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Model of granular layer encoding in the cerebellum

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Abstract

Involved in sensorimotor and even cognitive coordination, the cerebellum receives inputs from diverse brain areas. These inputs are recoded by the granule cells, the most numerous cells in the brain, and together with the inhibitory Golgi cells form the granular layer. A model of the granular layer is presented. It suggests that the granular layer performs a recoding of the mossy fibers into a sparse representation that permits noise reduction by the Golgi cell and facilitates learning in the molecular and Purkinje layer. Hence, the granular layer contains different signal processings that lead to a robust and efficient representation for coordination.

Keywords: Granule cell; Golgi cell; Sparse; Coding; Representation; Denoising; Plasticity

1. Introduction

The anatomical cohesion of the granular layer with the inhibitory feedback of Golgi cell (Go) suggests that the cerebellum functionality can be divided in two independent processing regions: the granular layer and the Purkinje layer. The diversity of Purkinje cells sharing the same parallel fibers (PFs) inputs suggests that the processing in the granular layer should remain essentially unsupervised. Its purpose is a recoding of the mossy fibers (MFs) inputs: (1) to transmit to Purkinje cells a complete contextual account of MF activity, (2) in a form that facilitate learning at the Purkinje cells and (3) that minimizes destructive interference between tasks being learnt. A sparse and distributed PFs representation that maximizes the mutual information between MFs

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and PFs and minimizes the statistical dependencies among PFs would fulfill these three roles [3,4]. Marr's codon must be adaptive for such a representation. The adaptation should rely on the statistical dependencies in the MFs signals that are created when an animal performs different activities. We consider the case when MFs inputs contain noise, and suggest new roles for the Go inhibition in the granular layer network.

2. Model

MF inputs terminate in glomeruli where granule cell (GC) dendrites and Go axons converge to make synaptic contacts. The GCs send their PF axons to the Purkinje cells and make contact with Go(s), which inhibit(s) every GC dendrites at the glomeruli. A Go integrates the output of about 6000 GCs and receive inputs from a number of MFs. In the granular layer, all synapses are excitatory, except for the Go axon.

The model assumes the relation between the firing frequencies of these cells to be

$$S = (WX - vz)^+ \quad \text{and} \quad z = (\mu^{\mathrm{T}} S + \gamma^{\mathrm{T}} X - \theta)^+, \tag{1}$$

where X and S are vectors that represent the firing frequency of the MFs and GCs, respectively, W is the weight matrix of their excitatory synapses, W_{ji} is the weight from the ith MF to the jth GC, z is the firing rate of the Go with v the weight vector of its synapses onto a GC ($v_j = \sum_i V_{ji}$), V_{ji} is the inhibitory weight of the Go to the GC dendrite superimposed over the W_{ji} synaptic connection, μ is the weight vector of the PFs synapses onto the Go, γ is the weight vector of the excitatory synapses of the MFs onto Go dendrites, $(\cdot)^+$ indicates positive values only ($\geqslant 0$). All weights are positive.

2.1. Sparse coding in the parallel fibers

The hypothesis is that different statistical dependencies in the MFs signals are created when an animal performs different activities. The statistical dependencies are assumed to create probabilities in the MFs that will be sparse along some directions. These sparsest directions and the MF–GC synaptic weights can be found using independent component analysis (ICA) algorithms [4]. The resulting representation in the GCs will be sparse, distributed and nearly statistically independent, which should facilitate further processing in the molecular and Purkinje layer.

Away from saturation, system Eq. (1) can be solved as a linear model: $S = AX + u$ with $A = (I - (1/(1 + \mu^{\mathrm{T}} v))v\mu^{\mathrm{T}})(W - v\gamma^{\mathrm{T}})$, $u = (\theta/(1 + \mu^{\mathrm{T}} v))v$. To perform ICA, the only relevant parameter is the matrix A. To deal with its redundancy, in this first stage of learning $\theta = 0$ and $\mu = 0$, eliminating feedback inhibition from PFs. In this case, $A = W - v\gamma^{\mathrm{T}}$, which is not positive restricted. This suggests that one role of direct mossy fibers inputs to the Golgi cell with the weights v and γ is to permit a richer encoding in the GC than would be possible otherwise with only the positive weights W.

