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

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Key words: electrolocation, dynamic population coding, burst spike, synchronous firing, neural model

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Abstract

Sensory systems utilize dynamical properties of neurons to extract features of spatiotemporally varying stimuli. We propose a dynamic population coding of sensory stimuli in which the stimulus features are encoded into a spatiotemporal firing pattern of neuron population. Using electrolocation of weakly electric fish as a model system, we study how the spatiotemporal features of electric field modulated depending on the distance and size of an object are encoded into the spatial distribution of and time interval between burst spikes of neuron population. We showed that the information about distance and size of object are represented as a function of the spatial area of and time interval between of the synchronously firing of neuron population in a higher nucleus.

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 to 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 represented on any map. The features are encoded into spatiotemporal firing patterns of relevant neuron population. The features of the patterns are not classified by the position of maximum firing neuron but by the dynamical properties of response activity of neuron population such as spatial area of synchronized firing zone and interval between successive synchronized firings. We refer to this type of population coding as "dynamic population coding". However, it is not yet clear how the neuron population represents the stimulus features based on the dynamic population coding. To study the neural mechanism generating dynamic population coding, we adopted electrosensory system of a weakly electric fish. The electrosensory system gives us an ideal system to address this issue, because the electrosensory system has a relatively simple structure and the role of its circuitry in processing behavioral signals across multiple parallel sensory pathways has been well studied [7].

Electrosensory system allows fish to locate and identify an object in the absence of visual cue 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 alternating voltage are modulated by an object, and they are measured by electroreceptors distributed over the fish body surface. An object, whose impedance is different from that of surrounding water, will alter the spatiotemporal pattern of transepidermal voltage, and its alternation is encoded into neuronal impulse trains by the electroreceptors. The information about the modulations of amplitude and phase encoded by the electroreceptors is conveyed to electrosensory lateral-line lobe (ELL) and then transmitted to torus semicircularis(TS) as shown in Fig.1.

When an object moves nearby fish body, the receptors receive the electric 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 represents 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 is no neuron tuned to each 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 using the ratio of maximum slope to maximum amplitude of the distribution of current across the skin over the body surface, suggesting that the information of object distance is encoded into the spatial firing pattern of receptor population. Experimental results [6,11] have also 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 spatiotemporal burst patterns of ELL neuron population. We propose that the information is encoded into spatiotemporal firing patterns of receptor population and ELL network. However, it is not yet clear by what kinds of dynamical properties of the neuronal populations 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 spatiotemporal variation of electric field around the fish body. We made also a model of electroreceptor distributed on the fish body surface and neural network models of ELL and TS to investigate by what kind of neural mechanism the features of EOD signals modulated by an object are represented in these networks. The models may reproduce qualitatively the experimental results [10]. We showed that the spatiotemporal features of electric field around the fish body are represented by the spatiotemporal patterns of burst firing of ELL neuron population. In TS network, the information about the distance and size of an object can be represented as a function of the spatial area of synchronous firing of neuron population and the interval between the successive synchronous firings.

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 eminentia granularis posterior (EGP) as shown schematically in Fig.1. In the present study, we consider only the detection of a resistive object, which has been well studied experimentally. The resistive object causes modulation of EOD amplitude, but not of EOD phase. Thus, our model includes only P-receptors and P-afferents which can respond to the amplitude modulation of EOD.

The information of EOD distortion induced by a resistive object is processed along the feedforward pathway from P-receptors → P-afferents → ELL → TS. The efferent signals from EGP are sent 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 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 14×41 receptor neurons distributing regularly on the side of body surface in which the object is. Each receptor neuron receives EOD stimulus whose amplitude is modulated by the object, where the magnitude of modulation is changed depending on the distance between the object and the receptor neuron. The P-receptor encodes EOD amplitude modulation (EOD AM) in a spike train of P-afferent. The network model of ELL consists of 10×35 basilar pyramidal (bp) neurons in a regular 2D-array. The model of single bp neuron consists of two compartments, soma and dendrite. The bp neuron encodes the increase of EOD AM in the timing of burst spike. The bp neurons send their signal to two higher centers, TS and EGP. The network model of TS consists of 10×35 neurons in 2D-array. The model of EGP consists of two types of neurons, EGP1 and EGP2. EGP neurons send back their signals to the ELL. Although the efferent pathway to ELL includes NP (nucleus praeeminentialis) besides EGP[2], we consider here only a direct effect of EGP, in order to regulate the range of dynamic response of ELL neurons.

