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Neurocomputing 32–33 (2000) 905–911

NEUROCOMPUTING

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# From hippocampus to V1: Effect of LTP on spatio-temporal dynamics of receptive fields

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Accepted 13 January 2000

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## Abstract

Recent studies have revealed novel effects [8,1,23,24,12,13] of patterns of neuronal activity and synaptic plasticity on the size and specificity of receptive fields. However, little has been done to quantify their effect on the receptive field *shape*. It has been shown that place fields are highly asymmetric such that, the firing rate of a place cell rises slowly as a rat enters a place field but the firing rate drops off abruptly at the end of the place field [15] in an experience dependent fashion. Here we present a computational model that can explain the results, based on NMDA-dependent LTP. Striking similarities between the hippocampal and striate receptive field dynamics are pointed out. Our model suggests that LTP/D could result in diverse phenomena such as phase precession in the hippocampal neurons and the origin of directional receptive fields in the striate cortex. It is suggested that the key feature underlying directionality and inseparable spatiotemporal dynamics is the asymmetric shape of the receptive field. © 2000 Elsevier Science B.V. All rights reserved.

**Keywords:** Direction selectivity; Navigation; Learning; NMDA; Skewness

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## 1. Methods

The CA1 neuron used for the mathematical model was adapted from the rate model of an adapting neuron by Wang [22]. The strength  $s$  of an excitatory synapses from CA3 to CA1 was modified by an amount  $ds$  according to the physiological learning rule [10,21]

$$ds = \int_0^T dt \int_1^{50} d\tau [A_{LTP} \exp(-\tau/\tau_{LTP}) f_{CA3}(t - \tau) f_{CA1}(t) - A_{LTD} \exp(-\tau/\tau_{LTD}) f_{CA3}(t + \tau) f_{CA1}(t)],$$

where  $A_{LTP} = 0.0006$ ,  $A_{LTD} = 0.9A_{LTP}$ ,  $\tau_{LTP} = \tau_{LTD} = 10$  mS, and  $T$  is the total duration of a given lap.  $f_{CA3}$  and  $f_{CA1}$  are the firing rates of the presynaptic CA3 and postsynaptic CA1 neurons, respectively.

## 2. Introduction

It has recently been shown that the place fields in CA1 are negatively skewed [15] such that the firing rate increases gradually as the rat enters the place field but drops off abruptly at the trailing edge of the field. A majority of these place fields are also directional [17], such that when the rat traverses the same region of space in the opposite direction the cell fires very little or no spikes at all. Further, at the beginning of a session the mean firing rate of place cells was equal in the first and the second halves of their place fields. However, with experience the place fields became asymmetric such that the mean firing rate was higher in the second half of the place field than the first [15]. Further, as documented earlier, the place field size also increases in an asymmetric fashion [12,13].

Thus, unlike the usual implicit assumption of a symmetric shape of receptive fields, the hippocampal receptive fields are asymmetric. The nature of this asymmetry is the opposite of that expected from the common properties of the principal cells such as spike frequency adaptation, which would result in the typical large phasic response in

