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SIMULATION OF MOVEMENT DETECTION BY DIRECTION-SELECTIVE GANGLION CELLS IN THE RABBIT AND SQUIRREL RETINA

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Abstract—A veto-gate model of movement detection by direction-selective ganglion cells in the vertebrate retina, first proposed by Barlow and Levick (1965), provides the basis for a model described in this study. The model is a simple network consisting basically of (1) two subunits that have receptive fields with a center-surround organization and an adaptational gain control, (2) a lateral inhibitory pathway, (3) a site of nonlinear interaction, followed by (4) a leaky temporal integrator. The model is tested by comparing its basic properties to those reported in the physiological literature on rabbit and squirrel direction-selective retinal ganglion cells. It is shown that the physiological findings on sensitivity to flashes, moving spots or slits, and ϕ -movement stimuli, can be mimicked quite well by our model. Similarities between the component processes of the subunits and known retinal processes are pointed out. The simulation studies shed a new light on some of the known properties and suggest several new, more revealing, physiological experiments. Such experiments are necessary to develop a full specification of this type of model and to fix more parameter values than is possible at present. Results of some critical experiments are predicted to enable physiologists to falsify or corroborate the model. The simulation studies also help to distinguish use from abuse of this type of model in explanations of psychophysical findings. For example, neither the most complete Barlow–Levick detector nor any stripped-down versions that retain a temporally extended lateral inhibition (which is essential to mimic the physiological findings), respond well to moving random-pixel arrays.

1. INTRODUCTION

1.1. Rationale

The primary goal of the present simulation study is to construct a model of movement detection that can simulate most physiological properties of direction-selective ganglion cells of at least two species—the rabbit and the squirrel. We attempt to relate the properties of the model to intraretinal processes and structures. The physiological findings reported by Barlow and Levick (1965), Michael (1968) and Wyatt and Daw (1975), among others, will be simulated as closely as possible with the model. The physiological requirements strongly constrain both the detailed structure of the model and several of its parameter values. The resulting model then proves to have properties that have not yet been tested in physiological experiments. Our simulations suggest new and more critical physiological experiments. In addition the study indicates that some reported psychophysical findings cannot be explained by versions of the Barlow–

Levick model that fit the selected physiological boundary conditions.

1.2. General properties and form of a Barlow–Levick type model

In electrophysiological studies movement-sensitive, direction-selective ganglion cells in the rabbit retina (Barlow & Hill, 1963; Barlow & Levick, 1965) and in the squirrel retina (Michael, 1968) have been characterized in some detail. The response of a direction-selective ganglion cell varies greatly with the direction of motion. The movement directions evoking a maximum and a minimum response are termed the preferred direction and the null direction, respectively. Usually these directions are 180 deg apart. An additional criterion for labeling a cell “direction-selective” is that its response is invariant to a change in contrast-sign (Barlow & Hill, 1963). The preferred direction has also been shown to be independent of color, contrast, ambient light level and of which part of the receptive field (RF) is traversed by the

stimulus (Barlow & Hill 1963; Maturana & Frenk, 1963). The RF diameter is always much larger than the smallest region from which a direction-selective response can be elicited. A majority of direction-selective ganglion cells in the rabbit retina respond with on and off discharges to stationary flashed spots of light, but the mechanism of direction selectivity does not correlate with the overall RF organization in on- and off-regions (Barlow & Levick, 1965; Michael, 1968).

Barlow and Levick (1965) proposed the following mechanism of direction selectivity: a subunit R (drawn to the right in Fig. 1 below, hence called "R") has an excitatory projection upon a "veto-gate" which receives a delayed inhibitory input from an adjacent subunit L. The veto-gate operates in such a way that the excitatory output from R is only transmitted if the delayed and/or temporally dispersed inhibitory signal from L does not coincide with it. A stimulus moving in the direction L-to-R will first excite L and then R. Because of the delay and/or temporal dispersion, the inhibition from L might just close the gate when the excitation from R arrives. Thus, L-to-R is the null direction, whereas R-to-L is the preferred direction. The RF of the ganglion cell is covered with subfields of this type, all with the same preferred direction. A delay is not strictly necessary as long as the inhibition, elicited by movement in the null direction, temporally overlaps the excitation.

Since the two nonlinearly interacting subfields are not spatially coincident, the Barlow-Levick model will be called a "bilocal" detector (van Doorn, Koenderink & van de Grind, 1984). The "Reichardt-detector" (e.g. Reichardt, 1959) is also of the bilocal type, but it contains a conjunction-gate instead of a veto-gate.

