

Smart Sensing Strategies: Insights from a Biological Active Sensing System

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ABSTRACT

Biological sensory systems efficiently and reliably monitor changes in real-world environments that are relevant to an animal's specific behavioral needs and goals. Understanding the sensory mechanisms and information processing principles that biological systems utilize for sensory data acquisition may provide useful guidance for the design and implementation of smart sensing systems in diverse engineering applications. Certain freshwater fish from South America and Africa, known as weakly electric fish, use self-generated electrical energy to actively probe their environment. The fish emit millivolt-level electrical discharges and detect microvolt-level voltage perturbations arising from nearby objects in the water. The fish are able to detect and localize targets in 3D space and assess target characteristics such as size, shape and electrical impedance. This electrolocation ability enables the fish to hunt and navigate at night and in turbid waters without the use of visual cues. To achieve reliable, real-time performance, the nervous system implements a number of smart sensing strategies, including efficient encoding, multiscale virtual sensor arrays, task-dependent filtering and online subtraction of sensory expectation.

INTRODUCTION

All animals are faced with the challenging task of extracting useful information about their environment from the barrage of stimuli impinging on their sensory receptors. In most real-world situations, a majority of the incoming information is irrelevant to the animal's survival needs. Of all the information contained in the rich, multi-channel, multi-modal data stream, only a small fraction is relevant to the animal's immediate behavioral needs and goals, such as finding food and avoiding predators. To address this

sensory data acquisition challenge, animals use a variety of neural and behavioral strategies for optimizing the content and quality of incoming signals, so as to enhance signals of behavioral relevance and suppress irrelevant background signals. Engineers face similar challenges when designing and implementing smart sensing systems for real-world engineering applications.

Sensory systems extract information by analyzing patterns of energy that are generated by or reflected from objects in the environment. In most cases, the energy originates from a source that is extrinsic to the sensing system. For example, visual systems typically rely on electromagnetic energy from the sun or other external light sources. An alternative sensing strategy that has been adopted by some organisms is to use self-generated energy to probe the environment (Nelson and MacIver 2006). The terms passive and active are often used as a convenient means of distinguishing between these two modes of sensing. The term “active sensing” originated in engineering to describe man-made systems that emit energy into the environment, such as radar and sonar (Bajcsy 1988). An interesting property of biological and man-made active sensing systems is that they can exert control over the properties of the energy source, such as its intensity, timing, directionality, or spectral characteristics. Bats, dolphins and electric fish are among the best known examples of animals that employ active sensing strategies.

