Neural mechanism of detecting interaural intensity differences in the owl's auditory brainstem for sound location

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Abstract In order to clarify the neural mechanism of detection of the interaural intensity difference(IID), we presented a neural model of a pair of VLVp units (the first site of binaural convergence of intensity information). We proposed that each value of IID is represented as a neuronal position of a firing zone gap which is generated in ICc shell by combining output of right VLVp with that of left VLVp. Based on this gap coding scheme, we clarified the functional role of the mutual inhibitory connections between R- and L- VLVp and of bilateral inhibitory projection from VLVp pair to ICc shell.

1. Introduction

Barn owls perform sound location based on analyses of interaural differences in arrival time and intensity of sound. Two kinds of neural signals representing the interaural time difference(ITD) and the interaural intensity difference(IID) are processed in anatomically separate pathways that start from the cochlea nuclei to the higher sensory brain modalities. ITD is used for detecting the horizonal direction of sound source and IID for the vertical direction. The neural map for detecting the spatial direction of sound source is formed in the brain of barn owls, based on the interaural arrival time and intensity information[1]. The neural pathway for the sound location with respect to horizontal direction has been actively studied experimentally[1-3] and theoretically[4,5]. The neural mechanism of detecting ITD with a remarkable high accuracy has been clarified based on the reasonable models of the neural pathway[4,5].

The neural pathway for the sound location with respect to vertical direction has also actively investigated anatomically and physiologically[6-9]. The neural information processing for detection of IID is made on neural pathway in parallel with the pathway of ITD detection before both the signals arrive at the lateral shell of central nucleus of the interior colliculus (ICc shell). The pathway for the IID detection is the angular nucleus in the cochlear nucleus (the first site of extraction only of amplitude information from sound signals) → the nucleus ventralis lemnisci lateralis pars posterior (VLVp, the first site of binaural convergence of intensity information) → ICc shell (the first site of convergence of ITD and IID information) → the external nucleus of inferior colliculus (ICx, where the brain map for sound location is generated)[1,7]. The IID sensitive neurons both in VLVp and ICc shell are turned in to a single frequency. The intensities of sound components with single frequencies are processed separately and simultaneously. Outputs of frequency-tuned IID sensitive neurons in ICc shell are integrated over all frequencies in ICx.

In order to clarify the neural mechanism of detection of IID, we present here a neural model of a pair of right and left VLVp units in which the signals of sound intensities coming from both the ears are combined to compare with each other. VLVp units are excited by sound received at the contralateral ear and are inhibited by sound at the ipsilateral ear[6-9]. inhibitory signals at each VLVp unit come from the contralateral VLVp unit. The right and left VLVp units are couple through bilateral mutual inhibitory connections[8,9].

The purpose of our study is to solve the two problems :

1. What functional role the bilateral mutual inhibition between right and left VLVp units plays in detecting IID,
2. How the outputs of both VLVp units are combined in the projection to ICc shell (the

input stage to the map of auditory space in ICx).

We propose in the present paper that each value of IID is represented as a neuronal position of a firing zone gap which is generated in ICc shell by combining a stepladder type of firing pattern of linear arrays of IID sensitive neurons in right VLVp unit with a reversed stepladder type of firing pattern in left VLVp. Investigating the response properties of a pair of VLVp units under stimulation of sounds with various intensities, we show how the bilateral mutual inhibition works effectively to keep the firing zone gap from broadening but from becoming too narrow, that is, disappearing. Thus, the combined projection of output signals of right and left VLVp units represents IID information definitely in the neural network of ICc shell independently of the absolute sound intensity.

2. The neural model of a pair of VLVp units

The pathway of intensity signals from the nucleus angularis(NA) to VLVp is schematically shown in Fig.1. Each VLVp unit includes multiple linear arrays (chains) of IID sensitive neurons. The neurons in each chain are arranged randomly. Each neuron receives excitatory inputs directly from the contralateral NA and inhibitory inputs indirectly from ipsilateral NA by way of the VLVp unit at the opposite side. The strength of inhibitory synaptic connection between both VLVp units declines systematically along the chains from dorsal to ventral side as shown in Fig.1 [6]. The system shown in Fig.1 works only under stimulation of sound component whose frequency is common. There exits an equivalent system for each frequency component of sound.

