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Gain modulation of recurrent networks

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Abstract

Gain modulation is an important mechanism by which attentional and other inputs modify the amplitude of neuronal responses without changing their selectivity. Gain modulation has been studied previously in feedforward circuits but not in recurrent neural networks. We show how gain modulation modifies the response of a recurrent network to feedforward inputs. Even modest gain modulation of the recurrent network can cause downstream neurons to switch from a state in which they are unresponsive to a stimulus to a state where they respond selectively. Funneling the recurrent connections of a network through gain modulated neurons allows the selectivity within the network to be modified by modulatory inputs. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Recurrent model; Switching; Gain modulation; Attention

1. Introduction

Neuronal responses can change over short time scales due to attentional effects and processes related to motor response selection and activation. Goldberg et al. [7] have recorded neurons in area LIP that only fire to stimuli that recently have appeared in their receptive fields, or to stimuli that have behavioral significance (see also [13]). One possible mechanism for this type of change is rapid modulation of synaptic efficacy, essentially a faster form of the same processes that account for changes in selectivity over much longer time scales during learning and development [14]. A second idea is that switching arrays shift the input to the neuron being modulated

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[3,10]. Here we explore another possibility, gain modulation of individual neurons within a recurrent network.

Gain modulation is a widespread mechanism by which neural responses amplitude is scaled while the selectivity of the neuron remains unchanged. Information about eye and head position is combined with visual input in parietal cortex through gain modulation of visual receptive fields [2,4]. Gain modulation has also been seen in V4 neurons as a function of attention [5,9]. The effects of gain modulation have been studied in feedforward networks [15,12,11], but not in recurrent networks. We show here that gain modulation within a recurrent circuit can dramatically affect both the activity of downstream neurons and the selectivity of the network itself.

2. Models and results

Our first model is a linear recurrent network as shown in Fig. 1a. The activity of neuron i within such a network of N neurons, u_i, is determined by solving

$$u_i = g_i\left(I_i + \sum_{j=1}^{N} W_{ij} u_j \right). \tag{1}$$

The first term within the parentheses is the feedforward input to neuron i, and the second term represents recurrent input from the other neurons in the network. W_{ij} is the weight of the synapse from unit j to unit i. The parameter g_i (this is a multiplicative factor not a function) is the factor by which we introduce gain modulation. Initially,

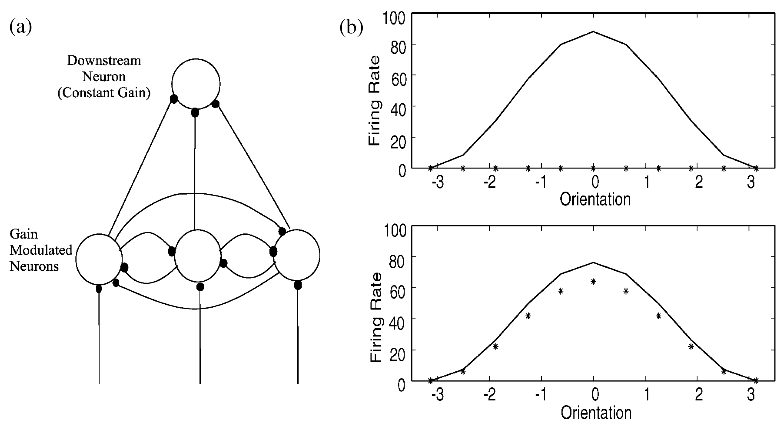

Fig. 1. (a) Gain-modulated neurons in a reccurent network driving a single down-stream neuron. The recurrent neurons are driven by stimulus input characterized by a single variable labelled ‘orientation’. (b) Upper panel: Response tuning curves of the downstream neuron when the network is not gain modulated (stars on x-axis indicating no response) and when it is gain modulated (curve). Lower panel: Response tuning curves of a representative neuron within the recurrent network in the unmodulated (stars) and modulated (curve) states.

we evaluate this network with all $g_i = 1$. In this case, we solve for the activities by expressing the rates and feedforward inputs in terms of a complete set of eigenvectors ξ_i^μ of the recurrent weight matrix, $\sum_j W_{ij}\xi_j^\mu = \lambda_\mu \xi_i^\mu$ for $\mu = 1, 2, \ldots, N$, where λ_μ are the eigenvalues. The solution is

$$u_i = \sum_{\mu=1}^{N} \left(\frac{\xi_i^\mu}{1-\lambda_\mu} \sum_{j=1}^{N} I_j \xi_j^\mu \right). \tag{2}$$

This equation displays the phenomenon of selective amplification if the largest eigenvalue, λ_1, is near (but < 1) 1 [1,6]. The factor $1 - \lambda_1$ in the denominator causes the $\mu = 1$ term to dominate, and we find

$$u_i \approx \frac{\xi_i^1}{1-\lambda_1} \sum_{j=1}^{N} I_j \xi_j^1. \tag{3}$$

We now study the effect of gain modulation by allowing the g_i factors to be different from one. We wish to study how large effects could arise from modest gain modulations, so we restrict our analysis to the case where all the g_i are close to one. This allows us to perform a perturbative calculation in powers of the quantities $g_i - 1$. To first order, it is possible to derive an analytic expression for the activity of unit i,

$$u_i \approx A\xi_i^1 + \frac{\lambda_1}{1-\lambda_1} \sum_{\mu \neq 1} \left(\frac{\xi_i^\mu}{\lambda_1 - \lambda_\mu} \sum_{j=1}^{N} I_j \xi_j^\mu \sum_{k=1}^{N} (g_k - 1)\xi_k^\mu \xi_k^1 \right). \tag{4}$$

The factor A, which we have not bothered to write out, depends on the input and gain factors. We leave out this expression because it plays no role in the switching function we are studying.