1.3. Basic physiological findings to be simulated by the model

(1) The responses are direction-selective, except for very low and very high stimulus velocities (Barlow & Levick, 1965; Michael, 1968; Oyster, 1968).

(2) The direction selectivity is insensitive to the mean field illuminance and to the sign and magnitude of contrast (Barlow & Hill, 1963; Maturana & Frenk, 1963).

(3) With increasing velocity the "total response" (the total number of spikes per sweep) continuously declines.

(4) The curve representing the maximum response amplitude as a function of velocity has an optimum (Wyatt & Daw, 1975).

Physiological experiments with two stationary and spatially noncoincident flashed stimuli have revealed the following additional properties of direction-selective ganglion cells.

(5) When a single nonmoving stimulus is flashed, it will elicit an on-response in almost any part of the ganglion cell's RF. Such a RF might contain many bilocal detector units. When two flashes presented at different loci in the RF are switched on in the preferred sequence, they will both elicit an on-response. When the flashes are presented in the non-preferred sequence, however, only the first one elicits an on-response. The same pattern is found for off-responses (Barlow & Levick, 1965, Fig. 6).

(6) When the temporal interval is varied between adjacent flashes that are displayed one after the other in the null direction, the response to the second flash is large for long and very short intervals but zero for intermediate intervals (Michael, 1968).

(7) When the spatial separation between the two flashed stimuli is increased, the inhibition decreases for the null sequence and the response is invariant for the preferred sequence (Barlow & Levick, 1965; Michael, 1968).

2. DEVELOPMENT OF THE MODEL

The model will be described stage by stage, going from the top to the bottom of Fig. 1. The gain modules in Fig. 1 will then be described in detail with the help of Fig. 2.

2.1. The subunit RF-structure

There are indications that the excitatory subunit of movement detectors in the mammalian retina is a cholinergic amacrine cell and that the inhibitory subunit is a GABAergic amacrine cell (Caldwell, Daw & Wyatt, 1978; Ariel & Daw, 1982; Masland, Mills & Cassidy, 1984). These neuronal elements may interact at the dendrite of a direction-selective ganglion cell (Torre & Poggio, 1978; Koch, Poggio & Torre, 1983). It seems reasonable to assume that the subunits have a center-surround organization (Werblin & Dowling, 1969; Marchiafava & Torre, 1978). This will be simulated by using a narrow Gaussian spatial weighting function (parameter w_c) for the center region and an antagonistic broad Gaussian weighting function (parameter

w_s) with equal area for the surround region (Enroth-Cugell & Robson, 1966; Rodieck, 1965). The distance between the centers of the left and right subunit-fields is termed the "span", s . The total spatial extent of each subunit's RF is determined by the truncation width of the Gaussian weighting functions (parameter w): see Fig. 1.

The weighted sums of the receptor signals of the center and surround regions of each subunit are fed into separate center and surround leaky integrators. The leaky integrators account for the temporal dispersion occurring when the graded potentials elicited by the visual stimulus are transmitted across synapses and spread over retinal cell bodies and dendrites. If y is the output and x the input function of the leaky integrator, the relation:

$$y(t + \Delta t) = y(t) \cdot \exp(-\Delta t/T) + h \cdot x(t); \quad (1)$$

approximately describes the decay of the contents and the accumulation of the input. The input weighting factor h will be normalized as $h = \Delta t/T$, where T is the time constant of the leaky integrator. If T is then also expressed in terms of the elementary timesteps, Δt , of the simulation ($T = N \cdot \Delta t$) it follows that:

$$y(n + 1) = y(n) \cdot \exp(-1/N) + (1/N) \cdot x(n); \quad (2)$$

where n indicates the sequence number of the simulation time steps. Usually $N \gg 1$ and $\exp(-1/N)$ can be replaced by $(1 - 1/N)$.

The model of Fig. 1 employs 2 different leaky integrators in each subunit's RF. In order to enable the gain module (see below for details) to generate appropriately timed on- and off-responses to moving stimuli, the center C and surround S each have their own relaxation time constant (T_c and T_s). As the signal from the surround is probably transmitted via an extra neuronal step T_s is assigned a larger value than T_c (Werblin & Dowling, 1969, their Fig. 10). The signals from the center and surround leaky integrators are fed into the gain modules, where they will be scaled—in a way to be described below in connection with Fig. 2—and combined by a subtractive inhibition.