The connections between the networks are as follows. (1) Receptors - ELL: Single bp neuron has a receptive field made by ON center-OFF surround connection with receptors. The bp neuron at (i, j) site of ELL network receives excitatory signal from P-afferent of a receptor at the relevant site of receptor network and inhibitory signals from P-afferents of the nearest neighboring receptors via granule cells. There is no direct connection between bp neurons. (2) ELL - TS: TS neuron at (i, j) site of TS network receives excitatory signals from bp neuron at (i, j) site and its nearest neighboring neurons in ELL network. (3) ELL-EGP: Each bp neuron connects reciprocally with EGP1 neuron, and makes only efferent connection with EGP2 neuron, as shown in Fig 1. EGP1 neuron receives all the outputs of bp neurons, and globally sends its output signal to all the dendrites of bp neurons through excitatory synapse. EGP2 receives the output of EGP1, and sends its output signal to all the dendrites of bp neurons through inhibitory synapse.

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

We made a 3-dimensional(3D) model of fish body extending 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

The responses of receptors and P-afferents to EOD AM signals 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-afferents 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 the two-point MacGregor model [12]. Although the multicompartment model of bp neuron and its simplified model have been proposed [3,4], these models have complicated dynamic processes to generate a burst spike. We used the two-point MacGregor model to reproduce easily the burst dynamics of bp neuron. The observed essential property of burst spike of bp neuron can be well described by adjusting the parameter values in the two-point MacGregor model.

2.5. Neural network model of TS

The TS neuron 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 neurons in the TS network are mutually connected through excitatory and inhibitory synapses made on the basis of ON center-OFF surround 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 the leaky-integrator neuron model. The EGP neurons regulate the range of dynamic response of bp neurons so as to become silent under application of the fish's own (unmodulated) EOD signals and as a result to sensitively respond to the modulated part of EOD signals induced by an object. The strengths of synaptic connections between EGP neurons and apical dendrite of bp neurons are adjusted based on Hebbian learning rule so as to generate the response property 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 networks to EOD AM signals induced by a moving object

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

Figure 2b shows the raster plot of burst spikes of 35 bp neurons located on the longitudinal center line of ELL network, corresponding to the center line of receptor network. The upstroke of temporal variation of EOD AM received by the receptor located on the position x is encoded in the burst spike patterns. It is seen in Fig.2b that the burst firing pattern of bp neurons shifts smoothly to the right on ELL network as the object passes from the head to the tail. Although the receptors on the fish body surface receive a spatiotemporally continuous stimulation of EOD AM signal, ELL network encodes the spatiotemporal correlation between receptor response activities in the spread and timing of burst spikes of bp neurons, that is, as a digital representation.

TS neurons generate a single spike under application of the burst outputs of bp neurons. The raster plot of spike timing of TS neurons, which are located on the longitudinal center line of TS network, is shown in Fig.2c. The firing TS neurons are localized on a finite region in TS network, and the spike timings of TS neurons in the region are synchronized, and the synchronized firing region in the network moves discontinuously, that is, hops along the longitudinal line in the network every time interval. Then, the area of firing region keeps constant and the time interval is also constant.

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

The distance and size of an object can be represented by the area of synchronized firing region and the time interval of the hopping of synchronized region, in TS network. Figures 2d and 2e illustrate the dependence of the area (S) and the hopping time interval T_{hp} on the distance and size of an object. It is seen in Fig. 2d that the area S and hopping time interval T_{hp} of synchronized firing region increases significantly with increasing the lateral distance (d) of object. As seen in Fig.2e, the hopping time interval T_{hp} changes significantly with changing the object size a, but the area S shows only a weak dependence on a, where a is the length of the side of cubic object.

The dependence of T_{hp} and S on d and a come from the dependence of two features of EOD AM, the maximum amplitude of EOD AM and the half maximum width of normalized EOD AM, on d and a. Our calculation of EOD AM shows that the maximum amplitude of EOD AM is increased with decreasing d and increasing a, while the width of normalized EOD AM increases with d but shows only a weak dependence on a. The magnitude of T_{hp} is mainly determined by magnitude of time interval between burst firing patterns in ELL network which is determined by the maximum amplitude of EOD AM. Thus, T_{hp} decreases with decreasing d and increasing a, because the increase of a cause the increase in maximum amplitude of EOD AM, and thereby result in the decrease of time interval between burst firing patterns in ELL network. The area S is mainly determined by magnitude of the spatial spread of burst firing pattern in ELL network which changes depending on the width of normalized EOD AM. Therefore, the dependence of S on d and a shown in Figs. 2d and 2e are straightforwardly explained based on the calculated dependence of the half maximum width of normalized EOD AM on d and a, respectively.

The result suggests that the size of an object is mainly represented by the time interval T_{hp} and the object distance is represented by a function of two characteristic dynamical properties of the synchronously firing TS neuron population, S and T_{hp}.

