Edge-Detection Filter Improves Spatial Resolution in the Electrosensory System of the Paddlefish

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Hofmann MH, Chagnaud BP, Wilkens LA. Edge-detection filter improves spatial resolution in the electrosensory system of the paddlefish. J Neurophysiol 102: 797–804, 2009. First published May 20, 2009; doi:10.1152/jn.91215.2008. In many fishes, prey capture is guided primarily by vision. In the paddlefish, the electroreceptors can completely substitute for the visual system to detect tiny daphnia, their primary prey. Electroreceptors are distributed over the entire rostrum, head, and gill covers, and there are no accessory structures like the eye to form an image. To accurately locate planktonic prey in three-dimensional space, the electroreceptors has to be improved by another mechanism. We have investigated information processing in the electrosensory system of the paddlefish at hind- and midbrain levels by recording single-cell extracellular activity. We stimulated with a linear array of electrodes that simulated a moving dipole field. In addition, global electric fields were applied to simulate the temporal component of a moving dipole. Some stimulation were done with sinusoidal fields. The fire rate of cells in the hindbrain followed the first derivative of the stimulus wave form. In contrast, the response of tectal cells were similar to the third derivative. This improves spatial resolution and receptive fields of tectal units are much smaller than the ones of hind brain units. The principle is similar to a Laplacian of Gaussian filter that is commonly used in digital image processing. However, instead of working in the spatial domain, the paddlefish edge detection filter works in the time domain, thus eliminating the need for extensive interconnections in an array of topographically organized neurons.

I N T R O D U C T I O N

Many fishes and amphibians can detect weak electric fields arising from other animals and use this information to find prey and avoid predators. This passive electrosensory system is present in lampreys, sharks and rays, lungfish, some amphibians, sturgeons and paddlefish, and in a few groups of advanced bony fish (Bodznick and Montgomery 2005; Wilkens et al. 2001; Zupanc and Bullock 2005). Electroreceptors are distributed over the head and, in some groups, also the trunk. The physiology of the receptors and the activity of primary afferent fibers has been well studied in many species (Bodznick and Montgomery 2005). In all electrosensory systems, afferent fibers project to a single hindbrain area, the dorsal octavolateral nucleus (DON) in nonteleosts, the electrosensory lateral line lobe (ELL) in teleosts. From there, information is sent to various targets in the midbrain, depending on the species (Bell and Maler 2005). There are some physiological studies of passive electrosensory centers in the midbrain (Bodznick 1991; Bullock 1984, Chagnaud et al. 2008; Knudsen 1978; Schweitzer 1986), but little is known about how the information is processed.

The paddlefishes (Fig. 1A) are the sister group of sturgeons and composed of only two living species. One of them, Polyodon spathula, is specialized in feeding on plankton. In contrast to the adults that filter feed nonselectively, juveniles pick out single water fleas (mainly daphnia), which they are able to localize with their electrosensory system alone (Wilkens et al. 2001). Single planktonic prey can be detected up to a distance of ≈8 cm (Wilkens et al. 2001). At that distance, however, localization becomes difficult because the receptors in the skin lack directional sensitivity except for the shielding effect of the body, due to the high skin resistance. Electrosensory receptor cells are located at the base of pores, the ampullae of Lorenzini (Fig. 1A, inset). Several pores form a cluster that is innervated by a small bundle of nerve fibers. This functional unit will be referred to as a “receptor.”

In all vertebrates, the midbrain tectum contains a map of the environment that represents the location of objects in space. In most fish species, the visual system dominates tectal input and gives precise information about location, e.g., of prey. In the paddlefish, a prominent projection from the hindbrain electrosensory area to the tectum is present (Hofmann et al. 2002), and behavioral studies have shown that the electrosensory system substitutes for vision in prey capture (Wilkens et al. 2001). Although retinal projections are highly directionally sensitive, benefiting from the presence of a lens, electroreceptors are not. The high spatial resolution required for electrosensory-based prey capture must therefore result from central processing. Here we show that the spatial resolution of electrosensory neurons is enhanced in the tectum, and we provide a hypothesis for how this is achieved.