2.2. The lateral pathway and the nonlinear interaction

The wave of inhibitory activity from the left subunit in Fig. 1, which passes first through a delay of d time units, must be able to suppress null-direction responses over a broad range of velocities (Michael, 1968; Wyatt & Daw,

Fig. 1. Bilocal detector model embodying the veto-gate proposal of Barlow and Levick. The subunit RF center (C) and surround (S) are represented by Gaussian weighting functions of different width at half height, but of equal area. The weighted sum is determined separately at the center and surround leaky integrators, the output signals of which (x_c for the center and x_s for the surround) are combined antagonistically in the gain module which produces an output signal y (y_L and y_R for the left and right hand modules, respectively), as explained in Fig. 2. The on and off-responses are transmitted as either excitatory (arrow) or inhibitory (small circle) input to the site of nonlinear interaction. The inhibitory pathway contains a delay d and a leaky integrator with time constant T_i . The output of the nonlinear interaction mechanism is fed into a final leaky integrator with time constant T_f . The parameters of the model, including those of the gain box of Fig. 2, are summarized in Table 1. The part of the model to the lower-left of the interrupted line only contributes to the output for stationary flashed stimuli (see text).

1975). Simulations showed that this cannot be achieved with a pure delay in the lateral inhibitory pathway. An additional temporal dispersion (inhibitory leaky integrator I , time constant T_i) is mandatory.

Poggio and Reichardt (1976) showed that the interaction between subunits of a motion detector *must* be nonlinear if the average response of the detector is to show direction selectivity. They showed that a minimal direction-selective model consists of asymmetrical, second-order interactions. If only nonlinearities up to the second order are taken into account, the output of a multiple input system is equivalent to the output of a set of linearly summing two-input systems. This justifies our decision to base most of the computer simulation studies on movement detectors with only two subunits and one

nonlinear interaction (representing the "veto-gate"): see Fig. 1.

A nonlinear, suppressive interaction that implements the veto-gate idea may be accomplished by shunting inhibition (Furman, 1965; Miller & Dacheux, 1976; Marchiafava, 1979), or by stochastic event (epsp) suppression in coincidence-detecting structures (van de Grind, van Schalm & Bouman, 1968). In both cases the output of the nonlinear stage can be approximately described as $e - \alpha \cdot e \cdot i$, where e and i are the excitatory and inhibitory inputs, respectively, and α is a constant. We therefore included this type of nonlinear interaction in our model (Fig. 1). The final leaky integrator F (with time constant, T_F) is included to account for the synaptic and electrotonic dispersion of activity in the dendritic tree of the direction-selective ganglion cell. Since our model does not include a spike generator, its output mimicks the soma potential of the direction-selective ganglion cell. The spike rates are assumed to be a reasonably straightforward reflection of the soma potentials of these cells.

2.3. The gain module

The lateral inhibition in the null direction should be conditional upon relative illumination in the receptive fields, not upon absolute (adapational) luminance values. Thus, some form of dynamic gain control has to be included. The gain modules serve this function: see Fig. 2.

The main mechanisms of visual light and dark adaptation have been shown to reside at the preganglionic level in the vertebrate retina (Dowling, 1967; Shapley & Enroth-Cugell, 1984). Therefore we have included an adaptational gain control in the individual subunits. A Weber-law adaptation mechanism has been shown to be suitable for this purpose (Barlow, 1965; van de Grind, Koenderink & Bouman, 1970; Koenderink, van de Grind & Bouman, 1970, 1971). The basic idea is that the summed and leaky-integrated center signal is divided by a signal representing an average taken over a larger area and a longer time period, $\langle x \rangle$ (see Fig. 2). Koenderink et al. (1970, 1971) showed that such a divisive feedforward gain control is equivalent to the multiplicative type of feedback gain control, which has recently been proposed for the turtle retina (Tranchina, Gordon & Shapley, 1984). The constant θ is added to $\langle x \rangle$ to represent the absolute threshold of the subfield light response (Fig. 2). Thus, the light-adapted center and surround signals equal

Fig. 2. Gain box of the model from Fig. 1. The long-term large-area average of subunit responses $\langle x \rangle$ is used to scale both x_c and x_s . An absolute threshold θ is added to the scale factor. The result is passed through a rectifying differentiator (RD). The center-surround interaction is implemented by a subtractive type of inhibition (indicated symbolically by a T-ending). Only the positive components of the output signal of this stage are transmitted to the nonlinear interaction stage. Whenever necessary the saturation stage keeps the responses within the physiological range.