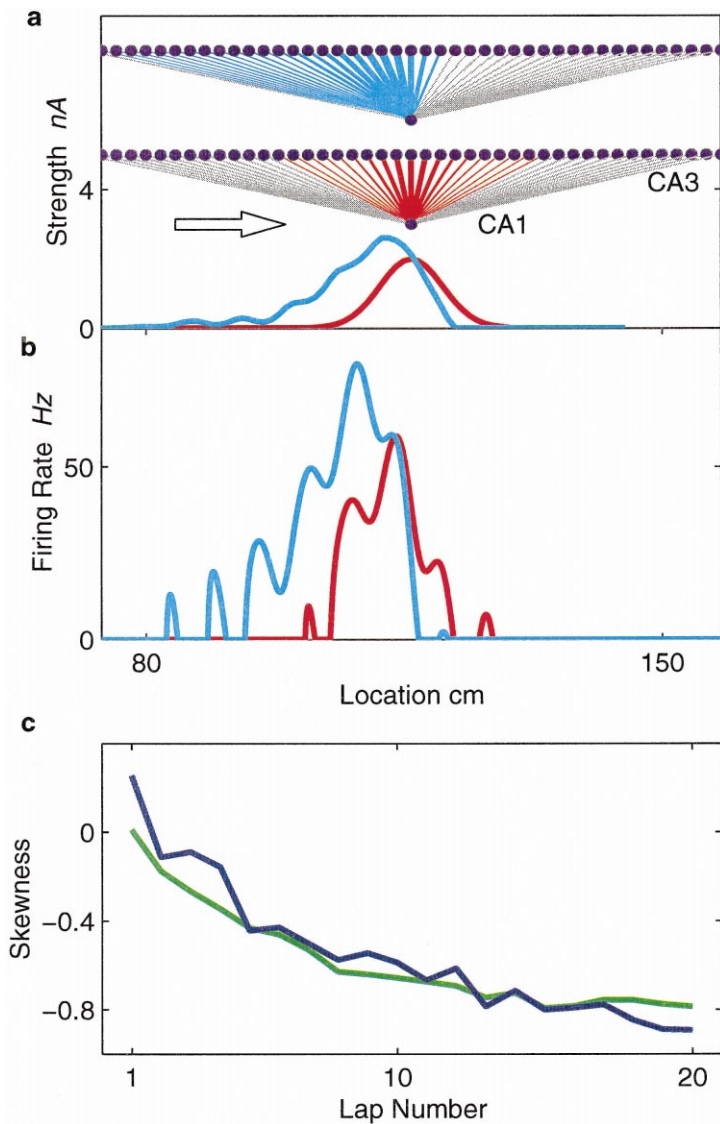
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Fig. 1. A computational model that can explain the change in place field properties with experience. (a) The rat traveled from left to right (arrow). Initially, the CA1 model neuron receives symmetric input from a large number of CA3 neurons (red lines). Hence the net synaptic current injected in the neuron was also symmetric (red curve). (b) However, the output of the neuron was positively skewed (red curve) due to spike-frequency adaptation. Due to LTP/D of the synapses with repeated traversals of the track, the net synaptic matrix became asymmetric (blue lines (a)), the net synaptic input current was negatively skewed (blue curve (b)), and the output of the CA1 cell was negatively skewed (blue curve (b)). In addition the location of the first and the last spikes in the place field shifted backwards and the size of the place field increased. (c) There was a gradual change in the skewness with experience and the output of the CA1 neuron (blue) was less skewed than the input (green) due to spike frequency adaptation. Thus the model captures all the phenomena documented in [15]. Unlike the usual models of learning which are based on a recurrent network, the above model is a purely feed forward network.

the early part of the place field followed by a small tonic response, i.e. a *positive skewness*.

### 3. Results

These phenomena can be explained using a computational model (Fig. 1) which uses the properties of long-term potentiation (LTP) and depotentiation (LTD) of NMDA-dependent synapses between CA3 and CA1 as follows.



An NMDA-dependent synapse is strengthened if the presynaptic neuron fires just before postsynaptic neuron, and depotentiated if the converse is true [6,9,3,10,14,21]. The pyramidal neurons in CA1 get their primary excitatory input from CA3, many of which are NMDA dependent. Hence, when a rat repeatedly traverses a region of space in the same direction the synapses from those CA3 neurons which have a place field before that of a CA1 neuron would be strengthened, with the amount of strengthening inversely proportional to the distance between the two place fields; whereas the synapses from those CA3 neuron that follow a CA1 place field would be weakened.

The place fields thus get a spatially symmetric input at the beginning of a session. The symmetry is then dynamically broken by the temporally asymmetric nature of NMDA-dependent LTP/D and the asymmetric experience, resulting in an experience dependent, directionally tuned, and spatially asymmetric place fields.

These results also reveal a mechanism which could underly the phenomenon of phase precession [18], where the phase of the  $\theta$  rhythm at which a neuron fires a spike steadily advances to an earlier phase as the animal moves through the place field. In addition to the excitatory input, the CA1 neurons also receive an oscillatory inhibitory input. Since the net excitatory input to a place cell increases monotonically with distance within the place field, the neuron would come out of the inhibition earlier as the rat travels farther, and hence the spike phase would exhibit an advancement.

