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REVIEW

Sensory flow shaped by active sensing: sensorimotor strategies in electric fish

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Summary

Goal-directed behavior in most cases is composed of a sequential order of elementary motor patterns shaped by sensorimotor contingencies. The sensory information acquired thus is structured in both space and time. Here we review the role of motion during the generation of sensory flow focusing on how animals actively shape information by behavioral strategies. We use the well-studied examples of vision in insects and echolocation in bats to describe commonalities of sensory-related behavioral strategies across sensory systems, and evaluate what is currently known about comparable active sensing strategies in electroreception of electric fish. In this sensory system the sensors are dispersed across the animal's body and the carrier source emitting energy used for sensing, the electric organ, is moved while the animal moves. Thus ego-motions strongly influence sensory dynamics. We present, for the first time, data of electric flow during natural probing behavior in *Gnathonemus petersii* (Mormyridae), which provide evidence for this influence. These data reveal a complex interdependency between the physical input to the receptors and the animal's movements, posture and objects in its environment. Although research on spatiotemporal dynamics in electrolocation is still in its infancy, the emerging field of dynamical sensory systems analysis in electric fish is a promising approach to the study of the link between movement and acquisition of sensory information.

Key words: electric fish, active sensing, sensory flow, electric image, reafferent noise, electrosensory lateral line lobe.

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Introduction

Animals strive to extract information from their environment. The efficacy with which information is obtained, that is, the amount of crucial information extracted from the total amount of information available to the animal, can be quantified taking an ideal observer approach (Geisler, 1989). This approach offers a unifying framework for the quantification of behavior with respect to the sensory information gained. In this review we will address how the interdependency between prior knowledge (internal model) of the world and physiological mechanisms can lead to specific active behavioral strategies or patterns that sculpt and influence the information gained (the action–perception cycle, see Fig. 1). We will start this review by focusing on well-established model organisms and describe behavioral strategies employed to optimize sensory input (i.e. insect vision and bat echolocation) before addressing similar issues in weakly electric fish. We specifically will focus on the impact of ego-motion to sensory information.

In philosophical terms, the question we pose is this: which information is necessary for an animal to achieve a representation of its world that is sufficient for its survival? This may be regarded as the classic inverse problem, in which an animal needs to determine the properties of an environmental source by means of the sensory signals it obtains. Approaching this from a Bayesian context showed that, for example, humans use prior knowledge to determine the properties of an object when faced with ambiguous sensory input (Adams et al., 2004). Changing the prior statistics in these experiments led to predictable changes in perception, hence priors are constantly updated based on the recently encountered natural statistics. The influence of these 'priors' on actual behavior can only be studied in well-designed and controlled reduced laboratory conditions. It is easier to study how behavior influences sensing if priors are ignored, and indeed studies of this nature have formed the basis of several seminal publications in the field of active sensing recently. Such studies are inspired by the approach of Henri Poincaré (Poincaré, 1902), who proposed that the only way to extract and disambiguate information from our environment is to relate sensory experiences to the agent's own body and its movements. Along these lines, the framework of embodied cognition holds that behavior should not be decomposed in functional information-processing modules but into behavior-generating modules (sensory-motor units). That is to say that there is no way of reducing behavior into input (perception) and output (action) because these are not separable [see chapter 6 in Brooks (Brooks, 1999)]. We will come back to these ideas at the end of our review, but point out that from the standpoint of dynamical systems, sensing may be understood as a means for guiding action and would not require solving the inverse problem.

In addition to the idea that behavior may actively be used to sculpt sensory information, one can go as far as to assign a form of structural knowledge to the Bauplan of bodies: evolution is in a sense a learning algorithm (Dennett, 1995) where resource-intensive neuronal processing is delegated to smart anatomical

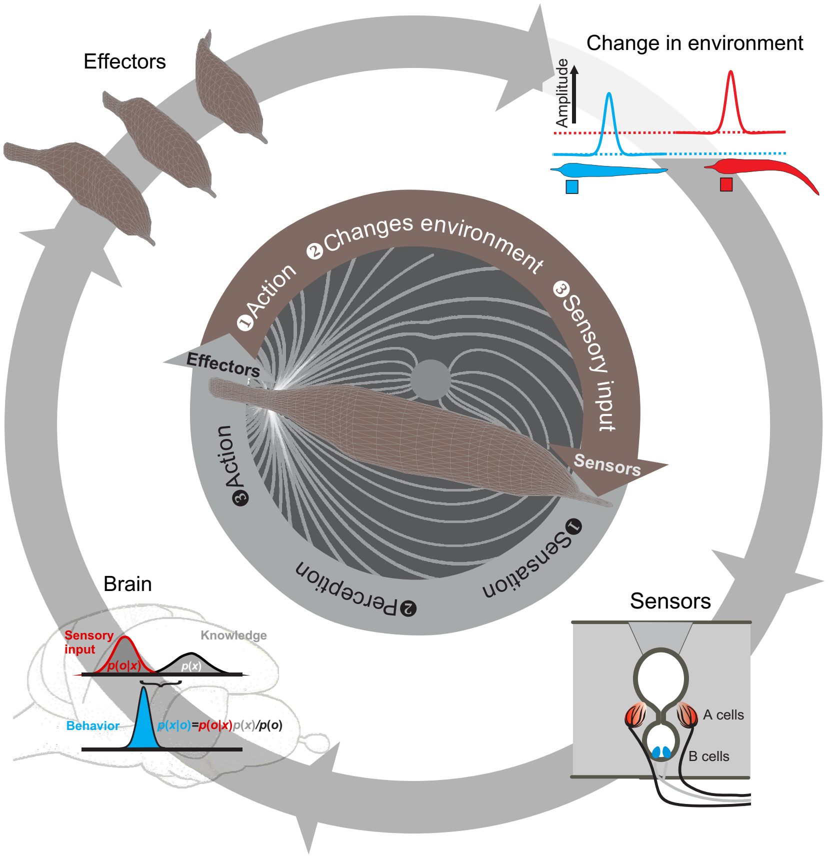


Fig. 1. Action–perception cycle in weakly electric fish. Sensory input (sensors) is evaluated (brain) with respect to the internal knowledge about the environment. Based on this integration, behaviors are generated (effectors). Movement of the body and the emission pattern of the electric organ discharges in turn change the upcoming sensory input (reafference).

solutions. In electroreception a number of such examples, termed pre-receptor adaptations, are well known (Bacelo et al., 2008; Castelló et al., 2000; Migliaro et al., 2005; Pusch et al., 2008).

From the above it is evident that sensing and acting are tightly linked, and a term that has been used increasingly to highlight various aspects of this sensorimotor loop is 'active sensing'. However, as we will see below, this term has different connotations depending on whether researchers focus on sensory or motor aspects of behavior. Active sensing often involves movements, yet in some cases movements are not needed, as is the case with the generation of electric fields. We will use the term active sensing strategies when referring to sensing strategies in which the sensory flow is shaped by movements (be it of the sensors or the animal). In contrast to this we will we use the term active sensing to describe the emission of energy without movements.

The classic definition of active sensing is that animals produce and emit energy, which serves as a carrier source that is then modulated by the environment. Following this definition, active sensing is a rare mode of sensing used in echolocation, active whisking, active sniffing, active touch (haptics) and active electrolocation. Active sensing systems must invest a considerable amount of energy, especially when a large range of the environment needs to be considered. Spherical spreading leads to a severe dissipation of carrier intensity, which is proportional to $1/r^2$. Because the same spreading loss occurs on the return to the animal, the effective intensity scales $\approx 1/r^4$ (Nelson and MacIver, 2006).

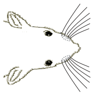
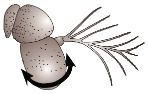
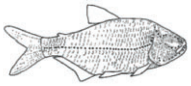
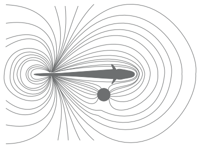
The term active sensing has also been used to describe situations in which the execution of movements generates or modulates sensory input. Motor activity has corollary consequences on the sensory information, termed reafference based on the works of von Holst and Mittelstaedt (von Holst and Mittelstaedt, 1950) and Sperry (Sperry, 1950). Thus action directly influences sensation and *vice versa*. This can be regarded as a form of an active sensing strategy, by which motor activity is being invested in a manner best suited for sensing (Gibson, 1962; Grant et al., 2009; Longden and Krapp, 2011).

A common denominator in both is the following logic: given a current state of sensory knowledge, if an animal moves in a certain direction and if its model of the reality is correct, it will perceive a predictable change in at least some parameters of the sensory information. If there is a mismatch between expected input and actual input, i.e. if the prior model of the world is erroneous, the model needs to be updated with respect to the current sensory input.