The membrane potential of each neuron is determined by the equation,

$$\frac{dV_X(k,i;t)}{dt} = \frac{1}{\tau_m}(-(V_X(k,i;t) - V_{rest}) + E_X(k,i;t) - I_X(k,i;t)), \tag{1}$$

where $V_X(k,i;t)$ is the membrane potential of i th neuron in k th chain tuned in to a common frequency ω within X-VLVp unit (X = R for right unit and L for left unit). V_{rest} is the membrane potential in the resting state, and $E_X(k,i;t)$ and $I_X(k,i;t)$ are the excitatory and inhibitory inputs, respectively.

The excitatory input current $E_X(k,i;t)$ commons to every neuron in k th chain and is given by

$$E_X(k,i;t) = W_E P_Y(\omega) S_{train}(t - t_{Y,k}), \tag{2}$$

where W_E is the strength of excitatory synaptic connection and $S_{train}(t)$ is a single sound train represented approximately by a gaussian function of t, and $t_{Y,k}$ means the time required for the sound signal propagation from Y ear to k th chain in X-VLVp unit. The propagation time $t_{Y,k}$ is changed randomly depending on k as

$$t_{Y,k} = t_{Y,0} + t_{Y,w}(rand(1) - 0.5), \tag{3}$$

where $t_{Y,0}$ is the average value and $t_{Y,w}$ is a width of random variation. $P_Y(\omega)$ is proportional to the power spectrum of frequency ω of the sound received at the Y ear. Here after, the pair of X and Y means X = R and Y = L or X = L and Y = R. When the interaural intensity difference takes a value IID dB, we have the relation $P_L(\omega) = P_R(\omega)10^{IID/20}$. The inhibitory input current $I(k, i; t)$ is given by the contralateral VLVp unit as shown in Fig.1 and represented as

$$I_X(k,i;t) = W_I(X,k,i) \sum_{l=1}^{N_{chain}} \sum_{j=1}^{N_{neuron}} U_Y(l,j;t-t_{RL})$$
$$\times H(|r_{max} - r(X,k,i) - r(Y,l,j)| - l_{dend}/2), \tag{4}$$

where $W_I(X,k,i)$ and $r(X,k,i)$ are the strength of inhibitory synaptic connection at and the distance from the dorsal edge to, respectively, i th neuron in k th chain within X-VLVp unit, $U_Y(l,j;t)$ and $r(Y,l,j)$ are the output and the distance, respectively, of j th neuron in l th chain in Y-VLVp unit, and t_{RL} is the time required for the signal propagation between R- and L-VLVp units. Here, H(x) is the ladder function, r_{max} is the length of a neuron chain, and l_{dend} is the length of dendrite of each neuron receiving outputs as shown in Fig.1. The output $U_Y(l,j,t)$ is given by

$$U_Y(l,j;t) = \frac{1}{1 + \exp[-(V_Y(l,j;k) - V_{th})/h_{vr}]}. \tag{5}$$

The synaptic strength $W_I(X,k,i)$ depends on the distance [6] as

$$W_I(X,k,i) = \frac{W_{I,max}}{1 + \exp[(r(X,k,i) - r_{max}/2)/d_{int}]}, \tag{6}$$

where $W_{I,max}$ and d_{int} are the maximum synaptic strength and the rate constant, respectively.

3. Response properties of the VLVp model

3.1. Firing patterns of each neuron chain

Manley et al.[6] have found that arrays of IID sensitive neurones in VLVp units show a stepladder type of firing pattern under application of sound stimulation, that is, neurons at the dorsal side are silent and neurons at the ventral side fire actively. They have shown also that the position of the neuron with half-maximum firing rate shifts monotonically with the value of IID, that is, the value of IID is coded in to the neuronal position of firing zone edge in each neuron chain.

We calculated the output $U_X(k,i;t)$ of every neuron (X,k,i) under application of sound with various values of IID, and obtained the total output $U_X(x_i;t)$ of X-VLVp at the position x_i along the chains, which is given by

$$U_X(x_i;t) = \sum_{k=1}^{N_{chain}} \sum_{j=1}^{N_{neuron}} U_X(k,j;t) \times H(|r(X,k,j) - x_i| - l_{dend}/2). \tag{7}$$

We show the values of $U_X(x_i, t_7)$ for X = R and L as a function of x_i for various IID in Fig.2A. The position x_{hmax} corresponding to the half-maximum output strength shifts in proportional to the magnitude of IID in both R- and L-VLVp units as it should do.

