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Place-to-Time Code Transformation During Saccades

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Abstract. A neural network model of the control system for saccadic eye movements is suggested. The parameters of the movement are represented in a topographically encoded array of neurons in the brain stem structure Superior Colliculus. The output of the network is a time course of the activity in premotor neurons. Suggested model is an extended version of existing feedback models and it can account for experimentally observed "weighted average effect". Accepted explanation for this phenomenon is the theory saying that the kinematic parameters of the movement are encoded as the "center of mass" of the activity hill in Superior Colliculus. Here a neural network implementation of this idea is presented for the one-dimensional case.

1 Introduction

Neural modelling has a long history and it is only recent development that shifted the motivation for this research from explanatory theories for biological phenomena towards computational devices barely reminding original inspiration. The limits of such approach, however, are now more and more visible, and the lack of new models is forcing researchers to seek closer contacts with the biology as the original source of ideas. An appropriate subject for neural modelling is the oculomotor system since its anatomical structure is relatively simple and well described and there are numerous results of neurophysiological experiments available. The most simple voluntary motor act performed by this system is a saccade. It is a movement that rapidly redirects the eye towards a new point in the environment, the interesting part of the external world being brought to the fovea. The formal description of the problem is straightforward: from the relative displacement of the target to the fovea it is neccessary to compute kinematic and dynamic parameters of the movement. Let us start the analysis with a brief summary of the experimental results available today.

Since the early experiments of Robinson [4, 5] it is clear that the input to the system is provided by two pathways: through the cortical structure called Frontal Eye Fields [1], and through the brain stem structure Superior Colliculus (SC) [6]. The functional organization of both regions is similar and was revealed by electrical stimulation and single cell recording experiments in behaving animals. Neurons are arranged in a topographic map, aligned with the movement space of the eye. A saccade is preceded by an activity in the map and the location of this activity determines the kinematic parameters of the movement. Each neuron has a "movement field" (term borrowed from the sensorial receptive fields) meaning that the activity (firing rate) of the neuron depends on the location of the saccade endpoint. For certain endpoint the activity of the neuron is the highest, decreasing with the euclidean distance of the endpoint from this point. Endpoints corresponding to the neurons in map are gradually shifted, forming a grid over the motor space. The activity preceding a saccade therefore forms a hill, with the top located at the neuron, whose endpoint corresponds to the endpoint of the intended movement. Surrounding neurons fire with progressivelly smaller intensity as the distance in the map increases. The map is two-dimensional [9] and little is known about the ultimate three-dimensional control of the gaze.

The output of the system is high frequency burst of activity in premotor neurons, where the intensity of this burst determines the velocity of the movement and the time integral (duration x intensity) determines the displacement of the eye. The ultimate control of the eye muscles is performed by motorneuron pools located in the pontine oculomotor nuclei. However most of the existing models are concerned only with the level of premotor neurons, assuming linear relationship between premotor and oculomotor structures. Two kinds of premotor neurons has been identified within the brainstem according to the lead time, by which their activity preceeds the movement. Medium lead burst neurons (MLB) have a lead time cca 10 ms, whereas long lead burst neurons (LLB) about 30 ms [7]. Another kind of neuron in the pathway from input to motor neurons is the pause cell. It is characterized by high activity during gaze fixation and silent behavior during the saccade. It was suggested that the activity of these cells inhibits the premotor neurons, saccades being initiaded by a pause cells blocade.

Most popular and widely accepted model of this system was suggested by D. A. Robinson (for recent version see [8]). According to this theory, the transformation of the spatial code in the input into the time course of the activity in premotor neurons is performed by a feedback loop in the brainstem. It is believed that the signal related to the time integral of the burst is fed back to the input via separate neural pathway. This closed circuit performs the neccessary place-to-time code transformation. Despite its success, Robinson's model fails to explain the phenomenon made visible by two kind of experiments. First, when two places in SC are simultaneously stimulated by currents with different intensities, resulting saccade is a "weighted vectorial sum" where the weights are the current intensities ([5]). Second, when one part of SC is deactivated e.g. by lidocain, parameters of the saccades are influenced in a systematic way, leaving the metrics of saccades corresponding to the center of deactivated zone intact [2]. These results could be explained by a theory stating that the kinematic parameters of the movement are encoded as the "center of mass" of the activity hill in SC. Presented model is an attempt to implement such computation into a biologically plausible neural network.