4. Concluding Remarks

We have shown the following result using our neural model of electrosensory system. The ability to generate the dynamic representations of distance and size of an object comes from the dynamic response properties of ELL and TS neurons. In ELL, the area of bp neuron population making burst firing within a finite time window is sensitively changed depending on the width of normalized EOD AM, which is changed depending on an object distance. The interburst interval is sensitive to the changes of object size and distance. The synchronization of firing of TS neurons may be generated by combining effectively the spatiotemporal features of ELL dynamical response with the network dynamics of TS, thereby making a stable, synchronously firing neuronal population into which distance and size of an object are encoded.

The present model have many parameters used for describing bp neurons, 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. However, the present model is insensitive to slight changes in parameter values, that is, the changes within the relevant reasonable ranges do not make any essential change in the results presented here.

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

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Figure Legends

Fig. 1. Our model of electrosensory system including the afferent signals from receptors and the efferent signals from the higher nucleus, EGP. The afferent signals are propagated along the solid lines, and the efferent signals are done along the dotted lines. ELL(electrosensory lateral-line lobe), TS(torus semicircularis), and EGP(eminentia granularis posterior).

Fig. 2. (a) Temporal variations of EOD amplitude modulation(EOD AM) induced by a cubic object moving from H to T. (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 relevant network corresponding to the longitudinal axis of fish (x-axis). The plots mean the timing of burst spikes of 35 different neurons on the center line of ELL and TS networks. (d)(e) Dependences of the area (S) and hopping time interval (T_{hp}) of synchronously firing regions of TS network, respectively, on the distance(d) and size(a) of a cubic object whose side length is a. The area S is represented by the number of neurons included in the synchronously firing region. The curves of S and T_{hp} are represented by the solid and dashed lines, respectively.

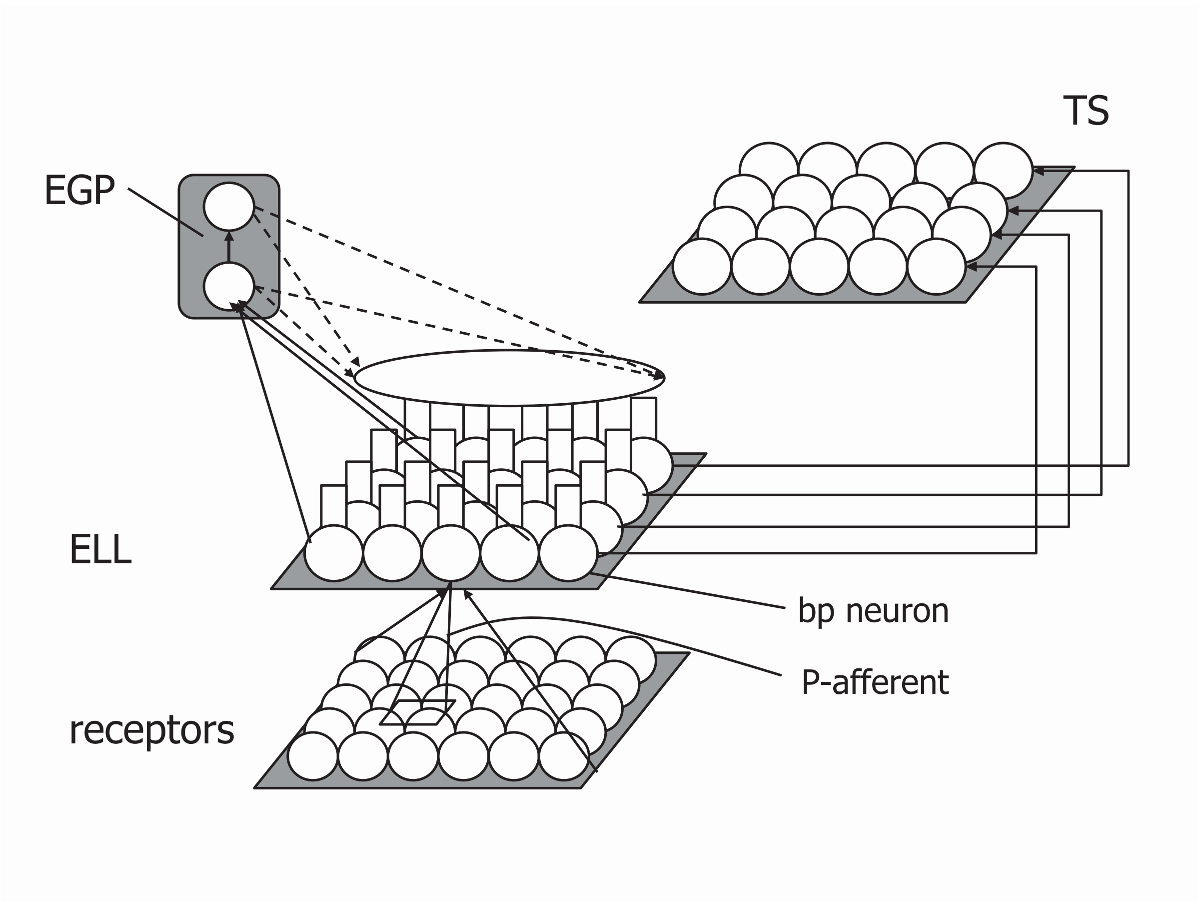

Figure 1. K. Fujita et al.