M E T H O D S

Animals

Fourteen paddlefish (Polyodon spathula Walbaum 1792) measuring 20–30 cm total length were used for this investigation. Paddlefish were obtained from the Hunnewell Hatchery, Missouri Department of Conservation, and kept in large bio-filtered and aerated tanks containing dechlorinated water that was raised to a salinity of 2% by the addition of stock salt. Before surgery the fish were anesthetized with MS-222 (1:10,000). Local anesthesia (0.4% Lidocaine, Sigma) was applied at the dorsal surface of the skull, repeated at 2-hr intervals, and the brain was exposed. Fish were then placed in the recording chamber, immobilized with 10–15 μl Tubocurarine (Apothecon) and the gills irrigated through the mouth with fresh, aerated water. The experiments comply with the “Principles of Animal Care,” Publication No. 86–23, revised 1985, of the National Institute of Health according to a protocol approved by the University of Missouri-St. Louis animal welfare committee.
Stimulation

The fish were stimulated with weak electric fields. Most stimuli were delivered by means of a linear array of 48 silver electrodes spaced 5 mm apart (see Fig. 1). The silver wires were incorporated into an acrylic holder and connected to a series of multiplexers (double pole multiple throw analog switches, DG407, Maxim). Another set of 48 electrodes was present 3 cm lateral to the first set. The array was placed parallel to the rostrocaudal axis of the fish at a distance of 0.5–1.2 cm from the edge of the rostrum (distances varied over the length of the rostrum due to variations in the width of the rostrum). The array extended from the tip of the rostrum to at least the caudal end of the gill covers, depending on fish size. A computer was used to control the multiplexers and to connect two of the silver wires to a stimulus isolation unit that served also as a voltage-to-current converter (A 395 linear stimulus isolator, WPI, Sarasota, FL). To simulate a moving dipole source, the first two electrodes were switched on and stepped with a constant speed through the array by computer. Two electrode configurations were used. In the parallel mode, the two active electrodes were neighboring electrodes in the array closest to the fish. This creates a dipole field that is oriented parallel to the fish’s long axis. In the perpendicular mode, one electrode in each array was active. In this mode, the dipole field was always perpendicular to the fish’s long axis. In both modes, we applied either a DC field or a sinusoidal field at 5 Hz. The DC field was further tested with opposite polarities. In the perpendicular mode, either the positive or the negative pole was always closer to the fish.

In this study, we applied the same waveform that is present at a certain receptor (red circle) during the simulated movement is shown in A, top. In the parallel mode, field strength changes as shown in B, top. C, top: response of a tectal unit to a moving DC dipole field. Note that the response is much sharper than the stimulus. D, top: In the parallel mode, some tectal units show 2 peaks. Bin width of peristimulus time histogram (PSTH) in C and D 100 ms. The photograph in A is modified after (13).

FIG. 1. A: paddlefish striking at dipole electrodes that create an artificial electric field. The long rostrum is covered with electroreceptors (inset: scale bar, 1 mm). The receptor cells are located at the base of pores that in turn are arranged into clusters. B: stimulator used to simulate a moving dipole source. Orientation of the dipole is either parallel (Par) or perpendicular (Per) to the fish’s long axis (MUX: multiplexer). Scale bar, 1 cm. In the perpendicular mode, the change in field strength at a certain receptor (red circle) during the simulated movement is shown in C, bottom. In the parallel mode, field strength changes as shown in D, bottom. C, top: response of a tectal unit to a moving DC dipole field. Note that the response is much sharper than the stimulus. D, top: In the parallel mode, some tectal units show 2 peaks. Bin width of peristimulus time histogram (PSTH) in C and D 100 ms. The photograph in A is modified after (13).

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In this study, we applied the same waveform that is present at a receptor in the skin while a dipole source passes the fish. The calculation of this waveform is explained in more detail in Hofmann and Wilkens (2005). In brief, the voltage measured by a receptor (Rec) was calculated at any given point in time as the sum of the potentials caused by the two source poles

\[
\text{Rec} = \frac{kQ_1}{r_1} + \frac{kQ_2}{r_2}
\]

where \(k\) is the Coulomb’s constant, \(Q_1\) and \(Q_2\) the point charges of the two source poles and \(r_1\) and \(r_2\) the distance to the poles. Depending on
size of the dipole (r_0 = size/2), its orientation alpha (0 is parallel to the movement direction and 90 perpendicular) and the closest distance d of the receptor to the dipole during the movement (P = 0), r_1 and r_2 are

\[ r_1 = \sqrt{[p - r_0 \cdot \cos(alpha)]^2 + [d + r_0 \cdot \sin(alpha)]^2} \]

\[ r_2 = \sqrt{[p + r_0 \cdot \cos(alpha)]^2 - [d - r_0 \cdot \sin(alpha)]^2} \]

p is the horizontal position at any given point in time. The same calculations were also applied to stimulate the model (see following text). All stimuli were calculated in a computer and converted by a CED system (1401 +, Cambridge) to the analog voltage.

