XXIII. NEUROPHYSIOLOGY[*]

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A. CONTRAST DETECTORS[†]

Lateral substractive inhibition may occur at the retinal bipolar level, thereby enabling a contrast-detection process in which each "contrast bipolar" cell could detect any spatial change of the intensity of light incident in its receptive field. In such a situation, the locus of the contrast bipolar cells that fire at any time gives the contour of any sharply contrasted image on the retina at this time. A contrast-detector ganglion cell receiving signals from an area that contains many contrast bipolar cells thereby senses a significant part of that contour as limited by the object size-ganglion field relationship. Its rate of firing is different for different shapes and sizes of the image and for different velocities of a moving image. It is, therefore, desirable to obtain simple expressions relating ganglion tone to the aforementioned parameters that are consistent with, and supported by, neurophysiological evidence.

In particular, we shall be concerned with the dependence of ganglion tone upon the length of the contrast, or edge, of the image and upon its velocity. By applying a process used to model a specific visual ganglion cell,[1] we can obtain one expression for such a dependence. The process to which we refer is the lateral (nonlinear) inhibition at the level of the ganglion cell dendrites. All that we require is, first, that there be a single horizontal dendritic layer for the contrast ganglion cell, and second, that signals arriving there from bipolar cells interact by lateral nonlinear inhibition. Either divisive inhibition of exponential inhibition would be adequate for this task. We chose, for simplicity, to use exponential inhibition[2] in our formulations.

For the sake of simplicity, we assume: First, that the contrast bipolars are uniformly distributed throughout the retina and that their number is large enough to permit the assignment of "linear density" (λ), the number of contrast bipolar cells per unit retinal length, as a constant. Second, we assume that bipolar cells give rise to pulses (action potentials) of constant amplitude (p) and constant duration (τ), and that they contain refractory periods of sorts.

If the image of a sharply contrasted object is stationary with respect to the retina, and l is the length of the edge in the contrast ganglion cell receptive field, this cell receives pulses from n_o contrast bipolar cells, in which

$$n_o = l\lambda. \tag{1}$$

If the image moves with respect to the retina, with velocity of absolute value u, the ganglion cell will receive pulses from n_e additional bipolar cells such that n_e is approximately given by

$$n_e = u \cdot \tau l\lambda^2. \tag{2}$$

The total number, n, of bipolar cells exciting the ganglion cell is given by

$$n = n_o + n_e = l\lambda(1+u\tau\lambda). \tag{3}$$

If the lateral exponential inhibition occurs, the contribution of a single bipolar cell to the activity of the ganglion cell is given by

$$p \cdot e^{-kp(n-1)}, \tag{4}$$

where k is a constant that determines the strength of the inhibitory action. Under the assumption that contributions are additive, the total activity, A_c, of the ganglion cell is given by

$$A_c = \sum p \, e^{-kp(n-1)}, \tag{5}$$

where the summation is over all of the bipolar cells that are firing, that is, n. Then,

$$A_c = np \, e^{-kp(n-1)}. \tag{6}$$

By substituting Eq. 3 in Eq. 6 and renaming the constants, we obtain

$$A_c = K_1 l(1+K_3 u) \, e^{-K_2 l(1+K_3 u)}, \tag{7}$$

where

$$K_1 = \lambda \, p \, e^{kp}$$

$$K_2 = k \, p \, \lambda$$

$$K_3 = \tau \, \lambda.$$

Let the frequency (tone), f, of the ganglion cell be linearly related to its activity; that is,

$$f = aA_c + b, \qquad f \geq 0, \tag{8}$$

where b, if positive, is the spontaneous firing frequency. A negative value of b may be interpreted as threshold.

