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An Efficient Learning Model for the Neural Integrator of the Oculomotor System

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Abstract : Certain premotor neurons of the oculomotor system fire at a rate proportional to desired eye velocity. Their output is integrated by a network of neurons to supply an eye position command to the motoneurons of the extraocular muscles. We develop a biologically plausible self-organizing neural network that can simulate this system, known as the neural integrator. This network intensively uses recurrent connections in its hidden layer. It learns by using a general supervisor that continuously minimizes several error-functions using the Levenberg-Marquardt algorithm and corrects all the weights. We also prove that the network can easily recover from various lesions and perform signal processing more complicated than just integration.

1. Introduction

The oculomotor system is responsible of all the eyes movements. These movements are either volunteer (such as pursuit or saccadic movements) or reflex (such as the vestibulo-ocular reflex : VOR). Let us explain a little bit more : the VOR moves the eyes in the head whenever the head moves, so that the line of sight does not change in space and images remain relatively stationary on the retina.

Thus, the oculomotor system receives different signals :

- from the *paramedian zone of the pontine reticular formation* (PPRF) for the volunteer saccadic movements.
- from the *retina*. The retina gives a signal proportional to the error between the fovea (center of the retina) and the target in a pursuit movement.
- from a *push-pull pair of semicircular canals* (located in the ears). These canals sense angular head velocity and use it as an eye-velocity command to execute the VOR).

All these signals are treated and then the oculomotor system sends command signals to eye-muscle motoneurons.

In brain, the signals are coded in the modulation of each discharge rate around a steady background rate of about 100 spikes/s. The motoneurons of the extraocular muscles, at the other end, drive the eyes with discharge rate (also coded as modulation around a background rate of about 100 spikes/s) that are proportional to a combination of desired eye velocity and position : the eye-velocity component overcoming orbital viscosity (it initially moves the eye), the eye-position component counteracting orbital elasticity (it maintains the eye in an eccentric position).

When the neurophysiologists studied the oculomotor system, they noticed that all the incoming signals were coded in term of velocity but the command signals sent to the eye-muscles motoneurons were coded in term of velocity and position : an integration was clearly occurring.

This concept is illustrated in fig. 1 to explain the generation of the command of a saccadic movement. We understand the role of the integrator : it produces the eye-position component from the incoming eye-velocity signal. The integrated signal is added to the first signal and there are both sent to the muscle-motoneurons.

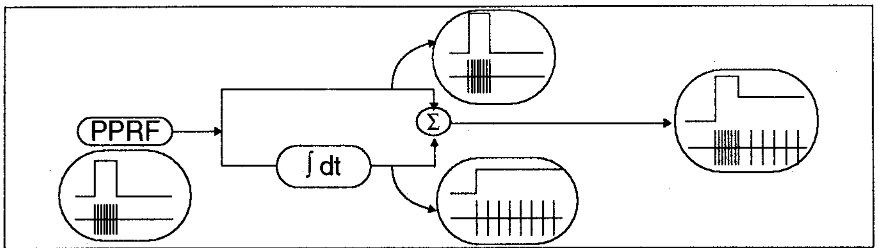

Fig. 1. Principle of generation of a saccadic movement.

2. The neural integrator

Fig. 2 shows the signal processing involved in the oculomotor system where we can distinguish three main inputs: the paramedian pontine reticular formation, the retina and the semicircular canals.

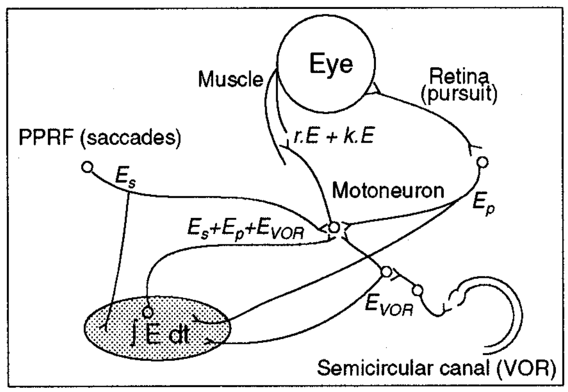

Fig. 2. Signal processing of the oculomotor system.