Calibration

Before each experiment, stimuli were calibrated to compensate for potential changes in salinity. The actual field strength across the tank was measured with two silver wires placed 20 cm apart. Then a sine wave was applied to the stimulus isolation unit by the computer with a fixed peak-to-peak voltage. A potentiometer at the input of the recording tank. The isolation unit was then adjusted to produce a 10 μV/cm² field in the recording tank.

Recordings

Neuronal activity was recorded with tungsten electrodes (5–20-MΩ; FHC, Bowdoinham, ME). The signals were amplified by a factor of 1,000 (AM Systems, Model No. 1700, Carlsborg, WA), filtered (notch 60 Hz, 300-Hz low-pass, 1.4-kHz high-pass), displayed on an oscilloscope (Tektronix, 2216, Richardson, TX), monitored on a loudspeaker, and stored on a computer. Spikes were separated from background noise using a custom macro (Igor Pro 5.0, Waveometrics). Because tectal units have a very low spontaneous activity, we used global fields as search stimuli (10 μV·cm⁻¹, modulated at 5 Hz). Data were analyzed with Igor Pro 5.0 and standard peristimulus time histograms (PSTHs) were plotted. Data presented here are based on 45 units in the tectum and 54 DON units.

Computer models

All calculations were done with IGOR 5 (Waveometrics). DON units show a spontaneous rate that can be modulated by electrical stimulation. We applied an integrate-and-fire model to simulated DON units. A membrane potential (V) in the model DON units depolarizes with time until a threshold is reached. This creates an action potential and the membrane potential is reset

\[ V(t) = V(t - dt) + Vbias + \xi(t - dt) + Vmod(t - dt) \]

if V(t) > 0 then V(t) = -100

The discrete time step dt used for the calculations is 100 μs. The reset potential is -100 mV and the threshold 0 mV. Vbias is the voltage that is added for each time step to increase the membrane potential steadily until the threshold is reached. Vbias determines the spontaneous frequency of the spike generator and was set to 0.28 mV which resulted in a spontaneous rate of ca. 29 Hz. We also added Gaussian noise ξ(t) with a mean of zero and a SD of 0.5 mV. The modulation voltage Vmod is determined by the level of transmitter released from primary afferent fibers innervating the DON unit. The filter properties of primary afferent fibers and DON units are well known and can be estimated as a derivative filter with an additional low-pass filter (Hofmann and Wilkens 2005; Hofmann et al. 2004). Therefore we differentiated the calculated field strength at the receptor and applied a low-pass filter (Igor Filter Design Lab, MPL low-pass filter: end-pass band, 7 Hz; start stop-band, 18 Hz; 10 dB, 31 Terms, error 0.501). The low-pass filter parameters were chosen to match the frequency response of DON units (Hofmann et al. 2004). This signal was then used as Vmod to modulate the integrate-and-fire model.

Tectal units show little ongoing activity and spike trains are very variable. Because coefficient of variance values of interspike intervals were always around 1, there is no evidence for any regular spike generator. We therefore model tectal units by assuming that spikes are triggered when the membrane potential reaches a certain threshold

\[ V(t) = V(t - dt) + \xi(t - dt) + Vmod(t - dt) \]

if V(t) > 0 then generate one spike

In the absence of Vmod, i.e., Vmod is zero, the membrane potential is driven only by internal noise, but no bias voltage depolarizes the cell and therefore no regular spontaneous activity is apparent as it is the case in DON units. Because tectal units receive their input from DON units, we modulated the tectal units with the same signal that modulates the DON units (i.e., the derivative of the calculated signal at the receptor, with the addition of a low-pass filter) and added two additional derivative steps. These two additional steps lead to response properties of the model that were very similar to the units recorded in live paddlefish.