Let us define z as

$$z \equiv l(1+K_3 u). \tag{9}$$

The maximum value of f occurs when $\frac{\partial f}{\partial z} = 0$, that is, for a value of z (represented by Z_{opt}), in which

$$Z_{opt} = \frac{1}{K_2}. \tag{10}$$

For a stationary object (u = 0) there is an optimum edge length in the retinal field which produces a maximum response. This is

$$l_{opt} = \frac{1}{K_2}. \tag{11}$$

For moving objects of constant edge length, l_o, there is an optimum velocity, U_{opt}, which produces a maximum f and is given by

$$U_{opt} = \frac{1}{K_3} \left(\frac{1}{K_2 l_o} - 1 \right). \tag{12}$$

In any case, the maximum frequency is given by

$$f_{max} = a \frac{K_1}{K_2 e} + b. \tag{13}$$

Since only the absolute value of the velocity u appears in the expressions above, a negative value for U_{opt} has no meaning. Therefore, for a given edge length, l_o, the maximum frequency can be obtained only if

$$K_2 l_o \leq 1. \tag{14}$$

The case $K_2 l_o = 1$ corresponds to the optimum stationary edge, that is, a maximum

ganglion tone that is due to a stationary edge, as given by Eq. 11.

Properties that are qualitatively similar to the ones described here — and that have oriented our work — have been reported for the group 1 ganglion cells in the frog's retina.[3,4]

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B. INSIGHT INTO NEURONAL CLOSED LOOPS FROM SHIFT-REGISTER THEORY[*]

In 1943, Pitts and McCulloch[1] produced three theorems showing that nets with circles could compute only those numbers that a Turing machine could compute with a finite tape. Recently, Minsky and Papert[2] have reported several theorems applicable to them, and our group has presented some in previous reports.[3-6] Since Wiener's pioneering treatment of nonlinear filters, little progress has been made, until last year when Caianiello published two items in Kybernetik.[7,8]

In the meantime, a theory of shift registers has grown up independently, depending on Galois Fields, initiated by Huffman's[9,10] analysis of their use in coding, and a subsequent evolution of theorems of limited generality.[11-24] It has not been recognized that all such devices were within the scope of nerve net theory, although the converse is not generally true in the present state of the art. As their theory is relatively complete[25-29] (except for fully nonlinear shift registers with inputs), it is clear that shift-register theory can sometimes be extended from Boolian functions of 0 and 1 to any finite field of integers, and in some cases to the field of real numbers,[30-32] and perhaps even of complex numbers.

There is no apparent reason why these theories may not ultimately be extended to all closed-loop structures in finite automata of neuron nets of proper neuromimes. We still do not know how to extend this theory to the general problems of nonlinear anastomotic nets with inputs.
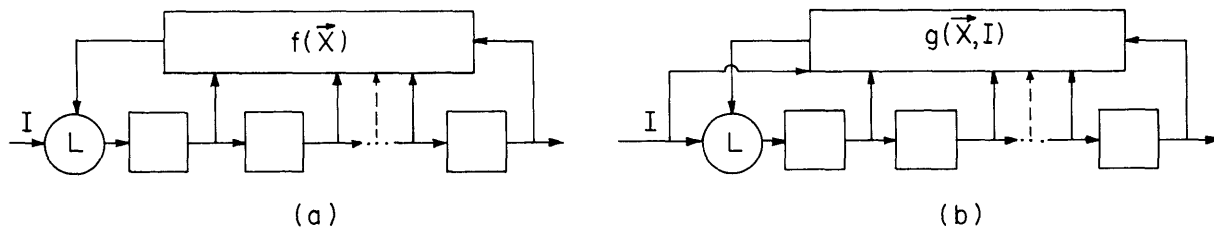

Fig. XXIII-1. Nonlinear feedback shift register for control (a) and command (b).

Even without that, the utility of these notions foreshadows a great extension of neuronal modelling in the design of circuits for command and control, as well as in the programming of commands for which shift registers are eminently suitable. We already have simple solutions for temporal sequences in nonlinear feedback shift registers.

For example, we have found conditions for driving the state of nonlinear feedback shift registers with input through any logical gate of types (a) and (b) (see Fig. XXIII-1). In this figure

I = Input

L = Logical gate

$\vec{X}$ = The vector that defines the state of the n delay elements of an nth-order shift register

$f(\vec{X})$ = Any Boolian function of the n components of $\vec{X}$

$g(\vec{X}, I)$ = Any Boolian function of the components of $\vec{X}$ and I.

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