$x_c/(\langle x \rangle + \theta)$ and $x_s/(\langle x \rangle + \theta)$, respectively. In case $\langle x \rangle \ll \theta$ the maximum gain value of $1/\theta$ is approached.

For reasons to be discussed below the Weber-scaled center and surround signals pass through rectifying differentiators (RD in Fig. 2). Then the scaled surround-signal is subtracted from the scaled center-signal. Subtractive inhibition, which makes the surround a "silent" RF component, is physiologically plausible. Transiently responsive rectifying amacrine cells in the turtle retina, for example, have a center that generates on- and off-responses and a purely inhibitory ("silent") surround (Marchiafava & Torre, 1978). A similar class of cells is hypothesized to function as subunit in the present model (the rectifying differentiators help to implement this assumption: see below). Finally, the signal passes through a saturation stage SAT, which limits the strongest transient peaks to keep them within a physiologically reasonable working range.

Responses of on-off direction-selective ganglion cells to a stationary bright spot are usually transient (Barlow & Levick, 1965; Caldwell et al., 1978). Long, narrow bars or spots moving in the preferred direction usually evoke a distinct on- and off-peak in the peristimulus time histogram. In addition there is evidence that also the *inhibitory* activity elicited by movement in the null direction is more or less transient

(Michael, 1968; Barlow & Levick, 1965, p. 491). The occurrence of these short-lasting responses supports the hypothesis that amacrine cells provide strong input to direction-selective ganglion cells. To mimic these findings rectifying differentiators (RD) are included in the gain module (Fig. 2). The RD subtracts its input at time t from its input at time $t + \Delta t$ and takes the absolute value of this difference. The temporal relation between the stimulus and the RD output determines whether it will be called an on- or off-response component. Without the rectifying differentiators the model may produce tonic response components in cases where the physiological results do not show them. As an example, suppose that a stationary spot is projected for a prolonged period of time onto the center region of the right hand subunit in Fig. 1. In the absence of rectifying differentiators the center signal would then dominate the surround signal in a sustained fashion and the ensuing prolonged excitation would reach the final output stage. This would be in conflict with the physiological findings. Some kind of rectifying differentiator therefore appears to be necessary. This conclusion is further supported by the following physiological findings.

(1) Intracellular recordings from amacrine cells show that they can generate transient and rectified responses (Werblin & Dowling, 1969; Kaneko, 1973; Toyoda, 1974; Marchiafava & Torre, 1978).

(2) Cholinergic amacrine cells release transmitter at both the on- and offset of illumination, but not in between (Masland et al., 1984).

We have thus arrived at a model as given in Fig. 1 with a gain module as schematized in Fig. 2. Table 1 summarizes the model par-

ameters. (Such a table suggests more degrees of freedom to fit physiological results than really exist. The choice of parameter values or ranges is strongly constrained by the required functions and the physiological findings: see Section 3.1.)

Before we confront this model with the physiological findings it is important to make a distinction between detector responses to real vs apparent movement. Without the connections to the lower-left of the dotted line in Fig. 1 the model readily mimicks most physiological findings for moving stimuli. However, it would then fail to mimick responses to flashes. The left subunit would then have a purely inhibitory role so its flash responses would not reach the final output. But, according to requirement (5) in Section 1.3 a single stationary flash should be able to elicit a response from *any* part of the RF. Therefore, we included the part of the model to the lower-left of the interrupted line in Fig. 1. This extension is based on the assumption that many subunits are serially connected within the RF of a single direction-selective unit. Moving stimuli will excite many subunits in succession and when movement is in the null direction, this will lead to a chain-wise inhibition. The left subunit in Fig. 1 will then be inhibited by the subunit to its left (not drawn) in exactly the same way as it inhibits the subunit to its right. The left input of the final integrator is therefore nonfunctional for a stimulus moving in the null-direction. Its activity cycle then precedes and does not significantly influence the one of immediate interest. In that case the model network functions as if the part to the lower-left of the dotted line in Fig. 1 were not there. For spatially separated nonsimultaneous flashes on the other hand, such as used in apparent-movement experiments, the left input to the final integrator does influence the results. Real movement and apparent movement activate the proposed network differently. Both types of stimuli should therefore be used in physiological experiments to fully analyze a Barlow-Levick type of bilocal detector. Experimenters have not always been aware of this problem.