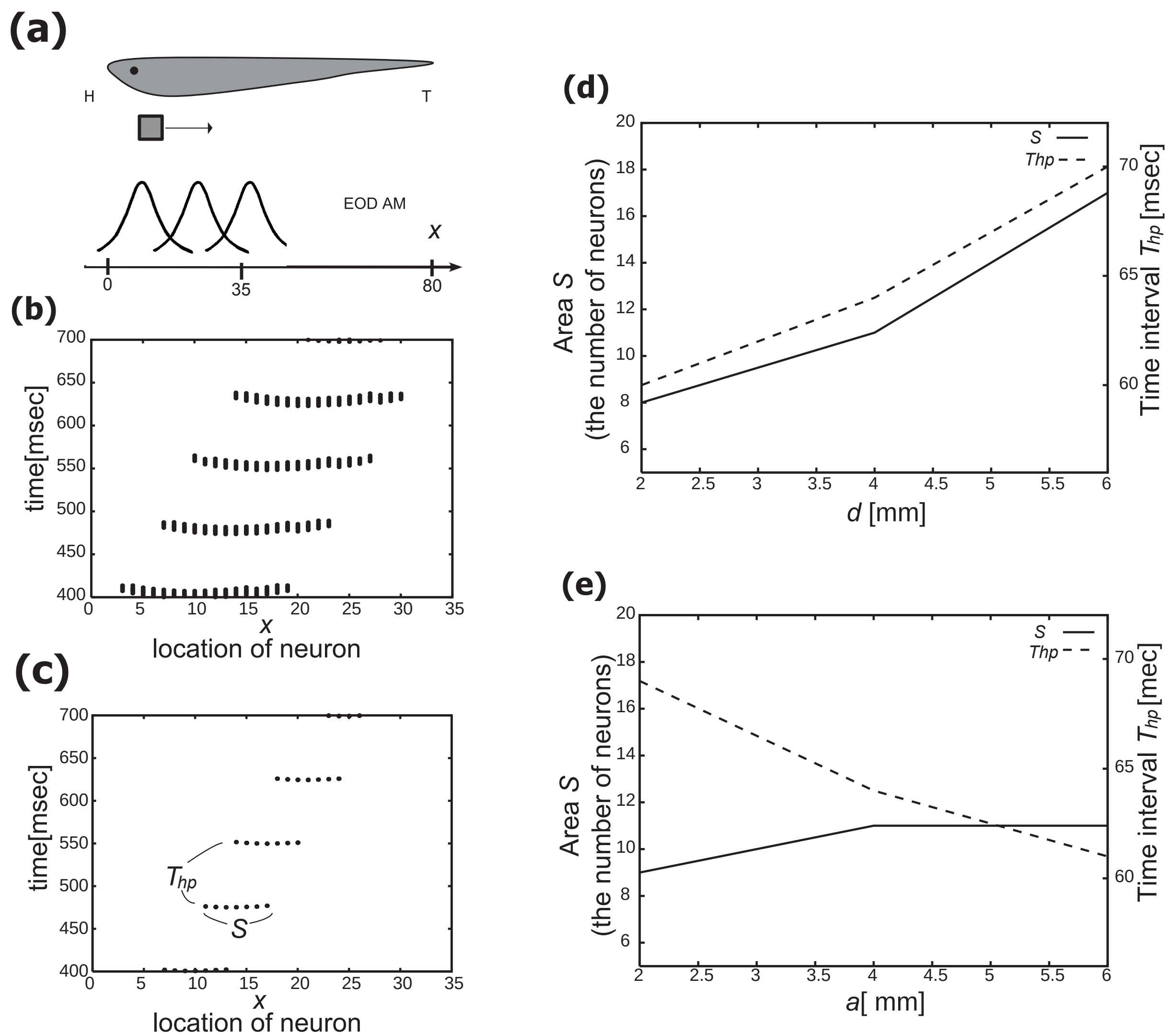

Figure 2. K. Fujita et al.

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 mechanisms of electrolocation, sound localization, and echolocation and visual recognition mechanism using the in silico method.

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