Comparison of Models for Subtractive and Shunting Lateral-Inhibition in Receptor-Neuron Fields

By G. G. FURMAN*

Bell Telephone Laboratories, Inc., Murray Hill, New Jersey

With 21 Figures in the Text

(Received April 12, 1965)

Summary. Two types of neuronal lateral inhibition in one-dimensional fields of receptors and neurons are considered. The first, which has been called subtractive inhibition in Limulus, is called subtractive inhibition (SI): it assumes that neuronal activity depends on the difference between the total excitation and inhibition. The second type is called shunting inhibition (SHI): it assumes that inhibitory influences cause a shunting of a portion of the excitation-produced depolarizing current. Consideration of the shunting model is dictated by its considerable physiological plausibility. The actions of SI and SHI, examined for a variety of coupling conditions and time-domain depolarizing input stimuli, are shown to be very different. The results indicate that SI is most suited for obtaining (1) a linearity between input and output, (2) a contrasting effect that does not depend on the presence of input discontinuities, and (3) a dependence of the contrasting upon input amplitude. SHI is especially useful if coupling coefficients can be varied to accommodate the various input functions or if, for fixed coupling coefficients, the class of input functions is limited. On the other hand, SI appears most suited for obtaining (1) a nonlinear input-output relation, (2) a relative contrasting only of discontinuities, and (3) a dependence of the contrasting upon input amplitude.

I. Introduction

Lateral inhibition of neurons, activated by a spatially distributed field of sensory receptors, has been found to occur in a number of sensory systems.

* Present address: Defense Research Corp., P.O. Box 3587, Santa Barbara, California.

Lateral inhibition of a subtractive type has been demonstrated in the compound eye of Limulus, and the quantitative relations have been investigated [1–7]. Such inhibition is called subtractive because a measure of the activity of any neuron may be obtained by subtracting its inhibitory inputs from the excitatory inputs. Thus the neuron is totally inhibited if its net inhibition is greater than the excitation.

More recently, a theory of lateral inhibition of a subtracting type has been developed in which the inhibitory inputs act to shunt or divert a portion of the excitation-produced depolarizing current, thereby reducing the neuron firing rate. This notion of shunting has a sound physiological basis [8, 9]. It has been shown that a shunting inhibition model accurately predicts results for a class of visual sensitivity-discrimination experiments [10]. The Weber's law relations which describe the Weber fractions for optical data are predicted by this model even if visual receptors are assumed to be linear rather than logarithmic.

Both subtractive and shunting types of lateral inhibition are capable of enhancing the image contrast in sensory fields of receptors and neurons. A well-known contrast-enhancement effect in human vision is the Mach band phenomenon [11]. Mach bands are...
illusory bands of light and dark that appear adjacent to the boundary between uniform fields that have unequal luminances. Mach bands act to enhance the boundary, thereby making small luminance differences between fields detectable. It will be shown that both subtractive and shunting inhibition can give rise to Mach bands. Lateral inhibition may also provide an explanation for the relatively high degree of frequency selectivity (i.e., sharpness of tuning) exhibited by primary auditory neurons [9].

Experimental evidence supports the presence of lateral inhibition within the receptor-neuron fields mediating visual [12, 13], tactile [14, 15], and auditory [16–19] sensation in mammals. This evidence rests, in part, on demonstrations that the activity of a region within such a field can inhibit (and be inhibited by) the activity of surrounding regions.

As the application of these modes of coupling to the mammalian cochlea has been considered [9], the background necessary for understanding the ensemble inter-unit interactions treated in this paper will, in part, be a repetition of portions of the earlier paper.

A comparison of the action of subtractive and shunting inhibition, under a variety of coupling conditions and positive, time-stationary inputs, shows them to be markedly different. They differ (1) in their capabilities for imposing an upper or lower bound on neuron firing rate, (2) in the linearity of their input-output relations, and (3) in the nature of the sensory image modifications that they can bring about.

In the present paper, we consider the consequences of applying these two modes of inhibition to one-dimensional sensory fields in general, these fields being composed of receptors and neurons. We discuss first a two-unit application of these two modes and then consider a larger population of interacting units, i.e., an ensemble of units, where each unit consists of a receptor and neuron.

