Networks of integrate-and-fire neurons using Rank Order Coding B: Spike timing dependent plasticity and emergence of orientation selectivity

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Abstract

Rank Order Coding is an alternative to conventional rate coding schemes that uses the order in which a neuron's inputs fire to encode information. In a visual system framework, we simulated the asynchronous waves of retinal spikes produced in response to natural scenes and used them to stimulate integrate-and-fire V1 neurons that implemented a standard learning rule based on spike timing. After propagating thousands of images, orientation like receptive fields arise in these neurons despite the fact that the input neurons never fired more than once. We also analyze the biological plausibility of such a network. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Recent experiments on the speed of processing in the visual system are problematic for classic rate coding schemes [10]. An alternative scheme uses the analog-to-delay transformation characteristic of retinal ganglion cells to produce an asynchronous wave of spikes in which information is encoded by the order in which cells fire [5]. As

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we showed in previous papers [3–5,11], the responses of an integrate-and-fire neuron can be made to depend on the relative order of firing of its afferents by progressively desensitizing the neuron each time one of the inputs fires. The desensitizing process could be achieved by a relatively simple mechanism involving feed-forward shunting inhibition. By modeling millions of these neurons in retinotopically organized maps using a specially designed neural network simulator called SpikeNET [3], we have found that even relatively simple feed-forward architectures that use these principles can perform complex visual processing tasks that include the recognition of faces in photographs [4]. In the face recognition network, learning was implemented using a supervised learning rule: the experimenter determined classes of images (different views of a same face) that different groups of neurons were taught to recognize. In the present study a similar propagation procedure was used, but we decided to let each group of neurons select it's preferred stimulus. The idea was to test whether self-organization of receptive field properties can occur even under conditions where conventional rate coding schemes cannot operate, i.e. under conditions where each neuron is only allowed to fire one spike. In the companion paper (Perrinet, Delorme, Samualides, Thorpe, this volume), we already reviewed how to implement a biologically plausible learning rule, namely spike time based plasticity. In this learning scheme, the weight change depends upon the order of discharge of the postsynaptic and the presynaptic neuron. The present paper aims at determining the influence of such a rule on neuronal selectivity when propagating natural images.

2. Architecture of the network

We used a network composed of two layers, the first one modeling the retina and the other one representing groups of neurons in V1. Stimuli were 8-bit grayscale natural images taken from a commercial database (Corel photo library). We took 2790 50×50 grabs at random positions from 600 natural images each having a resolution of 364×244 pixels. The original photographs included landscapes, city views as well as natural and man-made objects. Spike timing of arrays of ON-center and OFF-center cells values were calculated by a direct application of a 3×3 difference of Gaussian contrast filter on the image. The Rank Order Coding scheme assumes that strongly activated neurons will tend to fire earlier than weakly activated ones, and that the resulting asynchrony can be used to encode information about the image. The question here concerns the issue of whether neurons in the next level could learn to extract information about the image using a biologically plausible unsupervised learning strategy. The neurons in the V1 level were simple integrate-and-fire units organized in retinotopic homogeneous maps with 11×11 receptive field size initialized with random values (Fig. 1). When propagating a new image, neuronal activity was initially reset to 0. Then, as the propagation went on, neurons were progressively desensitized each time one of their inputs fired, thus making neuronal responses dependent upon the relative order of firing of the neuron's afferents. More precisely, let $A = \{a_1, a_2, a_3 \ldots a_{m-1}, a_m\}$ be the ensemble of afferent neurons of neuron i and $W = \{w_{1,i}, w_{2,i}, w_{3,i} \ldots w_{m-1,i}, w_{m,i}\}$ the weights of the m corresponding
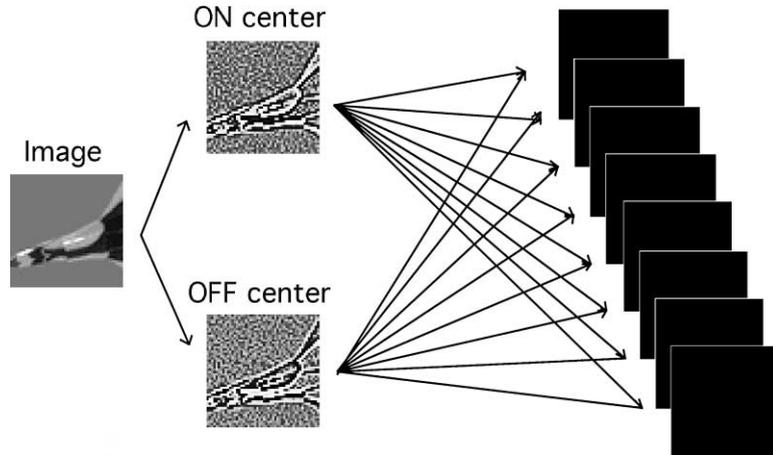
Fig. 1. Architecture of the network. Neurons were retinotopically organized into neuronal maps in which they shared the same synaptic weights. Whenever the synaptic weight of a neuron was modified, the same modification was applied to the entire population of neurons within the map. Inhibition is also present between each neuronal map: if a neuron spike, it inhibits all the neurons in the other maps with neighboring positions. This prevents all the neurons from learning the same pattern.

