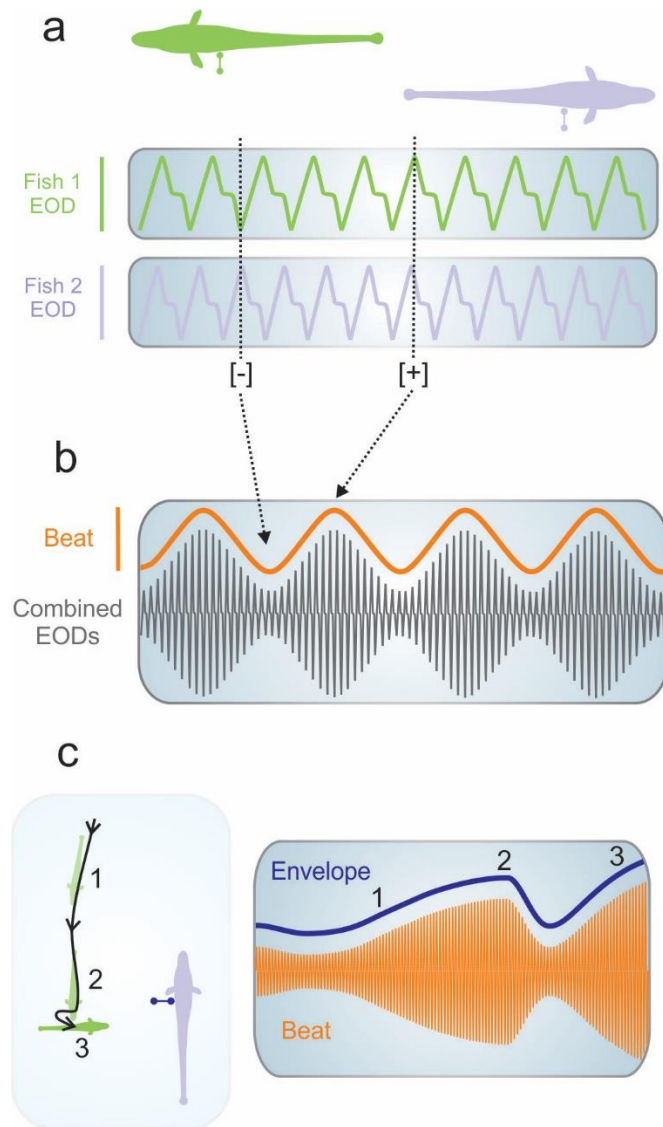
Figure 2. Conspecific signals and the influence of spatial interaction.

(a). Two separate, individual fish are depicted with receiving dipoles (green and purple) measuring their respective EODs. EODs are shown as continuous quasi-sinusoidal waveforms that differ slightly in frequency. Differences in frequency cause changes in phase, as depicted by the dotted black lines. Interactions of EOD waveform peaks and troughs create suppressions and additions in amplitude and are represented by [-] and [+], respectively.

(b). A depiction of the combined EODs of two static fish. Constructive and destructive interferences created by EOD phase differences result in the formation of a "beat" (orange).

Arrows point to examples of decreases and increases of beat strength caused by EOD interactions.

(c). Amplitude modulations of the beat (beat of the beat) result in the formation of an "envelope". Receiving dipole recordings (blue) from a stationary, receiver fish (purple) shows how the envelope strength changes as a function of distance as well as orientation. (1) A distant, sender fish will produce a weaker envelope that increases in strength as the sender fish approaches. (2) Envelope strength greatly increases when the two fish are in close proximity but quickly decreases as the zero potential plane of the sender fish crosses over the receiving dipole. (3) The strength of the envelope is affected not only by distance but also by orientation, with an optimal orientation resulting in greater envelope strength.
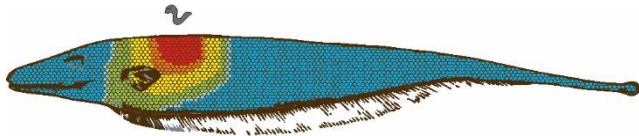
Figure 3. Local activation of the receptor array enables spatial localization of prey.

A representation of the tuberous electroreceptor array on an *Apteronotus leptorhynchus*. Local electrokinetic signals from a small prey item creates a gradient of activation along the sensory surface of the body. Warmer and cooler colors depict a higher and lower amount of receptor activation, respectively. This pattern of receptor activity provides sensory information for spatially localizing prey.
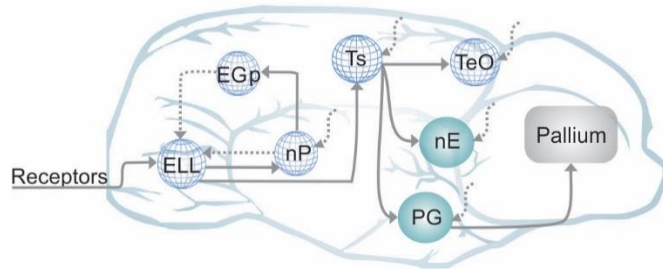
Figure 4. Electrosensory pathway and topographically mapped brain regions.

A depiction of an *Apteronotus leptorhynchus* brain with labeled brain regions and their respective connections. Electroreceptor afferents provide sensory input to the electrosensory lateral line lobe (ELL). The ELL is topographically mapped (globe symbol) and influenced by indirect feedback from the caudal lobe of the cerebellum (EGp) and by direct feedback from the nucleus praeminentialis (nP). Sensory information from the hindbrain ELL projects to the midbrain torus (Ts). Connections from the Ts project further to the optic tectum (TeO), the nucleus electrosensorius (nE), and the preglomerular nucleus (PG). A topographic organization is conserved to brain regions as far as TeO but is lost in the forebrain dorsal telencephalon (pallium). Dashed arrows represent brain areas additionally influenced by the pallium, though connections and interactions with the pallium have been less studied.