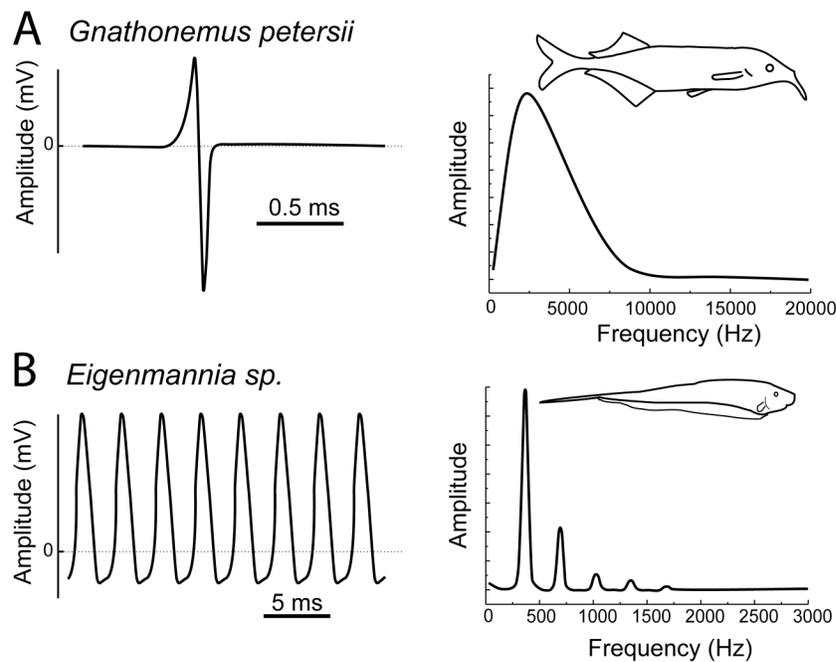


Fig. 1. Electric organ discharge (EOD) waveforms (left) and power spectra (right) for weakly electric fish with pulse-type (A) and wave-type (B) discharges. From von der Emde (1999).

ELECTROLOCATION

Certain freshwater fish from South America and Africa, known as weakly electric fish, use self-generated electrical energy to actively probe their environment. These fish generate electric fields using a specialized electric organ located in the tail region of the fish. The temporal properties of the electric organ discharge (EOD) can be qualitatively assessed by placing a pair of wires in the water near the fish and listening to the EOD signal on an audio monitor. The EOD patterns of weakly electric fish fall into two broad categories. Pulse-type fish (Fig. 1A) generate brief discharges separated by significantly longer gaps, such that the audio output sounds like a series of clicks. Wave-type electric fish (Fig. 1B) generate EODs with little or no gap between successive discharges, resulting in a quasi-periodic signal that sounds like a tone or hum.

The electric field has an approximately dipolar spatial structure (Knudsen 1975). Objects that differ in electrical impedance from the surrounding water such as rocks, plants, and prey, will perturb the flow of electric current near the fish. These perturbations give rise to changes in the local potential difference across the skin of the fish, referred to as the transdermal voltage (Nelson 2005). The transdermal voltage changes are monitored by specialized electroreceptor organs distributed over the skin of the fish. The active electrosensory system allows the fish to detect, identify and localize objects in its environment even in complete darkness. This capability is called electrolocation, in analogy to the echolocation capability of bats and dolphins. The active electric sense has a working range of a few centimeters for detecting small prey and about one body length for detecting larger objects.

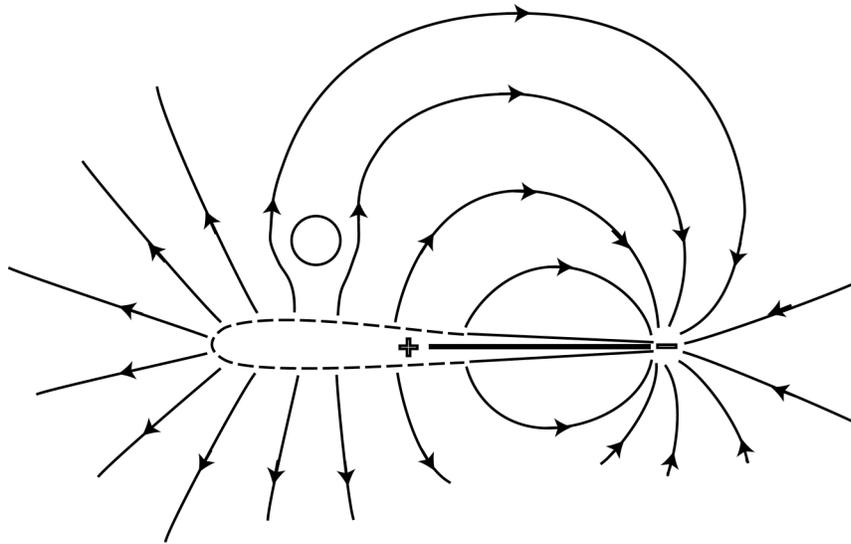


Fig.2. Principle of active electrolocation. The electric organ (horizontal black bar) gives rise to a dipolar field. Electric current follows the field lines (solid with arrows). A non-conducting object (circle) perturbs the flow of electric current, causing a local decrease in current density, which translates into a decrease in the voltage across the skin near the object. Redrawn from Heiligenberg (1977).

