Dynamic population coding for detecting the distance and size of an object in electrolocation

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Abstract

To clarify the neural mechanism of dynamic population coding in electrolocation carried out by electrosensory system of a weakly electric fish, we developed a model of fish body to describe numerically the spatiotemporal patterns of electric field around the body, and neural network models of electrosensory lateral-line lobe(ELL) and torus semicircularis(TS). The spatiotemporal features of electric field relevant to distance and size of objects are encoded into the spatial distribution and timing of burst spikes of ELL neurons. The information is represented more definitely as the area and timing of the synchronized firing pattern of TS neuron population.

1. Introduction

In early processing stages of many sensory systems, a stimulus is processed based on a specific map representing stimulus features. In the visual system, the features of visual stimuli are classified into elemental features such as boundary lines, their tilted angles, and colors and represented in the neuronal maps specific to each feature: in the somatosensory system, the tactile information is processed based on the somatotopical map representing the location of a touch on the skin. The activity pattern of neurons on the map is well described by a gaussian distribution whose maximum firing is given by the neuron tuned into the feature. This coding scheme has been well known as population coding. However, the populations of neurons in early stages may also carry information about features of stimulus which are not explicitly encoded into any map. The features are encoded into spatiotemporal firing patterns which are not classified by the position of maximum firing but by the dynamical properties of neurons such as distance between burst spikes and spatial range of synchronization of spike timing. We refer to this type of a population coding as "dynamic population coding". However, it is not yet clear how the neuronal population encodes the stimulus features in dynamic population coding. To clarify the neural mechanism of dynamic population coding, we study electrosensory system of a weakly electric fish. The electrosensory system gives us an ideal system to address this issue, because the electrosensory system has relatively simple structure and the role of its circuitry in processing behavioral signals across multiple parallel sensory pathways have been well studied [7].

Electrosensory system allows fish to locate and identify an object in the absence of visual cues and signals from other sensory systems [1]. Weakly electric fish generates the 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 fish 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 encoded into neuronal impulse trains by electroreceptors. The information about amplitude and phase modulation received by electroreceptors is conveyed to electrosensory lateral-line lobe (ELL) and then transmitted to torus semicircularis(TS).

When an object moves nearby fish body, the receptors receive EOD signals with spatiotemporal structure. The fish can perceive a unique image of object on the basis of somatotopical mapping of receptor signals on ELL, which represent the location of object on fish body surface. However, the information about the distance and size of an object are not explicitly represented on the somatotopical maps, that is, there are no neuronal maps for detecting the distance and size of an object. It has been demonstrated from the ethological experiments for pulse type fish [13] that the fish can measure the distance of object by using the ratio of maximum slope to maximum amplitude of the current distribution across the skin. Then, it is quite reasonable that they are encoded in spatiotemporal firing pattern of receptors and ELL network. Experimental results [6,11] have shown that the ELL neurons exhibit burst spikes under the application of electrosensory stimuli, suggesting that the features of the stimuli are represented by the burst patterns of ELL neurons. However, it is not yet clear by what kinds of dynamical properties of neuronal population the distance and size of an object are encoded.

To address this issue, we developed a model of fish body in order to describe numerically the spatio-temporal patterns of electric field around the fish body. We made also a model of electroreceptor distributed on the fish body and neural network models of ELL and TS to investigate what kinds of dynamic information induced in electric field are encoded in these networks. The models may reproduce qualitatively the experimental results [10]. Here we show that the spatiotemporal features of electric field around the fish body are encoded into the timing of burst firings of ELL neurons. The information of the distance and size of an object can be extracted by taking account of simultaneously the spatial area of synchronous firings of neuronal population and the time intervals between the firing spikes in TS network.

2. Model

2.1. Overview of our model

Electrosensory system consists of receptors, P-afferent nerves, electrosensory lateral-line lobe(ELL), torus semicircularis(TS), and eminential granularis posterior (EGP). The amplitude information of EOD distortion induced by a resistive object is processed in the feedforward pathway from receptors to TS via P-afferent and ELL. The feedback signals from EGP are sending back to ELL [2]. To investigate the neural mechanism by which the fish can detect the distance and size of a moving object, we made a neural network model of electrosensory system as shown in Fig.1.

We briefly describe the neural structure of each network. The receptor, ELL and TS networks are somatotopically connected with each other. Receptor network consists of two dimensional array of receptor neurons, each of which receives EOD stimulus modulated by an object, where the modulation are changed depending on the distance between object and receptor. The P-afferent encodes EOD amplitude modulation (EOD AM) into a spike train. The model of ELL neuron(basilar pyramidal(bp) neuron) consists of two compartments, soma and dendrite. The bp neuron encodes the increase in EOD AM into the timing of burst spike. The bp neurons project to two higher centers, TS and EGP, and EGP neurons project back to the ELL. Although the descending pathway of ELL has a more complex structure including NP(nucleus praeeminentialis) and EGP [2], we consider only a simplified model of EGP to regulate the dynamic range of ELL neurons.

