

A neural circuit model of emotional learning using two pathways with different granularity and speed of information processing

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Abstract

We propose a neural circuit model of emotional learning using two pathways with different granularity and speed of information processing. In order to derive a precise time process, we utilized a spiking model neuron proposed by Izhikevich and spike-timing-dependent synaptic plasticity (STDP) of both excitatory and inhibitory synapses. We conducted computer simulations to evaluate the proposed model. We demonstrate some aspects of emotional learning from the perspective of the time process. The agreement of the results with the previous behavioral experiments suggests that the structure and learning process of the proposed model are appropriate.

Key words:

neural circuit model; emotional learning; STDP

1 Introduction

Animals, including humans, learn on the basis of experience and memory, with emotions, and increase their survival probability through reactions involving emotional memory. Such learning is called emotional learning (Uwano and Ono, 1997; LeDoux, 1996). It was clarified that the primary region for emotional learning is the amygdala (LeDoux, 1996). LeDoux (1996) suggested on

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the basis of physiological and anatomic findings that two pathways, thalamo-amygdala (direct) and thalamo-cortico-amygdala (indirect) pathways, play important roles in emotional learning. The direct pathway can process faster than the indirect pathway, although the information is coarser. On the other hand, the indirect pathway processes information in more detail, but more slowly. The direct pathway may be particularly useful in situations requiring a rapid response; it is a rough processing system.

Armony et al. (1997) proposed a neural circuit model of emotional learning using two pathways with different granularity of information processing. However, the model cannot account for the time process of emotional learning because the model does not include a precise time process. Moreover, the model does not clarify the circuit problem whereby neurons in the memory consolidation site for emotion do not directly contact the central nucleus (CE) of the amygdala that provides the principal source of emotional outputs (Paré et al., 2004).

We propose a neural circuit model of emotional learning using two pathways with different granularity and speed of information processing. In order to derive a precise time process, we utilized a spiking model neuron proposed by Izhikevich (2007) and spike-timing-dependent synaptic plasticity (STDP) of both excitatory and inhibitory synapses. We conducted computer simulations to evaluate the proposed model. We demonstrate some aspects of emotional learning from the perspective of a time process.

The remainder of this article is organized as follows. In Section 2, we propose a neural circuit model of emotional learning using two pathways with granularity and different speed of information processing. Section 3 describes the results of a computer simulation to examine the proposed model. Section 4 presents our conclusions.

2 Proposed Model

Our proposed model network is shown in Fig. 1. The proposed model consists of sensory input, thalamus, cortex, and the amygdala. The route of the conditioned stimulus (CS) includes variable connections, whereas the route of the unconditioned stimulus (US) is fixed. In the thalamus, the neuronal groups directly connected to amygdala are partially received from the sensory input whereas the neuronal groups connected to cortex are fully received. This corresponds to a difference in the granularity of information processing. In the cortex, semantic conversion means that the primary features are converted to semantic features in the association cortex area through an excitatory and inhibitory network. The semantic conversion is supposed to be learned in a past.