In summary, motor actions occur in two distinguishable forms, namely, actuation and motion of sensors and motion of an animal through the environment (see Table 1). Both forms are involved in active sensing strategies that can be crudely divided into two mutually non-exclusive objectives of the actions taken by an animal: (1) to select or shape the sensory stream impinging on the sensors and (2) to generate spatiotemporal dynamics in the sensory flow that are suitable to extract information. In a more general form, ego-motions evoke sensory flow patterns and we here examine how active sensing strategies are used to sculpt such sensory flow patterns.

In the following sections we introduce examples of active sensing strategies in two well-investigated sensory systems. We will then extend our discussion to weakly electric fish, where behavioral data indicate that spatiotemporal properties of electrosensory input, i.e. electric flow, are probably a key element of a better understanding of electrosensory information processing.

Table 1. Examples of active sensing strategies

Principle	Examples		Sensory consequences
Actuation/motion of sensors or emitters	Many animals can move their pinnae to change the filter characteristics or orient their sensitivity. In bats, both their echo beam and the ears can be focused to form an attentional spotlight.		Shape the sensory input to be optimal for perception
	In active touch (haptics) as well as in whisking rodents the forces and temporal patterns of the active exploration of the environment are tuned to optimize sensory input.		
	Jumping spiders, flies, molluscs and vertebrates show active scanning movements of their eyes, which serve various aspects of sensing.		
	Mechanosensory systems such as hearing in flies or vertebrates share active adaptive movements based on molecular motors to fine-tune their sensitivity.		
Ego-motion through the environment	By inducing a flow field surrounding their body, blind cave fish generate a velocity-dependent sensory volume around their body.		Shape the spatiotemporal dynamics of sensory flow
	In weakly electric fishes, ego motions influence both the emitted and the perceived signals. There is evidence that animals adjust their kinematics to optimize their sensing volume, as well as indications that they actively maintain an ideal distance to objects during navigation.		
	Visually guided behaviors frequently depend on ego-motion-induced optic flow. The characteristics of optic flow are actively influenced to maintain optimal conditions for fast visual navigation.		

Behavioral examples of active sensing strategies

Active sensing strategies in insect vision

Sensory dynamics are best understood in the visual system, where the so-called optic flow has been studied in a variety of model organisms (Longden and Krapp, 2011; Srinivasan et al., 1999; Sun et al., 1992; Warren et al., 2001). Furthermore, there is a functional as well as neuronal understanding of how this optic flow is used to extract cues for navigation. The study of flies, bees and other visually oriented insects has provided clear examples of how sensory systems can achieve impressive behavioral performance with comparatively simple 'hardware', by actively influencing their sensory input.

In this review we limit ourselves to vision in insects, where the optic system is next to immobile with fixed-focus optics lacking stereopsis (Horridge, 1978). Although the eyes of flies have a relatively low resolution of approximately 3000 pixels per eye, these insects are nonetheless true acrobats, maneuvering at speeds of 700 body lengths per second (Franceschini et al., 2009). In contrast, humans running at their maximal speed (≈5.5 body lengths per second) or driving at 120 $\mathrm{km\,h^{-1}}$ (≈18 body lengths per second) move at sluggish speeds that are at best 2% of the flies' speed range! To achieve this seemingly effortless behavior, flies depend on the image shift on the retina during ego-motion, called optic flow, as their main source of information about the 3D layout of their surroundings (Egelhaaf, 2006).

Optic flow can be roughly separated into translational and rotational components. During a translational movement the relative motion of structures in the surroundings hold depth information: an object close to the animal will move faster on the retina than objects far away [motion parallax (Gibson et al., 1959)]. In contrast to this, optic flow during rotational movements does not hold any depth information (Koenderink, 1986). Thus it is the translational component that induces range-dependent optic flow (Buchner, 1984). Flying insects maximize this translational component of the optic flow using precisely structured sequences of movements (Collett and Paterson, 1991; Poteser and Kral, 1995; Srinivasan et al., 1991; Voss and Zeil, 1998). One frequently described behavior found in various species (Buelthoff et al., 1980; Collett and Land, 1975; Geurten et al., 2010; Ribak et al., 2009; Schilstra and Van Hateren, 1999; Wagner, 1986) is the so-called saccadic flight structure, as first described by Collett and Land (Collett and Land, 1975). This active sensing strategy segregates translational and rotational ego-motion (and corresponding optic flow) such that the time spent rotating is minimized. Using this strategy, the animals actively shape the visual input to enhance depth information (Boeddeker and Egelhaaf, 2005; Schilstra and van Hateren, 1999). Further reduction of rotational flow can be achieved by compensatory head movements and orientation saccades of the head (Boeddeker and Hemmi, 2010; Geurten et al., 2010; Schilstra and Van Hateren, 1999).

A number of behavioral experiments making use of manipulated optic flow have shown how optic flow is used. Early on, Kennedy (Kennedy, 1939) put forward the so-called optomotor theory according to which insects could regulate their flight by maintaining constant optic flow with reference to their surroundings (Fig. 2). Elegant evidence for this has been obtained in flies and bees. Both keep a constant optical flow when regulating their flight speed by means of lateral optic flow (Fig. 2A) or when orienting by aid of ventral optic flow during translational movement and smooth landing (Fig. 2B). Similarly, maneuvering through confined spaces, where insects successfully avoid obstacle collision, is generally thought to be mediated by balancing the optic

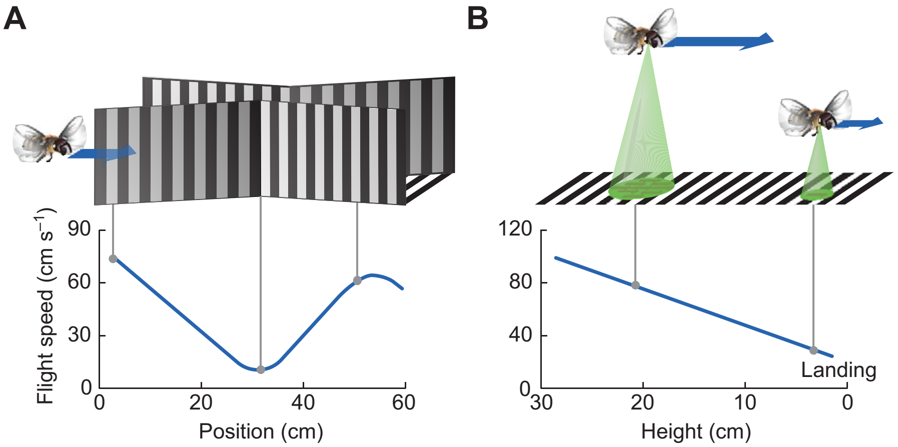


Fig. 2. Active sensing strategies in insect vision. (A) During flight, insects control their speed by monitoring translational optic flow. If the optic flow increases, e.g. when the walls with a stripe pattern of constant spatial frequency get closer, the insect lowers its speed (see graph below). Insects tend to center their trajectories in these flight tunnels in such a way that optic flow on both eyes is equal; this strategy is called the 'optic flow balancer theory'. (B) For landing, insects also maintain the optic flow constant during descending by decreasing their flying speed. Based on Srinivasan and colleagues (Srinivasan et al., 1999; Srinivasan, 2011).

flow between the left and right eyes (optic flow balancer theory) in a velocity-dependent manner (Srinivasan and Zhang, 1997; Srinivasan et al., 1991). Technical implementation of this astonishingly simple motor-control mechanism in flying robots has proven that this control mechanism suffices for autonomous take-off, landing, terrain following and head-wind compensation (Franceschini et al., 2007). Although compelling, the optic flow balancer theory (Fig. 2A) has been challenged and a revised optic flow regulator has been proposed (Serres et al., 2008). Another example for the use of optic flow is figure–ground separation. This describes the vital necessity to identify objects in front of a masking background. For flies, discontinuities in the optical flow field serve to indicate object boundaries and can serve to distinguish nearby objects from similarly textured backgrounds. While figure–ground separation depends on relative motion cues that are compared between nearby receptive fields (Kern et al., 1997; Srinivasan et al., 1991), distance estimation seems to rely on the speed of optic flow (Kirchner and Lengler, 1994). This was elegantly demonstrated by Srinivasan and Zhang (Srinivasan and Zhang, 1997) in an investigation of honeybee odometry. Bees measure the distance of a resource to their hive by integrating over the optic flow they have seen during flight. If the experimenter manipulates the optic flow during the trip to the source, the animal will signal the wrong distance to its conspecifics during a waggle dance in the hive.