3. SIMULATION RESULTS

3.1. The choice of parameter values

To make a modelling study more than an exercise in curve fitting one should preferably fix most or all model parameters. This is not strictly possible in our case, since we wanted to simulate

Table 1. Parameters of the movement detector

s :	distance between centers of the left and right subunit fields;
w_c :	Gaussian weighting constant for the center region;
w_s :	Gaussian weighting constant for the surround region;
w :	truncation width of the Gaussian weighting functions;
d :	delay in the inhibitory pathway;
T_c :	relaxation time constant of the center leaky integrator;
T_s :	relaxation time constant of the surround leaky integrator;
T_i :	relaxation time constant of the inhibitory leaky integrator;
T_f :	relaxation time constant of the final leaky integrator;
θ :	adaptation threshold;
Sat:	saturation level;
α :	inhibitory constant.

results obtained from different species, from different animals of the same species, and from cells varying in retinal eccentricity or other potentially important characteristics. Nevertheless it proved possible to strongly limit the range of variation of the parameters. All results reported below were obtained with the following narrow ranges of parameter values: w_c , 5–6; w_s , 9–12; w , 11–15; T_c , 6–10; T_s , 16–30; T_F , 5–8; $\theta = 1$; SAT = 10; α , 0.3–0.7; T_i , 10–25. Only s and d were varied over a somewhat greater range and their values are given in the legends to the figures. We did not systematically attempt to limit or decrease the ranges of variation of the parameter values. Distances are given in “distance units” (d.u.) and times in “time units” (t.u.) of the simulation, while velocities are given in “velocity units” (v.u. = d.u./t.u.). These units acquire real-world values by comparison of simulated to physiological results. A similar *post hoc* mapping is necessary to give real-world values to luminance units (l.u.) and response units (r.u.) of the simulation.

3.2. Simulation of physiological findings

(A) *Center-surround antagonism.* When the diameter of a spot, projected onto the center of one of the RF's of a bilocal detector, is gradually increased and the other subunit receives no input at all, the response rises steeply until the edges of the spot enter the surround region. After this peak the response slowly declines as the spot covers more and more of the surround. The resulting response curve (not shown) corresponds very well to the response pattern obtained from amacrine cells by Marchiafava and Torre (1978, their Figs 1 and 3).

(B) *Response to a moving bright bar.* Figure 3 shows the generation of the response to movement in the preferred direction. The final output of the bilocal detector has two distinct on- and off-peaks (Fig. 3d). This type of response is similar to that recorded from a direction-selective ganglion cell in the cat retina by Stone and Fabian (1966) and reproduced here in Fig. 3e. A null-direction response was completely absent. The responses to a moving dark bar are identical, provided that the stimulus contrast is the same.

(C) *Insensitivity to background light intensity and contrast magnitude.* As required, but as a rather trivial consequence of the structure, our model was insensitive to the background light intensity, except at extremely low luminances. It is more interesting to look at the influence of

Fig. 3. Responses to a bright bar moving in the preferred direction (pd). (a) Luminance at the center of the right-hand subunit changes between 1100 l.u. (bar) and 100 l.u. (background); velocity 2 v.u. The leading edge of the bar elicits an on-response and the trailing edge an off-response from the right-hand subunit (b). As the edges of the bar pass over the left subunit, on and off-inhibitory waves are generated (c). Due to the delay of 17 t.u., the inhibition only suppresses the tail of the right hand subunit's off-response. Consequently, the final output (d) consists of an on and off-response. (e) Response of a direction-selective ganglion cell in the cat retina to a similar stimulus (from Stone & Fabian 1966, reproduced with permission of the authors and Science; © 1966 by the AAAS). Comparison of (d) and (e) shows that 1 t.u. corresponds to 13 msec and 1 r.u. corresponds to 2.6 spikes/sec. Detector parameters: $s = 40$ d.u.; $d = 17$ t.u.

contrast. Barlow and Hill (1963) found that the discharge was almost uninfluenced by the intensity of the stimulus spot as long as there was sufficient contrast. Below a contrast of 1.2 they could hardly find a response at all. The simulation results for movement in the preferred direction are shown in Fig. 4a. For low contrasts the simulated response increases with contrast, whereas it is constant for high contrasts. Since inhibition is weak at low contrasts the null direction curve (Fig. 4b) has an optimum.

