ELSEVIER

Neurocomputing 32–33 (2000) 523–528

NEUROCOMPUTING

www.elsevier.com/locate/neucom

Temporally asymmetric Hebbian learning and neuronal response variability

Sen Song*, L.F. Abbott

Volen Center for Complex Systems and Department of Biology, Brandeis University, Waltham, MA 02454-9110, USA

Accepted 13 January 2000

Abstract

Recent experimental data have characterized a form of long-term synaptic modification that depends on the relative timing of pre- and post-synaptic action potentials. Modeling studies indicate that this rule can automatically adjust excitatory synaptic strengths so that the post-synaptic neuron receives roughly equal amount of excitation and inhibition and as a consequence fires irregular spike trains as observed *in vivo*. This rule also induces competition between different inputs and strengthens groups of synapses that are correlated over short time periods. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Hebbian learning; Spike timing; Variability; Competition; Balanced excitation

1. Introduction

Recent experimental results indicate that the induction of long-term potentiation (LTP) and long-term depression (LTD) at synapses in a variety of systems are highly sensitive to the relative timing of pre- and post-synaptic action potentials [2,3,6,11]. In experiments on neocortical slices [6], hippocampal cells in culture [3], and *in vivo* studies of tadpole tectum [11], long-term strengthening of synapses occurred if pre-synaptic action potentials preceded post-synaptic firing by no more than about 50 ms. Maximal LTP occurred when pre-synaptic spikes preceded post-synaptic action potentials by less than a few milliseconds. If pre-synaptic spikes followed post-synaptic action potentials, long-term depression rather than potentiation resulted.

* Corresponding author.

E-mail addresses: flamingo@volen.brandeis.edu (S. Song), abbott@volen.brandeis.edu (L.F. Abbott).

PII: S0925-2312(00)00208-3

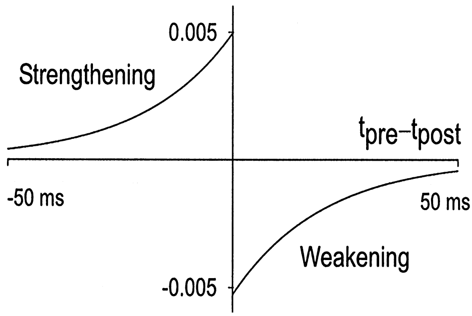

Fig. 1 . Temporally asymmetric Hebbian plasticity function. Graphed is the fractional change in synaptic strength produced by a pair of pre- and post-synaptic spikes occuring at t_{pre} and t_{post}, respectively. The curves in the plot are exponential functions.

2. Model

The experimental results are summarized schematically in Fig. 1. For the plasticity curve in Fig. 1, we have assumed that the area under the strengthening side of the curve is slightly less than the area under the weakening side. This means that pre-synaptic inputs that are not causally correlated with the post-synaptic response are weakened by temporally asymmetric Hebbian plasticity. This is important if the resulting synaptic modification rule is to be stable against uncontrolled growth of synaptic strengths. In our modeling studies, we examine how temporally asymmetric Hebbian plasticity acts on the excitatory synapses driving an integrate-and-fire model neuron with 1000 excitatory and 200 inhibitory synapses. The excitatory synapses are activated by uncorrelated or partially correlated Poisson spike trains at various rates. The model neuron also receives inhibitory input consisting of Poisson spike trains at a fixed rate of 10 Hz. In the simulations, excitatory synapses are subject to the plasticity rule shown in Fig. 1, while inhibitory synapses are held fixed. We also impose a lower bound of zero and an upper bound on the excitatory synapses.

3. Response variability

Experimental recordings from cortical neurons typically show large variabilities in their spike trains. However, as Softky and Koch [8] pointed out, it is difficult to obtain CV (coefficient of variation) values as large as those seen *in vivo*. However, a number of authors [4,7,10] have subsequently pointed out that irregular firing could be achieved if the amount of excitation and inhibition to a neuron are balanced. Neurons (simulated with an integrate-and-fire model) can operate in two different modes. In the regular firing mode, multiple synaptic inputs are integrated to generate an approximately constant input current that brings the neuron above threshold and produce steady firing. In the irregular firing mode, excitatory and inhibitory inputs to the neuron are more balanced and the mean level of synaptic current is insufficient to

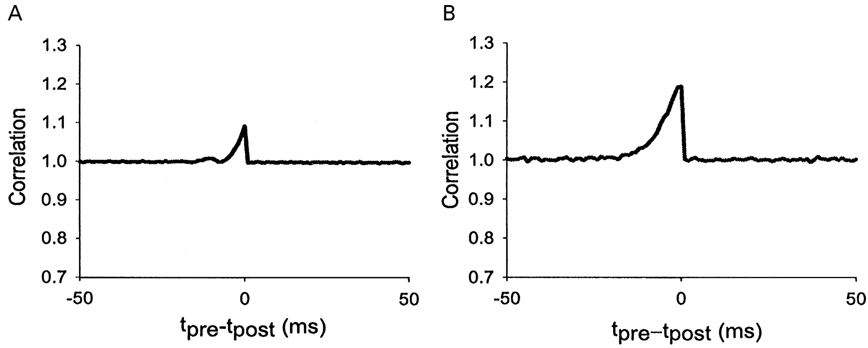

Fig. 2. Correlation between pre- and post-synaptic action potentials. The curve indicating the relative probability of a pair of pre- and post-synaptic spikes separated by the indicated time interval. (A) Regular firing mode. There is only a small excess of pre-synaptic spikes preceding a post-synaptic spike. (B) Irregular firing mode. The excess of pre-synaptic spikes shortly before a post-synaptic spike is much larger.