For example, a non-conducting object near the fish would block the flow of electrical current, causing the current lines to flow around the object as shown in Fig. 2. This decrease in current density would cause a localized decrease in voltage drop across the skin. Thus, a non-conducting object, such as a rock, casts a sort of electrosensory “shadow” on the surface of the fish. Conversely, a conducting object would increase the local current density, and hence increase the local transdermal voltage, giving rise to an electrosensory “bright spot” on the surface of the fish. Electrosensory images correspond to changes in transdermal voltage on the electroreceptor surface of the skin, just as visual images correspond to changes in light intensity on the photoreceptor surface of the retina. Since there is no functional equivalent to the lens of the eye, electrosensory images are blurred and the degree of blurring increases with target distance.

Relative motion between the fish and prey converts a static spatial image into a dynamic spatiotemporal pattern. Fig. 3 show a sequence of electrosensory images from a video reconstruction of a typical prey capture event (Nelson and MacIver 1999, MacIver and Nelson 2000). Initially, when the prey is first detected several centimeters from the fish, the electrosensory image is weak and diffuse (Fig. 3A, top). The image becomes progressively stronger and more localized as the relative distance between the fish and prey decreases. Just prior to capture, the image sweeps across the head at a distance of just a few millimeters, giving rise to an intense, focal image (Fig 3A, bottom). These dynamic changes in spatiotemporal image properties occur over a time course of less than one second, from the time of initial prey detection to the final capture.

STIMULUS CODING

The body of the fish is covered with approximately 15,000 electroreceptors, each of which acts like a miniature voltmeter and converts the local transdermal voltage into a sequence of nerve spikes. The conversion of transdermal voltage to nerve spikes is called stimulus coding. The nervous system implements several smart-sensing strategies for signal enhancement and background suppression at this first stage of signal processing. In species with wave-type electric organ discharges, the sensors are tuned to the frequency of the fish’s own EOD, with narrow, V-shaped tuning curves (Hopkins 1976). This frequency tuning improves the signal-to-noise ratio by filtering out background electrical noise in frequency bands that are unrelated to active electrolocation.

Another type of filtering takes place at this stage, which is related to the amplitude modulation (AM) frequency components of the signal. The AM frequency content depends on the speed and distance of the target object as it moves past the sensor array. Nearby, fast-moving targets will cause higher-frequency AMs compared to distant, slow-moving targets. Electroreceptors act as high-pass filters in the AM frequency domain, giving the strongest response to fast components of the AM signals (Nelson et al. 1997). If a target remains stationary relative to the fish, Afferent activity gradually adapts back to baseline firing with a multi-scale relaxation time course (Xu et al. 1996). The high-pass AM filtering properties and adaptation characteristics reflect the fact that *changes* in the local transdermal potential carry more behaviorally relevant information than the absolute magnitude of the transdermal potential. The high-pass AM filtering gives rise to a biphasic response profile, as shown if Fig. 3B. The peak of the afferent response is located ahead of the transdermal potential peak. As the electrosensory image moves

across the receptor array, there is a positive rate of change in transdermal potential on the leading edge of the image, generating a strong excitatory response in the afferents. Thus, the peak of afferent activity corresponds to where the electrosensory image is going to be located in the near future, rather than where it is currently located. The high-pass AM characteristics of afferent response dynamics give rise to a transformation of the raw electrosensory image that can be viewed as providing an estimate of the future prey location.