(D) *Velocity tuning curves.* Examples of simulated velocity tuning curves are shown in Fig. 5a–d. The total-response measure is plotted as a function of velocity in Fig. 5a and b for the preferred direction and null direction respectively. The maximum response is plotted in the same format in Fig. 5c and d. As can be seen by comparing the simulation results of Fig. 5 with the physiological findings of Wyatt and Daw (1975), which are reproduced in Fig. 5e, the physiological preferred-direction curves are mimicked quite well. Judging from the literature

Fig. 4. Total response measure for a spot moving in (a) the preferred direction (pd) and (b) the null direction (nd), both plotted as a function of contrast magnitude. (Note the logarithmic scale on the abscissa.) Contrast magnitude is defined as spot luminance divided by background luminance. The total response is calculated as the surface under the final output response curve. Detector parameters: $s = 15$ d.u.; $d = 5$ t.u. Stimulus parameters: background luminance 100 l.u., bar luminance variable, velocity 3 v.u.

the dependence of the null-direction response on velocity in direction-selective ganglion cells has not been explored in great detail. From the scarce data we have the impression that the null-direction responses of our model are too strong both at low (0.2–0.35 v.u.) and at high velocities (3.5–63 v.u.).

For increasing values of the delay parameter d the simulated response curves deviate more and more from the typical example of Wyatt and Daw (1975), included in Fig. 5e. The total response for intermediate to high velocities (2–20 v.u.) increases strongly both for the preferred direction and the null direction. The reason for this is that the inhibition is delayed too much to impede transmission of excitatory responses to fast-moving stimuli. Thus to prevent a conflict with results such as those of Wyatt and Daw, the delays should not be too long. To relate this to the physiology of the retina, it should be noted that, provided the well-known leaky cable model holds, the delay will be proportional to the length of the cellular processes (Jack, Noble & Tsien, 1975). Thus, our simulations suggest that *short-range interactions* are most important in establishing a strongly suppressive mechanism of direction selectivity in the retina.

(E) *Responses to sequences of stationary bars.* This simulation concerns an experiment by Barlow and Levick (1965, their Fig. 6, reproduced here as Fig. 6e). The onset of a first bar

is shortly followed by the onset of a second bar (presented at a different locus either in the preferred direction or in the null direction). Then, after both bars have been on for a relatively long period of time, they are switched off in the same sequence, with the same asynchrony as at onset. As in Barlow and Levick's experiment, the final output of the model for the null sequence consists of a brief on- and off-response to the first bar. For the reverse sequence, two on- and off-peaks are generated (Fig. 6a–d).

Barlow and Levick reported that the behavior demonstrated in Fig. 6e can be elicited from almost any part of the RF of direction-selective cells in the rabbit retina. We did not intend to simulate this with a single bilocal detector. The finding can be explained by assuming that the unit of Fig. 1 is serially repeated in the RF of the direction-selective unit and that the overlap between the many subunits is considerable.

(F) *Responses to sequences of stationary bars with a varying temporal interval.* As opposed to the previous experiment, the second bar is now presented *after* the first has been switched off, so there is no temporal overlap. Michael (1968,

Fig. 5. Simulated velocity tuning curves for total and maximum responses to movement in the preferred direction (a and c) and the null direction (b and d) for a bar of 100 l.u. on a background of 10 l.u. Detector parameters of the simulation: $s = 15$ d.u.; $d = 4$ t.u. The curves for the preferred direction can be compared to physiological results obtained by Wyatt and Daw (1975) for an on-type direction-selective ganglion cell (e). The total response R_{tot} in (e) is expressed in "number of spikes" (right ordinate, dotted line). The maximum response R_{max} (solid line in e) is the maximum number of spikes/sec (left ordinate). Part (e) is reproduced with permission of the American Physiological Society and the authors. Comparison of the simulation results to those of the physiological experiment shows that 1 v.u. corresponds to 0.5 deg/sec and that 1 r.u. corresponds to 2.4 spikes/sec.

Fig. 6. Simulation of the static flashed-bar experiment of Barlow and Levick (1965). Some of the original results are reproduced in e, with permission of the *Journal of Physiology* and the authors. The left hand column in (e) indicates the positions of the bars in the receptive field. The other two columns in (e) show retinal ganglion cell responses and the photomultiplier signals, which indicate when bar A and B (of the left hand column in e) are switched on and off. Our corresponding simulation results are shown in (a)–(d). The simulated response to the null sequence (first bar on the center of the left-hand subunit, second bar on the center of the right-hand subunit) only consists of a transient on- and off-response to the first bar (c). The reverse sequence (preferred direction) evokes on- and off-responses to both bars (d). One t.u. corresponds to 6.0 msec. Detector parameters: $s = 8$ d.u., $d = 18$ t.u. Stimulus parameters of the simulation: bar 1 is switched on at 10 t.u. and off at 110 t.u. Bar 2 is switched on at 30 t.u. and off at 130 t.u. Mean luminance 10 l.u., luminance of the bars 200 l.u.