bring the neuron above threshold. Instead, the neuron fires due to fluctuations in the total synaptic input, and this produces an irregular pattern of action potentials.

Fig. 2 shows the probability that an action potential fired by a post-synaptic neuron is preceded or followed by a pre-synaptic spike separated by various intervals for an integrate-and-fire model in the two modes of operation. The histogram has been normalized so its value for pairings that are due solely to chance is one. The histogram when the model is in the regular firing mode (Fig. 2A) takes a value close to one for almost all input–output spike time differences. This is a reflection of the fact that the timing of individual action potentials in the regular firing mode is relatively independent of the timing of the pre-synaptic inputs. In contrast, the histogram for a model neuron in the irregular firing mode (Fig. 2B) shows a much larger excess of pre-synaptic spikes occurring shortly before the post-synaptic neuron fires. This excess reflects the fluctuations in the total synaptic input that push the membrane potential up to the threshold and produce a spike in the irregular firing mode. It thus represents the causal influence of pre-synaptic spikes on post-synaptic spike times.

4. Temporally asymmetric Hebbian plasticity leads to an irregular firing state

For a neuron to operate in the irregular firing mode, there must be an appropriate balance between the strength of its excitatory and inhibitory inputs. A synaptic modification rule based on the curve in Fig. 1 can automatically generate the balance of excitation and inhibition needed to produce an irregular firing state [1]. To demonstrate this, we started the model in a regular firing mode by giving it relatively strong excitatory synaptic strengths. We then applied Poisson spike trains with the same average rate to the excitatory synapses. Because the area under the weakening part of the curve in Fig. 1 is greater than that under the strenthening part, excitatory synapses will get weaker if there is an equal probability of a pre-synaptic spike to

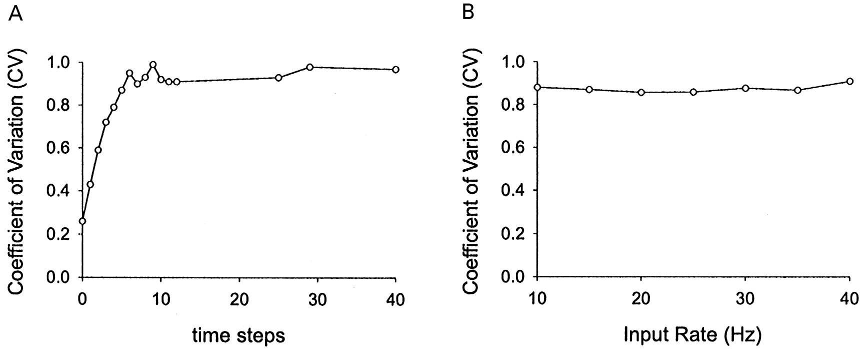

Fig. 3. Coefficient of variation (CV) of the output spike train of the model neuron. (A) Evolution of CV in a simulation where the neuron made a transition from a regular to an irregular firing state due to the action of the temporally asymmetric Hebbian plasticity on the synapses. (B) The equilibrium CV values of the post-synaptic interspike intervals for different input firing rates.

either precede or follow a post-synaptic spike. This is exactly what happens in the regular firing mode (Fig. 2A). As the plasticity rule weakens the excitatory synapses, the amount of excitatory input gets closer to the amount of inhibitory input, and the neuron enters the irregular firing mode, where there is a higher probability for a pre-synaptic spike to precede than to follow a post-synaptic spike (Fig. 2B). This compensates for the fact that the rule we use produces more weakening than strengthening on average. Equilibrium will be reached when the strenthening effect caused by the excess of pre-synaptic spikes (Fig. 2A) is balanced by the weakening effect caused by the flat baseline. This is achieved when the integrated product of the plasticity curve and the curve of correlation between pre- and post-synaptic action potentials reaches zero. The equilibrium state corresponds to a balanced, irregular firing mode of operation. Fig. 3A shows a transition from a regular (low CV) to an irregular (CV close to 1) firing state mediated by the temporally asymmetric Hebbian plasticity rule. The solid curve in Fig. 3B shows that temporally asymmetric Hebbian plasticity can robustly generate irregular output firing for a wide range of input firing rates.