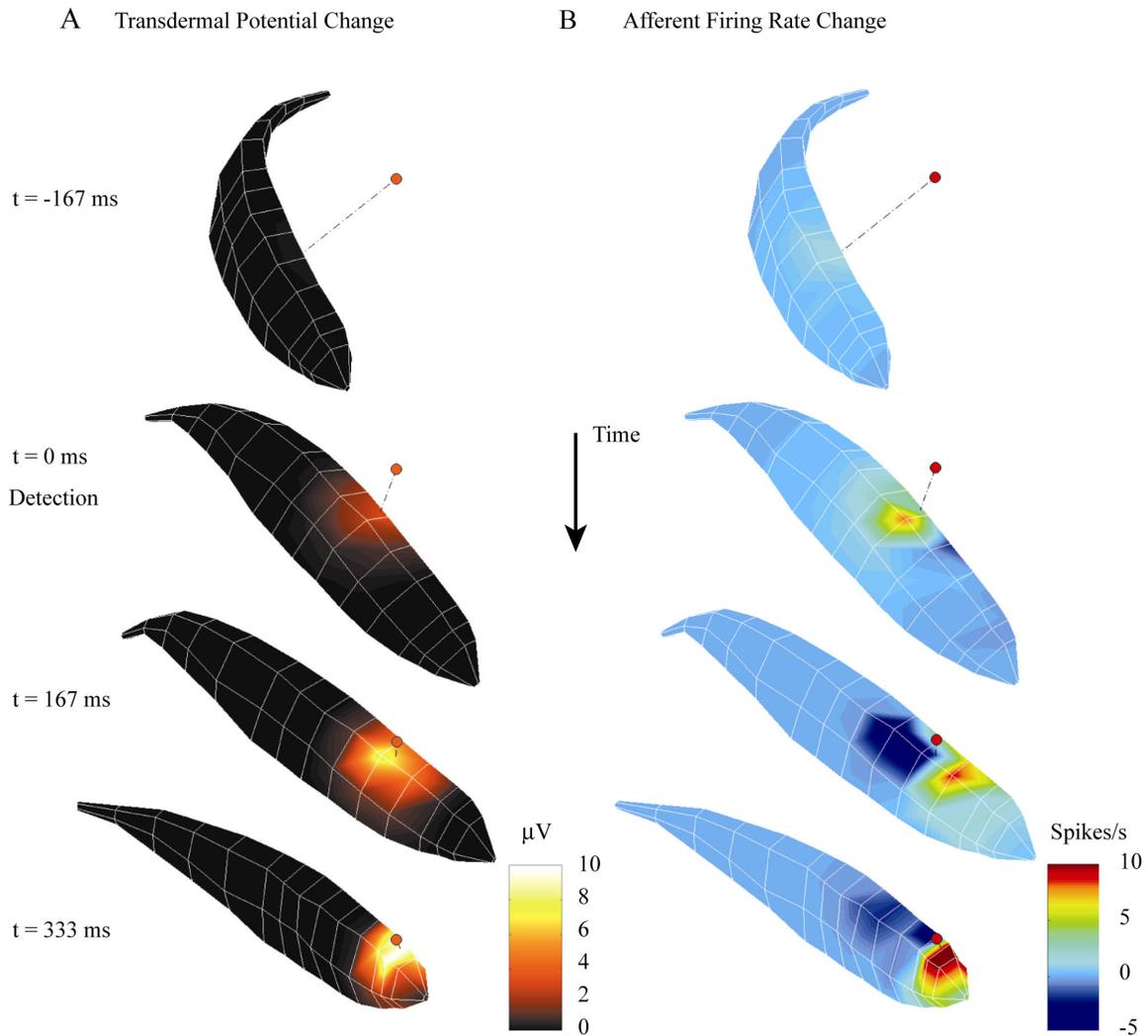


Fig. 3. Electrosensory images from a reconstructed prey capture event. The figure shows snapshots of the fish and prey at four different time points in the prey capture sequence. The left-hand column (A) shows the change in transdermal voltage induced by the prey (small red sphere). The right-hand column (B) shows the predicted change in spike activity on primary afferent nerve fibers. The dashed line indicates the shortest distance between the fish and prey. From MacIver and Nelson (2000).