3.2. Functional role of the bilateral mutual inhibition between R- and L- VLVp unit

In order to investigate what functional role the mutual inhibitory connection between R- and L- VLVp units plays in detecting values of IID, we examined the temporal variations of the outputs of R- and L- VLVp units. The calculated results are shown in Fig.2B. At first (to), both VLVp units receive only excitatory input, because any neuron in both VLVp units is in the resting state. Then, every neuron fires. After the whole firing (t_1), very strong inhibitory inputs reach to contralateral VLVp units. Then most neurons become silent, although the excitatory input is stationarily given. After t_2, the firing zones of both VLVp units increase gradually as time passes from t_3 to t_4. The firing zones decrease again gradually during the period from t_5 to t_6. Finally the firing patterns of both VLVp units are stabilized as seen in Fig.2B.

The mutual inhibition can work effectively not only for stabilizing the firing patterns of both VLVp units but also for determining definitely the positions of firing zone edges in both the units.

Especially, a suitable strength of mutual inhibition can keep the firing zone gap between both VLVp units from broadening but from disappearing, that is, the two firing zones from overlapping. Thus, the position of bottom of the firing zone gap created by the combined projection of the output signals of R- and L- VLVp units represents IID information quite stably and definitely. The firing patterns shown in Fig.2B shows clearly this functional role of the mutual inhibition.

4. Model of signal projection from a pair of VLVp units to a ICc shell unit

The two kinds of neural signals representing the interaural time difference (ITD) and the interaural intensity difference (IID) are converged firstly in the lateral shell of the central nucleus of the inferior colliculus (ICc shell). The maps representing ITD and IID, which are tuned in to single sound frequencies, are formed in ICc shell.

The value of ITD is represented by the position of firing neuron in the linear array of ITD sensitive neurons within ICc core[1,5]. The axones of ITD sensitive neurons in ICc core make excitatory synaptic connections with the neurons in ICc shell, whereas the axons of main neurons in R- and L- VLVp units make inhibitory synaptic connections with the main neurons in ICc shell[8,9].

We proposed in the present paper the model showing how the map can be generated in ICc shell by the excitatory inputs from ICc core and the inhibitory inputs from R- and L- VLVp units. Then, ITD and IID are represented along the axes perpendicular mutually

as shown in Fig.3. The main neurons in ICc shell are arranged in the form of a lattice. The neuron in ICc core, which is tuned in to a single value of ITD, as shown in Fig.3. The neurons in each column are received bilaterally the outputs of R- and L- VLVp units at the relevant position through inhibitory synapses as shown in Fig.3.

Thus, the lattice array of main neurons in ICc shell functions as the map in which the value of ITD is represented along the column direction and the value of IID is represented along the row direction as shown in Fig.3. Under application of binaural sound stimulus, only one neuron group in the arrays within ICc core fire, where the ITD selectivity of the neuron group corresponds to the value of ITD of the stimulus. Therefore, the neurons in only the row of the lattice corresponding to the ITD value receive the excitatory inputs. On the other hand, each neuron in the row receives inhibitory inputs from R- and L- VLVp units. The neurons in the narrow gap, whose position corresponds to the value of IID of the stimulus, do not firing as shown in Fig.3. Therefore, the neuron in the lattice corresponding to the value of IID is not inhibited by the outputs of R- and L- VLVp units. Thus, the neuron in the lattice, which is firing under application of the sound with a pair of definite values of ITD and IID, can represent the value of ITD by its position along the column direction and the value of IID by its position along the row direction.

This functional model is consistent with the observed result [8] that the outputs of a pair of VLVp units are projected to ICc shell with bilateral inhibitory connections. The coding scheme based on the firing zone gap , in which values of IID are represented by neuronal positions of the bottom of the gap, is quite reasonable, because this scheme is the simplest solution to stable and accurate coding of IID as long as the IID information is propagated to ICc shell through the bilateral inhibitory connection.