II. Four Inhibitory Models

We have mentioned that two modes of interaction are considered. With each of these modes it is possible for the direction of lateral information flow to be either forward or backward (Fig. 1). The coupling coefficient \( a \) determines the degree of interaction, while inhibition is effected by the inputs in the forward case or by the outputs in the backward case.

Let \( v_1 \) and \( v_2 \) be the inputs to the two units and let \( i_1 \) and \( i_2 \) be their outputs. Only when the inputs are presented one at a time (when there is no inhibition present) does \( i_1 = v_1 \) and \( i_2 = v_2 \). In general, the subtractive mode of inhibition is characterized by the functional relations \( i_1 = v_1 - g(v_2) \) and \( i_2 = v_2 - g(v_1) \) for forward inhibition; and \( i_1 = v_1 - g(i_2) \) and \( i_2 = v_2 - g(i_1) \) for backward inhibition. The shunting mode* of inhibition is characterized by the functional relations \( i_1 = v_1/[1 + h(v_2)] \) and \( i_2 = v_2/[1 + h(v_1)] \) for forward inhibition; and \( i_1 = v_1/[1 + h(i_2)] \) and \( i_2 = v_2/[1 + h(i_1)] \) for backward inhibition, where \( h > 0 \).

If there are more than two units, forward and backward subtractive inhibition are described by the relations
\[
i_k = v_k - \sum_{j \neq k} g_{kj}(v_j) \quad \text{and} \quad i_k = v_k - \sum_{j \neq k} g_{kj}(i_j),
\]
and forward and backward shunting inhibition are described by the relations
\[
i_k = v_k / \left[1 + \sum_{j \neq k} h_{kj}(v_j)\right] \quad \text{and} \quad i_k = v_k / \left[1 + \sum_{j \neq k} h_{kj}(i_j)\right].
\]

As a simple case, we consider \( g \) and \( h \) to be linear (or piecewise linear) functions of their arguments. Hence, we have four coupling situations for the two units:

1. Forward subtractive with \( g(v) = av \),
2. Backward subtractive with \( g(i) = ai \),
3. Forward shunting with \( h(v) = av \) for \( v \geq 0 \) and \( h(v) = 0 \) for \( v < 0 \), and
4. Backward shunting with \( h(i) = ai \) for \( i \geq 0 \) and \( h(i) = 0 \) for \( i < 0 \).

For \( v_1, v_2 \geq 0 \) the assumptions, resulting expressions, and plots for the above appear in Figs. 2 through 5, respectively.

All four types of coupling create some contrast enhancement, as it is easily shown that the output contrast ratio \( i_1/i_2 \) is greater than the input contrast ratio \( v_1/v_2 \) for \( v_1 > v_2 \).

If we let the two inputs vary while keeping their ratio fixed (i.e., \( v_2 = \alpha v_1 \), where \( \alpha \) is a constant), then dissimilarities among the four types are seen. The output contrast ratio is independent of \( v_1 \) for the subtractive types (1 and 2) since \( i_1 \) and \( i_2 \) are proportional to \( v_1 \).

For shunting inhibition (types 3 and 4), \( i_1, i_2 \) and \( i_1/i_2 \) all depend on \( v_1 \). With forward shunting, these three variables saturate to asymptotic values, as given in Fig. 4. For backward shunting, with \( 0 < q < 1 \), only \( i_1 \) saturates, while \( i_2 \) and \( i_1/i_2 \) are linear functions of \( v_1 \) for large \( v_1 \). However, with backward shunting, if \( q = 1 \) then for large \( v_1 \) we have \( i_1 \) and \( i_2 \) proportional to \( 1/v_1 \) and \( i_1/i_2 = 1 \) (see Appendix 1 for a proof).

III. Model of Shunting-Inhibition

A number of physiological studies have shown that neuronal inhibition is characterized by increased membrane conductance to certain ions (for recent reviews on this subject see references [20–22]).

Consider a group of neurons, each connected in some complex fashion to one or several receptor cells. *The origin of the term “shunting” will become apparent in a later discussion.*