Fig. 2 clearly shows that a single integrator is shared by all the conjugate oculomotor systems.
Let's characterize this integrator. It was first proposed in 1968 by Robinson and for the neurophysiologists, it has something fascinating : it's the first time that the role of a biological neural network is described in a very sharp way in mathematical terms :

$$y(t) = \int x(t)\, dt.$$

The question of the location of this integrator raised many problems. Finally, Cheron et al (1986) and Cannon and Robinson (1987) showed that it lies in the nucleus prepositus hypoglossi, behind the abducens nuclei. [6]
Becker and Klein (1973) showed, from measurements of the drift of the eye in eccentric positions in the dark, that the time constant, T_n, of the leaky neural integrator in humans is on order of 20 seconds.

3. The different models

The question arises of how to build an integrator with neurons. Positive feedback has always been the favored hypothesis. If cells could excite themselves through local network connections, the activity, once started would be persevered : integration ! Two problems immediately appear : one must integrate the eye-velocity signal without its important background rate and build an integrator with a leak rate corresponding to a time constant of 20 seconds out of neurons with a membrane time constant of 0.005 s (in other words, an increase of four orders magnitude is required). Moreover, the system must be robust : it may not be sensitive to small fluctuations in its parameters.

3.1. Basic models

The first model was proposed by Robinson (1970) who simulated the integrator analogically. He proposed a black box whose transfer function was calculated by several measurements of gain, phase lags, time constant, ... The model was correct but it didn't have the faculty of learning.

The first neural network idea is to connect two neurons with lateral connections. Indeed, the lateral feedback model or laminar network model is a very important type of feedback models, frequently encountered in brain networks : this type of network allows us to elaborate biologically plausible network.

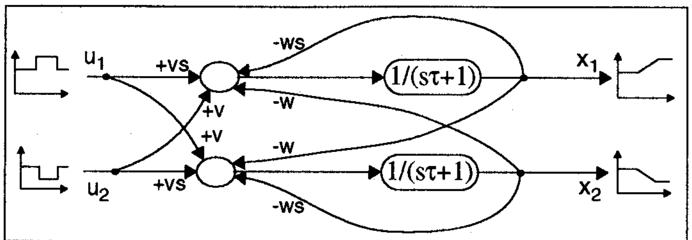

Fig. 3. Basic model of two neurons (Cannon, Robinson [2]).

We see that the dynamics for an individual neuron were modelled by a first-order process with a time constant, τ, of 5 ms. This value is an upper limit for τ based on measurements on membrane potential transients induced by current injection (Rall, 1960).

It's possible to prove that if δu_1 and δu_2 are equal but opposite deviation for a constant level (with $-\delta u_2 = \delta u_1 = \delta u$) the transfer function of each neuron is:

$$\frac{\delta X_1(s)}{\delta U(s)} = -\frac{\delta X_2(s)}{\delta U(s)} = \frac{(v_s - v)\backslash\tau}{s + (1 + w_s + w)\backslash\tau} = \frac{(v_s - v)\backslash\tau}{s + \frac{1}{T_n}} with T_n = \frac{\tau}{1 + w_s + w} \quad (1)$$

We see that if w_s-w = -0.99975 with τ equal to 5 ms and v_s-v = 0.01, then the step response of neuron 1 is that of a simple, first-order, leaky integrator with a time constant of 20 s and a gain of 2.0. On the other hand, if we calculate the transfer function for the case $\delta u_1 = \delta u_2$ (i. e. : the background rate), we find that the step response of neuron 1 is a first-order integrator with τ=2.5 ms and a gain of 1.0. Thus, it's possible to control independently the time constant and gain for DC and push-pull signals.

It's important to notice that this system is the first to solve the two main difficulties for the simulation of the integrator : integrating only the push-pull signals and not the background rate, obtaining a time constant of 20 s.The problem with that system is its weakness : a change of 0.005 in w or w_s change τ from 20 to 1 s !

3.2 Other models

This model generated several other models in order to obtain more robustness. The disadvantage is the fact that all the weights of the connections are fixed and it's impossible for the system to learn something and act like a biologically plausible network.

4. Our learning model

We use the basic network of Arnold and Robinson [3] that is the extension of the model of fig. 3. This network consists of a push-pull input (from, i.e., the semicircular canals), a variable number of interneurons and two motoneurons (fig. 4.). All the neurons were modelled by a summer followed by a first-order lag with a time constant of 5 ms.

