A neural model of electrosensory system for detection of position and moving direction of an object in electrolocation

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Abstract:
Weakly electric fish generates electric field around its body using electric organ discharge and can accurately detect the location of an object using the modulation of electric field induced by an object. Objects with electric properties different from those of the surrounding water distort the electric field around fish’s body depending on the size, distance and electric properties of objects. It is not clear yet how the fish recognizes the properties of an object such as its electric property, location and size based on its electric image. As the first step to clarify the neuronal mechanism of electrolocation, we developed a model of fish body by which we describe numerically the spatio-temporal patterns of electric field around the fish body. We made also neural models of electroreceptors distributed on the fish body and of electrosensory lateral line lobe(ELL) to investigate what kinds of information of electric field distorted by an object they detect. The models reproduce qualitatively the experimental results about the detections of size, distance, and moving directions of an object. We show that the ability of ELL neuron to detect the direction of object movement parallel to the fish body is generated by the spatially inhomogeneous pattern of electric field along the fish body from head to tail, which is induced originally by the electric organs in the tail of fish.

1. Introduction

The brain perceives the environment by the acquisition of its “sensory image”. In visual system, various features of an object such as structure, contrast, and color are encoded in parallel by the peripheral nervous system, and these features are bound in the visual cortex to make an visual image of an object. Auditory system also uses the encoding and binding mechanisms similar to the visual system to make an auditory image of sound source. However, the entire neural mechanism of sensory imaging in visual and auditory systems has not been known yet, because these systems have complex processing mechanisms realized based on complex neural structures. The electrosensory system gives us an ideal system to investigate the neural mechanism of sensory imaging, because the electrosensory system is relatively simply structured and the role of its circuitry in processing behavioral signals across multiple parallel sensory pathways have been well studied.[1,2].

Electrosensory system allows fish to locate and identify an object by binding various features of an object in the absence of visual cues and signals from other sensory systems. Weakly electric fish generates an electric discharge in its tail, and the current flow resulting from this electric organ discharge(EOD) causes a voltage to develop across the fish’s skin. The amplitude and phase of EOD modulated by an object are measured by electroreceptors distributed over the body surface. An object, whose impedance is different from that of surrounding water, will alter the spatio-temporal pattern of transepidermal voltage, and its alternation is detected and encoded into neuronal impulse trains by electroreceptors. The information about amplitude and phase modulation encoded by electroreceptors is conveyed to electrosensory lateral-line lobe(ELL), as shown in Fig. 1.
skin. However, the neuronal mechanism by which the central nervous systems of the fish compute the ratio has not been clear yet.

As the first step to clarify the neuronal mechanism of electrolocation, we developed a model of fish body by which we describe numerically the spatio-temporal patterns of electric field around the fish body. We made also neural models of electroreceptors distributed on the fish body and of electrosensory lateral line lobe (ELL) to investigate what kinds of information of electric field distorted by an object they detect. The models reproduce qualitatively the experimental results [1] about the detections of size, distance, and moving directions of an object. Here we show that the ability of ELL neuron to detect the direction of object movement parallel to the fish body is generated by the spatially inhomogeneous pattern of electric field along the fish body from head to tail, which is induced originally by the electric organs in the tail of fish.

![Figure 1 Neural circuits involved in electrolocation.](image)

Electroreceptors are distributed on the fish’s body surface. ELL is a first sensory nucleus converging the information of amplitude and phase in EOD signal encoded by receptor.

2. Model

2.1 Change in the transepidermal electric potential induced by an object at various positions

We calculated the change of voltage across the skin of the fish, based on the model presented by Hoshimiya et al. [4]. The fish was placed in a water container, as shown in Fig. 2a. The model of fish consists of a body surrounded by skin of high resistivity and an electric dipole made by the electric organ, as shown in Fig. 2b. The front end of this organ becomes negative with respect to its rear end. Then, the electrostatic potential at each point in the body and the external space was calculated simultaneously in the case where objects with various electric properties were put on a point in the space [5].

2.2 A model of electroreceptor and afferent nerve

P and T receptors are distributed on two-dimensional body surface. The response of P and T receptors and their afferents to the voltage across the skin induced by an object were calculated using our electroreceptor model [6].