Active sensing strategies in echolocation – temporal aspects

Compared with a continuously sampling sensory system, active senses are confronted with the question of when to invest energy for sensing and how long to do so. A well-understood example for this is the echolocation system of bats. However, even passive senses do not work in a perfectly continuous manner. For example, humans blink their eyes at 1–2 Hz with saccades occurring at ~4 Hz. While the role of saccadic suppression ('change blindness') is a matter of debate (Martinez-Conde et al., 2004), it shows that temporal discontinuities in sensing are also present in non-active senses. Because calls are emitted discontinuously in echolocation in bats, this sensory system shows how both spatial and temporal aspects of an active sensing strategy can be regulated depending on the behavioral goal. Here the interactions between sensing and motor behavior are range and velocity dependent. The task for a bat, flying at ~10 m s^{-1} (Ulanovsky and Moss, 2008), is to find and catch non-predictably moving prey. This requires either a detailed acoustic scene reconstruction, or a sequential approach utilizing a few salient acoustic features (for information on which cues are known to be used, see Fig. 3A). As shown below, it seems that bats actively structure their sensorimotor repertoire to extract context-dependent information in a manner optimally adapted to the physical constraints of echolocation following the latter strategy.

Based on the echolocation call rate, three stages can be distinguished: search, approach and terminal buzz phase (Simmons et al., 1979) (Fig. 3B). With decreasing target distance the call rate increases and the call duration decreases, while the bandwidth of the calls increases and intensity decreases (automatic gain control). Initially, low bandwidth and longer calls are well suited to detect prey and determine distance by analyzing the echo modulations (Schnitzler et al., 1983). The reduced call duration is beneficial for keeping calls and echoes separated at increased call rates. At high call rates, the use of shorter calls, together with an increase in bandwidth, enhance the accuracy of distance determination. Accuracy can be further enhanced by not focusing the echo beam exactly on the target, but keeping the target centered at the maximum slope of the beam (Fig. 3C) (Yovel et al., 2010). This behavior meets an optimality criterion for localization, though at the expense of decreased detection sensitivity. In addition, once the bat has detected a prey item, it will narrow its acoustic gaze on the target (Fig. 3D) such that the acoustic gaze angle of a given call becomes a predictor for the flight trajectory at the consecutive call. This is similar to focusing on a target visually.

The Doppler-shift compensation is velocity dependent and the best understood sensorimotor loop in bats. Here the bat is faced with the physical problem that the frequency of the echo does depend on the relative speed between the sender end emitter of the echo. Hence when a bat approaches a target at fixed speed, the received echo frequency shifts towards higher frequencies (Schnitzler, 1968). For determining the modulations in the echoes due to prey, many bats have an acoustic fovea, which contains neurons that are exactly tuned to a fixed echo frequency (Dear and Suga, 1995; Simmons et al., 1996). To keep the echoes within this preferred range, the bats actively stabilize the echo by adjusting their call frequency in a velocity- and range-dependent manner (Hiryu et al., 2008).

The senses described so far share that the animals can actively shape the sensory input through active sensing strategies. This is achieved by adjusting the motor patterns to serve one sensory modality, and/or by deciding when and where to emit the energy.

Sensory flow in weakly electric fish

Focusing on sensory flow in electrolocation of both mormyrid and gymnotid weakly electric fish, we will start by describing the

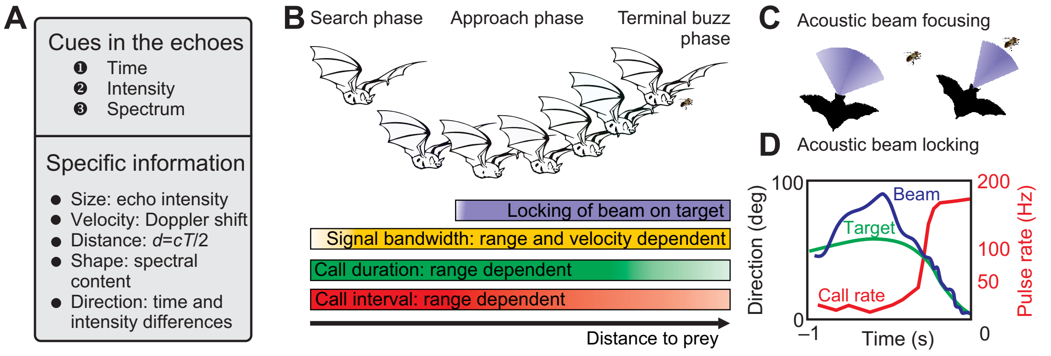


Fig. 3. Active sensing strategies in echolocation. (A) Bats can use different cues in their echoes to guide their consecutive actions (*c*, speed of sound; *T*, pulse-echo delay). (B) Foraging and prey capture are structured into phases. Throughout the approach, several properties of the calls are adapted depending on the nearness to the target. The colored bars underlying each parameter indicate the direction of change in that specific parameter. For example, signal bandwidth can be actively increased towards the terminal phase. (C) During foraging, the call beam is off target and wide, while it focuses on the target in the later phases, thereby enabling adaptive prey following as opposed to ‘predictive strike’ strategies. (D) The beam focusing is shown in a single example of a prey-catching sequence, showing nicely that the call rate and the focusing of the beam work together (modified from Ghose et al., 2006).

principal aspects of the physical inputs relevant in electrolocation and then describe some remarkable sensory capabilities of the elephantnose fish, *Gnathonemus petersii*. We will argue that these behaviors suggest that active electrolocation relies on information embedded in sensory flow rather than on static sensory cues alone. Consequently, we then describe behavioral examples where the electrosensory input is likely to be actively influenced. This finally leads us to review the current knowledge of spatiotemporal sensory flow dynamics in electrolocation.

Elephantnose fish can be trained to recognize different properties of objects based on electrolocation. These properties include the size, distance, impedance and shape of an object based solely on electric image properties (Budelli and Caputi, 2000; von der Emde, 2006; von der Emde and Fetz, 2007; von der Emde et al., 2010).

Here we shortly recapitulate the known parameters essential for electrolocation. Electric image (EI) is a term used to describe the change of the voltage distribution across the animal’s skin due to object-induced modulation in the self-generated electric field. At present we have only a basal understanding of which parameters of these, in many situations ambiguous, sensory images are relevant for behavior (Lewis and Maler, 2002; von der Emde et al., 1998). Most evidently, the location of a simple object can be detected by locating the peak modulation in the EI, while object distance can be estimated from the relative width of the EI. This last aspect shows that EIs are ambiguous as their properties depend on which region of the animal’s body they are cast upon. This means that even the simple metrics suitable to determine the distance to a single object differ depending on the body region [e.g. head region *versus* trunk region (Hofmann et al., 2013; Migliaro et al., 2005; Sanguinetti-Scheck et al., 2011)]. Even worse, if two or more objects are close to one another, the EIs interfere and can lead to non-linear summations (Budelli et al., 2002; Caputi and Budelli, 2006; Migliaro et al., 2005). Hence multiple factors lead to EIs being both complex and potentially ambiguous. Below we discuss data on the specific behavioral paradigm of gap detection, in which *G. petersii* does astonishingly well given the complexity of EIs described above.

In a recent study testing the electroacuity of *G. petersii* it was shown that these fish can discriminate objects separated by small gaps (limit ~1 mm) from solid objects of equivalent volume (Fig. 4A,B) (Fechler et al., 2012). The electroacuity depended on lateral object distance, i.e. for larger distances gaps needed to be larger in order to be detectable (Fig. 4B). As mentioned above objects in close proximity interact and superimpose non-linearly (Fig. 4C,D), and a modeling study had predicted that the just noticeable spacing between two objects of 20 mm diameter should be ~20 mm (Babineau et al., 2007). However, the electroacuity determined behaviorally in *G. petersii* is ~10 times better than this (note, however, that conductivity and shape of the objects were different in the model compared with the behavioral experiments). To tackle how it is possible for the fish to perform so well, Fechler et al. measured the EIs with the gapped object being placed 5 mm lateral from the animals’ skin (Fechler et al., 2012). They found a weak gap-specific electrical signature (see their fig. 7), which might provide an EI cue for gap detection at close distance. However, given that the gap detection worked up to much higher distances, we measured the EIs for 2 and 20 mm gaps also at higher lateral distances (Fig. 4E). Again, a clear electrical signature of the gap was present at close distances, but this was no longer measured at 17 or 27 mm distance. While this does not exclude the possibility that the animals may extract relevant cues even at these distances, it is clear that these would be weak and susceptible to noise. Thus it may be relevant to investigate whether, instead of relying on a stationary analysis of EIs (that is, taking the information from a single EI only), fish may do better based on cues from consecutive images. We now turn to a brief description of how such spatiotemporal parameters may enhance electrolocation.