If y_i is the output of the interneuron i, we can deduce:

$$\tau \dot{y}_i + y_i = \sum_{j=1}^{N} w_{ij} y_j(t) + \sum_{k=1}^{2} v_{ik} u_k(t) \quad (2)$$

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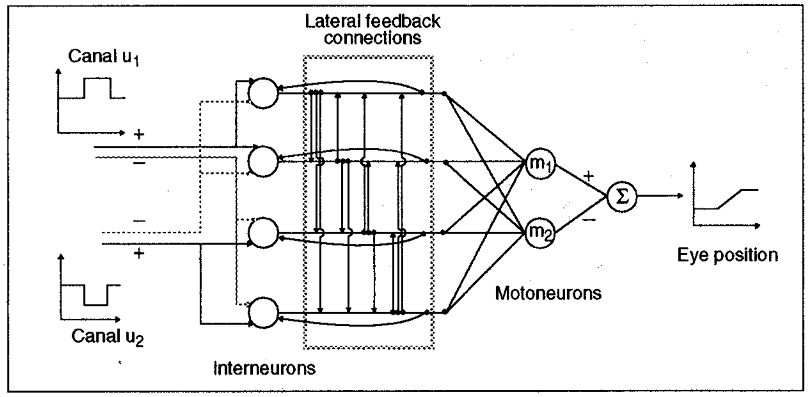

Fig. 4. Learning model for the integrator.

The input of each motoneuron is the weighted sum of the activity of each interneuron : $m_i = \Sigma\, z_{ij} \,.\, y_j$. And finally, the eye position is given by the difference of the firing rates of the two motoneurons : $e_{eye} = m_1(t) - m_2(t)$.

4.1. Learning algorithm

How can we learn a network to integrate ? The solution of back-propagation must be discarded because of the first-order lags combined with a recurrent lateral networks.

We choose a more biologically plausible solution : a general supervisor of all the weights using a general feedback. This supervisor continuously verifies if the output signal is the right integral of the input signals. This system is shown in fig. 5.We use an optimization technique in order to continuously verify if the integrator's working properly. This supervision consists in the minimization of an error-function whose variables are the weights of the full network.

The problem was to choose an optimization technique that could be very quick and that could support the minimization of an error-function depending of a lot of variables.

We chose the Levenberg-Marquardt algorithm which can minimize the sum of the squares of *m* nonlinear functions in *n* variables. In our case, the n variables are the weights v_{ij}, w_{ij} and z_{ij}.

The Levenberg-Marquardt algorithm is a popular alternative to the famous Gauss-Newton method and is of the trust-region type.

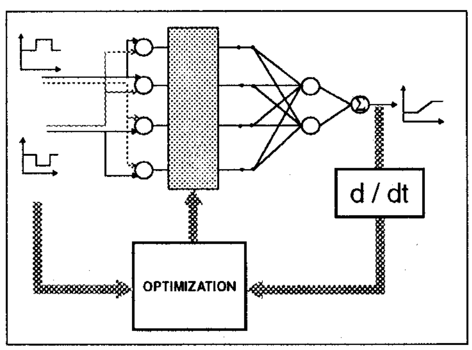

Fig. 5. Supervision of the neural network.

So, if $F(x) = \Sigma f_i(x)^2$, we must find a vector p such that $F(x + p)$ leads us to the minimum very quickly.The quality of the chosen method is due to the fact that it can ultimately achieve a quadratic rate of convergence, despite the fact that *only first derivatives* are used to compute the search direction p. The number of iterations to find a minimum can be, at least, divided by two in comparison with a classical steepest-descent algorithm. [4].

An important question is the correct choice of the error-functions $f_i(x)$. We obtain a first approximation of the desired weights thanks to a fitting between the output curve and a desired curve (so we fixed f_k equals $\varphi(v_{ij}, w_{ij}, z_{ij}, t_k) - y_k$ where f_k is the

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k^{th} error-function, φ is the output of the network at time t_k and y_k the desired output of the network at time t_k). After only about 300 iterations, we obtain a neural network which can properly integrate; we must now learn it to have an human behavior.

We choose thus as error-functions a combination of two parameters : the rate at which images slip across the retina must ideally be null and the time constant of the leaky integrator must equal 20 seconds. After about 50 iterations, we get a correct neural network that simulates the integrator of the oculomotor system.

The continuous supervision system of the network only calculates these error-functions and verifies if the system maintains itself at the minimum. If the system leaves the minimum, new weights are immediately determined and applied.

We developed a training model with four and then sixteen interneurons.

4.2. Results

The training with 16 interneurons provides us some interesting results. Fig 6. shows the integrated signal and its derivative (that ideally must fit the input signal).

First of all, the training leads automatically to a push-pull distribution of the inputs to hidden layer weights v_{ij} (fig. 7.).