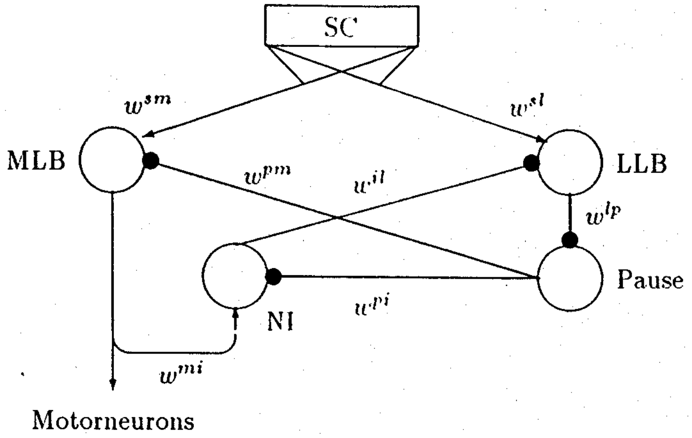

Figure 1: One module of suggested model. Arrows denote excitatory synapses, black dots inhibitory. See text for more details.

2 The Model

The activity of each neuron will be described by a real number from the interval $< 0, \text{max. frequency} >$, where max. frequency varies with the type of neuron. Let us consider a one-dimensional topographic map in SC spanning infinitely in both directions (border effect are neglected). If the endpoint of the movement is at the position x_t relatively to the fovea then the activity of the x-th neuron in the map is described by $SC_x(t) = g(d(x_t, x))$. Here $d(x_t, x)$ is the euclidean distance and g is some monotonically decreasing function. Let this function be identical for all neurons in the map. If we now define coordinates with zero aligned with the fovea a saccade with the amplitude x_t will be preceded by an activity spread described by $f(x - x_t)$. One should notice that this function is symetric i.e. $f(-x) = f(x)$. It is easy to show that for every symetric function it holds $\int x f(x) dx = 0$. Let us now compute the integral

$$\int x f(x - x_t) dx = \int (x_1 + x_t) f(x_1) dx_1 = \int x_1 f(x_1) dx_1 + x_t \int f(x_1) dx_1,$$

where the substitution $x_1 = x - x_t$ was used. The first integral in the rightmost expression is zero, and the result is

$$x_t = \frac{\int x f(x - x_t) dx}{\int f(x - x_t) dx}. \tag{1}$$

This is the equation for computing the "center of mass" of the activity spread in SC as mentioned in the introduction. In Fig. 1 is a neural network realizing this computation. It should be noted that this is only one module whereas the whole system supposedly consists of several thousands of such modules. Let us describe the sequence of events within this module.

The saccade is preceded by an activity hill in SC, the center of mass of this hill determines the displacement (motor error). It is supposed that this hill remains constant for cca. 70 ms. Two separate synaptic connections emmanates from SC: first, topographically weighted, enters LLB, second with an equal weights enters MLB. MLB innervates directly Motorneurons and its activity is in the same time integrated in Neural integrator (NI). This signal is fed back and subtracted from LLB activity. Here the suggestion recently made by Moschovakis el al. [3] was used, namely that the feedback loop is closing at the level of certain burst neurons in the brainstem. Pause neuron fires constantly with high frequency, blocking MLB, until it is inhibited by LLB. This is the moment when the actual movement begins: MLB is deblocked and starts to fire the burst of activity. The saccade lasts until the activity of LLB decreases under certain threshold. The main idea of this model is simple - LLB is the place where the computation of eq. 1 is performed. The integral in numerator is computed by the convolution of the SC activity with a simple line (topographically arranged weights SC $\rightarrow$ LLB), the integral in denominator is computed in MLB by a simple spatial summation and fed back through the NI. The formal description of the model is following. Input-output function of both MLB and LLB is linear within the range $< 0, I_{max} >$:

$$f(I) = \begin{cases} 0 & \text{if } I < 0 \\ kI & \text{if } I \in < 0, I_{max} > \\ \text{max. frequency} & \text{otherwise.} \end{cases}$$

Input (somatic potential) for MLB is given by

$$I_{MLB}(t) = \int w^{sm} f(x - x_t) dx - w^{pm} Pause(t),$$

where w^{sm} and w^{pm} are constants, $f(x - x_t)$ is the activity in SC, dx denotes spatial integration and $Pause(t)$ is the Pause cell activity. For LLB is the input

$$I_{LLB}(t) = \int w^{sl} x f(x - x_t) dx - w^{il} NI(t),$$

where similar notation as before was used. The activity of NI is described simply by

$$NI(t) = \int_0^t w^{mi} MLB dt - w^{pi} Pause(t) = t w^{mi} MLB + C,$$

where 0 is the starting time. Here it is supposed that the integrator is reset by the Pause cell to a zero value after each saccade, therefore C is zero. Note that the activity of MLB is constant for a sufficient period of time. The activity of Pause cells is described by

$$Pause(t) = \begin{cases} \text{max. frequency} & \text{if } w^{lp} LLB(t) < \Theta \\ 0 & \text{otherwise,} \end{cases}$$

where Θ is the threshold which is sufficiently small. The duration of saccade is controlled at the level of LLB and saccade stops when the LLB activity decreases to zero.