An influential study focusing on dynamical cues in contrast to the static ‘one-shot’ cues from electric images was a theoretical approach where the detectability of prey-like items in front of a cluttered background was modeled (see Fig. 5B) (Babineau et al., 2007). In front of a relatively large background, the signal due to a small prey item in the foreground was found to be weak (~4% different from the background). Thus the background electrically masked the nearby prey, a problem generally referred to as the figure–ground separation task. Akin to the extraction of objects based on the visual flow in flies, fish may solve this task by analyzing spatial disparities between objects in the foreground and background (called motion parallaxes) that arise during movement. This was confirmed in the model by considering motion between fish and prey. This made the prey’s signature move across the electroreceptor array, whereas the signature of the background remained spatially uniform and stable

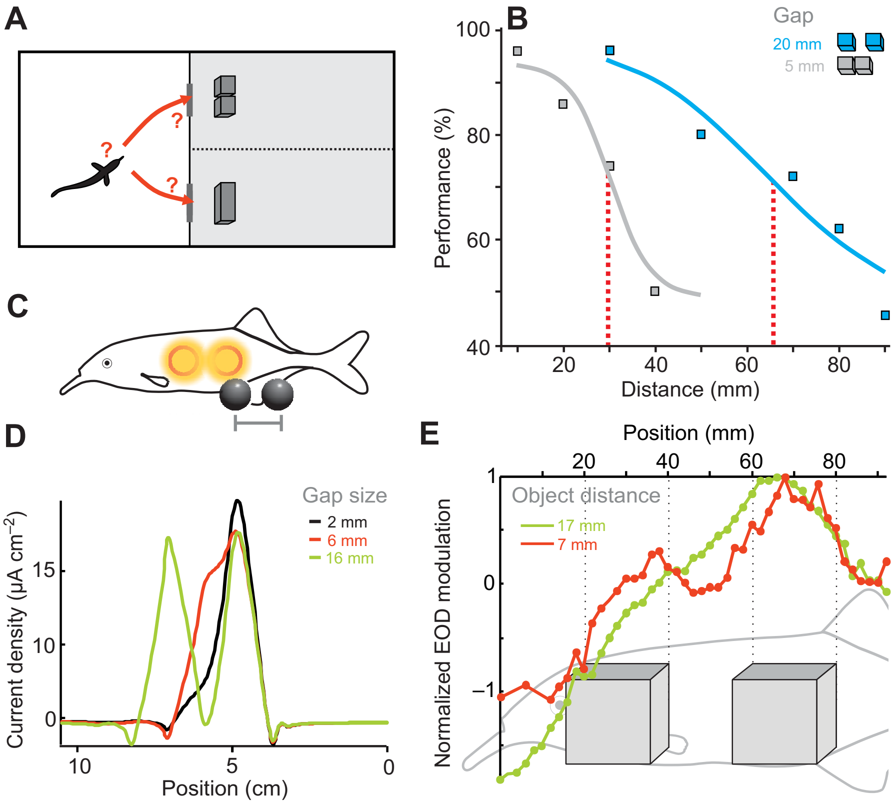


Fig. 4. Electric flow and gap detection. (A) In a behavioral task, *Gnathonemus petersii* is trained to discriminate a ‘combined object’ (two cubes separated by a small gap) from a solid object of the same size. (B) The behavioral data show that *G. petersii* can be trained to discriminate the gapped object from a solid object of equal volume. Gap detection critically depends on the size of the gap and the nearness to the animal: the smaller the gap the closer the objects have to be presented in order to detect the gap. Correct discrimination limits are shown by the vertical lines intersecting the fitted functions at the 75% level [data modified from Fechler et al. (Fechler et al., 2012)]. (C,D) The superposition effect as modeled for a small pair of objects (3×3×3 mm). Depending on the gap size, the static electric images (EIs) sum in a non-linear manner and will possibly be non-discriminable (modified from Engelmann et al., 2008). (E) Measured EIs (positive modulation values are normalized to the maximum modulation) for a 20×20×20 mm object with a 20 mm gap (see blue trace in B). While the electric signature of the large gap (‘notch’) is readily visible if the objects are close to the animal (7 mm lateral distance), it is no longer present if the lateral distance is increased (17 mm). However, the animals are still able to distinguish this gap even for further lateral distances in the behavioral task (see blue trace in B). See Hofmann et al. (Hofmann et al., 2013) for methodology of EI measurements.

(Babineau et al., 2007). As a consequence, the signal that was barely noticeable under stationary conditions became detectable through its spatiotemporal signature (Fig. 5A,B).

While we cannot decide whether such cues underlie the unexpectedly good electroacuity in the gap-detection task by *G. petersii*, recent experimental data in which fish were trained to discriminate differently shaped objects in front of moving and non-moving backgrounds strongly favor the idea that relative motion can enhance electrolocation (see Fig. 5C) (Fechler and von der Emde, 2013).

Sensorimotor patterns in electrolocation behavior

The above example indicates that fish are able to extract information more efficiently through relative motion cues than is possible with static electric cues alone. In light of the works of Babineau and colleagues (Babineau et al., 2007), it seems that active sensing strategies will specifically become relevant in conditions where the signal-to-noise conditions are bad, as is the case during prey capture in cluttered environments. If this is the case, one can expect to find stereotypical movements in electrolocation similar to what we presented for echolocation and vision. Ultimately, the motor repertoire in such strategies depends on motor capabilities of the animal as well as on the anatomical and physiological organization of the electrosensory system. Still, we expect that similar principles govern active sensing strategies in the differing electrosensory systems of gymnotiform and mormyrid fish.

Indeed, stereotyped ‘probing motor acts’ (PMAs) have been described qualitatively for mormyrids during novel-object probing (Toerring and Belbenoit, 1979; Toerring and Moller, 1984; von der Emde, 1992). These PMAs also occur in two-alternative forced-choice experiments. Here PMAs are frequent in the early learning phases, whereas their occurrence decreases once the behavioral task has been accomplished (von der Emde, 1992). This has been interpreted in the way that in order to analyze objects in detail, these motor acts are needed, whereas once a task has been learned, animals optimize their search strategy such that only relevant object features are investigated. Moreover, some PMAs disappear in individuals with a silenced electric organ, further pointing to their role in active electrolocation (Toerring and Belbenoit, 1979). The extent to which PMAs can be described quantitatively, e.g. based on an underlying set of prototypical movements (Braun et al., 2010; Geurten et al., 2010), and how they influence electrolocation is currently under investigation (Hofmann et al., 2013) (see below).

Detailed quantitative descriptions of electrosensory behavior allowed assessing the electrosensory consequences of active sensing strategies. Based on the analysis of prey-catching behavior in *Apteronotus albifrons* (MacIver et al., 1997; Nelson and MacIver, 1999), MacIver and colleagues showed that the sensory and motor volumes of *A. albifrons* are omnidirectional, a result that has been confirmed for *Gymnotus omarorum* (Pereira et al., 2012; Snyder et al., 2007). A specific motor pattern is in line with the hypothesis of active alignment of sensory and motor capabilities. During foraging, *A. albifrons* swims with a body pitch angle of approximately −30 deg. This increases the volume of water that is sampled in a certain amount of time (sensory volume) by optimally exposing it to the body region of highest electroreceptor density (MacIver et al., 2010; Nelson and MacIver, 1999). This increase in sensory volume comes at considerable energetic costs due to the increase of drag forces during tilted swimming (MacIver et al., 2010). A comparable gait was also found for *G. petersii*, which forages with a body pitch angle of approximately −18 deg (Hollmann, 2008; von der Emde et al., 2008). Notably, the motor volume of *G. petersii* can be expected to differ from that of *A. albifrons* due to its carangiform swimming style. Nonetheless, similar constraints seem to have led to comparable motor strategies to enhance electrolocation.

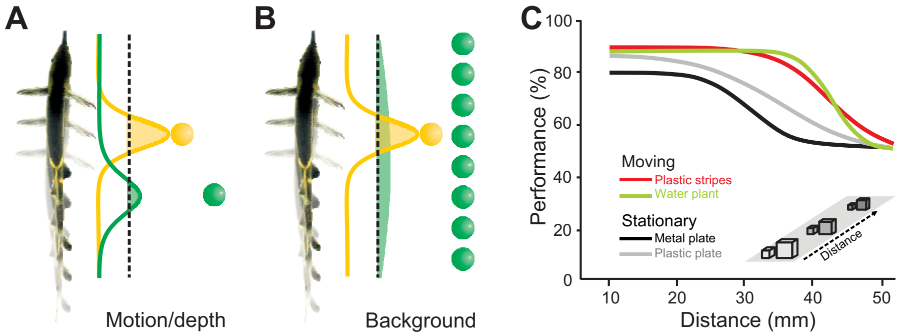


Fig. 5. Electric flow and figure–ground separation. (A) Swimming back and forth beside objects might be useful for determining object distance using motion parallax cues. (B) In the presence of relatively uniform objects in the background (green circles), the signal-to-noise ratio between the background and foreground is enhanced due to the blurriness of the background. This, together with motion, could in theory enhance detectability in figure–ground separation situations (Babineau et al., 2007). (C) Object discrimination performance of *G. petersii* as a function of the distance to the objects that had to be distinguished (cubes of different volumes). Discrimination performance drops with distance in the presence of stationary backgrounds. Similar to B, moving structured backgrounds, here either a natural or a plastic plant, improve the range over which discrimination is achieved significantly [data in C were redrawn after Fechler and von der Emde (Fechler and von der Emde, 2013)].