Neurons in the striate cortex are directionally tuned [7] and they have slanted spatiotemporal receptive fields [16,19,11,2], i.e. the response latencies are shorter and the firing rates are larger as the stimuli are flashed farther along the preferred direction. These phenomena are similar to the directionally tuned, negatively skewed place cells [15] with phase precession [18] in the hippocampus (Table 1). The shortening of latencies is akin to phase advancement. As mentioned above, shortening of latencies could arise due to an increasing excitatory input with distance along the preferred direction. Thus, the inseparability of the spatiotemporal receptive field could arise due to an asymmetric distribution of firing rate, or the net excitatory input, within the receptive field. While the spatiotemporal dynamics of striate receptive fields has been studied extensively, the skewness of the firing rate distribution as a function of position has received little attention. Similarly, the development of the spatiotemporal receptive dynamics of the striate fields, similar to that demonstrated for the hippocampus [15] are yet to be demonstrated.

Hence, we propose that the slanted spatiotemporal receptive fields in the striate cortex could arise due to a mechanism similar to the one proposed here for the asymmetric place fields, namely strengthening of NMDA-dependent synapses as a result of sequential neuronal activation during natural scene viewing or spontaneous activity in the retina [20] during early development, which are similar to the rat running back and forth through the environment. The initial thalamocortical synaptic matrix could be symmetric and hence directionally untuned. Small fluctuations in the skewness of the undeveloped synaptic matrix would then be amplified by sequential (even if symmetric) activity, resulting in asymmetric firing rate (and hence latency)

Table 1

Hippocampus	V1
Directional place fields	Directional receptive fields
Asymmetric firing rate distribution	Asymmetric firing rate distribution
Advancement of phase with distance	Shortening of latencies along preferred direction
Prediction of future location?	Prediction of future stimulus position?
Experience-dependent change in asymmetry	??

distribution. A delayed inhibition proportional to the net excitatory drive on the principal cells with asymmetric receptive fields would result in direction selectivity. Such a model of the origin of direction selectivity suggests that if either the synaptic plasticity or the sequential activity of neurons were abolished during development, the neurons in striate cortex would lose direction selectivity. Support for such a phenomenon has been provided by experiments which show that when cats are reared in an environment with 8 Hz strobe lighting, the direction selectivity and spatiotemporal inseparability are extinguished [4]. This could occur because the strobe rearing at 8 Hz (period = 120 ms) prevents the sequential activation of neighboring neurons in the striate cortex within the window of LTP ( $< 50$  ms). Further, preliminary studies have indicated that when the NMDA receptors are pharmacologically blocked, the asymmetric expansion of place cells is extinguished [15].

The origin of such directional spatiotemporal dynamics in striate cortex has been intensely debated [5] and are difficult to study experimentally. The work presented here suggests that the hippocampus, with its well documented highly plastic synaptic matrix, may provide a valuable tool towards understanding such phenomena. It is important to note that unlike the previous works, the mechanism proposed here neither requires the existence of recurrent excitatory connections, nor the existence of two subpopulations of thalamic cells with differing delays [5].

Thus, history-dependent asymmetric shape of a receptive field could be a general property of receptive fields in the brain. Such an asymmetric shape may reveal the plasticity mechanisms underlying the formation of these receptive fields and may allow an animal to predict the upcoming event, such as the location of a visual stimulus or a spatial location, via an experience-dependent encoding of a sequence of past events.

## References

- [1] L.F. Abbot, K. Blum, Functional significance of long-term potentiation for sequence learning and prediction. *Cerebral Cortex* 6 (1996) 406–416.
- [2] D.G. Albrecht, W.S. Geisler, Motion selectivity and the contrast-response function of simple cells in the visual cortex, *Visual Neurosci.* 7 (1991) 531–546.
- [3] B. Gustafsson, H. Wigstrom, Hippocampal long-lasting potentiation produced by pairing single volleys and brief conditioning tetani evoked in separate afferents, *J. Neurosci.* 6 (1986) 1575–1582.

