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Model of granular layer encoding in the cerebellum

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Abstract

7 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
9 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
11 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
13 processings that lead to a robust and efficient representation for coordination.

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

1. Introduction

17 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
19 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
21 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
23 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
25 distributed PFs representation that maximizes the mutual information between MFs

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

2. Model

7 MF inputs terminate in glomeruli where granule cell (GC) dendrites and Go axons
 8 converge to make synaptic contacts. The GCs send their PF axons to the Purkinje cells
 9 and make contact with Go(s), which inhibit(s) every GC dendrites at the glomeruli.
 10 A Go integrates the output of about 6000 GCs and receive inputs from a number of
 11 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

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

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

2.1. Sparse coding in the parallel fibers

23 The hypothesis is that different statistical dependencies in the MFs signals are created
 24 when an animal performs different activities. The statistical dependencies are assumed
 25 to create probabilities in the MFs that will be sparse along some directions. These
 26 sparsest directions and the MF-GC synaptic weights can be found using independent
 27 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.

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

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

1 well-characterized statistical structure in the MFs. Different types of inputs would
 2 provide a different statistical structure, but would not change the results, given that
 3 a sparse representation can be obtained in the GCs. In the simulations, the GCs re-
 4 ceived between 4 and 64 MFs inputs, organized in patches of different sizes, 2×2 ,
 5 3×3 , 4×4 , 6×6 and 8×8 patches. In order to build the desired sparse and dis-
 6 tributed representation at the GCs, a conventional ICA algorithm was used to learn
 7 the matrix A [2] with the *natural gradient* improvement [1]. A biologically plausible
 8 implementation of the learning algorithm could also have been used instead [3,4]. The
 9 ICA basis obtained after learning over 16 000 patches of natural images are shown in
 10 (Fig. 2). The ICA algorithm was used to compute the weights A , then the positive re-
 11 stricted weights W , and γ were computed by minimizing their respective values, given
 12 that we set $V_{ji} = A_{ji}^2$ (see below). The GCs were constructed from two sets, one with
 13 $S_1 = (AX)^+$ and another with $S_2 = (-AX)^+$, in order to retain most of the information
 in the original image.

15 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
 17 GCs and provide the right amount of inhibition in order to optimally denoise them.
 18 The noisy MFs inputs are modeled as $X' = X + \varepsilon$, where ε is Gaussian with zero
 19 mean. We note $S' = (AX')^+ = (Y + \varepsilon')^+$ the noisy outputs of the GCs. Consistent
 20 with the hypothesis usually underlying ICA (ICA as a maximum likelihood based on
 21 the same prior for all sources [7]), we can assume that the probabilities involved in
 22 each GCs are identical, i.e. the Y_i and ε'_i have almost the same distributions for all
 23 i . We can thus consider the S'_i as independent realizations of the same scalar random
 24 variable $(\bar{Y} + \bar{\varepsilon}')^+$, and write $(1/N) \sum_i S'_i \approx E[(\bar{Y} + \bar{\varepsilon}')^+]$. Noting that \bar{Y} is a positive
 25 variable and that the noise is small, a first-order approximation to the distributions
 26 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
 27 it is possible to estimate the noise variance by computing $z'/N = \mu^T S' - \theta$, which is
 the Golgi cell summing over the PFs input ($\mu = 1$, in theory).

29 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 ,
 31 $P(Y) = \alpha \exp(-\alpha Y)$ [5]. The term $\alpha Var(\varepsilon')$ is precisely the inhibition of Go in our
 32 model scaled by $2/N$, setting $\theta = E[\bar{Y}]$. Given that the noise is amplified by A at the
 33 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
 35 information is local to the glomeruli.

4. Results

37 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,
 39 whereas the image quality degrades gracefully. The optimal denoising was computed

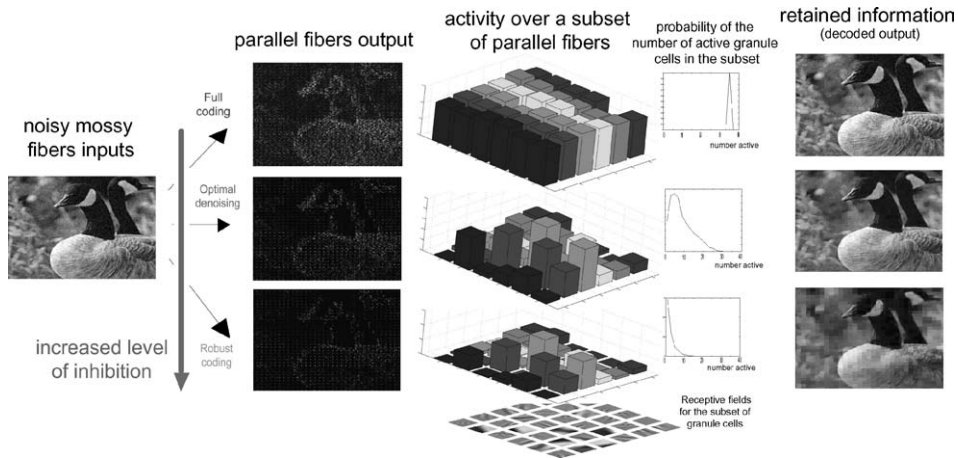


Fig. 1. Encoding by the GCs of noisy MFs inputs for different level of Go inhibition. The same set of 72 ($=2 \times 36$) GCs (positive) is used for coding the entire image by patches of 6×6 pixels. In total, it is equivalent to using 80 000 GCs to encode the entire image (*parallel fibers output*). 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.

- 1 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
- 3 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 ($\alpha = 0.13$).
- 5 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).

1 5. Discussion and conclusion

5.1. Denoising with sparse variables

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

7 Many cerebellar models have used a random weight matrix W with arbitrary Go
8 inhibition to determine the number of active GCs. In our simulations this strategy
9 leads systematically to information loss in the encoding of the PFs. Other models used
10 a representation that decorrelates the MFs inputs, (equivalent to performing principal
11 component analysis (PCA)) [6,8]. With this encoding, the retained information is high,
12 but the coding is not *lifetime* sparse as the number of GCs active is at its maximum
13 most of the time. PCA minimizes *population* sparseness and not *lifetime* sparseness
14 [9].

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

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