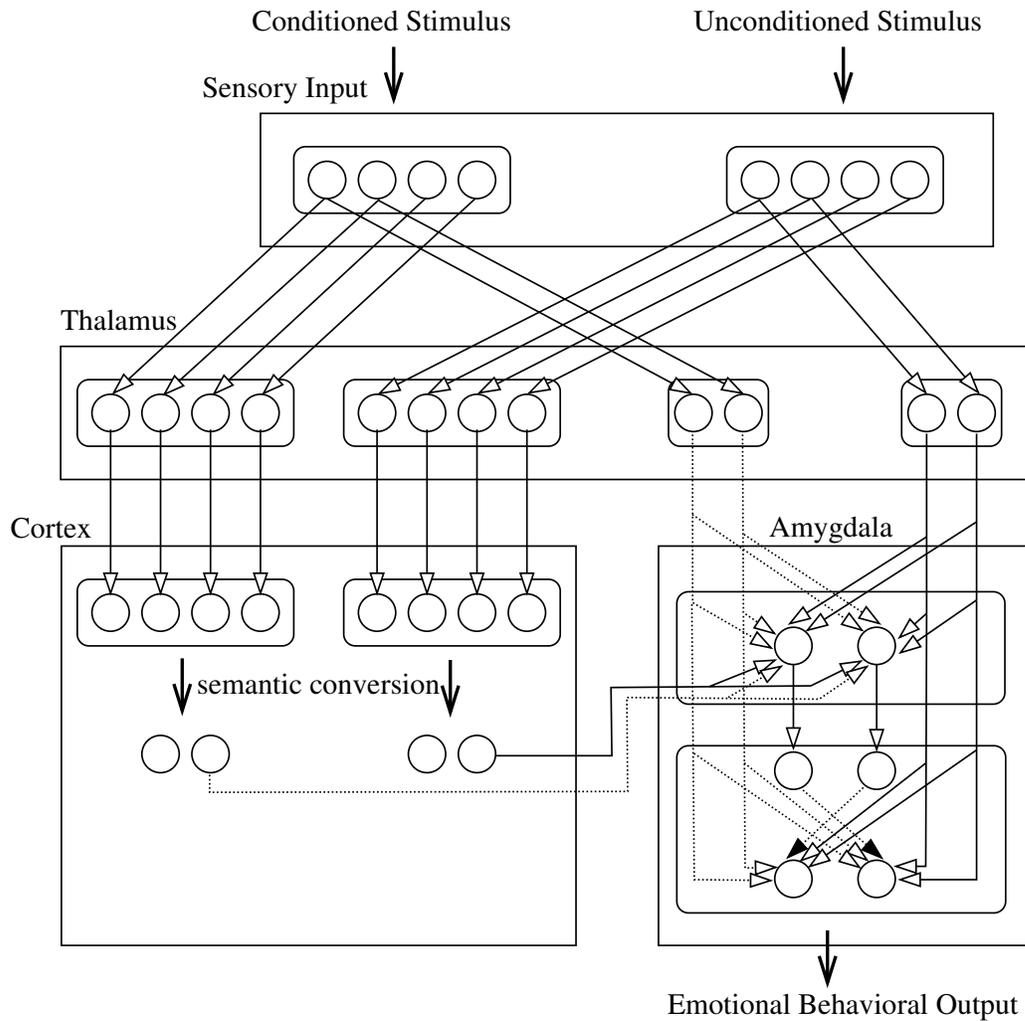


Fig. 1. Proposed model. Solid and dotted connections indicate fixed and variable connections, respectively. Opened and filled arrowheads indicate excitatory and inhibitory connections, respectively.

In the amygdala, the lower side is the medial sector of the central amygdala (CEm) that provides the principal source of emotional outputs (Paré et al., 2004), whereas the upper part is the lateral division of the central nucleus (CEl), including the lateral capsular division (CEc). Wilensky et al. (2006) showed that the central nucleus (CE) is involved not only in the expression but also in the acquisition of emotional learning. The CEl receives input from both the cortex and the thalamus, whereas the CEm receives from only the thalamus. That is, the CEl is a full memory consolidation site whereas the CEm is a partial one. Thus, the inhibitory interneurons between the CEl and CEm are supposed to compensate for the partial memory consolidation of the CEm. Here, the left and right sides of the amygdala are supposed to be opposed to each other, for instance, for fear and calmness.

In order to derive a precise time process, we utilized a spiking model neuron proposed by Izhikevich (2007). The model neuron was reduced from a number of biophysically accurate Hodgkin–Huxley-type neuronal models to a two-dimensional system ordinary differential of the form

$$\dot{v} = 0.04v^2 + 5v + 140 - u + I_{\text{ext}}(t) \quad (1)$$

$$\dot{u} = a(bv - u) \quad (2)$$

with the auxiliary after-spike resting

$$\text{if } v \leq 30 \text{ mV, then } \begin{cases} v \leftarrow c \\ u \leftarrow u + d. \end{cases} \quad (3)$$

The external current $I_{\text{ext}}(t)$ is expressed as

$$I_{\text{ext}}(t) = - \sum_i g_{\text{syn}i}(t)(V - V_{\text{rev}}). \quad (4)$$

$$g_{\text{syn}i}(t) = \begin{cases} w_i A_i \frac{t-t_i^f}{\tau_i^2} \exp\left(-\frac{t-t_i^f}{\tau_i}\right) & \text{if } t \leq t_i^f \\ 0 & \text{if } t > t_i^f \end{cases} \quad (5)$$

Here, v represents the membrane potential of the model neuron, u represents a membrane recovery variable, a , b , c , and d are dimensionless parameters, t is time, $g_{\text{syn}i}(t)$ is the time-varying synaptic conductance for the i -th spike, V_{rest} is the reversal potential, w_i is the weight ratio, A_i is the maximum amplitude, t_i^f is the arrival time, and τ_i is the time constant. The parameter set for regular spiking (RS), $a = 0.02$, $b = 0.2$, $c = -65$, and $d = 8.0$, is used for excitatory neurons, whereas the parameter set for fast spiking (FS), $a = 0.10$, $b = 0.2$, $c = -65$, and $d = 2.0$, is used for inhibitory neurons.

