Does the temporal precision of spike coincidences represent animal's elevated expectation of predictable events?

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Abstract

In a delay response task, neuron pairs in the monkey's motor cortex show spike synchrony at timings of a GO instruction following a delay period. Besides, the temporal precision of the synchrony at the later timing becomes higher. Therefore, it is thought the change in the precision of the synchrony represents degree of the elevated expectation for external events. To understand the mechanism, we construct a computational model in which spike-timing-dependent synaptic plasticity (STDP) organizes the predictive synchrony. The proposed model can reproduce the change in the precision of the synchrony without any updating mechanism of the internal dynamics.

Introduction

If a monkey is trained on a delay response task in which a GO signal to instruct a motor response follows a delay period with one of preset intervals, pairs of neurons in monkey's primary motor cortex show significant spike synchrony at the timings when the GO signal is expected to appear (Riehle et al, 1997). The significant synchrony is observed unless the GO signal is actually presented. It is also found that the temporal precision of the synchrony at the later timing becomes higher (Riehle et al., 2000). Therefore, it has been thought that this synchrony is internally generated and highly involved in animal's anticipation of predictable external events and that the temporal precision of the synchrony represents degree of the anticipation. However, the underlying mechanism and the actual meaning of the phenomenon remain unclear. In the present study, we conduct numerical simulations with a computational model in order to understand the organization of such an activity.

Methods and materials

A neural activity representing an internal time must be essential to predict occurrence times of external events. Though such an activity itself is an important problem to be studied, we here assume that time information is represented by spikes that are loosely time-locked to a CUE signal. Each of these loosely timed spikes (LT spikes) occurs around after a fixed interval from a CUE signal, showing temporal jitters of 10-20ms trial by trial. In our model, a group of primary motor neurons (20 neurons) are innervated by two kinds of afferents: ones are background afferents through which Poisson spikes with mean firing rates of 10-30Hz are delivered, and the other ones are LT afferents through which superposition of LT spikes and Poisson spikes with a low firing rate are delivered. The background afferents to the single neuron consist of 1000 excitatory and 300 inhibitory synapses. The LT afferents consists of 300 synapses and each of them delivers a couple of LT spikes, times of which are randomly and uniformly generated within the delay period. All the excitatory synapses of both the afferents are modified by a spike-timing-dependent plasticity rule (STDP rule) proposed by Song et al. (2000). In addition, the neurons receive the excitatory inputs initiated by the sensory GO signal. The proposed model engages in the simulated task similar to the experiment. In a trial set, 500 learning trials are followed by 50 test trials. In the learning trials, the excitatory input representing the GO signal is given to each of the neurons at a timing that is randomly chosen among three preset ones. On the other hand, in the test trials, the GO input is not presented. The spike data obtained in the test trials are used for unitary event analysis, which detects spike coincidences occurring more significantly than expected by chance (Grün et al., 2002). In the analysis, we take the 1-10, typically 5ms, coincidence window (equivalent to a bin) that defines a precision of spike coincidences between neuron pairs, and the 100ms sliding time window in which firing rates of the neurons are locally calculated. If the actual number of spike coincidences significantly exceeds the expected ones calculated from the firing rates of the pair in a sliding time window, the bin in the middle of the sliding window is defined as a significant bin.

Results

In the learning trials, both types of the synapses compete according to the STDP rule. As a result, the achieved synapses show bimodal distributions in terms of the synaptic strengths, which is consistent with the previous study (Song et al., 2000). To see the detailed synaptic configuration, a relation between timings of the individual LT spikes and the corresponding LT synapses is investigated. It is found that the synapses for the LT spikes occurring immediately before the timings of the GO signal are strongly potentiated. This is because the excitatory inputs by the GO signal evoke the post-synaptic spikes, which makes causal relations for the synapses mediating the LT spikes occurring immediately before the post-synaptic spikes. Thus, the timings of the GO signal are associated with the LT afferents for the LT spikes occurring immediately before the timings of the GO signal through the causality detection function of the STDP.

Unitary event analysis is applied to the spike data of the test trials. Among all the 190 pairs, some pairs (~10%) show significant spike coincidences around at the two or three expected times of the GO signal. To make the further investigation, we count the significant time bins using analyzed data of 10 trial sets. The obtained histogram of the counts has distinguished peaks at the timings of the GO signal. These peaks show robustness even if the mean firing rate of background inputs increases from 10 to 30Hz, which is achieved by the activity regulation function of the STDP rule to reduce the gain of the background inputs. Next, we change the size of the coincidence window for the analysis, such as 1, 2, 5 and 10ms, in order to see the time course of the precision of the synchrony. The result indicates the following tendency: the all the three peaks are observed in the case of the large window of 10ms, but the height of the earliest peak becomes lower as the smaller window is taken. The result implies that the later predictive synchrony has the higher temporal precision. This is due to the fact that the synaptic distribution of the LT afferents responsible for the latest timing of the GO signal is more strongly biased toward the maximum strength than that of the ones for the earliest timing.

Conclusion

The proposed model can explain the organization of the predictive synchrony observed in the experimental study. Besides, the model gives an insight about the time course of the temporal precision of the predictive synchrony: the increase in the precision is reproduced simply by the synaptic organization under a noisy condition. It may be thought that some monitoring mechanisms, which judge whether the GO signal is presented or not, are necessary when the internal dynamics such as the increase in the synchrony precision is updated according to the situation. The present study, however, gives an alternative account for the phenomenon.