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THE PURKINJE UNIT OF THE CEREBELLUM AS A MODEL OF A STABLE NEURAL NETWORK

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Abstract.

A basic neural network is built keeping the real neural connectivity around the Purkinje cell of the cerebellar cortex. The output of a neuron is the transformation, by a linear or non-linear firing function, of the summation of weighted inputs. Covariance learning rules are used for synaptic weights. It is assumed that only synapses between mossy fibers and granule cells, and between parallel fibers and Purkinje cell, are modifiable. The output range of such a unit is studied in the linear and non-linear case searching extremas of the output with respect to mossy fiber inputs. Asymptotic stability is then shown for an isolated linear unit with conditions on several parameters, studying solutions of an associated time-delay equation. This result can be applied to a non-linear unit.

1. Introduction

The study of learning and memory in the cerebellar cortex involves various topics such as, for example, nets acting like pattern associator (Marr 1969; Albus 1971; Fujita 1982), or the identification of circuits to implement classical conditioning (Thompson 1990).

In this paper, the preliminary study of the stability of a functional unit built around a Purkinje cell, and called for this reason a Purkinje unit (Chauvet, 1986), is offered. The Purkinje unit is defined as a hierarchical neural network with external inputs (mossy fibers, climbing fiber and "external context"), and a unique output. The global neural network is thus a network of neural networks. This hierarchy allows us to demonstrate and to anticipate certain comportments of the network at the higher level from the study of the lower levels, specifically from interactions between Purkinje units and their own individual properties (Chapeau-Blondeau and Chauvet, 1991).

Regarding learning and memory abilities, it is shown that Purkinje units are asymptotically stable. Therefore, construction and study of networks composed of Purkinje units is possible with biological constraints, i.e., (i) real connectivity, (ii) specific activating or inhibiting synaptic property, (iii) anatomical hierarchical structure. Stable properties of the network suggest a mathematical interpretation of the functional properties of the cerebellar cortex. However, neurons in a Purkinje unit are assumed to satisfy covariance learning rules (Sejnowitz, 1977; Chauvet, 1986).

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2. Representation of a Purkinje unit

2.1 Description of a Purkinje unit

Output activity along the Purkinje cell axon and input activity along the climbing fiber are respectively denoted as *Y* and *V*. Fig. 1 shows a Purkinje unit with notations as follows: the input pattern $\underline{U}$ is a vector with *g* elements (the number of granule cells) 1 or 0 that represent information propagated along the

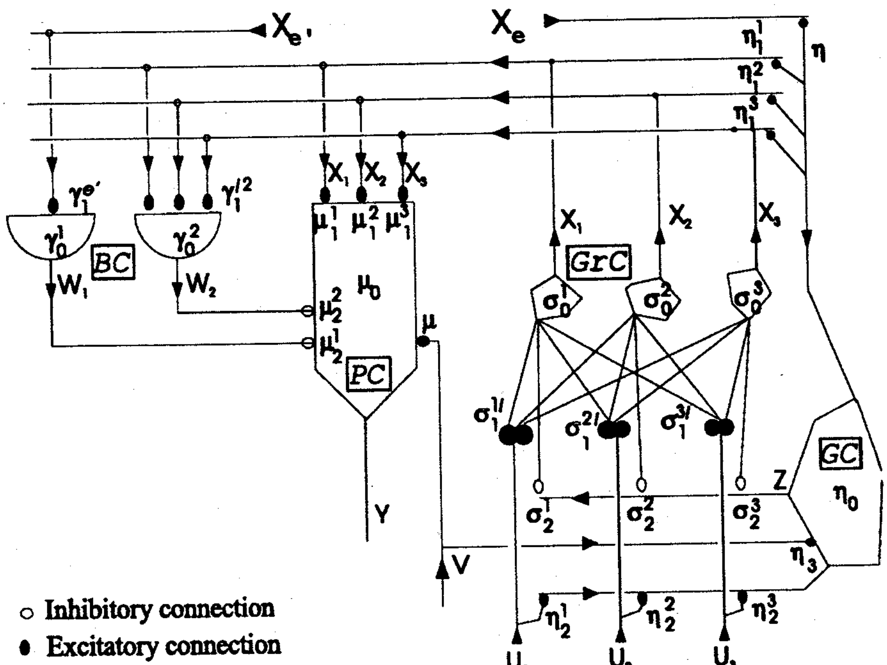

Figure 1:A Purkinje unit. *GC* represent the Golgi cell, *PC* the Purkinje cell, *GrC* the Granule cells and *BC* the basket cells.

g mossy fibers. External context is defined by X_e and $X_{e'}$, i.e. activities propagated along the parallel fibers that are connected with the Golgi cell or with the star cells or basket cells that belong to the unit but do not issue from this unit. X_i is the activity on the parallel fiber that originates in granule cell *i*. Other neurons in the unit are the Golgi cell and *b* star or basket cells. All the synaptic weights are positive and are included in the following equations. σ_l^{ij} and μ_1^i are assumed to be modifiable and positive.