The network models of ELL and TS consist of neurons arranged in 2D lattice. The connections between two networks are as follows. TS neuron at (i, j) site receives the input signals from bp neuron at (i,j) site and its nearest neighbor neurons in ELL network. Each bp neuron connects reciprocally with EGP1, and makes only feedback connection with EGP2, as shown in Fig.1. EGP1 receives all the outputs of bp neurons, and diffusively sends its output signals to all the dendrite of bp neurons. EGP2 receives the output of EGP1, and sends its output signal to all the dendrites of bp neurons with inhibitory synapses.

2.2. Model of fish body for calculating EOD modulations induced by an object

We made a 3-dimensional(3D) model of fish body based on the 2D model proposed by Hoshimiya et al. [8]. The detail of our model is described in Ref. [10].

2.3. Models of electroreceptor and afferent nerve

P-receptors are distributed on two dimensional body surface as shown in Fig.1. The responses of P-receptors and P-afferents to EOD AM were calculated using our electroreceptor model [9].

2.4. Neural network model of ELL

We made a neural network model of ELL based on its anatomical structure [5]. The bp neurons receive not only the P-afferent signals but also the efferent signals from the higher unit, EGP. A bp neuron is excited directly by inputs from central P-afferent nerves and inhibited indirectly via granule cells by inputs from peripheral P-afferents. The model of bp neuron consists of soma and apical dendrite, which were made based on two-point MacGregor model [12]. Although the multicompartment model of bp neuron and its simplified model have been proposed [3,4], these models have complex dynamics to generate a burst spike. We used two-point MacGregor model to reproduce easily the burst dynamics of bp neuron. The essential property of burst spike can be well described by the two-point MacGregor model.

2.5. Neural network model of TS

The TS model was made based on the soma model proposed by Doiron et al. [4], whose dynamics is described by active Na and K channels. The TS neurons are mutually connected with excitatory and inhibitory synapses on the basis of ON center-OFF surrounding connection.

2.6. Model of EGP

The EGP network consists of two types of neurons, EGP1 and EGP2. The models of EGP1 and EGP2 neurons were made based on a leaky-integrator neuron model. The EGP neurons regulate the dynamic range of bp neurons so as to make them silent under the stimulation by only the fish's own EOD signals and to sensitively respond to only the EOD modulation induced by an object. The synaptic weights between EGP neurons and apical dendrite of bp neurons are adjusted by Hebbian learning process so as to generate the function mentioned. The details of the EGP model and its functional role in regulating the ELL dynamics are described in Ref. [5].

3. Results

3.1. Response properties of ELL and TS network to EOD modulation induced by a moving object

Figure 2a shows the temporal variations of EOD modulations induced by a moving object, which are received by the receptors located on the center line of the receptor network along the longitudinal axis of fish body. The object moves from the head(H) to the tail (T) of fish, keeping the lateral distance of an object constant, as shown in Fig.2a. The amplitude modulations of EOD were calculated using the model of fish body described in section 2.2. As shown in Fig.2a, the Gaussian-like EOD amplitude modulation (EOD AM) propagates on the receptor network without changing the shape during the movement of an object. The maximum amplitude and width of Gaussian-like EOD AM shown in Fig.2a change depending on the distance and size of an object.

Figure 2b shows the raster plot of burst spikes of 35 bp neurons located on the center line of ELL network, each of which represents the upstroke of EOD AM received by the receptor located on the position x along the longitudinal axis of the fish body. It is seen in Fig.2b that the burst firings of bp neurons shift smoothly on ELL network as the object passes from the head to the tail of the fish. Although the receptors on the fish body receive a spatiotemporaly continuous patterns of EOD modulations, the bp neurons can represent the spatiotemporal correlation of receptor activity induced by EOD modulations by the discrete signals, that is, the timing of burst spikes.

TS neurons generate a single spike by receiving the burst outputs of bp neurons. The raster plot of spike timing of TS neurons, which are located on the center line of TS network, is shown in Fig.2c. In Fig.2c, the spike timings of TS neurons in a region are synchronized, and the synchronized firing region in the network moves discontinuously along the center line in the network every time interval. Then, the area of firing region keeps constant and the time interval is also constant. The distance and size of an object are possible to be represented by the area of synchronized firing pattern and the time interval of the hopping of synchronized region.