5. Correlation-based Hebbian modification

Correlating different synaptic inputs so they are more likely to arrive together in a cluster is an effective way of increasing their ability to evoke post-synaptic action potentials [5]. This enables them to grow stronger together while weakening other synapses that are not part of the cluster. This effect can be seen in Fig. 4. In this study, we introduced correlated bursts into a group of synapses. We randomly picked intervals from an exponential distribution. At the start of each interval, we randomly picked 20% of the neurons from the correlated group and fired them at a random time around the start of the interval with a mean jitter of 2 ms. As the result of the temporally asymmetric Hebbian plasticity, the correlated group ended up with much

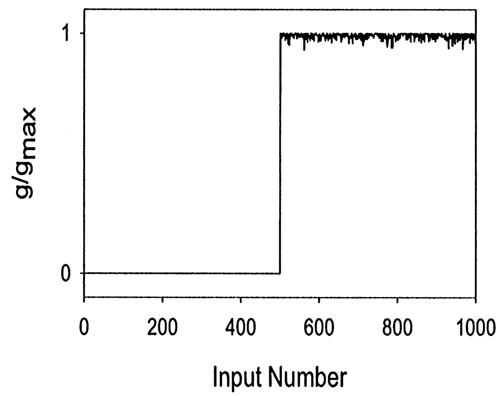

Fig. 4. Synaptic strengths for synapses in an uncorrelated group (input number < 500) and a correlated group (input number > 500). $g/g_{\max}$ is the synaptic conductance as a fraction of the maximal conductance.

larger synaptic strengths, while the strengths of the other group were essentially driven to zero. Correlations have a large effect only when the correlation time constant is fast, which is to say, on the time scale of the plasticity function. In another study [9], we generated spikes trains with a correlation function that decays exponentially with time. We found that when correlation decayed rapidly, the correlated group ended up with larger synaptic strengths. However, this effect disappears for larger correlation times, and at intermediate correlation times the synapses of correlated group were even weakened. We also observed that temporally asymmetric Hebbian plasticity is insensitive to the average rate or degree of variablility of the synaptic inputs. In sum, temporally asymmetric Hebbian learning enforces competition among synaptic inputs and selectively favors groups with fast correlations.

6. Conclusion

Temporally asymmetric Hebbian plasticity automatically leads to a balanced, irregular firing state in which pre- and post-synaptic spike times are causally correlated. It regulates both the firing rate and the coefficient of variation of post-synaptic firing over a wide range of input rates. Temporally asymmetric Hebbian plasticity shows the basic feature of Hebbian learning, the strengthening of correlated groups of synapses. However, it also displays the desirable features of firing rate independence and stability and introduces competition among inputs in a novel way.

References

[1] L.F. Abbott, S. Song, Temporally Asymmetric Hebbian Learning, Spike Timing and Neuronal Response Variability, in: M.S. Kearns, S.A. Solla, D.A. Cohn (Eds.), Advances in Neural Information Processing Systems, Vol. 11, MIT Press, Cambridge, MA, 1999, pp. 69–75.

[2] C.C. Bell, V.Z. Han, Y. Sugawara, K. Grant, Synaptic plasticity in a cerebellum-like structure depends on temporal order, Nature 387 (1997) 278–281.
[3] G-q. Bi, M-m. Poo, Activity-induced synaptic modifications in hippocampal culture:dependence on spike timing, synaptic strength and cell type, J. Neurosci. 18 (1998) 10 464–10 472.
[4] G. Bugmann, C. Christodoulou, J.G. Taylor, Role of temporal integration and fluctuation detection in the highly irregular firing of a leaky integrator neuron model with partial reset, Neural Comput. 9 (1997) 985–1000.
[5] R. Kempter, W. Gerstner, J.L. van Hemmen, Hebbian learning and spiking neurons, Phys. Rev. E 59 (1999) 4498–4514.
[6] H. Markram, J. Lubke, M. Frotscher, B. Sakmann, Regulation of synaptic efficacy by coincidence of post-synaptic APs and EPSPs, Science 275 (1997) 213–215.
[7] M.N. Shadlen, W.T. Newsome, Noise, neural codes and cortical organization, Curr. Opin. Neurobiol. 4 (1994) 569–579.
[8] W.R. Softky, C. Koch, Cortical cells should spike regularly but do not. Neural Comput. 4 (1992) 643–646.
[9] S. Song, K.D. Miller, L.F. Abbott, Competitive Hebbian learning through spike-timing-dependent synaptic plasticity, submitted for publication.
[10] T.W. Troyer, K.D. Miller, Physiological gain leads to high ISI variability in a simple model of a cortical regular spiking cell, Neural Comput. 9 (1997) 971–983.
[11] L.I. Zhang, H.W. Tao, C.E. Holt, W.A. Harris, M-m. Poo, A critical window for cooperation and competition among developing retinotectal synapses, Nature 395 (1998) 37–44.

Sen Song is a graduate student in the Biology Department at Brandeis University. His research examines the computational properties of networks of spiking neurons and the functional consequences of spike based learning rules.

L.F. Abbott is the Nancy Lurie Marks Professor of Neuroscience and the Director of the Volen Center for Complex Systems at Brandeis University. His research explores the effects of recurrent connectivity and both short- and long-term synaptic plasticity on the functional properties of cortical circuits.