RESULTS

Responses of tectal neurons to a moving DC stimulus

In these experiments, we recorded neuronal activity at different levels in the electrosensory system of the paddlefish while stimulating with a linear array of electrodes that creates a moving weak electric field in the water around the fish. Figure 1B shows the experimental setup with the location of the stimulating electrodes. An active electrode pair is stepped through the array to simulate a DC field that moves with a speed of 10 cm s⁻¹ from rostral to caudal corresponding to the movement of planktonic prey at the normal swimming speed of the paddlefish. Two electrode configurations were used. In the parallel configuration, the dipole field is oriented parallel to the fish’s long axis; in the perpendicular mode, the dipole field is oriented perpendicular to the fish’s axis. We applied either a DC field or a sinusoidal field at 5 Hz. The physical properties of electric fields in homogenous media are relatively simple, and the field potential at any point around a source can be calculated easily (10). Thus we can calculate the electric field signature at a certain receptor during stimulation, i.e., we know exactly what the receptor “sees.” Therefore the stimulus traces in the following figures do not reflect the applied stimulus but rather the electric field signature at a fictive receptor in the skin. We then recorded from tectal neurons to see how they respond to the moving field. Figure 1, C and D, shows the responses of two tectal units that have a much sharper response profile than the stimulus. If stimulated in the perpendicular mode, only a single burst of spikes is present (Fig. 1C), but if stimulated in the parallel configuration, some units showed two bursts (D). In neurons with a higher spontaneous rate, we also noted that there is an inhibitory phase before and after the burst. This resembles the center-surround organization of retinal ganglion cells.

Electrosensory neurons in the first relay station, the hind-brain DON, have a relatively high spontaneous rate that is modulated by electric stimuli. Cathodal stimuli increase the spike rate and anodal stimuli decrease the rate (Hofmann et al. 2005). Because tectal units have a low spontaneous rate
(4.31 ± 3.19 Hz, n = 21), a rate decrease is hardly measurable. We therefore compared the responses to normal and inverted stimuli by changing the polarity of the dipole. We recorded 42 tectal units and 24 showed a clear response to the moving DC stimulus. Most units showed a single peak in the peristimulus time histogram (PSTH) (Fig. 2, A–C, red histograms). When stimulus polarity was reversed, these units responded in two ways, depending on dipole orientation. In the perpendicular mode, a single peak was present, but either shortly before or after the peak to the original polarity (i.e., positive pole closer to the fish, Fig. 2, A and B, blue histograms). In the parallel mode, the units showed no spikes at the time when they had strong excitation to the original polarity (positive pole was leading), but smaller peaks shortly before and after that time (Fig. 2C, blue histogram). Many units showed two peaks, separated by a pause to the original polarity in parallel mode (Fig. 2D, red histogram) and a single peak at the center when polarity was reversed (Fig. 2D, blue histogram). While inspecting these plots, we found that the response pattern is equivalent to the third derivative of the stimulus. The green traces in Fig. 2 show the calculated field strength at the receptor and the black trace the third derivative of it. For the perpendicular orientation, one electrode is always closer to the fish and the electric field signature at a receptor shows only a single polarity (monophasic). The third derivative then has four phases with two major peaks, one positive and one negative. Figure 2, A–D, shows that the third derivative of the stimulus is a good approximation of the response pattern for tectal units. The stimulation with normal and reversed polarity was helpful in the tectum because tectal cells have low spontaneous rates and only the positive side of the derivative would result in increased spike rate. By reversing the polarity of the stimulus, the

![Recordings](http://jn.physiology.org/)

**Fig. 2.** Top: response of 2 units in the tectum to a moving DC dipole field oriented perpendicular to direction of movement (A and B) and the same units stimulated with a dipole oriented parallel to direction of movement (C and D). The green trace is the calculated field strength at the receptor. The red and blue bars represent the PSTH to stimulation with alternate dipole polarities. The black trace is the third derivative of the stimulus. Two kinds of neurons are represented: ones that directly follow the 3rd derivative (A and C) and others that follow the inverted derivative (B and D). Bottom: same as top, but spike trains were produced by a computer model.
derivative is also inverted and we can test whether the responses correlate with the now inverted derivative.