5. Functional merits of the coding scheme based on the firing zone gap

In order to investigate the functional merits of the gap coding scheme in which values of IID are represented by the neuronal positions of the bottom of the firing zone gap, we considered another possible coding scheme, the overlap coding scheme in which values of IID are represented by the neuronal positions corresponding to the overlap between both the firing zones. In order to examine which coding scheme generates better representation of IID, we calculated the response firing patterns of a pair of VLVp units in both the coding schemes induced by sounds with various intensities. The results are shown in Fig.4. In the calculation, we adjusted the strength of mutual inhibitory coupling so that the response becomes ideal for each coding scheme under application of a sound with a standard intensity in the case of IID = 0. In the gap coding scheme, the firing patterns with a narrow sharp gap are obtained over the wide range of sound intensities as shown in Fig.4A. In the overlap cording scheme, the width of overlap region is changed quite sensitively depending on the sound intensity as shown in Fig.4B. As the intensity

is strengthened, the overlap region disappears. As the intensity is weakened, the region becomes wider. This means that IID of strong sound can not be detected and IID of weak sound is detected only with a low accuracy. On the other hand, the gap coding scheme can make IID detection stable and accurate independently of sound intensity over a wide range of the intensity.

The bilateral mutual inhibitory connection plays an essential role in producing the difference in accuracy of IID detection between the gap and overlap codings. The firing patterns of both VLVp units becomes a stepladder type, because the strength of inhibitory synaptic connection changes with neuron position as shown in Fig.1. The neurons in the region of X-VLVp unit receiving signals from the silent region of Y-VLVp unit can fire because of no inhibitory input. Furthermore, the neurons in the silent region of Y-VLVp unit are kept from firing by the inhibitory input from the firing region of X-VLVp unit. Therefore, the firing patterns of both VLVp units stabilize each other through the mutual inhibition as shown in Fig.2B. The firing zone gap becomes quite stable. On the other hand, in the overlap coding scheme we can make an ideal overlap zone adjusting the inhibition strength for a single strength of sound so that the excitatory inputs are balanced with the inhibitory inputs in the overlap region. However, even if we succeed in balancing both the inputs for a sound intensity, the balance is easily broken by changing the sound intensity as shown in Fig.4B.

Furthermore, if IID is represented in the overlap coding scheme, the signal projection from a pair of VLVp units to ICc shell must be made through excitatory synaptic connections. This is not the case.

6. Conclusion

The sound location of owl respect to vertical direction is made based on analysis of the interaural intensity differences(IID). In order to clarify the neural mechanism of detection of IID, we presented a neural model of a pair of VLVp units in which the signals of sound intensities coming from both ears are combined to compare with each other. In the present model, the information of IID is represented by position of the firing zone edge in the chains of IID sensitive neurons in both R- and L- VLVp units. The mutual inhibitory coupling can induce the cooperative formation of clear firing zone edge in both R- and L-VLVp units so that the firing zones in both units do not overlap with each other but the firing zone gap becomes as narrow as passible.

In order to clarify the neural mechanism by which IID information is bound with ITD information so that the neural map for sound location is generated in ICc shell, we presented a neural model of ICc shell network. The ICc shell neuron sensitive specifically to a pair of specific values of ITD and IID is made by the excitatory inputs from ICc core encoding ITD and the inhibitory inputs from bilateral VLVp units encoding IID. We

showed how effectively the firing zone gap made in bilateral VLVp units transmits IID information to ICc shell by the inhibitory signals.

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Figure Captions

Fig.1. Schematic diagram of pathway of intensity signals. Each VLVp unit receives an excitatory input from the contralateral nucleus angularis(NA) and an inhibitory input from the contralateral VLVp unit. Linear arrays of main neurons in VLVp units function as IID detection units. Each neuron gathers outputs of neurons at the opposite side with its dendrite. The inhibitory synaptic strength decreases systematically from dorsal to ventral. The triangle shows the variation for the connection from right to left VLVp units

Fig.2.(A) Firing patterns $U_X(x_i, t_7)$ of right VLVp (broken line) and left VLVp (solid line) induced by sounds whose IID is 4, 8, 12, and 16 dB at t_7 (see (B)). (B) temporal variation of firing patterns $U_X(x_i, t)$ of R-VLVp (broken line) and L-VLVp (solid line) during the period from t_0 to t_7. The patterns become stable after t_6.