The solid connections shown in Fig. 1 are fixed, whereas the dotted connections are variable, that is, they are learned by STDP, which is a minute time resolution version of the well-known Hebb learning rule. The STDP profile of excitatory synapses has been observed electrophysiologically (Markram et al., 1997; Bi and Poo, 1998; Froemke and Dan, 2002). From the profile, postsynaptic potentials arriving after presynaptic potentials induce long-term potentiation, and postsynaptic potentials arriving before presynaptic potentials induce long-term depression. Froemke and Dan (2002) derived a numerical description of the increase and decrease rates of synaptic plasticity $w(\Delta t)$ from electrophysiological data as follows:

$$\Delta w(\Delta t) = \begin{cases} \frac{1.02}{n} \exp\left(\frac{-|\Delta t|}{15.5}\right) + 1 & \text{if } \Delta t > 0 \\ -\frac{0.52}{n} \exp\left(\frac{-|\Delta t|}{33.2}\right) + 1 & \text{if } \Delta t < 0, \end{cases} \quad (6)$$

where Δt (ms) is the temporal difference from a postsynaptic spike to a presy-

naptic spike and n is the number for which the maximum rate is obtained.

On the other hand, Murakoshi and Suganuma (2007) indicated that the STDP profiles of inhibitory synapses are quite different. They suggested that the asymmetrical timing STDP rule for inhibitory synapses observed by Haas et al. (2006) functions successfully in forming a semantic network with an exception. The results of the preliminary computer experiment showed that the symmetrical timing STDP rule for of inhibitory synapses observed by Woodin et al. (2003) functioned successfully for emotional learning in the amygdala in this study. Murakoshi and Suganuma (2007) formulated the symmetrical STDP rule observed by Woodin et al. (2003) as

$$\Delta w(\Delta t) = \left[1.50 * \exp(-0.004 * (\Delta t^2)) - 0.50 * \exp(-0.0003 * (\Delta t^2)) \right] / n + 1. \quad (7)$$

3 Simulation

We conducted computer simulations to confirm our proposed neural circuit model of emotional learning using two pathways with different granularity and speed of information processing. The membrane potential was calculated by the Euler method with a time step of 0.01 ms. We utilized latest-neighbor interaction (Zhu et al., 2006) as a spike paring rule, in which at any time instant only the latest-neighbor pairs of pre- and postsynaptic spikes contribute to plasticity.

The parameters used in these simulations are shown in Table 1. All parameters are biologically plausible values. The difference in propagation delay between the direct and indirect pathways was 7–73 (ms) by electrophysiological observations (Uwano and Ono, 1997). The simulation results between 27 and 53 (ms) were successful, and we now give the simulation results at 40 (ms). For simplicity, the total number of neurons was 50, that is for the minimum formation. n for excitation and inhibitions were 60 and 150, respectively, which were taken from numbers of spike pairs in electrophysiological experiments (Froemke and Dan, 2002; Woodin et al., 2003). Reversal potential for excitatory synapse was about 0 mV (Goforth et al., 1999), and reversal potential for inhibitory synapse was about -70 mV (Martina et al., 2001). When intensity for sensory input was 6.0, the frequency of neuronal firings was about 13 Hz, which was usually observed as an electroencephalogram frequency of human brain. Time constant for excitatory and inhibitory synapses were 1.0 ms and 8.0 ms, respectively, which were converted to single exponential formulation expressed as Eq. (5) from electrophysiological observations (Zhou and Hablitz, 1998; Meis and Pape, 2001). Since the number of neurons was minimum, an amplitude by single synapse is not significant in itself, that is, the balance

Table 1
List of parameters.

Parameter	Value
Total simulation time (ms)	80,000
Total number of neurons	50
Number for which the maximum rate is obtained for excitation, n	60
Number for which the maximum rate is obtained for inhibition, n	150
Duration of stimulus (ms)	19,000
Interval between stimulus (ms)	1,000
Intensity for sensory input	6.0
Difference of propagation delay between direct and indirect pathways (ms)	40
Propagation delay (except for from thalamus to CEm) (ms)	5.0
Propagation delay from thalamus to CEm (ms)	10.0
Maximum weight ratio	1.0
Initial value of weight ratio	0.2
Time constant for excitatory synapse	1.0
Time constant for inhibitory synapse	8.0
Maximum amplitude of excitatory synapse	1
Maximum amplitude of inhibitory synapse	-115
Reversal potential for excitatory synapse (mV)	0.0
Reversal potential for inhibitory synapse (mV)	-70.0

of the total amount of excitatory and inhibitory input is significant. When maximum amplitude of excitatory synapse was fixed at 1, simulations were succeeded with maximum amplitude of inhibitory synapse between -100 and -128 . We now give the simulation results at -115 . This means that the total amount of inhibitory input is more necessary than that of excitatory input.