Fig. 6, reproduced in Fig. 7c) reported that for very short intervals, the preferred direction response to the second bar was facilitated slightly while the null direction response to the second bar was unimpaired. For intermediate intervals, the null direction response was completely suppressed whereas the preferred-direction response was neither facilitated nor inhibited. For long temporal intervals, the preferred direction response was constant and the null-direction response recovered slowly. This behavior was simulated in great detail by our model (Fig. 7). Note that “apparent facilitation” is obtained for the preferred direction without the inclusion of an explicit facilitation mechanism in the model. It is caused by the off-response of the first flash. Thus wrong conclusions about facilitation could be drawn from the responses of this type of network if every spike occurring after the onset of the second flash were counted as a response to this flash (Michael, 1968).

The assumption that the effective inhibition is subjected to a delay and a leaky integrator operation (Fig. 1) seems justified by the observation that the null-direction response curve is first constant, then falls *steeply* to zero and finally recovers *slowly*. If the pathway only contained a leaky integrator a decline would already be expected for very short inter-flash intervals in Fig. 7. If there were only a delay, a much steeper recovery would be expected (as well as a steep fall at about 30 msec).

(G) *Spatial distribution of inhibition*. To reproduce finding (7) of Section 1.3, one needs a direction-selective unit with more than 2 subfields. In our bilocal model inhibition in the null sequence cannot diminish gradually while excitation in the preferred sequence is required to be constant. The inhibition and excitation arise from the same subunit output in our model and always change in the same way when the stimulus is altered. In principle a subunit with a separate spatially-asymmetric inhibitory channel could account for the observations, but there are no physiological findings to support such a proposition. We therefore simulated multiple-

Fig. 7. Simulation of the temporal interval experiment by Michael (1968), which is described in the text. Two flashes are presented one after the other, either in the preferred (a) or in the null sequence (b). The total response to the second flash is plotted as a function of the time interval between the flashes. Data obtained by Michael (1968) are replotted in (c), where ($\square$) refer to movement in the preferred direction and ($\blacksquare$) to movement in the null direction. Detector parameter values: $s = 15$ d.u.; $d = 70$ t.u. Stimulus parameters of the simulation: bar 1 is switched on at 5 t.u. and off at 25 t.u. mean luminance 10 l.u., bar luminance 110 l.u. Comparison between simulation results and real-world values shows that 1 t.u. = 2.9 msec and 1 r.u. = 0.024 spikes.

subunit Barlow–Levick systems. In one version the delay in the inhibitory pathways from 4 separate L-units (L and R refer to the convention of Fig. 1 again) depended linearly on the distance to the one R-subunit (in agreement with cable theory: Jack et al., 1975). The inhibitory signals generated by different subunits were summated, passed through a common leaky integrator and fed into the nonlinear interaction stage. In other respects this model conformed to the scheme of Figs 1 and 2. Because of the small number of subunits in the simulation both the null and the preferred sequence response amplitude vs flash-distance curves had a somewhat ragged appearance (not shown). Nevertheless the basic physiological findings of Barlow and Levick (1965) and Michael (1968) for this experiment were mimicked quite well. The output for the preferred sequence is almost constant for increasing distance between the flashes, whereas in the null-direction increasing distance led to increasing response. In the other version of the multiple-subunit model inhibition-strength was assumed to be a decreasing function of the distance from the R-unit, whereas the delay was kept constant, irrespective of the distance. This led to similar results.

In both multiple-subunit versions of the model the degree of overlap, calculated as $(w - 0.5s)/w$, is a significant factor in shaping the mentioned response curves. If the overlap is too small, the spot might hit a surround region and not elicit any lateral inhibition at all. For our model we found that an overlap of 73% mimicks the physiological behavior very well. This result suggests that a fairly high degree of overlap is necessary in a multiple-subunit movement detector. The preferred-direction response declined with increasing overlap, but since the null-direction response remained strongly suppressed, the degree of direction selectivity tended to stay high.