Fig.3. Schematic description of functional connections of the lattice of main neurons in ICc shell with the array of ITD sensitive neurons within ICc core and with the arrays of IID sensitive neurons within R- and L- VLVp units. Arrows in the ICc shell network denote the excitatory synapses and short bars denote the inhibitory synapses.

Fig.4. Neural representations of IID based on (A) the gap coding scheme and (B) the overlap coding scheme in the three cases where the sound intensity is strong (top figure), standard (center), and weak (bottom). The broken and solid lines denote $U_X(x_i, t_7)$ for X = R and L, respectively. The dotted line shows $U_R(x_i, t_7) + U_L(x_i, t_7)$.
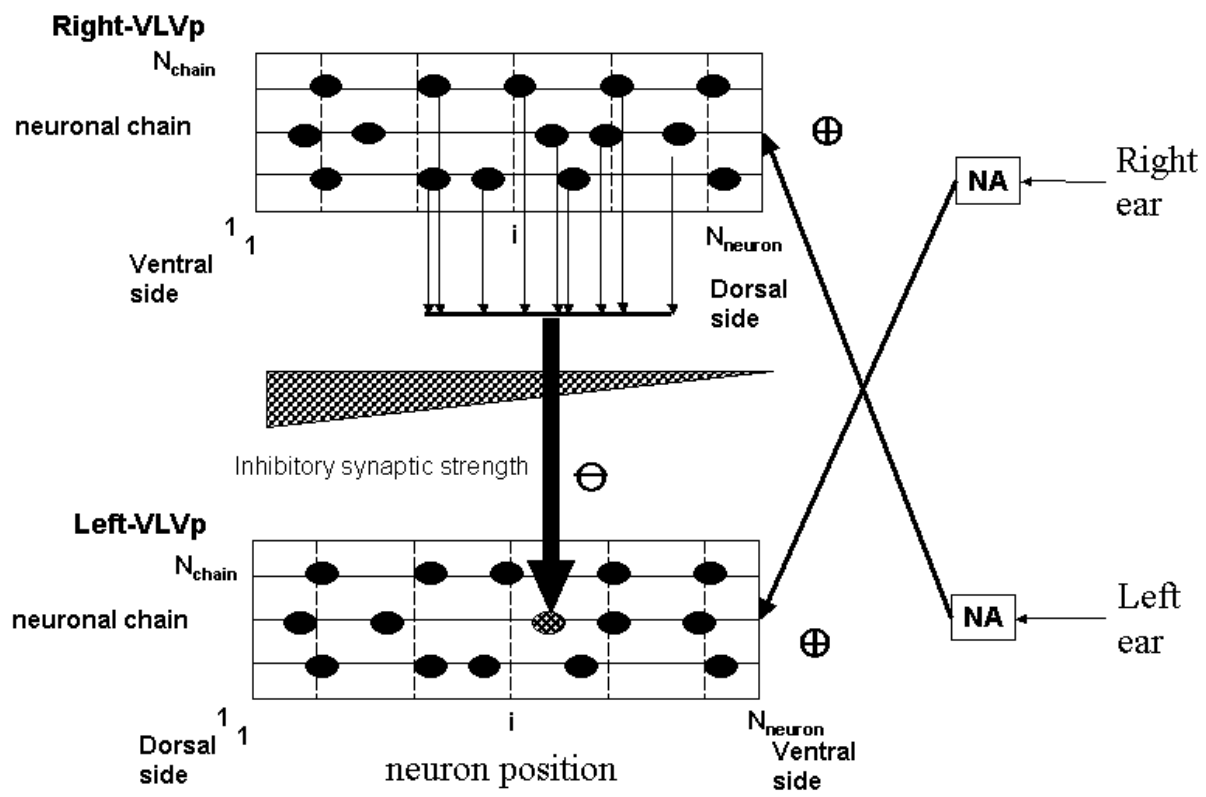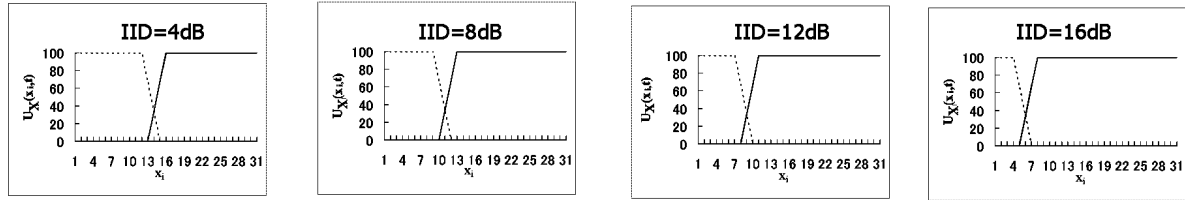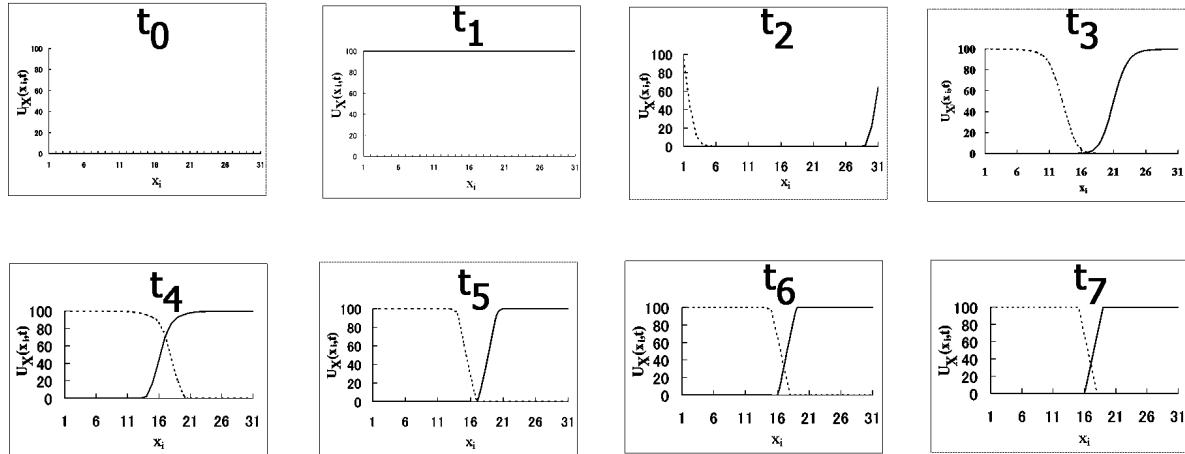
Figure 1. K. Fujita et al.