connections; let $\mathrm{mod} \in]0,1[$ be an arbitrary modulation factor. The activation level of neuron i at time t is given by

$$Activation(i,t) = \sum_{j \in [1,m]} \mathrm{mod}^{order(a_j)} w_{j,i}$$

where $order(a_j)$ is the firing rank of neuron a_j in the ensemble A. By convention, $order(a_j) = +\infty$ if neuron a_j has not fired at time t, setting the corresponding term in the above sum to zero. This kind of desensitization function could correspond to a fast shunting inhibition mechanism.

Whenever a neuron reached its threshold, it spiked and inhibited neurons at equivalent positions in the other maps so that only one neuron would respond at any particular location. Every spike also triggered a time based Hebbian-like learning rule that adjusted the synaptic weights according to [1] electrophysiological results (Fig. 2). Let t_e be the date of arrival of the EPSP at synapse of weight W and t_a the date of discharge of the postsynaptic neuron

if $t_e < t_a$ then $\mathrm{d}W = \alpha(1 - W)\mathrm{e}^{-|\Delta o|/\tau}$,

else $\mathrm{d}W = -\alpha W \mathrm{e}^{-|\Delta o|/\tau}$,

where Δo is the difference between the date of the EPSP and the date of the neuronal discharge (expressed in term of order of arrival instead of time). α is a constant that controls the amount of synaptic potentiation and depression. In the current simulations its value was fixed at 0.02, in accordance with biological data. We adjusted the
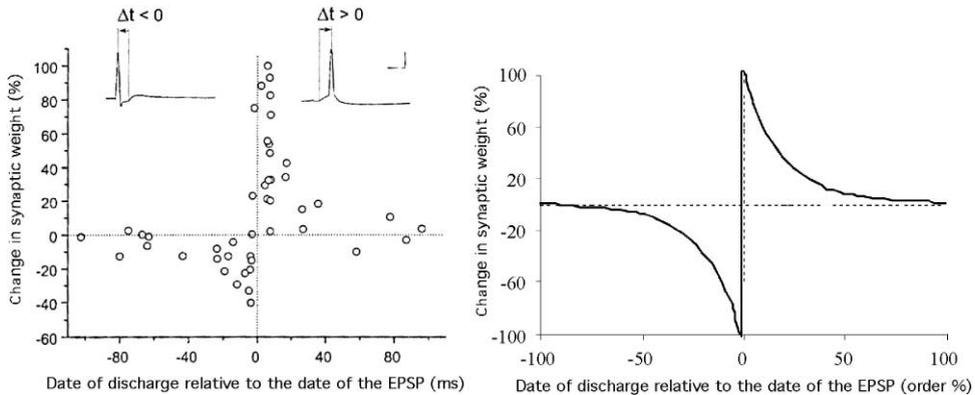
Fig. 2. (A) Synaptic weight modification as reported by Bi and Poo [1]. Hippocampal neurons were recorded and stimulated in culture with 1 Hz pairings of presynaptic and postsynaptic discharges. If the postsynaptic spike precedes the EPSP, the synapses is strengthened, otherwise, it is depressed. (B) Learning rule implemented in the model: to keep the network homogeneous, we express this rule in the order of EPSP arrival domain instead of the time domain. Adapted from Bi and Poo [1].

relation between order of arrival and time difference in order to obtain a value for τ close to 20 ms.

During all the simulations, neuronal thresholds were kept constant but the sum of all the synaptic weights was renormalized for each neuron. This kind of renormalization offers the advantage of not constraining neurons in term of discharge probability and in the distribution of their synaptic weights.

3. Results

After propagating the 2590 photographs, we observed different sorts of selectivity that included contour orientation, end-stop and blob cells (Fig. 3). Note that the use of small receptive fields at the level of the retinal input means that only information at the smallest spatial scale is present. Including retinal receptive fields at larger scales would have resulted in a wider range of spatial frequencies. Mathematical simulations have shown that orientation-selective receptive fields can emerge spontaneously when using natural photographs with a sparse decomposition [8]. Since we used strong inhibition between maps of neurons, the receptive field decomposition of Fig. 1 must have a substantial sparse component.