2.3 A neural model of ELL

The ELL neuron, basilar pyramidal (bp) cell, responds selectively to a rise of EOD amplitude [1]. Figure 3 shows a model of bp cell made based on the anatomical structure. The bp cell receives the afferent spikes through the excitatory synaptic connection from the central region of receptive field and the inhibitory synaptic inputs with time delays via granule cells receiving afferent spikes from peripheral region of receptive field. Thus, bp cell has ON center-OFF surrounding connection between bp cell and receptors, as shown in Fig. 3. The membrane potentials of bp cell and ith granule cell, \( V_{bp} \) and \( V_{gr} \), are determined by

\[
\frac{dV_{gr}}{dt} = \frac{C}{\tau_{er}} \left( -g_{er} m^2 h (V_{bp} - V_{gr}) - g_{ex} n^4 (V_{bp} - V_{es}) - g_{es} (V_{es} - V_p) + I_{a} + I_{nb} \right),
\]

\[
\frac{dV_{bp}}{dt} = -V_{bp} + w_{ex} (V_p - V_0),
\]

\[
X_{er}^{'} (t) = \frac{1}{1 + \exp(-V_{er}^{'} - V_{er}^{\infty})/\xi_{er}},
\]

\[
I_{nb} = \sum_{i=1}^{N_i} w_{nh} X_{er}^{'} (t - \tau_{er}),
\]

\[
\frac{dV_{bp}}{dt} = -g_{es} (V_p - V_0).
\]
\[ I_{ex} = \sum_{j=1}^{N_d} g_{y_j} (V_{y_j} - V_{E_y}) \]  

where \( g_y \) and \( E_y \) \((Y=Na, K, L)\) is the conductance and equilibrium potential of Na, K, and leak channels, respectively, and \( n \) is the gating probability of Na and K channels. \( I_{ex} \) is the excitatory synaptic current induced by the afferent inputs from the central region of receptive field and \( I_{inh} \) is the inhibitory synaptic current induced by the outputs of granule cells. \( X_{gr}^{-1} \) is the output of granule cell which is described by a sigmoidal function of \( V_{gr}^{-1} \), and \( \tau_i \) is a time delay of output of granule cell.

The sensitivity of bp cell to increase in EOD amplitude comes from the ON center-OFF surrounding connection between bp cell and receptors, by which excitatory signals are followed by the inhibitory signals with time delays via granule cells. The time delay comes from the signal propagation over a long distance from the receptors at the surrounding area of the receptive field of the bp cell and from the time delay arising from the signal mediation by granule cells. The bp cell fires when the amplitude of EOD distortion is increased, but becomes silent soon due to the delayed inhibitory currents from the granule cells, because the firing rate of granule cell is also increased with the increase of the EOD distortion.

Fig. 3 A model of ELL. Bp cell receives excitatory synaptic currents induced by the afferent spikes from receptors c1-c3, and inhibitory currents induced by afferent spikes from receptors, R1-R3, L1-L3. The inhibitory currents have different time delays depending on the distance between bp cell and receptor.

3. Results

3.1 EOD distortions around fish’s body induced by a resistive object

Figure 4 shows the changes of transepidermal voltage induced by a resistive object, which is defined as the difference between

\[ V_{T} = V_{EOD} - V_{B} \]
transepidermal voltage under the existence of an object and that in the absence of an object. Three curves in Fig. 4 represent the voltage changes calculated at positions on body surface in the case where the object is placed at the positions along the direction perpendicular to the fish body. Each receptor on body surface receives the different electric field depending on the location of object. It is seen in Fig. 4 that the deviation of transepidermal voltage induced by an object decreases as the object goes away from the fish body surface.