A gap coding of IID

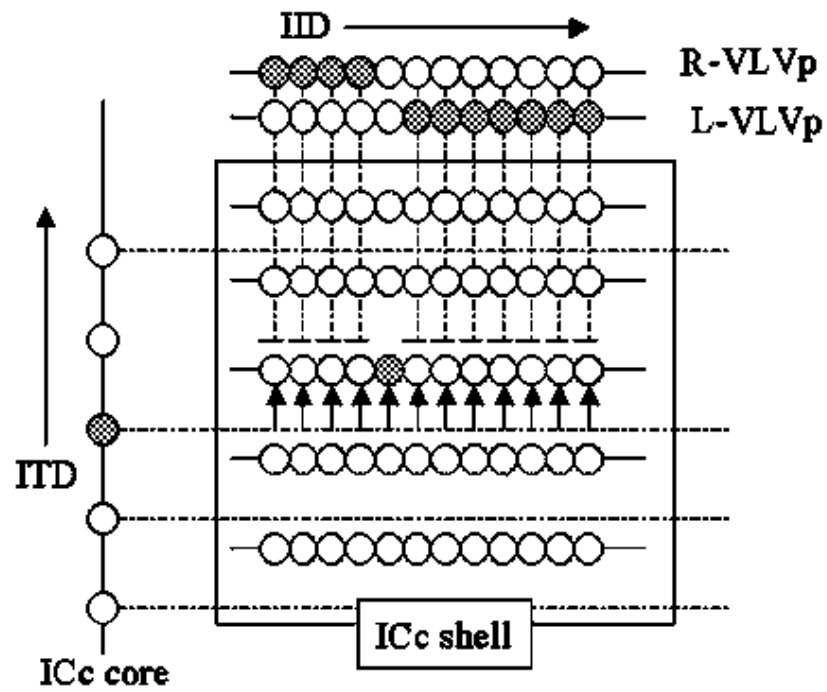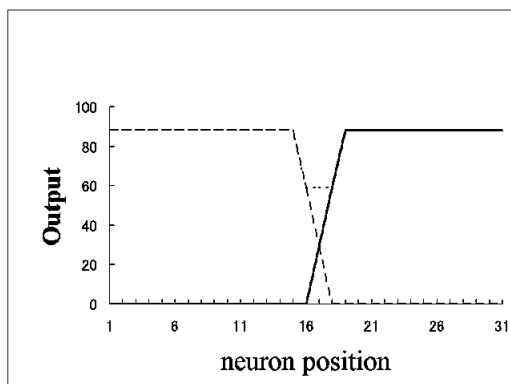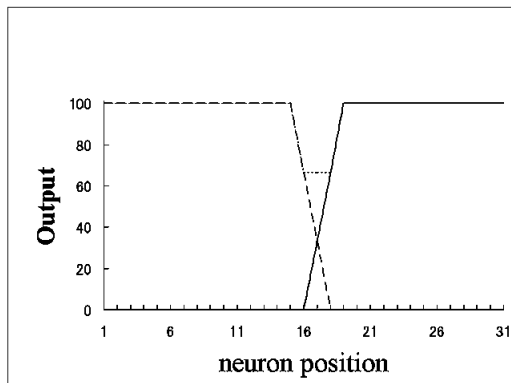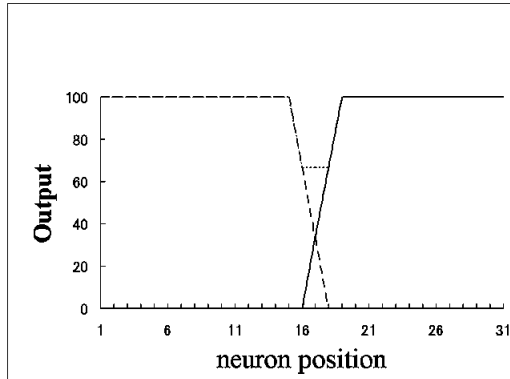# B Temporal variation of firing pattern for IID=0

Figure 2. K. Fujita et al.
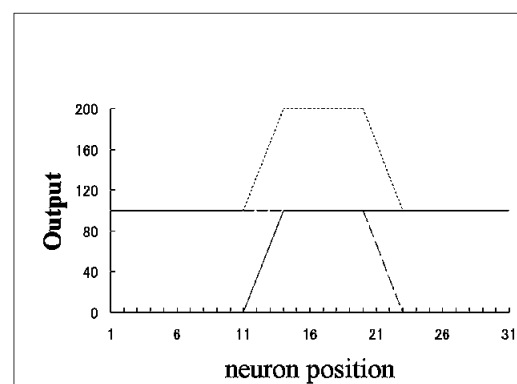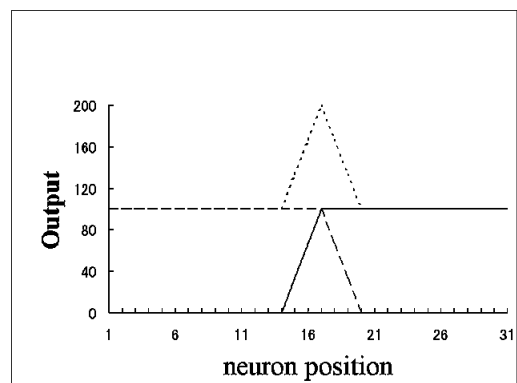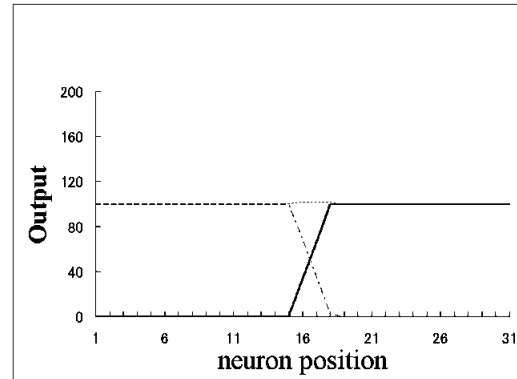
Figure 3. K. Fujita et al.

A gap coding

B overlap coding

Figure 4. K. Fujita et al.