The output *S* of a neuron is $S = F(s_0 + \sum_{i=1}^{n} a_i E_i)$ where there are *n* synaptic weights a_i and inputs E_i, and s_0 a basic activity . F is a firing function that is taken equal to identity or equal to a sigmoïd defined by: $F(s) = (1 + e^{-as})^{-1}$ with $a>0$. With this model of neuron, equations which give *Y* as a function of inputs and unit parameters are deduced from figure 1 (Chauvet, 86).

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2.2 Definition of a symmetrical unit

We call a symmetrical unit a simplified Purkinje unit, for which:
$\forall i,j \in \{1,...,g\}$, $\sigma_0^i=\sigma_0$, $\sigma_1^{ij}=\sigma_1^j$, $\sigma_2^i=\sigma_2$, $\eta_1^i=\eta_1$, $\eta_2^i=\eta_2$, $\beta_{ij}=\beta_j$, $\mu_2^i=\mu_2$, $\gamma_0^i=\gamma_0$, $\gamma_1^{ij}=\gamma_1$
We then obtain:

$$X = F(\sigma_0+\sum_{j=1}^{g}\sigma_1^j U_j - \sigma_2 F(\eta_0+g\eta_1 X+\eta_e X_e+\eta_3 V+\eta_2\sum_{j=1}^{g} U_j)) \ , \qquad (1)$$

and $$Y = F(\mu_0+\sum_{i=1}^{g}\mu_1^i X+\mu V-b\mu_2 F(\gamma_0+g\gamma_1 X+\gamma_1' X_e')) \qquad (2)$$

With a firing function equal to identity, the expressions of X and Y are:

$$X = \frac{1}{1+g\sigma_2\eta_1}(\sigma_0-\eta_0\sigma_2+\sum_{j=1}^{g}(\sigma_1^j-\sigma_2\eta_2)U_j-\eta_e\sigma_2 X_e-\sigma_2\eta_3 V) \ , \qquad (3)$$

and $$Y = \mu_0-b\mu_2\gamma_0+\sum_{i=1}^{g}(\mu_1^i-b\mu_2\gamma_1)X+\mu V-b\mu_2\gamma_1' X_e' \qquad (4)$$

Learning rules are: $$\frac{d\sigma_1^i}{dt}(t) = \beta_i(X(t)-\overline{X}(t))(U_i-\frac{1}{2}) \ , \qquad (5)$$

and $$\frac{d\mu_1^i}{dt}(t) = \alpha_i(X(t)-\overline{X}(t))(Y(t)-\overline{Y}(t)) \qquad (6)$$

with $\alpha_i,\beta_i<0$ for $1\leq i\leq g$, where $\overline{X}$ and $\overline{Y}$ are the weighted means of X and Y. For a time-dependent function $S(t)$, $\overline{S}(t)$ is defined by: $\overline{S}(t)=\frac{1}{M}\int_0^T S(t-\tau)e^{-\frac{\tau}{T}}d\tau$ with $M=\frac{T(e-1)}{e}$.

All results obtained for a symmetrical unit are valid for a Purkinje unit.

3. Mathematical study of retrieving

3.1 Output range in a linear symmetrical unit

We may now search extrema of function $\underline{U}\rightarrow X(\underline{U})$ in E defined by $E=\{\underline{v}\in\mathbb{R}^g \ / \ v_i=0 \ ou \ 1, \ 1\leq i\leq g\}$. The graph of X is a hyperplan for which the derivative with respect to U_j is $(\sigma_1^j-\sigma_2\eta_2)$. If E is bounded then the function $X(\underline{U})$ admits one minimum, denoted X_{min}, and one maximum, denoted X_{max}. Because the positivity constraint implies $X(\underline{U}=\underline{0})\geq 0$ and denoting E_+ the function such that ($E_+(x)=1$ if $x>0$ and $E_+(x)=0$ if $x<0$), X is at maximum for :

$$X_{max} = X(\ \underline{U_+^*}\ ) \ \text{ with } \ \underline{U_+^*} = (\ E_+(\sigma_1^j-\sigma_2\eta_2)\ )_{1\leq j\leq g} \ . \qquad (7.1)$$