We simulated emotional learning of fear and calmness, which are opposed to each other. For fear, snake and painful are CS and US, respectively; for calmness, rope and agreeable are CS and US, respectively. Figures 2 and 3 show simulation results for rope and snake, respectively. The sensory input that corresponded to each period was set at $I_{\text{ext}}(t) = 6.0$. Thus, each corresponding neuron periodically fired during each period. In the first period in both simulations, snake for the CS and painful for the US were associated. In the third period in both simulations, rope for the CS and agreeable for the US were

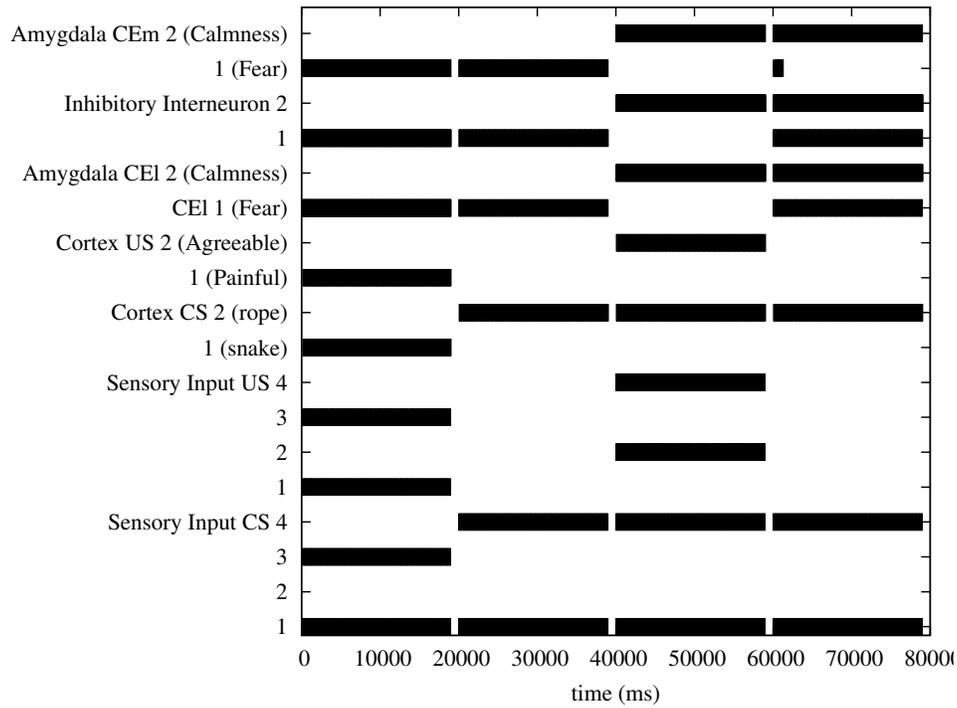


Fig. 2. Simulation result for rope.

associated. The second period was examined only for the only snake–painful association. The fourth period was the final examination for both associations. The second period of Fig. 2 shows that the emotional reaction was fear for the rope input. This is because the association between rope and agreeable had not been learned. The final result, the fourth period, of Fig. 2 shows that emotional reactions for rope input were both fear and calmness at first; however, the fear reaction disappeared after a while. This result is consistent with the time process of the emotional reaction of the human (LeDoux, 1994). The result for snake as shown in Fig. 3 is similar to the result for rope; however, the calmness reaction disappeared after a while.

We also conducted an inactivation simulation of the cortex for the CS. In Fig. 4, the model neurons in the cortex for CS were inactivated during the fourth period. The fear reaction continued to appear despite the rope sensory input. This result is consistent with the results obtained with experimental lesions of the cortex (Teich et al., 1988).