To further quantify this, we measured the response width in 13 DON and 24 TM units. In the perpendicular mode, the responses showed a decrease in spike rate followed by an increase, and we measured the time between both. In tectal units, the sequence of rate decrease and increase was sometimes reversed. This was the case in 6 of 16 units. In the parallel mode, there was a single peak with increased spike rate and a decrease in spike rate before and after it (6 units) or two peaks with increased spike rate centered around a drop in spike rate (17 units). In this mode, we measured the time difference between the two events with decreased or increased spike rate. We then multiplied the values with the speed of movement to get the equivalent in distance from the receptive field center in centimeters. In perpendicular mode, average response width for DON units was $5.21 \pm 0.61$ cm ($n = 13$) and for TM units $1.61 \pm 0.31$ cm ($n = 16$). In the parallel mode, response width was $6.82 \pm 0.58$ cm ($n = 11$) for DON units and $2.92 \pm 0.61$ cm ($n = 23$) for TM units. The response width’s for DON and TM units was significantly different ($P < 0.001$, t-test) in both modes. For each stimulus mode, we then calculated the stimulus at the receptor and the first to third derivative (Fig. 3). Note that the first derivative is inverted because DON cells invert the signal because they respond with increased firing rate to cathodal stimulation. For the third derivative, we showed also the inverted form because in some tectal cells the responses was inverted. Below these derivatives, we plotted for each unit the timing of the maximal decrease and increase in spike rate. All times were calculated relative to the center of the receptive field. Figure 3 shows that the response width is larger in DON units compared with tectal units. In the DON, the peaks or valleys correspond to the relative minima or maxima of the first derivative and in the tectum they correspond to the third derivative.

**Modeling tectal neurons**

We have developed a computer model that takes the moving stimulus as input. Previously we have shown that the response of neurons in the hindbrain electrosensory center (DON) can be described as the first derivative of the stimulus (Hofmann et al. 2004). We modeled a DON neuron by calculating the first derivative of the stimulus and used this signal to modulate the spike rate of an integrate-and-fire spike generator. Then we took the demodulated signal and calculated its second derivative. This signal is now the third derivative with respect to the original moving DC stimulus. This signal was fed into a simple threshold driven spike generator to simulate the spike train of tectal units. The responses of real tectal units are very similar to the modeled spike train, which shows that their behavior can indeed be explained by just three successive derivatives (Fig. 2, E–H).

**Stimulations with DC and sinusoidal stimuli**

Probably the most common wave form used to stimulate the electrosensory system is a sine wave. However, a sine wave is a special case because the waveform is not changed by a derivative function. Only the phase is shifted, by 90°. We can use this to test our hypothesis that the response of tectal units represent the third derivative of a stimulus. If we apply a sine wave, there should be no difference between DON and tectal (TM) units, except for a phase shift. Instead of moving a DC field along the fish, we applied a slowly moving 5-Hz sine wave. Now we can analyze the response in more detail by plotting each spike time not only with respect to the position of the stimulus along the rostrum but also to its phase relationship to each sine wave cycle.

The results are shown in Fig. 4. DON units have a relatively high spontaneous rate, but outside the receptive field spikes are not in phase with the stimulus ($n = 16$). On approaching the receptive field, spikes are accumulated at a certain phase angle.
Then there is a phase reversal with a high degree of phase coupling at the center of the receptive field. When leaving the receptive field there is again a phase reversal before the phase coupling ultimately disappears. These phase reversals were previously described and are present also in primary afferent fibers (Hofmann et al. 2002). However, the point here is whether there are differences between DON and TM units. We recorded 46 TM units and 36 responded to the 5-Hz scan stimulus. Although the plots look different the overall response is very similar, the only difference being that TM units have little spontaneous activity. But they both show strong phase coupling in the center of the receptive field and two phase reversals. Furthermore, the width of the receptive field is similar. The width was measured by calculating the time between the first significant phase coupling and the last significant phase coupling. To determine significant phase coupling, we calculated the synchronization coefficient (7) and the Rayleigh statistic (1). Z values >4.6 indicate significant phase coupling. E and F: response of a DON (E) and a tectal unit (F) to a global field stimulus that was changed in time to simulate a moving DC signal. The DON unit follows the 1st derivative (black trace in E), the tectal unit the 3rd derivative (black trace in F) of the stimulus (green trace in both).