Another important aspect of stimulus coding is related to the statistical properties of the afferent spike trains. Spike activity is irregular on short time scales, giving rise to a “sputtering” sound when listening to the spike activity on an audio monitor. Although afferent spike trains are irregular on short time scales, they show a remarkable degree of regularity on intermediate time scales of 100–200 msec. Spike train regularization on this time scale significantly enhances the detectability of weak signals by decreasing the effective background noise from spike train fluctuations (Brandman and Nelson 2002; Ratnam and Nelson 2000). Information-theoretic measures have been used to demonstrate that afferents accurately encode information about the temporal waveform of AM signals within the behaviorally relevant bandwidth. The information content in the spike train is on the order of one bit per spike, resulting in overall information rates of several hundred bits per second per afferent nerve fiber. (Gabbiani and Metzner 1999).

VIRTUAL SENSOR ARRAYS

The next stage of electrosensory information processing takes place in the central nervous system in a structure called the electrosensory lateral line lobe (ELL). The ELL is the sole recipient of electrosensory primary afferent input and thus all electrosensory information needed to support electrolocation passes through this structure. A key organizational feature of the ELL is that it contains multiple topographically organized maps of the fish’s body surface (Heiligenberg and Dye 1982; Shumway 1989a). Electrosensory images that appear as spatially localized voltage perturbations on the fish’s skin are transformed into spatially localized patterns of neural activity in parallel maps (Fig. 4). Each of these maps can be viewed as a sort of virtual sensor array.

As shown in Fig. 4A, the ELL of wave-type electric fish contains four subdivisions, each with its own topographic map of the electroreceptive periphery. The medial map is devoted to processing information from the passive electric sense, which detects low frequency electric fields of extrinsic origin. The three lateral maps are devoted to the active electric sense based on the fish’s own electric organ discharge. Each active electrosensory afferent nerve fiber trifurcates as it reaches the ELL, providing each of the three active maps with essentially identical input. The three maps are denoted by their anatomical locations as CMS (centromedial segment), CLS (centrolateral segment) and LS (lateral segment).

In general, ELL principal neurons filter the incoming electrosensory image data with spatiotemporal filtering properties that vary across the different maps (Shumway 1989b, Krahe et al. 2008). In contrast to the 15,000 active electroreceptors on the skin of the fish, there are approximately 2800 principal neurons in the CMS map, 1400 principal neurons in CLS, and 900 in LS (Maler, in press). The principal neurons in these three maps can be viewed as virtual sensors with spatial and temporal filtering properties that are unique to each map. The LS map, with only 900 principal neurons, has the highest degree of convergence from skin electroreceptors, with each principal neuron receiving input from approximately 1000 afferents. By performing extensive spatial averaging, the LS map exhibits the best sensitivity to weak stimuli, but has relatively poor spatial resolution. In contrast, the CMS segment, with 2800 principal neurons, has much less spatial convergence (only about 40 afferents per principal neuron) and thus has good spatial resolution but relatively low sensitivity to weak signals. The CLS segment has properties that are intermediate between CMS and LS.

