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EXPANSION AND SHIFT OF HIPPOCAMPAL PLACE FIELDS: EVIDENCE FOR SYNAPTIC POTENTIATION DURING BEHAVIOR

Mayank R. Mehta and Bruce L. McNaughton

ARL Division of Neural Systems, Memory and Aging
Department of Psychology
University of Arizona
Tucson AZ
E-mail: Mayank@NAMA.Arizona.EDU
E-mail: Bruce@NSMA.Arizona.EDU

ABSTRACT

Rat hippocampal neurons fire in a spatially selective fashion [1]. We show that place fields enlarge (by 75%) and shift (by $1.4cm$) in a direction opposite to the direction of movement of the rat, within a few traverses of a route, even if the environment has been experienced extensively on previous days. The expansion is not a result of locomotion or neural activity per se because it reoccurs when the rat runs on a different track immediately after running on the first one. This provides an evidence for systematic changes in neuronal firing properties due to and during experience. The results are consistent with the predictions of models [2, 3] of learning of sequences via Hebbian [4] synaptic potentiation. Thus, these data provide an evidence for Hebbian synaptic enhancement during behavior, and show that such learning occurs even when a rat enters a highly familiar environment after a day's absence.

Although it is a common belief that learning occurs via Hebbian long term potentiation (LTP) of the synapses, there is little evidence to suggest that such changes indeed occur during behavior. With the present technology, it is not possible to measure the strength of individual synapses during behavior. Most of the experiments on LTP involve artificial stimulation of brain tissue. These experiments show that the NMDA receptor mediated LTP is associative [5] and temporally asymmetric [6] –i.e. it occurs only if the postsynaptic neuron is depolarized within a short duration ($\sim 100ms$) *after* the spiking of the presynaptic neuron. It is not obvious that the anatomical connections between the neurons and the pattern of neuronal firing during behavior is indeed such that the pre and the post synaptic neurons have the required order of activation so as to strengthen the synapse. Thus it is important to investigate whether Hebbian LTP occurs during behavior. Given the present technological constraints, one has to devise

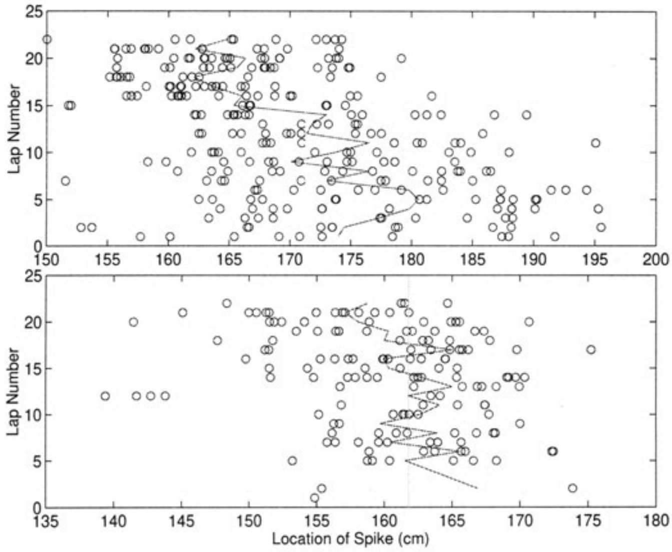

Figure 1. The location of the rat when two isolated cells (top and bottom panels) fired a spike is indicated by open circles, as a function of the lap number. The mean value of the locations of all the spikes fired by a cell during a lap corresponds to the location of the place field at that time. The place field locations during successive laps are joined by a solid line. The average value of all the spikes across *all the laps* corresponds to the place field center and is indicated by a light vertical line. The amount of firing per lap increased with time. In fact the cell in the bottom panel did not fire at all during some of the early laps. Further, the lap specific place field center shifted backwards.

indirect measures which would allow us to detect the consequences of changes in synaptic strengths. We have therefore looked for systematic changes in neuronal firing properties during behavior, which could arise due to Hebbian LTP.

The majority of experiments on LTP have been carried out on neurons of the Hippocampus. When a rat explores an environment, the neurons in the CA1 and CA3 regions of the hippocampus are known to fire in a spatially selective fashion [1] and are often called place cells. The region of space where a neuron fires selectively is called it's place field. A large number of neurons were recorded simultaneously [7] from two rats as they ran repeatedly in a counterclockwise direction on the perimeter of an elevated, rectangular track.

The closed linear track was mapped onto a straight line for the purpose of analyses, with the rats running in the direction of increasing distance. Fig. 1 shows the location of each spike, from two different cells, as a function of the lap number. As can be seen, the amount of firing increased with experience and the location of the center of mass of the lap specific place field moved in a direction opposite to the direction of movement of the rat.

However, these data are noisy. Few spikes (~ 10) were emitted by each cell during each lap. In order to do a statistically meaningful analysis of changes in place field properties, the 'ensemble averaged place field profile' of a population of cells was computed for each lap, as follows. For each place field, the location of the place field center (averaged over all the laps) was subtracted from the location of each spike, thereby obtaining the relative location of each spike. The firing rate as a function of the distance from the center, averaged across all the cells, gives the average place field profile of a population of cells. This profile was computed separately for each lap. Such an analysis corresponds to evaluating the ensemble average over all the place fields for each lap as opposed to the usual, time average over all the laps for each cell. The area under the 'ensemble averaged place field' curve is called the size of the place