Once a prey item is detected, *A. albifrons* catches it in a stereotypic manner. This includes a reversal in swimming direction and movements that bring the prey onto the dorsal filament, a region on the dorsum of the fish that shows an increased receptor density (Carr et al., 1982; Castelló et al., 2000; Franchina and Hopkins, 1996). During this orienting response, fish follow a 'close the gap strategy' with P-type afferent responses predicting the future position of the prey (MacIver et al., 2001; Nelson and MacIver, 1999; Nelson et al., 2002). Such a strategy enables the fish to continuously account for movements of the prey, even after the initial detection. During the final phase before the catch, a decrease in body pitch angle and tail bending was measured, i.e. the fish seek a rigid body posture (MacIver et al., 2001). This is interpreted as an active effort to reduce reafferent noise (Nelson, 2005). The PMA 'stationary probing' described for mormyrid fish may be interpreted similarly, although further quantification is needed (Toerring and Belbenoit, 1979).

The active placement of fovea-like sensory structures, as described for the dorsal filament in prey-capture behavior of *A. albifrons*, is also evident in the 'side-searching' behavior (Lannoo and Lannoo, 1993). This behavior is exclusively linked to foraging. Here *A. albifrons* rolls its body to one side and swims with the dorsal surface leading. Similar to this, many mormyrid species also have body regions with increased receptor densities (Hollmann et al., 2008) and these seem to be actively aligned during prey capture, foraging and object inspection (von der Emde, 2010; von der Emde et al., 2008).

Active relative motion with respect to external cues has been found in the 'electromotor response' initially investigated by Heiligenberg for Gymnotiformes (Heiligenberg, 1973a; Heiligenberg, 1973b). During this behavior, fish track the oscillation of nearby objects either in the transversal or in rostro-caudal direction. Heiligenberg created an illusionary transversal motion of two objects placed laterally to either side of the fish, using objects that changed their rostro-caudal dimensions (two blades shifting against each other). Even though this illusion was not perfect, fish adjusted their lateral position depending on object size in an apparently sensory optimal distance (Heiligenberg, 1973a). This is reminiscent of the optokinetic response in flies, which adjust their lateral position inside a flight tunnel depending on the stripe pattern of the walls and the resultant optic flow (Srinivasan et al., 1999) (see Fig. 2). Comparable data have been published for *Eigenmannia virescens*, where smooth shelter pursuit behavior becomes noisier if animals need to depend on electrolocation cues alone. This additional noise arises from additional back-and-forth oscillations performed by the fish (Fortune, 2006; Stamper et al., 2012). Similar behavior can be found in the shelter following data published for *Sternopygus* under dim light conditions (Rose and Canfield, 1993). These active relative motions in relation to the stimulus are interpreted as a means to shift the spatiotemporal dynamics of the sensory input towards the dynamic range of the sensory system (Stamper et al., 2012). Moreover, they can be used to generate sensory flow in relation to stationary objects (e.g. 'lateral va-et-vient') (Hofmann et al., 2013; Toerring and Belbenoit, 1979).

Active tail bending during electrolocation has been described as an electrosensory probing behavior that is likely to be employed to actively modulate the local EI signature of an object (Bacher, 1983; Behrend, 1984; Heiligenberg, 1975; Stamper et al., 2012; Toerring and Moller, 1984). During this behavior, fish stay stationary next to an object while the tail and trunk are bent towards the object. As a consequence, the EI is subject to large (predictive) distortions influencing both intensity and contrast (Bacher, 1983; Caputi, 2004; Chen et al., 2005; Engelmann et al., 2008; Heiligenberg, 1975; von der Emde et al., 2008). The analysis of these distortions over time could be used to determine the lateral distance to an object (Sim and Kim, 2011).

Thus far we have considered classic locomotor patterns. We now turn to the question of when energy is being emitted by the fish. While the electric organ discharge (EOD) frequency (fEOD) in wave-type gymnotids is stable on short time scales, the inter-EOD intervals of pulse-type mormyrids are context dependent and can be actively varied. Regularization of the EOD rhythm, i.e. a sustained increase to a high EOD rate, was reported for probing behaviors (Toerring and Moller, 1984; von der Emde, 1992) and for a special prey-capture behavior in the field (Arnegard and Carlson, 2005). During prey capture, the duration of regularization lasted approximately half a second, while regularization for longer duration was observed during two-alternative forced-choice tasks (Schwarz and von der Emde, 2001; von der Emde, 1992). Such a sustained increase in fEOD could reflect the effort to reach maximum temporal acuity. Moreover, an increased frequency while moving at a constant speed increases the spatial acuity, as the distance between two emitted EODs is smaller. This might be important during the dynamic analysis of the electrosensory input (see next section).

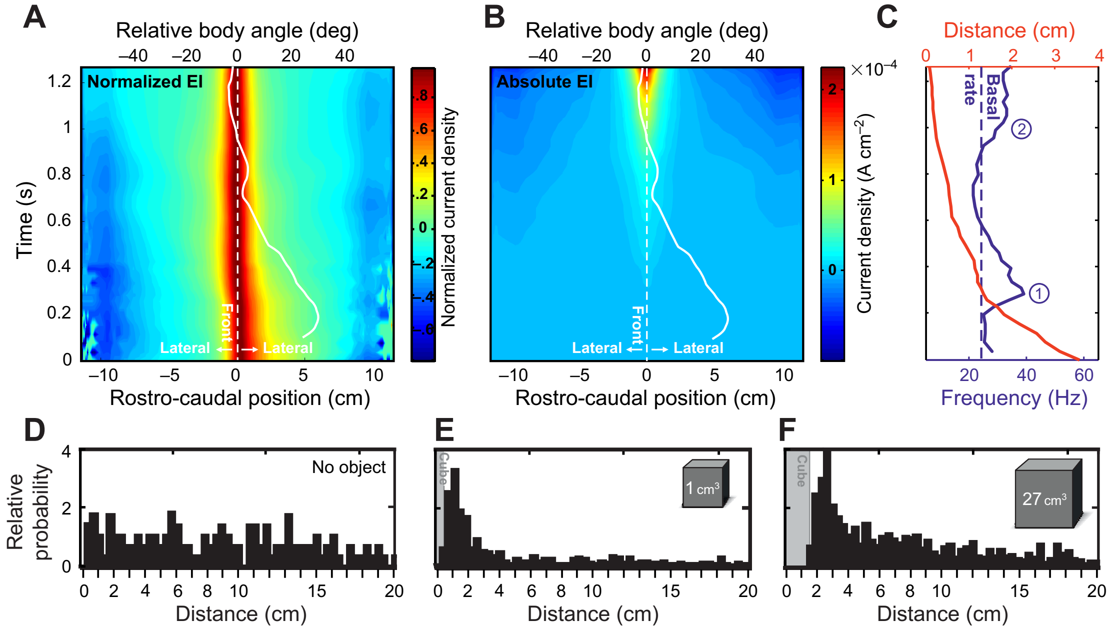


Fig. 6. Spatiotemporal electric image (EI) calculated for a natural approach sequence of *G. petersii* (A–C) and object detection distance based on novelty response (D–F). (A,B) Normalized (A) and absolute (B) spatiotemporal EIs while a fish approached a metal cube (27 cm^3) on an almost linear trajectory. Time is plotted on the *y*-axis; the object was reached at 1.2 s. The EIs are calculated for a linear patch of skin from the tip of the Schnauzenorgan to the tail and plotted as a function of the rostro-caudal position along the equator of the fish with the left side plotted at negative positions (bottom *x*-axis). The orientation of the fish's main body axis with respect to the object is shown by the white line (top *x*-axis). (C) Change of electric organ discharge (EOD) frequency and the distance (head of the animal to the center of the object) for the sequence shown in A. At the time highlighted by the '1', a brief increase in EOD rate (novelty response) occurred. Similarly, when the fish is very close to the objects the EOD rate is increased for a longer time while scanning the object ('2'). (D–F) Relative probability of the occurrences of the novelty response collected for different distances during unrestrained behavior. Data were pooled for all approach sequences within a radius of 20 cm to the objects for seven fish. In the absence of an object (D) the probability is almost evenly distributed over distance, while in the presence of an object (E,F) the probabilities are higher in an area surrounding the objects. Considering the novelty response as a measure of the fish detecting a change in its environment, this shows that *G. petersii* detects objects in a size-dependent manner at close distances (0.5–1.5 cm) only.