**Spatial versus temporal information processing**

There are two ways to calculate the derivative. It can be obtained in the time or space domain. As a stimulus source projects its electric field onto the skin of the paddlefish, a spatial derivative, the difference in field strength between neighboring receptors in a distributed array, can be computed. The alternative method would be to calculate the first derivative in the time domain. The signal at individual receptors changes over time in the same way it does over space. This is because a source field follows a straight path along the fish as it forages for prey. Here, time and space are equivalent. To find out whether paddlefish calculate the derivatives over time or space, we employed a global field stimulus with one electrode in front of the animal and one behind. This creates a homogeneous field strength in the tank (some distortions are present due to the fish’s body). We then applied a signal that simulates the electric field signature of a moving prey. The changes in field strength at a certain receptor are identical to the change in intensity it would perceive during movement. The only difference is that there is no spatial component. A moving DC source does both, it projects a spatial image onto the skin and changes over time with respect to a nonmoving sensor. With our global field electrodes the signal changes over time only, but at any given moment, the field strength is the same at all skin locations.

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**FIG. 4.** Responses of a DON unit (A, C, and E) and a tectal unit (B, D, and F) to a moving DC (A and B) and a moving 5-Hz stimulus (C and D). In contrast to DON units, tectal units show a more localized response to a moving DC (B) but have a very broad receptive field if stimulated with a moving sinusoidal stimulus (D). C and D, results from a slow scan. The top graph shows a PSTH (bin width, 0.5 s), the middle graph a phase plot, and the bottom graph the z values during the scan. Z values >4.6 indicate significant phase coupling. E and F: response of a DON (E) and a tectal unit (F) to a global field stimulus that was changed in time to simulate a moving DC signal. The DON unit follows the 1st derivative (black trace in E), the tectal unit the 3rd derivative (black trace in F) of the stimulus (green trace in both).
We tested 33 DON and 25 TM units for their response to a stimulus simulating the changes of the electric field over time of a passing prey item. Figure 4 shows two units, one in the DON (E) and one in the tectum (F), stimulated with the global field. Both units show a response pattern similar to the ones obtained by stimulating with a moving DC source. We measured the response width as described above and found that TM units averages at 1.53 ± 0.42 s (n = 25) and DON units at 4.9 ± 0.73 s (n = 33). The response width of tectal units was significantly smaller as in DON units (P < 0.001, t-test). The response of the DON unit follows the first derivative whereas the tectal unit follows the third derivative. This suggests that the derivatives are calculated in the time domain and not over space.

**DISCUSSION**

The mechanism used by the paddlefish to analyze an electrical image is similar to an algorithm used in digital image processing. In fact, it is equivalent to a method for edge detection called Laplacian of Gaussian filter (LoG) (Marr and Hildreth 1980). The LoG filter is a two-step process. First, a Gaussian smoothing is applied to eliminate pixel noise, acting essentially as a low-pass filter. Then, the second derivative is calculated. Zero crossings in the second derivative indicate points in the image with the steepest slopes (i.e., edges). The paddlefish also has a low-pass filter, combined with a derivative filter, already at the level of hindbrain neurons in the DON (Hofmann et al. 2005). In the tectum, two additional derivative steps are added. A LoG filter only makes two derivatives, but to detect the zero crossings, a third step is needed to convert the zero crossings into a relative maximum or minimum. The function of the LoG filter is demonstrated in the space domain (Fig. 5).

However, paddlefish want to know the location of the source, not the “edges” of the signal. The electric field signature of a passing prey has a characteristic form that depends on prey orientation (Wojtenek et al. 2001). If the prey is oriented such that its dipole field is parallel to the fish’s long axis, the signal at each receptor will be biphasic with the steepest slope exactly at the point in time when the prey is centered over the receptor (Fig. 5A). The steepest slope, however, is exactly what a LoG filter defines as an edge. If the prey is oriented with its dipole field perpendicular to the fish’s long axis, the steepest slope of the signal will be a little off-center but still close to center (Fig. 5B). In this case, a tectal unit would fire a little too early (or too late, depending on polarity), but this may not be critical for a fish with such a big mouth. Finally, as shown in Fig. 5C, the LoG filter is ineffective for localizing a sine wave except for a change in phase.

Comparing the original signal with the Laplacian, it becomes apparent that the Laplacian leads to a smaller receptive field and thus an increase in spatial resolution. Individual electoreceptors have no directional sensitivity, except for the shielding effect of the fish’s body. This is in sharp contrast to the visual system where photoreceptors are highly directionally sensitive due to the presence of an image-forming lens. In the electroreceptive system, a Laplacian filter seems to replace in a crude form the focusing property of a lens.