$$\int w^{sl} x f(x - x_t) dx - w^{il} NI(t) = 0.$$

Substituting the value for NI and then MLB gives

$$\int w^{sl} x f(x - x_t) dx - t w^{p} \int f(x - x_t) dx = 0,$$

where $w^{p} = w^{il} w^{mi} w^{sm} k$ is the product of the weights. Finaly we have

$$t = W \frac{\int x f(x - x_t) dx}{\int f(x - x_t) dx}. \qquad (2)$$

Here $W = w^{sl}/w^{p}$. Eq. 2 means, that the duration of the saccade is a linear function of the "center of mass" of the activity hill in SC.

3 Results

Simulations were performed with a neural map consisting of 50 neurons covering the range 0-25 deg. In Fig. 2 are the results when input parameter (motor error) was varied from 3 to 20 deg. Duration was measured in time steps (1 step = 1ms), MLB output in dimensionless units scaled to the interval $< 0, 1000 >$. In Fig. 3 were two places (8 and 16 deg resp.) simultaneously stimulated (following methodology from [5]). First current was held constant, second was varied from 0 to the intensity of the first one. For all data linear regression was performed, resulting line is plotted.

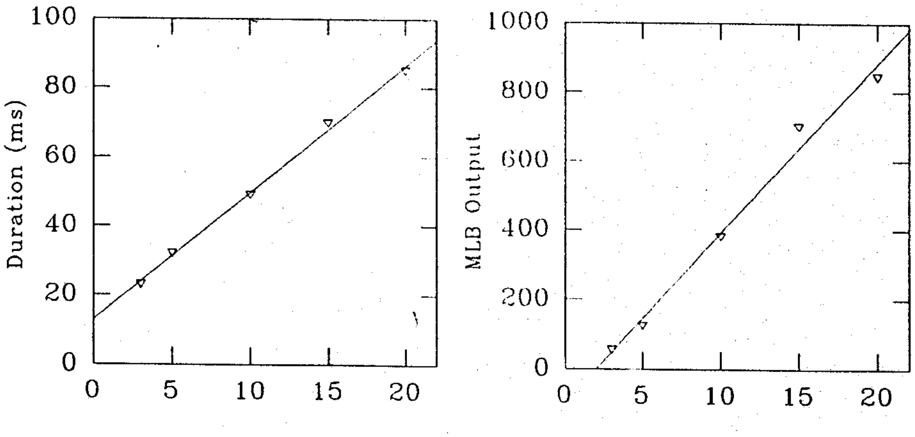

Figure 2: Simulation results for five input values of motor error.

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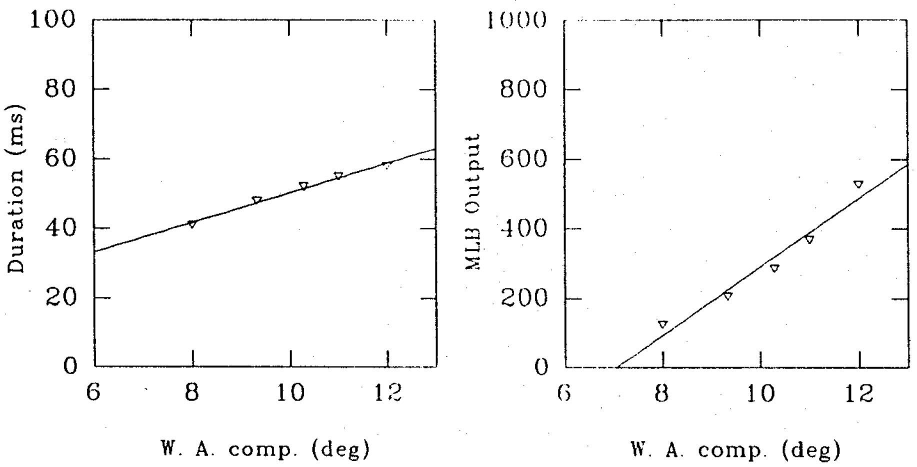

Figure 3: Double stimulation experiment. X axis is computed weighted average.

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