In contrast to regularization, EOD patterns during foraging and feeding are more variable (Schwarz and von der Emde, 2001; von der Emde, 1992). A particular pattern (novelty–response) consists of brief EOD accelerations that occur in advance of a prey directed strike or coincide with the detection of a novel object (Fig. 6D–F) (Arnegard and Carlson, 2005; Hopkins, 1986). These responses may also be regarded as a way to adjust the sampling rate to maintain a constant level of change in the sensory input. When encountering an unexpected object, a 'reflex-like' increase in fEOD probably ensures that the novel item is sampled with a high enough spatiotemporal resolution to be able to extract meaningful information from the temporal EI, similar to bats increasing their call rate towards prey during the final approach phase. Comparable increases of fEOD were found to coincide with escape responses mediated by Mauthner cell activation, which is another example where an increase in frequency ensures a high enough spatiotemporal resolution during a fast movement (Comas and Borde, 2010).

Electric fish show a variety of motor patterns linked to electrolocation. These patterns have a direct impact on the electric flow and are arguably used to actively modify it. These patterns hence can be considered active sensing strategies (overview in Table 2).

Naturalistic electric flow, reconstruction and analysis

An important step to better understand active electrolocation is its reconstruction and quantitative analysis. Although a number of studies have investigated the spatial formation of EIs and the influence of objects within a static electric scene (for a review, see Caputi and Budelli, 2006), information about spatiotemporal EI dynamics is sparse (Babineau et al., 2007; Chen et al., 2005; Hofmann et al., 2013; Sim and Kim, 2011; Sim and Kim, 2012).

Recently, technical advances in principle allow the recording of EIs in moving fish (Harrison et al., 2011). At present, however, most data are based on computational models (finite or boundary element methods). In these approaches, the sensory input can be modeled based on defined movement sequences. The available data are based on simplified motions, e.g. va-et-vient motion or idealized tail bending motion (Babineau et al., 2007; Hofmann et al., 2013; Sim and Kim, 2011; Sim and Kim, 2012), on reduced and thus simplified artificial trajectories (Chen et al., 2005), or on actual sequences of behavioral recordings (Assad et al., 1999; MacIver et al., 1997; Nelson and MacIver, 1999). Similar to the approach of Assad and MacIver, we here use a natural object scanning behavior sequence of *G. petersii* to calculate and examine the electric flow for mormyrids for the first time (Fig. 7A–C). The most obvious difference in the electric flow can be expected to be found between pulsatile (most mormyrids) and wave-type signaling species (most gymnotiforms). In contrast to wave-type signaling species, the pulsatile EOD emission will pose specific constraints on electro-motor patterns. At the same time, these patterns offer a direct readout of the electro-motor responses to sensory stimuli on-line (novelty responses or other forms of transient changes in EOD rhythms, see above). The sequence reproduced in Fig. 7 [see Hofmann et al. (Hofmann et al., 2013) for detailed description of methodology] includes at least two prominent PMAs: a tangential

Table 2. Active sensing strategies in weakly electric fish

Strategy	Possible electrosensory consequences	Reference
Body pitch	Increase of sensory volumen (*Apteronotus*), positioning of fovea (*Gnathonemus*)	Engelmann et al., 2008; Hollmann et al., 2008; Snyder et al., 2007
Rigid body posture	Reduction of reafferent noise	Nelson and MacIver, 1999; Toerring and Belbenoit, 1979
Fovea–stimulus alignment	Active use of fovea, increase of spatial acuity, noise reduction	Lannoo and Lannoo, 1993; MacIver et al., 2001; Pusch et al., 2008
Relative motion (va-et-vient)	Shift spatiotemporal dynamics of sensory input towards the dynamic range of the sensory system, generation of temporal slopes	Babineau et al., 2007; Hofmann et al., 2013; Sim and Kim, 2012; Stamper et al., 2012; Toerring and Belbenoit, 1979
Relative motion (tail bending)	Change in contrast, calculation of lateral distance by temporal slope ratio	Bacher, 1983; Behrend, 1984; Heiligenberg, 1975; Stamper et al., 2012; Sim and Kim, 2011
fEOD regularization/sustained increase	Increasing sampling rate, i.e. information per time and information per distance	Schwarz and von der Emde, 2001; Toerring and Belbenoit, 1979; von der Emde, 1992
fEOD brief increase	Control the amount of change of the incoming sensory input	Arnegard and Carlson, 2005; von der Emde, 1992

In the left column, text in parentheses indicates exemplary probing motor acts that can be attributed to the strategy. Studies where aspects of these behaviors have been addressed are shown to the right.

fEOD, electric organ discharge frequency.

PMA with a brief increase in EOD frequency and a lateral va-et-vient scanning PMA with a more regular EOD pattern. The temporal pattern of the EI modulation (tEI; Fig. 7B,C) is calculated for three locations at the body. If temporal EIs only depend on the distance from an object, the tEI should correlate with the distance perfectly. This is not the case (Fig. 7B), reflecting that tEIs are influenced by body posture, body–object interplay and pre-receptor mechanisms.

Clearly the temporal sequences are complex and this has probably made in-depth analysis of natural EI sequences difficult. A future challenge in this line of research will be to derive quantitative data on PMAs (Braun et al., 2010). This then will enable us to determine whether individual PMAs are linked to specific electric flow patterns. Avoiding these complexities by analyzing simplified behaviors, initial progress has been made towards better characterizations of electric flow and potential electrosensory cues contained in flow generated through simple behaviors. Using artificial and highly stereotyped tail movements, it was suggested that the ratio between tEI slope during bending the tail towards and away from an object might serve as a measure for lateral object distance (Sim and Kim, 2011). Furthermore, in va-et-vient movements, the calculation of a temporal slope-amplitude ratio (tSAR) based on the tEI was recently documented to be a suitable measure for lateral object distance (Hofmann et al., 2013; Sim and Kim, 2012). This measure was shown to be size invariant and independent from movement direction (Hofmann et al., 2013). Thereby, the tSAR potentially is equally powerful for distance estimation as the pure spatial SAR measure (von der Emde et al., 1998). How well such measures can be used in the analysis of complex electric flow remains to be tested.

Neuronal hardware: implication of active sensing strategies

Sensory systems usually operate in the background of permanent movement: even if an animal does not move its body, its sensors are typically in motion (e.g. eye and whisker motion, see Table 1). This implies that the relevant stimulus always contains reafferent components. Important information used to achieve behavioral goals such as locomotion towards an object, stopping before it, avoiding obstacles and following moving objects is embedded in the spatiotemporal sensory flow. How the nervous system is able to extract and enhance relevant signals using motion is an open and challenging question.

An extreme example showing that motion requires neuronal control and sensors is the metamorphosis found in tunicates: once the mobile larva makes permanent contact with the substrate and becomes sessile, it digests most of its brain. In a pointed way, this exemplifies the need of a brain for a moving body (MacIver, 2008). We now discuss aspects of the neuronal mechanisms that are possibly important for the analysis of electric flow in the electrosensory system, focusing on pulse-type mormyrid fish.

Neuronal architecture and plasticity

A segregation of information into complementary channels has been found in many sensory systems (Metzner and Juranek, 1997). In mormyrids, this is already realized at the level of the tuberous electroreceptors, where information on amplitude and amplitude/phase of the local electric field are separately encoded (see Fig. 1, sensors: A and B cells) and processed in two parallel maps within the electrosensory lateral line lobe (ELL) of the hindbrain. The mormyromast electroreceptor afferents provide an example of temporal coding, as the latency of the first spike conveys all the information about amplitude and phase of the local EOD (Gómez et al., 2004; Sawtell et al., 2006; Szabo and Hagiwara, 1967). These fixed response latencies are essential in relaying the sensory information. By coinciding with the corollary discharge input (juxtalobar) the reafferent input from the electroreceptors is presumably converted to a rate code (e.g. Bell, 2001), although evidence for both temporal and rate coding have been found in the output of ELL (Gertz et al., 2012).