- [4] A.L. Humphrey, A.B. Saul, Strobe rearing reduces direction selectivity in area 17 by altering spatiotemporal receptive-field structure, *J. Neurophysiol* 80 (1998) 2991–3004.
- [5] J.C. Feidler, A.B. Saul, A. Murthy, A.L. Humphrey, Hebbian learning and the development of direction selectivity: the role of geniculate response timings, *Network: Computation Neural Systems* 8 (1997) 195–214.
- [6] D.O. Hebb, *The Organization of Behavior*, Wiley, New York, 1986.
- [7] D.H. Hubel, T.N. Wiesel, Receptive fields of single neurons in cat striate cortex, *J. Physiol* 148 (1959) 574–591.
- [8] W.B. Levy, in: *Computational models of learning in simple neural systems*, eds. R.D. Hawkins, G.H. Bower, (Academic, New York) (1989) 243–305.
- [9] W.B. Levy, O. Steward, Temporal contiguity requirements for long-term associative potentiation/depression in the hippocampus, *Neuroscience* 8 (1983) 791–797.
- [10] H. Markram, J. Lubke, M. Frotscher, B. Sakmann, Regulation of synaptic efficacy by coincidence of postsynaptic APs and EPSPs, *Science* 275 (1997) 213–215.
- [11] J. McLean, L.A. Palmer, Contribution of linear spatiotemporal receptive field structure to velocity selectivity of simple cells in area 17 of cat, *Vision Res.* 29 (1989) 675–679.
- [12] M.R. Mehta, B.L. McNaughton, Expansion and shift of hippocampal place fields: Evidence for synaptic potentiation during behavior. *Proceedings of CNS\*96*, 741–745 (1996), Plenum Press.
- [13] M.R. Mehta, C.A. Barnes, B.L. McNaughton, Experience dependent asymmetric expansion of hippocampal place fields, *Proc. Natl. Acad. Sci. USA* 94 (1997) 8918–8921.
- [14] M.R. Mehta, B.L. McNaughton, Lack of experience dependent place field expansion in the dentate gyrus and NMDA dependence of the effect in CA1. *Society for Neuroscience meeting*, Abstract #196.7 (1997).
- [15] M.R. Mehta, M.A. Wilson, Experience dependent asymmetric shape of hippocampal receptive fields. *Society for Neuroscience meeting*, Abstract #758.3 (1998), *Neuron* 25 (2000) 707–715.
- [16] J.A. Movshon, I.D. Thompson, D.J. Tolhurst, Spatial summation in the receptive fields of simple cells in the cat's striate cortex, *J. Physiol.* 283 (1978) 53–77.
- [17] J. O'Keefe, J. Dostrovsky, The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat, *Brain Res.* 34 (1971) 171–175.
- [18] J. O'Keefe, M.L. Recce, Phase relationship between hippocampal place units and the EEG theta rhythm, *Hippocampus* 3 (1993) 317–330.
- [19] R.C. Reid, R.E. Soodak, R.M. Shapley, Linear mechanisms of directional selectivity in simple cells of cat striate cortex, *Proc. Natl. Acad. Sci.* 84 (1987) 8740–8744.
- [20] A.A. Penn, P.A. Riquelme, M.B. Feller, C.J. Shatz, Competition in retinogeniculate patterning driven by spontaneous activity, *Science* 279 (1998) 2108–2112.
- [21] G. Bi, M. Poo, Synaptic modification in cultured hippocampal neurons: Dependence on spike timing, synaptic strength, and postsynaptic cell type, *J. Neurosci.* 18 (1998) 10464–10472.
- [22] X. Wang, Calcium coding and adaptive temporal computation in cortical pyramidal neurons, *J. Neurophys.* 79 (1998) 1549–1566.
- [23] X. Wang, M.M. Merzenich, K. Sameshima, W.M. Jenkins, Remodeling of hand representation in adult cortex determined by timing of tactile stimulation. *Nature* 374 (1995) 71–75.
- [24] M.A. Wilson, B.L. McNaughton, Dynamics of the hippocampal ensemble code for space. *Science* 261 (1993) 1055–1058.

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