4. Spike time based plasticity and Rank Order Coding

The desensitization mechanism used in the Rank Order Coding scheme means that, for a neuron to be selective to a particular stimulus, high synaptic weights should be
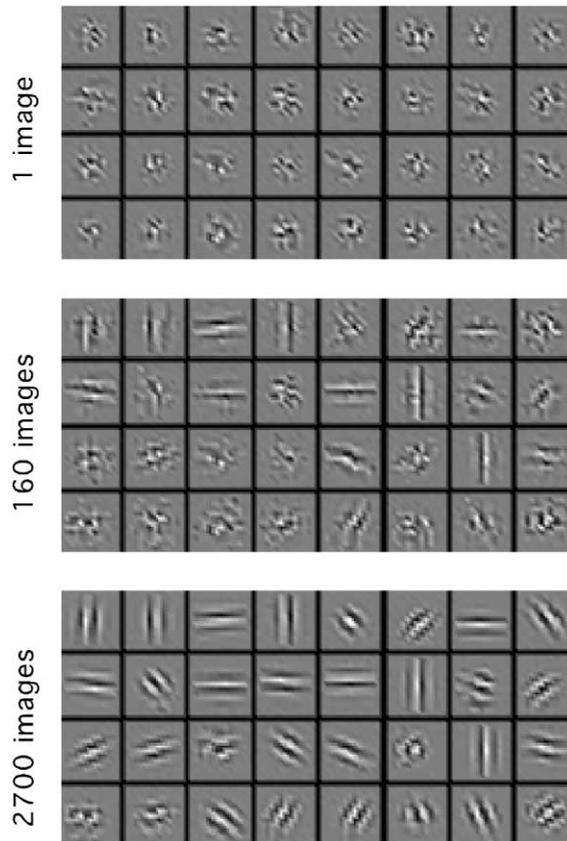
Fig. 3. Pattern of connectivity of 64 maps of V1 neurons inhibiting each other. The pattern of connectivity of neurons were initialized with two arrays (ON and OFF) of size 11×11 whose synaptic weights were distributed according to a randomized Gaussian function (the reconstruction process display here take into account both of these arrays, synapses from ON-center neurons being counted as positive and those from OFF-center neurons being counted as negative). Following propagation of a stimulus, the sum of input synaptic weights was renormalized so that the net input to each neuron remained constant. However, thresholds and convergence speed factors were not adjusted and remained constant during the whole simulation. Note that only the first neuron to fire at each location will undergo weight modifications. After propagating thousands of images, coherent receptive fields were found to arise naturally for these 64 maps of neurons.

assigned to inputs that fired first. Thus in a natural learning procedure, early activated synapses were strengthened whereas late activated synapses were depressed. In previous work, we have used a similar strategy for face detection and recognition in natural images [4,11].

We suggest that spike time based plasticity could induce a similar effect. As it can be derived from Fig. 2, early activated synaptic weights will always be reinforced whereas late activated synaptic weights will systematically be depressed. Other synapses with intermediate activation latencies will be alternately depressed or reinforced depending

on the neuron spike latency, and, on average, they will converge towards intermediate synaptic weight values. In other words, the spike-timing based learning rule could well be appropriate for implementing the rank order coding hypothesis.

5. Biological plausibility

Despite several simplifications, the model used here may not be too unreasonable with respect to biological plausibility. First, concerning the image presentation, the waves of action potentials triggered by a sequential presentation of images in our model could reflect activation reaching V1 resulting from saccadic eye movements. Second, the neuronal model used is very simple and does not include details of the dendritic structure. However, recent studies have shown that dendritic inputs tend to linearize at the soma [6] so that the integrate-and-fire simplification of neurons is not unreasonable and can account for electrophysiological recordings in the visual system [9]. Third, since the integration time of post synaptic potentials leading real neurons to spike is in the range of a few milliseconds, we considered we could ignore the decay in the membrane potential that would normally occur. Finally, with respect to the Rank Order Coding scheme, the fast desensitization mechanism that makes neurons selective to the relative order of firing of their afferent could be implemented using fast shunting inhibition or membrane conductance variations that have been observed recently in the visual system [2]. Moreover biological learning mechanisms, similar to the one we used in the present model, have been shown to depend on very small difference in latencies between the input and the output cell discharge date [7,1]. We considered this rule in the order of EPSP arrival dimension instead of the time dimension to keep neuronal integration, desensitization and learning processes homogeneous. This assumption make the network quite robust since, if the relative order of spikes in the input layer remains constant, changes in the exact latencies of the input spikes (i.e. changes that could depend on the luminance of the stimuli) should not dramatically change the dynamics of the learning mechanism.

The results show that plausible synaptic learning rules can be used to develop selective neuronal responses in networks of neurons using Rank Order Coding. This type of selectivity can develop even under conditions where classic rate coding can be excluded since none of the neurons was allowed to emit more than one spike. We suggest that the sorts of synaptic modification rule described recently in experimental studies could well provide a biologically plausible way to implement temporal coding schemes such as Rank Order Coding.

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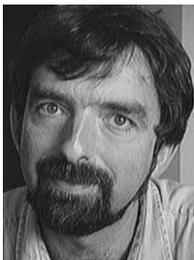
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