The changes of transepidermal voltage induced by a moving object are shown in Fig. 5. Six curves in Fig. 5 represent the voltage deviations calculated at points on body surface in the case where the object is placed at six positions described by the value of X in the figure. These positions are occupied in order by the object as it moves from left side (head of the fish) to the right side (tail of the fish) along the longitudinal axis of the fish. That is, receptors at each position on the body surface receive the potential relevant to the location of object whose magnitude is determined depending on the distance between the receptor and the object. It is seen in Fig. 5 that the deviation is increased as the object moves from head to tail. This is because the effect of electric organ on the deviation becomes large as the object moves to the tail. This result suggests that the fish may detect the location of an object based on the transepidermal voltage changes over the whole body surface.

3.2 Response properties of afferent and bp cell induced by a static object

The responses of receptor afferent and bp cell to the change of transepidermal voltage induced by an object are shown in Fig. 6. Fig. 6a shows the temporal variation of the transepidermal voltage at the position $x = -10$ on the body surface, which is generated by EOD modified by an object with lateral distance $L$ shown in Fig. 4. The amplitude of transepidermal voltage is increased by an object. We describe the temporal variation of transepidermal voltage by a sinusoidal wave, because any resistive object induces no phase distortion of EOD. Figures 6b and c show spike patterns of receptor afferent and bp cell induced by the transepidermal voltage shown in Fig. 6a, respectively. Both the firing rates are larger than the relevant rates evoked by fish’s own EOD. The afferent generates almost regular pattern of firing, while the firing pattern of bp cell becomes irregular because bp cell receives complex synaptic inputs consisting of excitatory and inhibitory inputs with various time delays.

Figure 7 shows the firing rate of receptor afferent and bp cell as a function of the distance between the fish and the object. It is shown in Fig. 7 that both the rates changes as the negative power of the fish-object distance. This suggests that the information about the distance of an object from the fish may be
encoded into the firing rate of afferent and bp cell. The firing rate of bp cell decays with increasing distance more rapidly than that of receptor afferent. The experimental results obtained by Bastian[1] has tendency opposite to our result. This discrepancy comes from that the complex feedback processes in ELL are not taken into account in the present model.

3.3 Response properties of afferent and bp cell induced by a moving object

Figure 8 shows the change in receptor afferent activity at x=-10 due to the moving of an object in parallel to longitudinal axis of the fish. It is seen in Fig. 8 that the activity is increased as the distance between the receptor(at x=-10) and the object is decreased. The activity is reduced noticeably in comparison with the activity induced by fish’s own EOD, when the object is at the tail side. This is consistent with the observed data obtained by Bastian[1].

Figure 9 shows the spike patterns of the bp cell induced by an object moving along the fish axis. As seen in Fig. 9, the firing rate of the bp cell induced by an object passing from the head to the tail, shown in Fig. 9(A), is larger than that induced by an object passing reversely, shown in Fig. 9(B). This indicates that the bp cell can discriminate the moving direction of an object. The difference in the spike pattern comes from the spatially inhomogeneous pattern of electric field along the fish body from head to tail, which is generated originally by the electric organs in the tail of fish. Because the EOD distortion is slightly decreased as the position is changed from the tail side to the head side, the magnitude of EOD distortion induced by an object moving to the tail is larger than that induced by an object moving to the head. This position dependence of EOD distortion makes the inhibitory inputs to the bp cell asymmetric with respect to the moving direction of an object. This result suggests that the fish uses positively the inherent, spatial inhomogeneity of electric field around its body for detecting the information about object movement.

Fig. 6 (A) Temporal variation of transepidermal voltage induced by an object. Spike patterns of (B) afferent and (C) bp cell.

Fig. 7 Dependence of activity of (A) afferent and (B) bp cell on the lateral distance of an object.
4. Concluding Remarks

We have investigated what kinds of information of EOD distortion induced by an object the receptor afferent and bp cell detect. We have shown that the lateral distance of an object is encoded into the firing rate of receptor afferent and bp cell, and the moving direction of an object is discriminated by bp cell whose ability comes from the inhomogeneous spatial pattern of original EOD around fish body.

The firing rates of afferent and bp cell depend not only on the distance of an object but also on its size: these firing rates increase with decreasing the lateral distance of an object, and increase also with increasing the size. ELL must discriminate effectively the effects of distance and size of an object. To solve the problem, we will extend our model of the fish body from 2-dimensional body to the 3-dimensional body.

References