3.2. Neural representation of the distance and size of an object in TS network

Figure 2d and e illustrate the dependences of the area and the hopping time interval of synchronized firing region in TS network on the distance and size of an object. It is seen in Fig.2d that the area (S) and hopping time interval (Td) of synchronized firing region increases significantly with increasing the lateral distance (d) of object. The hopping time interval Td changes significantly with changing the object size a, but the area S shows only a weak dependence on a. These results suggest that the size of an object is mainly represented by the time interval Td and the object distance is represented by a function of two characteristic dynamical properties of the synchronously firing TS neuron population, S and Td.

The ability to generate the dynamic representations of distance and size of an object comes from the dynamic properties of ELL and TS neurons. The nonlinear processing of burst generation enables bp neuron to effectively encode the width and maximum amplitude of EOD AM into a burst timing. In ELL, the area of burst spikes within a time window is sensitively changed depending on the width of normalized EOD AM, which is considered to well represent an object distance. The interburst interval is sensitive to the changes of object size and distance. The spike synchronization of TS neurons may be generated by combining effectively these features of ELL bursts, thereby making a stable, synchronously firing neuronal population for detecting distance and size of an object.

4. Concluding Remarks

We have shown that spatio-temporal correlations of EOD modulations induced by a moving object are effectively encoded into spatial distribution and the timing of burst firings of bp neuron population in ELL, and that the information about distance and size of an object included in the EOD modulations is well represented by the area of synchronous firing of TS neuron population and the time interval between the synchronous firings, respectively.

The present model have many parameters used for describing bp neuron, EGP neurons, and ELL and TS networks. We adjusted these parameter values so that each network model can reproduce the functional role in detecting the distance and size of an object. The present model are insensitive to slight changes in parameter values, that is, the changes within the reasonable ranges do not make an essential change in the results presented here.

The distance and size information encoded by the TS network are bound with each other in a higher nucleus, optic tectum(OT), to make unified image of object. OT receives signals from the visual system besides electrosensory system. OT binds the visual and electrosensory information to make a unique image of external world, which is useful for the communication and survival of the fish. Further study is to investigate how visual and electrosensory information are bound in OT to make an adequate behavior in the relevant image of environment.

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Figure Legends

Fig. 1. A model of electrosensory system including the feedforward signals from receptors and the feedback signals from a higher nucleus, EGP. The feedforward signals are denoted by the solid lines, and the feedback signals are denoted by the dotted lines. ELL(electrosensory lateral-line lobe), TS(torus semicircularis), and EGP(eminetial granalis posterior).

Fig. 2. (a) Temporal variations of EOD amplitude modulation(EOD AM). (b) (c) Raster plots of burst spikes of ELL neurons (b) and single spikes of TS neurons(c). The plots are shown for only ELL and TS neurons which are located on the center line of 2D network along the longitudinal axis of fish, or x-axis. (d)(e) Dependences of the area (S) and time interval(Td) of synchronous firing patterns of TS network on the distance(d) and size(a) of an object. The curves of S and Td are represented by the solid and dotted line, respectively.