Similarly, denoting E_- the function such that $E_-(x)=0$ if $x>0$ and $E_-(x)=1$ if $x<0$, X is at minimum for:

$$X_{min} = X(\ \underline{U_-^*}\ ) \ \text{ with } \ \underline{U_-^*} = (\ E_-(\sigma_1^j-\sigma_2\eta_2)\ )_{1\leq j\leq g} \ . \qquad (7.2)$$

This result shows the interest of the loop {granules-Golgi-granules}. The

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value $(\sigma_I^j - \sigma_2\eta_2)$ can be either negative or positive. As a consequence, the difference between two outputs of X for two different patterns of $\underline{U}$ is greater than if X depended only on σ_I^{ij}.

The function Y: $X \rightarrow Y$ is defined in $[X_{min}, X_{max}]$ and is an affine function. Therefore it takes its extrema only in X_{min} and X_{max}.

In this case, the loop {parallel fibers-Basket cells-Purkinje cell} has the same application as in the Granule cell subsystem: the $(\mu_1^i - b\mu_2\gamma_1)$ value increases the differences between different inputs of X.

We note that only one pattern of $\underline{U}$ can represent either the best or the worst performance.

3.2 Output range in a non-linear symmetrical unit

For such a unit, X and Y are non-linear with respect to U_j. The number of local extrema of functions $X(U_j)$ and $Y(U_j)$ are more numerous than in the linear case because the derivatives of these two functions vary about zero. Indeed, the derivative of $X(U_j)$ is:

$$\frac{dX}{dU_j} = F'(\sigma_0 + \sum_{j=1}^{g} \sigma_1^j U_j - \sigma_2 F(z)).(\sigma_1^j - \sigma_2 F'(z).(g\eta_1 \frac{dX}{dU_j} + \eta_2)) \quad ,$$

therefore $\frac{dX}{dU_j} = \frac{F'(x)}{1 + g\eta_1\sigma_2 F'(x)F(z)}(\sigma_1^j - \sigma_2\eta_2 F'(z))$ where x and z depend of U_j.

F' is a strictly positive gaussian function so that the sign of the derivative of $X(U_j)$ takes the sign of $(\sigma_1^j - \sigma_2\eta_2 F'(z))$. We see that if $\sigma_2\eta_2$ is not too far from σ_I^j, or z and $F'(z)$ vary sufficiently (i.e F is non-linear), the derivative varies about 0. The same holds for $Y(U_j)$. The derivative depends on the sign of $(\sum_{i=1}^{g} \mu_1^i - bg\mu_2\gamma_1 F'(w))$ and on the derivative of $X(U_j)$. Plotting functions X and Y of $\sum_{j=1}^{g} U_j$ with different sets of parameters, we find graphs with two or three local minima and two or three local maxima, including the bounds.

3.3 Intrinsic stability of a symmetrical unit

In this section we study the asymptotic stability of variables X, Y, and modifiable synaptic weights, when all entries are constant. The only sources of time variation are learning differential equations. In such a case, it has been proved that a unit with linear transfer function is asymptotically stable. Numerical simulations have yielded the same result for a unit with a transfer function.

Equation (1) is rewritten as $X(t) = A_0 + \sum_{i=1}^{g} A_i \sigma_1^i(t)$. Because the weighted mean is linear and equal to identity when applied to constants, using equation (5), we obtain:

$$\frac{d\sigma_1^i}{dt}(t) = \beta_i \sum_{j=1}^{g} A_j(\sigma_1^i(t) - \overline{\sigma_1^i}(t))(U_i - \frac{1}{2}) \text{ for } 1 \le i \le g \quad . \tag{8}$$

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Still using equation (5) and setting k=1, it is possible to deduce all the synaptic weights $\sigma_i^j(t)$ from $\sigma_i^1(t)$. Let i=1 in equation (8):

$$\frac{d\sigma_1^1}{dt}(t) = K\left(\sigma_1^1(t)-\overline{\sigma_1^1}(t)\right) \quad K=\sum_{j=1}^{s} A_j\beta_j(U_j-\frac{1}{2}) \text{ and } \forall t\in[-T,0],\ \sigma_1^1(t)=\sigma_1^0(t). \quad (9)$$

We have to note that K=0 if $\underline{U}=\underline{0}$ and in all other cases K<0.