The trained network seems biologically plausible : if we examine the output signals of the interneurons, we can note that neurons tend to be either sensitive to eye velocity as well as eye position (burst-tonic) or to eye position alone (tonic). We have also noticed the presence of position and velocity signals in opposite direction that has been noted only rarely in monkeys. All these signals are similar to the neural recordings held in the Faculty of Medicine in Mons.

We trained the network of 4 interneurons by forcing a push-pull distribution of the input weights : we found a solution for the network (which integrated properly) but this solution was not biologically plausible because all the interneurons outputs were burst-tonic. No tonic interneurons appeared : this fact probably discards the model proposed by Robinson in 1985 [1].

We can also remark that we couldn't find any kind of order in the distribution of the lateral connections weights w_{ij}. Fig 8. shows a 3D plot of the weights w_{ij} (i , j = 1..16): this *«chaos»* produces an integrated signal.

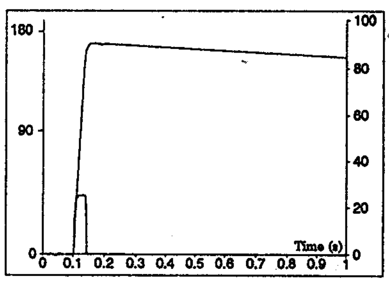

Fig 6. The integrated signal and its derivative

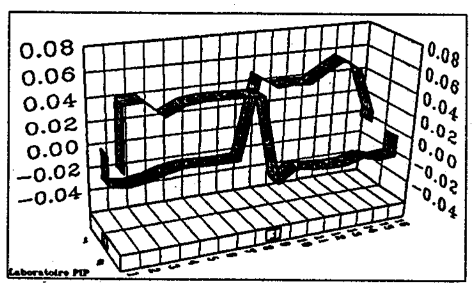

Fig 7. The distribution of the input weights v_{ij} (i between 1 and 2, j between 1 and 16)

4.3. Recovery from lesions and learning

We can measure the correctness of our model by simulating some common lesions. All these lesions were applied to the 16 interneurons network (the more robust). We demonstrate that our model can recover from the more common lesions : hemilabyrinthectomy, a lesion of the peripheral sensory receptors on one side.

Hemilabyrinthectomy was simulated by removing the inputs from one of the canals (we kept only the background rate of 100 spikes/s). After only 250 iterations, the net-

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work was able to integrate properly with only a single canal input.

We killed an interneuron to study the effect : the time constant fell from 20 to 1 seconds (just normal with only 16 interneurons) but after 200 iterations, the time constant of 20 s was recovered with 15 interneurons.

We also learned our model to induce post-saccadic drift. This was done experimentally by having a subject watch a random dot pattern while making spontaneous saccades. After each saccade the entire pattern slid briefly in the direction opposite to the saccade. After several hours, the subjects' eyes would spontaneously drift backwards after making a saccade in the dark. This was simulated in 150 iterations (fig. 9.). This illustrates the ability of the neural integrator to perform signal processing more complex than just integration in order to reduce retinal slip.

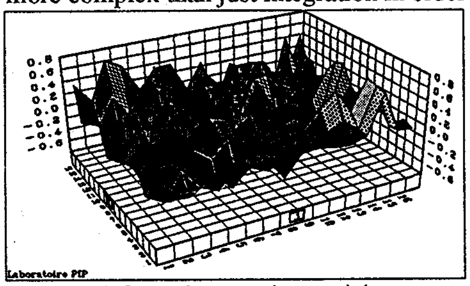

Fig. 8. Lateral connections weights w_{ij} (i and j between 1 and 16)

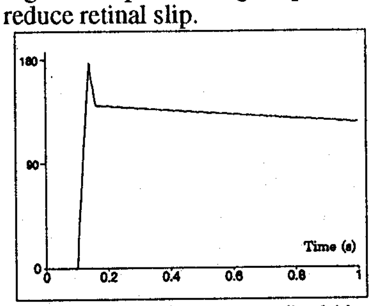

Fig. 9. Induced post-saccadic drift

5. Conclusion

An efficient learning model is proposed for the neural integrator of the oculomotor system. It has the ability of learning and recovering from lesions quite quickly. But this model remains quite simple, a more biologically plausible network will be developed by using a parallel processing and characterize some parts of the network (just like in the brain).

Moreover, the field of applications is wide and large : the first interest of the simulation of the oculomotor system appears in vision (one can apply the VOR to a camera to avoid low acuity). But, more generally, neural integrators can be used in any process control which use feedback loops.

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