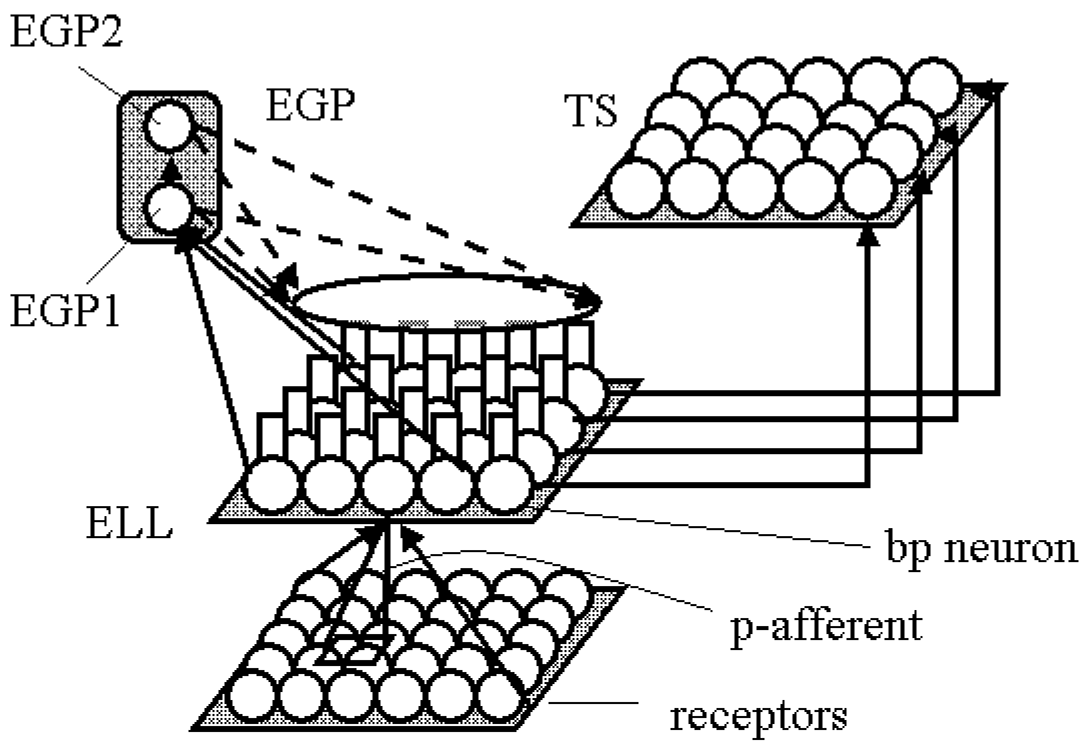

Figure 1. K. Fujita et al.

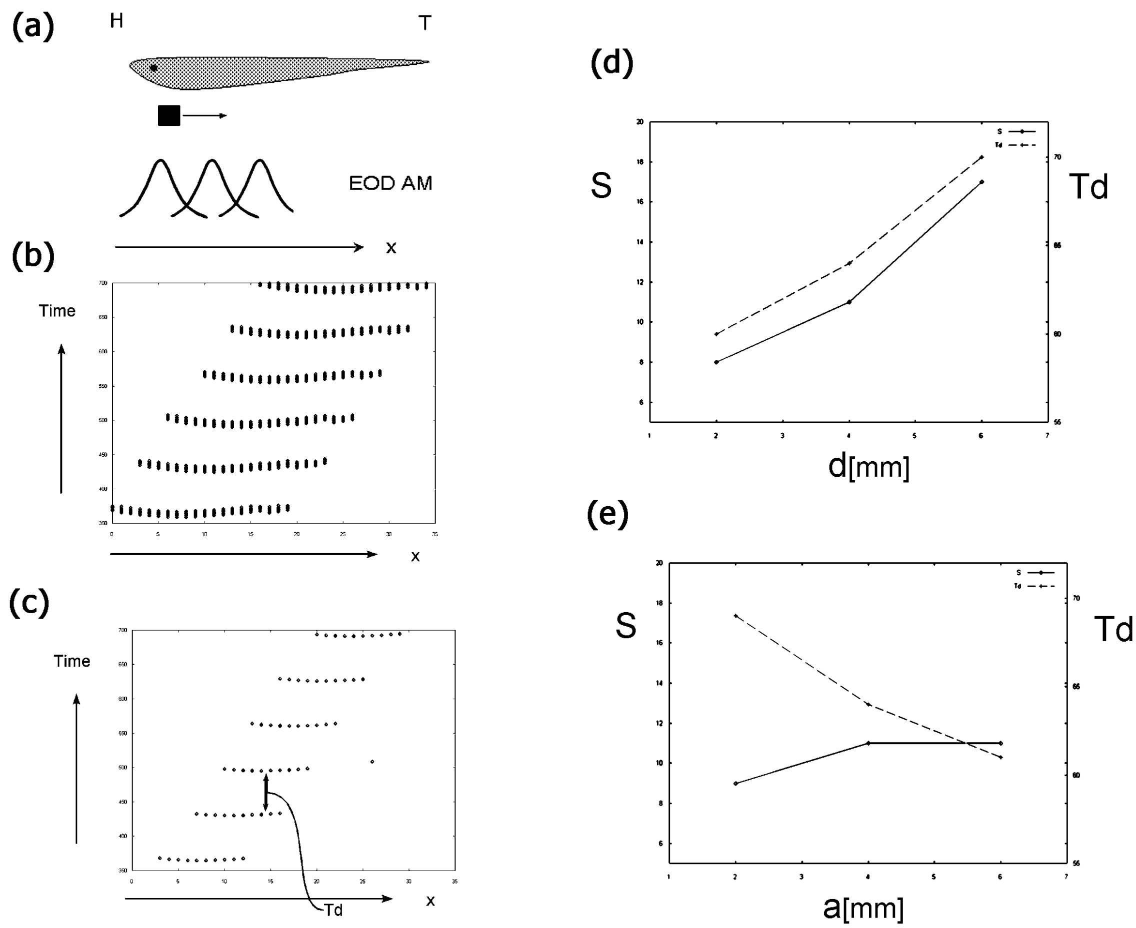

Figure 2. K. Fujita et al.

Biosketches

Kazuhisa Fujita is presently a student in the Graduate school of Information Systems at the University of Electro-Communications. His research interest is to clarify the neural mechanism of electrolocation.

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