In digital image processing, a LoG filter is usually one of the more time-consuming and complex image computations. Each pixel of the original image is converted into a new pixel depending on the brightness of the original pixel and its neighbors. Brightness gradients in an image can have a large range of scales. There are sharp changes from pixel to pixel or more gradual changes across the whole image. To capture the slow changes, the LoG filter has to compute for each pixel a large number of neighboring pixels. This means that for a neuronal model that acts in the space domain, each neuron has to be connected with almost all other neurons in the array and in an orderly fashion with each connection weighing differently according to distance. Paddlefish solve the problem by calculating the derivatives in the time domain.

In a realistic prey-catching scenario, the paddlefish cruises at a constant speed. As a ram ventilator, they swim constantly throughout life. Thus in an encounter with a planter, the prey would pass over the receptor array, also with a constant speed. At any given point in time, the “electrical image” on the array has a characteristic form (see Fig. 5, A and B). But while the

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**FIG. 5.** Color-coded visualization (left) and electric field signature of a horizontal transect of the image (right) showing the effect of a Laplacian of Gaussian filter (LoG) filter. Color scale: red, positive; blue, negative; black, 0. A. top: electric field signature of a moving dipole field oriented parallel to the fish’s long axis. Bottom: 3rd derivative of the original signal. B: same as A, but the dipole field is oriented perpendicular to the fish’s long axis. C: a sinusoidal signal is moved along the fish. Because a derivative filter applied to a sine wave changes the phase but not the shape, the derivative filter is ineffective.
prey moves in space, it also moves in time. Because the relative speed can be assumed to be constant, time and space are equivalent. As a consequence a single receptor will receive, over time, exactly the same signal that is present spatially at a fixed time over the whole array. Analyzing this signal in the time domain is equivalent to analyzing a stationary electrical image on the skin spatially. But it has some advantages. In an array of receptors, each receptor has its own spontaneous rate and sensitivity. Receptor mismatch can introduce large amounts of noise. Noise could be adjusted centrally, but this is not necessary if the relevant information is present in the activity of a single receptor over time. There is no receptor mismatch if only one receptor is used and scanned over the image. The other advantage is that spatial analysis of an array is limited in space to the size of the array, but temporal analysis is not. Each receptor is in principle a scanner with infinite range. Limited only by signal-to-noise ratio, each receptor produces a continuous signal that represents the full electric field signature from the point where the signal emerges above the noise to the point where it fades into the noise again, regardless of the dimensions of the fish. The signal is then analyzed in the time domain by a low-pass filter and a series of differentiators. The advantage is that the output of the neuron is a function of the current state and the previous history of input, a typical temporal filter. The same information that a spatial analysis has to obtain from a large number of neighbors is present in the previous history of stimulation of a single neuron. This may be the reason for the lack of a topographic map in the DON. Neurons in the DON have well-defined receptive fields, but they are not arranged topographically (Hofmann et al. 2005). This would be important if each neuron had to communicate with its neighbors, but not if information is processed in the time domain. In the tectum, electrosensory neurons may be topographically organized, but we have shown here that at least the derivative filter in tectal neurons operates in the time domain.

Paddlefish take advantage of a number of special, fortunate circumstances that apply during feeding. First, it can be assumed that the prey target is a point source on a featureless background. This is the equivalent of detecting fireflies on a dark night. Second, in contrast to fireflies, the paddlefish is moving, whereas the targets are suspended relatively motionless in the water column. The direction and speed of the target over the array is predictable. This enables the receptor to work in a scanning mode and eliminates receptor mismatch problems. It also allows the LoG filter to work in the time domain, thus eliminating the need for a large number of interconnections between neurons. Third, the signal waveform is predictable. The fastest change of field potential occurs when the prey is over the receptor and this is what the LoG filter defines as an edge.

We have found here for the first time a neuronal implementation of a LoG filter that helps to improve spatial resolution in the electrosensory system. This filter may also be used in other sensory systems with receptors distributed over the entire body and without accessory structures to enhance spatial resolution. Our results also show that spatial problems can be solved in a much easier way in the time domain given constant movement where time and space are equivalent. This latter principle may be of relevance for a much wider range of natural and technical sensors.

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