The circuitry of the ELL is well known (for reviews, see Bell et al., 2005; Meek et al., 1999) and can be considered to be composed of two parallel modules similar to ‘on’ and ‘off’ modules of the retina, in which the input from the EIs is transformed into a spatial activity pattern across the somatotopic maps in the ELL. These modules are essential for the encoding of modulations in the EIs that can be higher or lower than the normal water impedance. The circuitry of the ELL is well suited for the discrimination of reafferent sensory input from external sensory stimuli such as a nearby predator or prey items (Bell et al., 2008). Specifically, proprioceptive information, as well as corollary discharge and electrosensory signals conveyed to the ELL through parallel fibers from cerebellar regions, can be used to predict the electrosensory consequences of the animal’s own behavior (e.g. Bastian, 1995; Bastian, 1999; Sawtell, 2010). Coincidence of these centrally

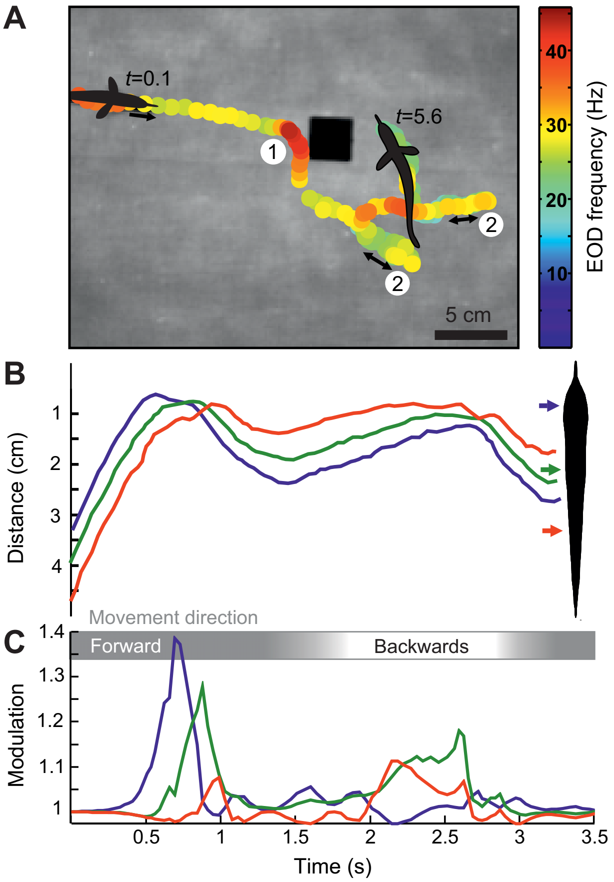


Fig. 7. Temporal electric image during complex probing behavior. (A) Part from a trajectory of *G. petersii* exploring a metal cube (27 cm^3). The position of the animal's head at successive electric organ discharges (EODs) is show by the colored circles. The circle color corresponds to the EOD frequency. Several probing motor acts can be seen in this short sequence, two of which are indicated by numbers: (1) tangential probing with a brief increase in EOD frequency; (2) object scanning using the va-et-vient probing motor act (PMA). *t*, time (s) – compare with abscissa in C. (B) The absolute distance of three positions ('receptors', see colored arrows on the right side for position reference) to the cube during the initial 3.5 s of the sequence in A. (C) Modeled temporal change of the local modulation of the EOD amplitude for the three 'receptors' considered in B.

originating predictive signals ('negative images') with predictable sensory inputs will result in a context-dependent suppression of such reafference. This cancellation mechanism is adaptive. Association of parallel fiber inputs and the activity of the ELL efferent neurons can lead to the generation of negative images (anti-Hebbian) of predictable electrosensory inputs. Thereby, the mechanism can fine-tune the suppression by continually generating and updating sensory predictions on the basis of associations between central signals and current sensory inputs (Fig. 8). Adaptive filtering could thus allow external electrosensory signals to be detected more easily [for a recent extensive review, see Bell et al. (Bell et al., 2008)].

While the cancellation operates relatively fast, the adaptive tuning of the negative image is probably too slow to completely adjust this mechanism to match sudden effects. Assuming that the development of the anti-Hebbian plasticity depends on the number of EODs during which a constant sensory input is presented, it would take several seconds for the effect shown in Fig. 8 to develop at an EOD rate of 80 Hz. Consequently, an animal would have to move comparatively slowly in order to benefit from the anti-Hebbian plasticity during object inspection. Indeed, this might be true for at least some described PMAs [e.g. stationary probing (Toerring and Moller, 1984)]. For complex movements this implies that there is either an additional mechanism for cancellation of reafferent input [such as an inhibition that is proportional to excitation derived from non-plastic and fast parts of the circuitry (e.g. Lewis et al., 2007)], or that the animal does not try to completely cancel reafferent input in order to take advantage of the sensory flow for the extraction of meaningful information.

In light of active behavioral strategies described above, we argue that reafference offers a wealth of information to the animals. For example, as suggested by Sim and Kim (Sim and Kim, 2011), temporal EI dynamics due to tail movements could in theory be used to determine object distance during electrolocation. It is thus likely that, rather than being removed completely, fish actively seek to obtain specific aspects of a reafferent sensory flow. Circuits such as the ELL could act as novelty filters in which sensory input is filtered to accentuate differences between successive images (electric flow).

Spatial coding

Arguably, the somatotopic organization of the ELL may be ideal for the analysis of spatial electric images, because the *x* and *y* coordinates of an object could be directly read out from the location of the excitation peak in the ELL maps. Object distance (*z*) would require additional measures related to the amplitude and width of the EIs, and Lewis and Maler (Lewis and Maler, 2001) proposed a simple way to obtain the relevant measures from the activity map in the ELL. To do so, the width of the active neuronal population as well as an estimate of the mean activity in this population would need to be extracted. These measures would be most reliable if the mean amplitude were to be based on wider spatial tuning function, while a narrow tuning would increase the reliability of image width information (Maler, 2009b). Hypothetically, the two parallel maps in the ELL might be a way to establish such parallel processing of the amplitude and width parameters discussed above. In some respect, this would be comparable to the parallel processing in the maps of gymnotiform electric fish (Krahe et al., 2008; Maler, 2009a).

Alternatively, slopes could be extracted from a temporal rather than from a spatial approach, provided that neurons in the ELL were to compute differences between successive EODs. Based on theoretical considerations (Brown and Bäcker, 2006), it was recently shown for the gymnotiform ELL that tuning width variation of receptive fields might optimize the estimation of different stimulus features (Maler, 2009b). For the extraction of 2D location parameters at finite distances, narrow spatial tuning is beneficial, whereas 3D parameters will in addition require wider spatial tuning functions. Extracting information from the blurred EIs encoded in a temporal fashion of extreme precision hence should best be based on both narrowly and broadly tuned receptive fields. Indeed, receptive fields in the medial zone of the ELL have been found to be narrow (Metzen et al., 2008) and these results have been confirmed using naturalistic objects for stimulation, where wider receptive fields also were found (Gertz et al., 2012). It remains to be investigated whether the two maps in the ELL of mormyrids differ with respect to their spatial tuning functions in a way similar to gymnotiforms.

Narrow tuning and the presumed underlying low degree of convergence in the ELL have a significant cost. Keeping spatial sensitivity high leads to a considerable discrepancy with respect to

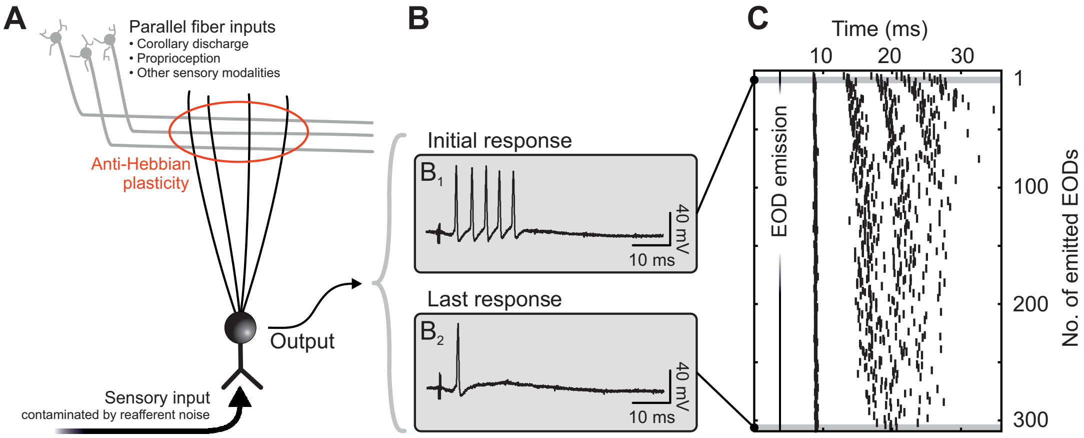


Fig. 8. Reduction of reafferent noise by anti-Hebbian plasticity. (A) Simplified schematic of the electrosensory lateral line lobe (ELL). Principal cells integrate peripheral sensory input with signals conveyed by a granule cell parallel fiber system. The interneurons mainly involved in this have been omitted from this scheme. Negative images are formed *via* changes in the strength of parallel fiber synapses according to an anti-Hebbian learning rule. (B,C) Adaptation of a response of an efferent (LF cell) neuron of the ELL to the sudden appearance of a small conductive cube. (B) Original recording traces. Top: initial response directly after start of stimulus presentation. Bottom: response after ≈300 electric organ discharges (EODs; average EOD emission ≈2.5 Hz). (C) Raster plot of the neuronal activity with number of emitted EODs increasing from top to bottom (*y*-axis). In the absence of the object, this cell was silent but started spiking on the first presentation of the object (see gray horizontal bar on top; the corresponding original recording is shown in B_1). After pairing the object over 300 EODs, the intensity of the sensory response was greatly diminished (see gray horizontal bar at bottom; the corresponding original recording is shown in B_2).

the range to which ELL units are able to detect the presence of objects or discriminate between distances (Künzel et al., 2012). Preliminary data shows that single neurons in the mormyrid ELL would allow detection of objects within a range below the behavioral detection range. To investigate this we are currently examining up to what distance ELL neurons are able to detect the presence of an object. With increasing distance, the detection probability decreases steeply, and seems to fail beyond a maximum of 30 mm. This is reflected in our finding that in discriminating two object positions, the minimal detectable inter-object distance increases with increasing lateral distance. Hence, slight differences can be resolved very close to the receptors, while further away the difference needs to be considerably larger. Hence it is conceivable that up-stream neurons will pool information from spatially neighboring ELL efferents in order to increase the working range for both detection and discrimination. Evidence for this has recently been found for the distance up to which neurons respond to an object, showing that pooling responses of three neighboring cells in ELL significantly increases the detectability (Gertz, 2013).