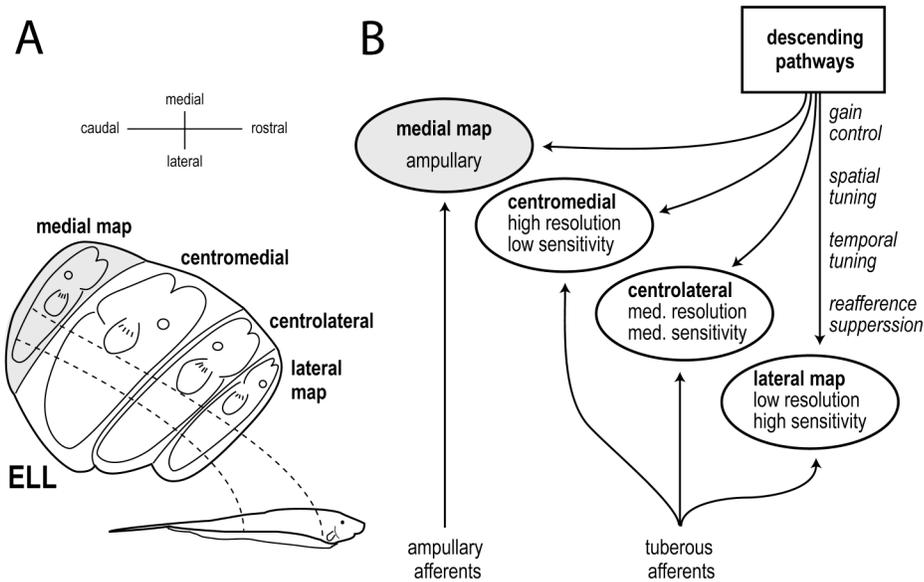


Fig. 4. The ELL can be viewed as an adaptive, multi-scale array of virtual smart sensors. (A) Illustration of the right ELL showing four topographic maps of passive (gray) and active (unshaded) electrosensory input. Modified from Heiligenberg and Dye (1982). (B) Principal neurons in each map process the primary afferent input with differing spatial, temporal and sensitivity characteristics. Descending signals provide gain control, frequency tuning, and suppression of background noise. From Nelson 2005.

TASK-DEPENDENT ADAPTIVE FILTERING

The ELL receives extensive descending input from higher brain centers. Descending input far surpasses primary afferent input in terms of total number of synapses. These descending pathways carry contextual information that is useful for adaptive signal processing, including electrosensory feedback signals, sensory signals from other modalities, proprioceptive signals related to body posture, and efference copy signals related to outgoing motor commands (Berman and Maler 1999). As shown in Figure 4B, the ELL can thus be visualized as a bank of adaptive spatiotemporal filters. Each filter bank contains an array of principal neurons that can be thought of as smart virtual sensors. These smart sensors pool raw data from the peripheral sensor array and process it in an adaptive, task-dependent manner. For example, prey-related signals and communications-related signals evoke different frequency tuning and spike-timing properties of these smart sensors, resulting in the optimal encoding of both stimulus categories (Chacron et al. 2003). It has been suggested that the different types of sensory processing carried out in the ELL—adaptive gain control, spatial filtering, temporal filtering, reafference suppression and common mode rejection—are likely to be representative of a class of canonical signal processing strategies employed in sensory systems in general (Berman and Maler 1999).

GENERATION AND SUBTRACTION OF SENSORY EXPECTATION

A number of studies have demonstrated that the neural circuitry of the ELL plays an important role in suppressing certain “expected” components of incoming electrosensory information, particularly those components for which an animal's actions have predictable sensory consequences (Bastian 1995, Bell 2001). This mechanism is responsible for adaptively suppressing electrosensory signals in wave-type electric fish associated with tail-bending movements which reposition of the electric organ relative to the sensor array (Bastian 1995, Bastian et al 2004). Adaptive background suppression has also been observed in association with a type of EOD-related noise in pulse-type fish. In both cases, the smart virtual sensors of the ELL adaptively construct a “negative image” of the expected pattern of sensory input. This sensory expectation is built up over a period of several minutes. The negative image is formed by correlation-based learning mechanisms operating at descending pathway synapses (Bell 2001).

SUMMARY

Weakly electric fish can detect, localize, and characterize sensory targets in their environment using an active electric sense. Active electrolocation relies on target-induced perturbations in the fish's self-generated electric field. Using the active electric sense, fish are capable of discriminating differences in size, shape, distance and impedance of target objects. To achieve reliable, real-time performance on these tasks, the nervous system implements a number of smart sensing strategies, including efficient encoding, multiscale virtual sensor arrays, task-dependent adaptive filtering and online subtraction of sensory expectation.

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