The important term for our purposes is the second one in Eq. (4). This indicates that gain modulation changes the pattern of the population response of the network, not simply its amplitude. Consider a downstream neuron with response given by

$$v = \sum_{j=1}^{N} \xi_j^\nu u_j \tag{5}$$

with $\nu \neq 1$. The downstream neuron is connected to neuron j of the recurrent network through a synapse of weight ξ_j^ν. Because $\nu \neq 1$, this neuron will be completely insensitive to patterns of activity in the recurrent network proportional to ξ_i^1. However, when the recurrent network is modulated, the second term in Eq. (4) shows that the pattern of network activity picks up terms proportional to the other eigenvectors of the recurrent weight matrix. Using Eq. (4), we find that

$$v \approx \frac{\lambda_1}{(1-\lambda_1)(\lambda_1 - \lambda_\nu)} \sum_{j=1}^{N} I_j \xi_j^\nu \sum_{k=1}^{N} (g_k - 1)\xi_k^\nu \xi_k^1. \tag{6}$$

The activity of this unit vanishes if all the g_i are equal to one, or indeed if they are all equal to each other. However, when the recurrent network is gain modulated in

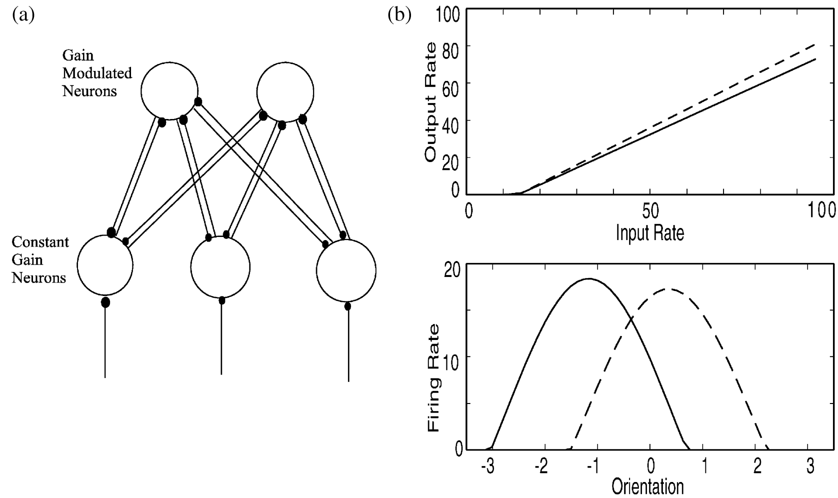

Fig. 2. (a) Recurrent network with a ‘pointer’ neuron architecture. All the recurrent connections are funneled through a set of gain modulated neurons. (b) Upper panel: the input–output curve of a gain modulated neuron before and after gain modulation. Lower panel: the change of selectivity for one of the constant gain neurons due to gain modulation. The dashed and solid response tunning curves correspond to the dashed and solid gain curves in the upper panel.

a nontrivial way, the downstream unit responds. Furthermore, the amplitude of v is amplified by the original factor $1/(1-\lambda_1)$. Fig. 1b (upper panel) shows the output of the downstream neuron in a simulation. Although the recurrent network neurons change their activities only slightly after gain modulation (Fig. 1b, lower panel), the downstream neuron's activity changes dramatically. It is switched from a nonresponsive to a selectively responsive state.

Hahnloser et al. [8] have proposed an architecture for recurrent networks in which the recurrent connections are funneled through a set of what they call ‘pointer’ neurons. Gain modulation of these neurons is a powerful way to modify network behavior because they effectively control the strength of the recurrent connections. In a second model, we have studied this form of gain modulation. The network has the structure shown in Fig. 2a. All the recurrent connections between the constant gain neurons project through a set of gain modulated neurons. In the example we studied, the connection from unmodulated neuron i to modulated neuron μ has strength $g_\mu \xi_i^\mu$ and the return connection has strength ξ_i^μ. Here g_μ is the gain modulation factor for neuron μ. The firing rates of the constant gain neurons are then governed by Eq. (1) with $W_{ij} = \sum_\mu g_\mu \xi_i^\mu \xi_j^\mu$. The eigenvectors of this matrix have components ξ^μ and have the eigenvalue g_μ. Recall that selective amplification occurs when one of the eigenvalues is close to one. By modulating the gain factors, we can control which of the eigenvectors has an eigenvalue near one, and hence which eignevector determines the selectivity of the network. Fig. 2b shows that the selectivity of one of the unmodulated neurons is shifted significantly when a small change is made in the gain of the modulated neurons.

3. Conclusions

Modulation that changes the gain of selected neurons by a small amount can have a dramatic effect on the responses of other neurons within a recurrent network. Downstream neurons can switch between unresponsive and selectively responsive states, and network selectivity can be significantly modified. Thus, gain modulation is a good candidate mechanism for major behavioral decision functions involving switching and shaping of selectivity.

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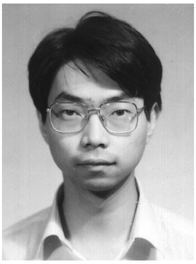

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