Spatial Processing in the Electrosensory System
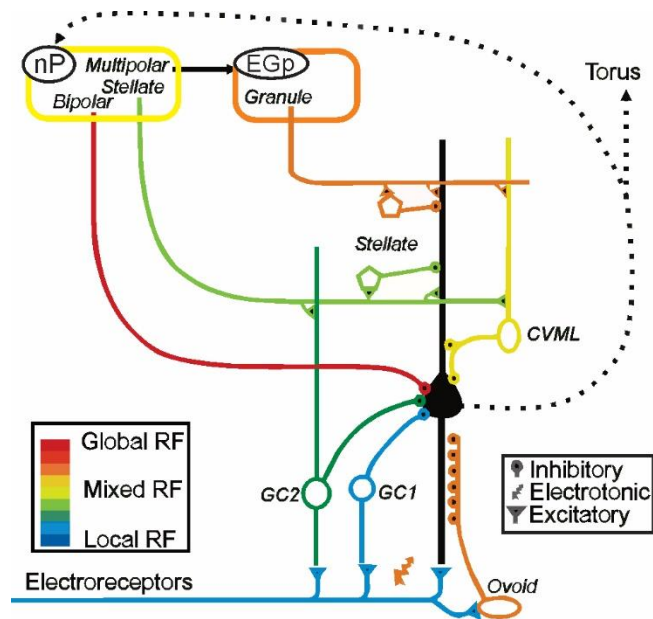
Figure 5. Circuitry of the ELL and immediate projections.

A simplified schematic of the electrosensory lateral line lobe (ELL) focusing on a particularly relevant set of connections with pyramidal cells is depicted. The progressive, cool to warm color scheme shows the size of receptive fields for a given cell type. More local receptive fields are depicted by cooler colors (blue and green), global receptive fields are shown in warmer colors (red and orange), and mixed receptive fields are shown with an intermediate color scheme (yellow), as described within the lower left box of the figure. Each electroreceptor provides sensory input to the ELL. Within the ELL, initial input is received by granule cells (GC1 and GC2), ovoid cells, and pyramidal cells (black hub). Pyramidal cells are the sole output neurons of the ELL, sending sensory information to the midbrain Torus semicircularis. A major source of input to ELL pyramidal cells comes from feedback pathways through the nucleus praeminentialis (nP) and the caudal lobe of the cerebellum (EGp). Stellate cells of the nP regulate the local direct feedback pathway (green) and form the basis of the "sensory searchlight" hypothesis. Bipolar cells of the nP provide global direct feedback, however the role of bipolar cells and global direct feedback has not been extensively studied. An indirect feedback pathway from the nP travels through the EGp and influences pyramidal cell activity. This schematic is not a comprehensive diagram of ELL connections, as other less obviously relevant pathways are not shown for the purpose of clarity.

Spatial Processing in the Electrosensory System
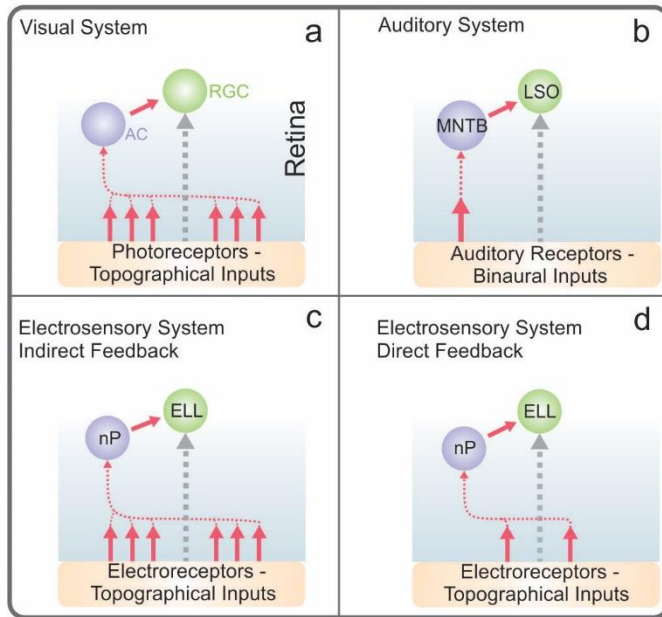
Figure 6. Shared network elements and potential feedback / lateral inputs contributing to localization and spatial processing.

In the visual system **(a)**, photoreceptors convey topographically organized visual input to retinal ganglion cells (RGCs) through additional layers of retinal circuitry. Most notably, amacrine cells (AC) influence RGC output and contribute to mechanisms such as background-suppression. A simplified depiction of sound localization in the mammalian auditory system is shown in panel **(b)**. Binaural input from the ipsilateral side is sent to the lateral superior olive (LSO), while sensory input from the contralateral side is sent to the LSO by way of the medial nucleus of the trapezoid body (MNTB). Direct excitatory input to the LSO and indirect inhibitory input illustrate an early mechanism of spatial processing in the auditory system**.** Panels **(c)** and **(d)** show how electroreceptors provide topographical input to the ELL through a feedforward pathway, while the nucleus praeminentialis (nP) provides two forms of feedback input onto the ELL, an indirect feedback **(c)** and a direct feedback **(d)**. Compared to the visual and auditory systems described above, different modes of feedback in the electrosensory system house shared network elements and are potentially involved in localization and spatial processing. In all panels, we color the pathway leading to feedback inputs or lateral inputs in red and the direct feedforward pathway in grey. Note that these diagrams are intended as simplified flow-charts.