It is clear that if K=0 then σ_1^1 is constant and equal to its initial value. Similarly, if $\sigma_1^0(t)$ is constant then σ_1^0 is a solution of equation (9) because the weighted mean of σ_1^0 is σ_1^0. This, together with equations (8), implies that the efficacies σ_1^i do not vary and that X is therefore constant.

Let us now assume that K<0 and $\sigma_1^0(t)$ are not constant. We need additional transformations to solve this case. First we have introduced an auxilliary function g such that: $\sigma_1^1(t) = \frac{dg}{dt}(t)e^{-\frac{t}{T}}$. After putting g in equation (9) and applying the change of variable u=t-τ in the integral, we obtain:

$$\frac{d^2g}{dt^2}(t) = (K+\frac{1}{T})\frac{dg}{dt}(t)+\frac{K}{M}(g(t-T)-g(t)) \ . \quad (10)$$

The initial function g_0 is calculated by σ_1^0.

It is possible to show the convergence of σ_1^1 using the three following steps (P. Chauvet et al., submitted).

(i) The characteristic equation P for (10) is calculated:

$$P(\lambda) = \lambda^2-(K+\frac{1}{T})\lambda+\frac{K}{M}-\frac{K}{M}e^{-\lambda T} = 0 \ ,$$

where λ is a complex number. The complex roots of P are pairwise conjugated and the set of zeros is infinite, countable and all zeros of P can be ordered in a sequence $\lambda_1, \lambda_2, \ldots$, such that $|\lambda_k|\to\infty$ when $k\to\infty$. For any real a, the number of zeros whose real parts are greater than a is at most finite. All zeros have finite multiplicities (Gorecki, 1989).

(ii) The complex roots of P are localized using asymptotic formulas. We deduce that real parts x_k of complex roots of P are strictly negative if:

$$|K|Te < 4k^2\pi^2(e-1) \ . \quad (11)$$

(iii) g is expressed as a linear combination of terms $\left(w_k(t)e^{\lambda_k t}\right)$, where w_k is a polynomial of degree equal to the multiplicity of the root λ_k minus one. Then, because the two real roots are of multiplicity 1, we obtain $\sigma_1^1(t)=a_1+\frac{dg_1}{dt}(t)e^{-\frac{t}{T}}$ where g_1 is built with complex roots only. With condition (11), σ_1^1 converges with time. As a consequence, synaptic weights σ_1^i and output X converge. From this result and using the same method we have shown that synaptic weights μ_1^i and Y converge.

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4. Discussion and conclusion

In this paper a Purkinje unit has been studied in two cases: (i) when formal neurons are linear, (ii) when formal neurons fire with a sigmoïd transfer function. The condition of stability for an isolated unit has been mathematically determined in the linear case. The capacity of the memory of a simplified unit has been studied by searching for the number of local extremums of the function that associates the output of the unit with an element of the input pattern. In the case of a linear unit, the explicit values of the patterns are obtained for the global minimum and maximum. In the case of a non-linear unit, the number of local extrema can be very high if the transfer function is sharply no-linear. The capacity of classification and separation of patterns is highly increased.

However, further numerical simulations have shown that the results of stability can be extended to the case of a Purkinje unit with non-linear transfer functions (P. Chauvet et al., submitted). The mathematical study of linear neurons in the Purkinje unit is of great interest because of the possible prediction of the sense of variation of synaptic weights. Specifically, they have been determined together with the outputs X and Y as a function of inputs X_e , $X_{e'}$, and V. The sense of variation of synaptic weights of a unit depending of other units that are connected with it, via outputs X and inputs X_e and $X_{e'}$, can be calculated, leading to specific logical variational learning rules for the network of Purkinje units.

The condition of asymptotic stability for the network of Purkinje units has been determined using mathematical method. The same condition of stability has been found for one unit plus a set of conditions on those parameters that are included in the global connectivity of the unit. The network including the delays of transport of activity between units has been implemented on a parallel computer system with transputers. All these different methods lead to a better and more coherent interpretation of the ability of the cerebellar cortex to store and retrieve patterns of activity.

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