Besides mere spatial aspects, receptive field properties may also enhance the spatial contrast in a way similar to mechanisms found in the visual system (Sherman, 1979). The complex receptive fields on the trunk could be specifically useful for detecting small moving objects (Metzen et al., 2008). These authors suggested that non-foveal neurons receiving input from the trunk of the animal are better in detecting motion than neurons receiving input from the Schnauzenorgan. Future research directed towards the spatial coding in the dorsolateral segment of the ELL is required to consolidate these predictions.

This review has put together a number of studies exemplifying that the body of weakly electric fish itself can be compared with the vertebrate retina: foveal and parafoveal regions of the sensory mosaic are distributed over the body and hence the body needs to be oriented similarly as saccades in foveate vision. An advantage of this distributed sensory system might lie in the fact that it enables omnidirectional sensing (at a short range matched to the motor space), whereas cephalization and the associated foveation of senses at the head region has led to the need of local sensor motions enabling sequential but highly accurate sampling of the environment.

Temporal aspects

As introduced above, latency-coded sensory input is being transformed through a temporal gating mechanism into rate-based information in the ELL, which is subjected to plastic modulations depending on prior sensory input. Indeed it was shown that the behavioral sensitivity of electric fish to novel stimuli depends on the time-averaged mean of the prior sensory input, so that responses following long periods of stationary input are enhanced (Caputi et al., 2003; Röver et al., 2012). The plastic feedback to the ELL and the formation of anti-Hebbian plasticity (Fig. 8) are in agreement with these results. One could expect that the responsiveness in the ELL would be suppressed under perfectly static condition. This is similar to the visual system, where fixation and suppression of eye movements leads to fading (Troxler's effect). As a result, neurons in the ELL would be highly sensitive to changes in the environment. Alternatively, comparable to the effect of eye movements, small body motions in electric fish may suppress complete adaptation in a static environment (Stamper et al., 2012).

The relevant parameters for electric flow analysis are the differences in locally measured EI amplitudes over time. The difference in local EOD amplitude between successive EODs would enable measurement of the temporal slope parameter discussed above. In contrast to the spatial coding based on the somatotopic maps of the ELL, temporal coding is not dependent on a high number of electroreceptors and a moving animal may in principle be able to obtain object information by analysing the reading of a single electroreceptor in time. During va-et-vient behavior, the peak of activity in the ELL would move somatotopically while the animal scans an object. Thus, in order to decipher the sensory input in its temporal pattern, spatially disparate data need to be compared. This is different for a temporal approach in which successive inputs from a single location are compared. The circuitry of the ELL as briefly explained above is well suited to enable an EOD-by-EOD comparison of the sensory input under non-stationary conditions. This means that the ELL is appropriate for performing the operation needed to calculate the electric flow.

Neural and behavioral dynamics

At present, our understanding of how the complexities of sensorimotor behaviors may be linked to neuronal processes is scarce. Here it may be helpful to look at sensorimotor interaction following the approach of dynamic systems and embodied cognition (Calvo and Gomilla, 2008). This approach highlights the inherent interdependence between the internal states, the sensory input and the motor variables. All these components are modeled as coupled sets of differential equations that determine the dynamics of the whole system. In this context, behavior is a temporal sequence of states (sensory, motor and internal variables) that evolve to a limit set (either a fixed point or a limit cycle). In less abstract terms, the neural activity depends on the relationship of the agent with the environment. This activity is then translated into changes of the motor-control parameters to satisfy a ‘need’ that is defined in the pattern of activity of forebrain structures.

The solution is not achieved by a sequence of processing steps in different neural structures but by continuously interacting neural systems that are mutually constrained. Such systems have the advantage of less computational load in the classic sense, they are fast in finding a solution, they have comparable higher tolerance to noise and they are independent from starting conditions (Pfeifer et al., 2008; Sporns, 2002).

A thought experiment for electric fishes, using this rationale (Spencer et al., 2009), could be a task in which they need to reach an object. Detection of the object means that a population of neurons responds differently in the part of ELL that corresponds, due to the topological organization, to the place on the skin where the image of the object is projected. A rather simple sensorimotor loop could make the electric fish move in a way (fovea stimulus alignment) that displaces that activity to the part of the ELL that maps the foveal regions (front of the head or Schnauzenorgan). This would make the fish orient to the object. If the sensorimotor loop also produces an increase of the activity in the ELL, this will not only orient the fish towards the object but also guide an approach. This can be seen in Fig. 6A,B, where we show a sequence of a fish both orienting and approaching an object. Fig. 6A shows the relationship between the centering of the EI with the decrease in relative angle to the fish, what we call orienting in this example. Fig. 6B shows that there is an increase in the intensity of the image that relates to the decrease in fish–object distance plotted in C. The pairing between the spatial relationship between the fish and the object and the properties of the resultant image obtained might occur in a loop in which the change in image causes a change in behavior, and the change in behavior causes a change in the image. This is referred to as ‘continuous reciprocal causation’ (Clark, 1997).

The sensors interact dynamically with the world by means of the motor system in order to generate a specific pattern of neural activation. Consequently, there is no need for a central representation (or a solution of the inverse problem). The ‘goal’ to reach the object is achieved by following this heuristic rule learned in the course of evolution. Schemes like this can be nested to achieve more complex behaviors. Experiments addressing building blocks of motor control do indeed suggest that complex motor patterns are based on adaptable cortical motor plans (Graziano et al., 2005).

Even though this framework might be controversial to the understanding of biological systems, it has been successfully applied in robotic design (Metta et al., 2008; Zibner et al., 2011). This approach conceives cognitive agents as managers of a versatile neural architecture consisting of coupled dynamical systems in flexible interaction. This means that an animal, depending on current needs, activates flexibly wired building blocks that behave as dynamical systems.

Conclusions

A variety of model systems have shown that temporal dynamics are an important feature of sensory stimuli. Applying two mutually non-exclusive approaches, animals can actively shape this input. These concern either movement of the whole animal and/or parts of its sensors, or the adjustment of properties of the energy being emitted for sensing.

Contrary to the wealth of data concerning active sensing strategies in other sensory systems (e.g. vision or echolocation), knowledge concerning the role active sensing strategies in shaping sensory flow is scarce in weakly electric fish. Recent theoretical and behavioral studies strongly advocate that the analysis of sensory input over time plays a key role in the sensory performance of electric fish. In light of this we have accumulated an overview of the movement strategies that have been described so far. The most prominent pattern found in mormyrids is stereotyped object scanning behaviors (PMA), whereas research in the wave-type Gymnotidae has revealed stereotypic movements associated with foraging and prey capture and the ‘electromotor response’ in object tracking. An additional way in which pulse-type weakly electric mormyrid fish can directly shape the sensory flow is through active changes in the EOD frequency. These changes in the sampling pattern seem to be context dependent. Several of the active sensing strategies in electric fish are reminiscent of active sensing strategies described for insect vision or echolocation in bats (see Table 2). However, it remains to be shown in detail which sensory cues are related to these patterns and whether fish actively seek to stabilize specific parts of the dynamic sensory input.

To solve these issues, we see two immediate needs: quantitative analysis of natural behaviors to determine whether the described PMAs are consistently occluding in a specific electrosensory context, and the numerical investigation of the electrosensory flows occurring during such behaviors. In the majority of studies thus far, motor patterns have been characterized qualitatively, and likewise the sensory input and consequences associated with a given behavior has been analyzed qualitatively. Amongst other courses, we here advocate for a joint approach in which modeling of sensory flow during natural behavior should be combined with a quantitative segregation of the underlying motor components [prototypes in the sense of Braun et al. (Braun et al., 2010)]. This will allow an investigation of these components regarding specific flow patterns similar to what has been shown for visual systems.

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Author contributions

All authors participated in the conception, writing, drafting and revising of the manuscript. All unpublished data presented here are based on work by V.H. and J.I.S.-S. that was conceptualized and designed by J.E., V.H. and L.G.-S. and analysed by V.H., J.I.S.-S. and J.E.

Competing interests

No competing interests declared.

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