To illustrate the model, the MFs inputs in the following are assumed to be encoding the pixels of natural images (Fig. 2). These images are used to provide a

well-characterized statistical structure in the MFs. Different types of inputs would provide a different statistical structure, but would not change the results, given that a sparse representation can be obtained in the GCs. In the simulations, the GCs received between 4 and 64 MFs inputs, organized in patches of different sizes, 2×2, 3×3, 4×4, 6×6 and 8×8 patches. In order to build the desired sparse and distributed representation at the GCs, a conventional ICA algorithm was used to learn the matrix A [2] with the *natural gradient* improvement [1]. A biologically plausible implementation of the learning algorithm could also have been used instead [3,4]. The ICA basis obtained after learning over 16 000 patches of natural images are shown in (Fig. 2). The ICA algorithm was used to compute the weights A, then the positive restricted weights W, and γ were computed by minimizing their respective values, given that we set $V_{ji} = A_{ji}^2$ (see below). The GCs were constructed from two sets, one with $S_1 = (AX)^+$ and another with $S_2 = (-AX)^+$, in order to retain most of the information in the original image.

3. Denoising: a new role for the Golgi cells

We show here that the Go is able to estimate the variance of the noise in the GCs and provide the right amount of inhibition in order to optimally denoise them. The noisy MFs inputs are modeled as $X' = X + \varepsilon$, where ε is Gaussian with zero mean. We note $S' = (AX')^+ = (Y + \varepsilon')^+$ the noisy outputs of the GCs. Consistent with the hypothesis usually underlying ICA (ICA as a maximum likelihood based on the same prior for all sources [7]), we can assume that the probabilities involved in each GCs are identical, i.e. the Y_i and ε_i' have almost the same distributions for all i. We can thus consider the S_i' as independent realizations of the same scalar random variable $(\bar{Y} + \bar{\varepsilon}')^+$, and write $(1/N)\sum_i^N S_i' \approx E[(\bar{Y} + \bar{\varepsilon}')^+]$. Noting that $\bar{Y}$ is a positive variable and that the noise is small, a first-order approximation to the distributions yields $E[(\bar{Y} + \bar{\varepsilon}')^+] = E[\bar{Y}] + (p_{\bar{Y}}(0)/2)Var(\bar{\varepsilon}) + o(Var(\bar{\varepsilon})^2)$, which demonstrates that it is possible to estimate the noise variance by computing $z'/N = \mu^{\mathrm{T}} S' - \theta$, which is the Golgi cell summing over the PFs input ($\mu = 1$, in theory).

Finally, we make use of the result that the best estimator $\hat{Y}$ of a noisy positive sparse variable $Y + \varepsilon'$ is $\hat{Y} = (Y - \alpha\, Var(\varepsilon'))^+$ for an exponential distribution for Y, $P(Y) = \alpha \exp(-\alpha Y)$ [5]. The term $\alpha Var(\varepsilon')$ is precisely the inhibition of Go in our model scaled by $2/N$, setting $\theta = E[\bar{Y}]$. Given that the noise is amplified by A at the MF–GC synapse, the noise variance is amplified by AA^{T}. The Go inhibition at each synapse was modulated by setting $V_{ji} = A_{ji}^2$ to counteract this noise amplification; all information is local to the glomeruli.

4. Results

Encoding by the GCs of noisy MFs inputs for different level of Go inhibition is shown in Fig. 1. As inhibition level increases, the number of GCs active decreases, whereas the image quality degrades gracefully. The optimal denoising was computed