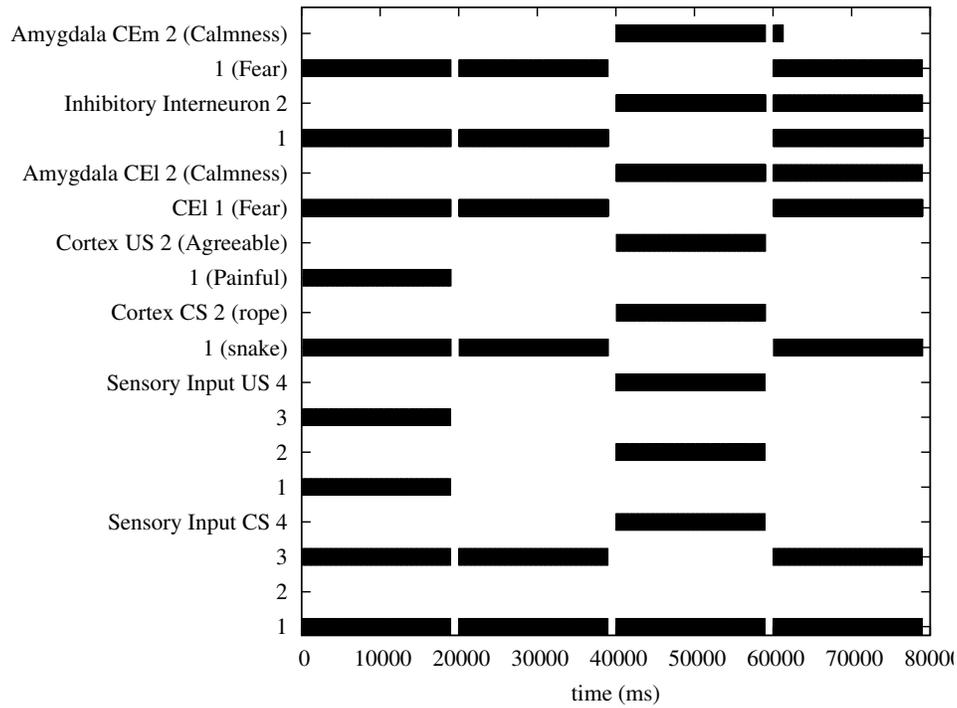


Fig. 3. Simulation result for snake.

4 Conclusions

We have proposed a neural circuit model of emotional learning using two pathways with different granularity and speed of information processing. In order to derive a precise time process, we utilized spiking model neuron proposed by Izhikevich (2007) and STDP of both excitatory and inhibitory synapses. We demonstrated some aspects of emotional learning from the perspective of the time process by conducting computer simulations. The agreement of the results with the previous behavioral experiments suggests that the structure and learning process of the proposed model are appropriate.

The proposed model is only one possibility for emotional learning. Thus, we hope to verify the structure and learning process suggested in this study through actual biological experiments.

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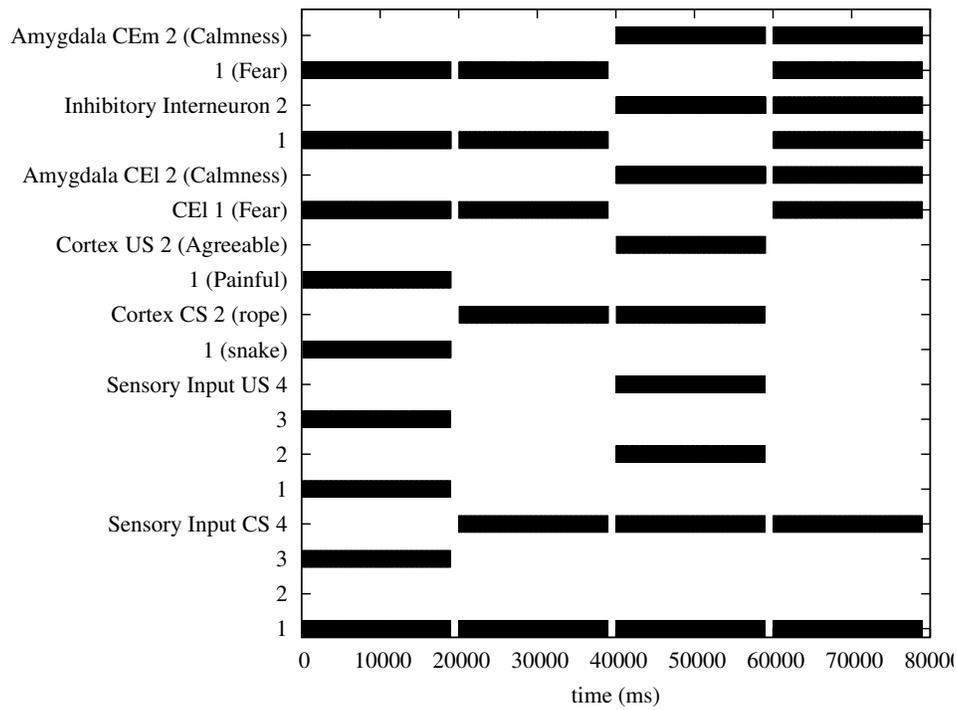


Fig. 4. Simulation result with lesion of cortex for rope.

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