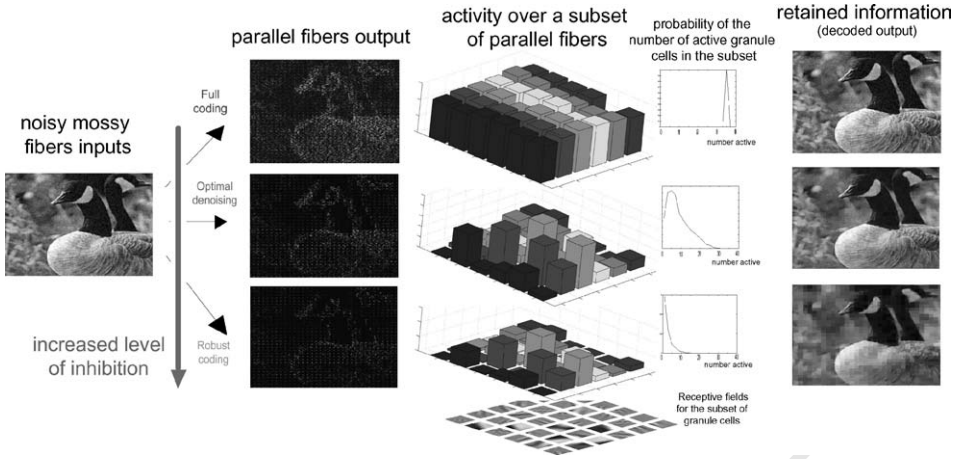

Fig. 1. Encoding by the GCs of noisy MFs inputs for different level of Go inhibition. The same set of 72 ($=2 \times 36$) GCs (positive) is used for coding the entire image by patches of 6×6 pixels. In total, it is equivalent to using 80 000 GCs to encode the entire image (*parallel fibers output*). The average activity of the GCs over all patches is shown in the next column. The rightmost column shows the decoded output using all 80 000 GCs. *Robust coding* demonstrates that the coding is robust to higher level of inhibition and that the image quality degrades gracefully using this encoding scheme.

Fig. 2. Images are used to illustrate the potential statistical structure present in MF inputs. A pixel of the image represents the firing rate activity of a MF. (Left) Learned receptive fields (8×8 pixels) for 64 of the GCs. Each small image shows the MFs inputs that give the maximum GC response. Denoising by Go inhibition. (2nd Left) Original image. (Center) The noisy MFs inputs, using Gaussian noise with a standard deviation of 0.4 of the original image' standard deviation. (Right) Denoised image, reconstructed from PFs activity with overlapping receptive fields.

using the known noise variance injected in the MFs inputs. The receptive field of the GCs were 6×6 MFs pixels. Similar results were obtained for more realistic GCs receptive field sizes (2×2 or 3×3). Similar results (Fig. 2) were obtained as well when the Go was used to estimate the noise variance as described above ($\alpha = 0.13$). The cell summed over the responses of the PFs ($\mu = 1.7 \times 10^{-8}$, $\theta = 0.0085$), or PFs and MFs ($\mu = 1.7 \times 10^{-8}$, $\theta = 0.0098$, not shown).

5. Discussion and conclusion

5.1. Denoising with sparse variables

Since the density of a super-Gaussian random variable, like the exponential density, has a sharp peak at zero, it can be assumed that the small values of S correspond in fact to pure noise, i.e. that their true value should be $S = 0$. Thresholding such values to zero thus reduces noise [5].

Many cerebellar models have used a random weight matrix W with arbitrary Go inhibition to determine the number of active GCs. In our simulations this strategy leads systematically to information loss in the encoding of the PFs. Other models used a representation that decorrelates the MFs inputs, (equivalent to performing principal component analysis (PCA)) [6,8]. With this encoding, the retained information is high, but the coding is not *lifetime* sparse as the number of GCs active is at its maximum most of the time. PCA minimizes *population* sparseness and not *lifetime* sparseness [9].

We suggest that one role of the Go accomplished by summing over all PFs (and MFs) is to construct an estimate of the variance of the noise present. To construct this estimate, we assumed that all PFs had the same noise. If there are multiple noise contributions, these could be estimated by different Gos converging on the same GCs. In this case, the current model still holds, since the variance of independent variables adds, e.g. $Var[x + y] = Var[x] + Var[y]$. Therefore, for optimal noise reduction, one simply needs to sum the inhibition from multiple Gos at the GC, a likely scenario (D'Angelo, personal communication).

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