3.3. Predictive simulations and proposed experiments

(A) *Sequences of stationary bars with varying degrees of temporal overlap.* Despite the many physiological experiments on direction-selective ganglion cells, a modeller cannot always find the answers to essential questions of model-construction in these reports. For example, it is hard to decide from literature data whether or not on- and off-component responses interact directly. We assumed that they do in our bilocal

movement-detector model. It is possible in principle to falsify or corroborate such an assumption in physiological experiments. One such experiment, which we have simulated and which is similar to the one of Fig. 6, runs as follows. The on- and offset asynchronies between temporally overlapping spots are varied from zero to the duration of the first flash (when “on” of the second flash coincides with “off” of the first). The left bar is projected onto the center of the left subunit, the right bar onto the center of the right subunit. The bars are switched on and off in the null as well as in the preferred sequence. If on–off interactions do occur, there will be a reversal in direction selectivity when the onset of the second bar approaches the offset of the first bar. For the preferred sequence the onset of the second bar will elicit an inhibitory wave suppressing the off-response to the first bar, while for the null sequence the on- and off-responses are unimpaired.

(B) *Insensitivity to moving random-dot patterns.* A very interesting finding in our simulation study was that the Barlow–Levick type of bilocal detector is relatively insensitive to moving random-pixel arrays. In such a pattern contiguous dots or pixels are randomly given either zero luminance (black) or a luminance of $2\langle L \rangle$, if $\langle L \rangle$ is the average luminance.

The insensitivity holds both for the null direction and the preferred direction and it results from the fact that the inhibition has a temporally-dispersed character (Fig. 8). The center, surround, and lateral-inhibitory leaky integrators in the circuit sustain a substantial amount of inhibition at any moment after the onset of movement of the noise pattern. Yet they cannot be missed in this model if one wants to mimick results such as those of Fig. 7 (Michael, 1968) and the response suppression over a broad range of velocities in the null direction (Barlow & Levick, 1965).

Our simulations showed that the Barlow–Levick detector described in this paper is much less sensitive to moving noise patterns than a conjunction-gate type of detector (Reichardt, 1959). In order to compare the Barlow–Levick scheme with that of Reichardt we implemented the latter type of detector in the unidirectional form outlined by van de Grind, Koenderink and van Doorn (1986). The Reichardt-detector simulation program was a slight modification of a program originated by Koenderink and van Doorn (personal communication). It implements (1) a nonlinear interaction of the multi-

Fig. 8. Model responses to a random-dot pattern moving in the preferred direction. The luminance at the right-hand subunit's center is given in (a). The pattern continuously evokes on- and off-responses from both subunits. In the lateral inhibitory pathway these responses are converted into a sustained inhibition (b). This results in a small final output (c). With equal parameter settings a bar moving in the preferred direction evoked a maximal response of 7 r.u. Note in (c) that a maximum is reached when the random-dot pattern first crosses the right-hand subunit-center. This transient response is due to the slow build-up of lateral inhibition. The steady-state response to random-dot movement in the null direction was of almost equal amplitude as in the preferred direction. Detector parameters: $s = 15$ d.u., $d = 5$ t.u. Stimulus parameters: background luminance 100, modulation depth 1.0, velocity 3 v.u.

plicative type (Excitation left $\times$ Excitation right) and (2) a delay in the projection from the left onto the right subunit. With moderate pixel luminance values, the simulated veto-gate detector responded about 100 times weaker to moving random-pixel patterns than this version of the Reichardt conjunction-gate detector.

At this point it is of importance to underline a crucial difference between a Reichardt and a Barlow-Levick type of bilocal detector. In the former there is no compelling reason to postulate a temporal dispersion in the lateral pathway, since it is commonly envisaged as a narrow velocity-bandpass system. An integrative lateral interaction would ruin the velocity-tuning. For the Barlow-Levick detector on the other hand, the wide rejection band for velocities in the null direction can only be obtained if inhibition is dispersed in time. Even if the rectifying differentiators, the on-off interactions, visual adaptation and the lateral delay were eliminated from the model, and for a wide range of center-surround interaction principles, we found the same result: *the Barlow-Levick type of movement detector is insensitive to moving random-dot patterns.*

(C) *Responses to moving sinusoidal gratings.* Moving sinewave gratings have been used exten-

sively in vision research, except in the study of direction-selective ganglion cells. Therefore our simulation results for moving sinewave gratings may have predictive value. Due to the rectifying property of the model, its responses exhibit a frequency-doubling effect (Fig. 9a and b). This effect has also been described for responses of amacrine cells to light flicker in carp (Toyoda, 1974) and cat (van de Grind, 1981, Fig. 2) and even for psychophysically measured flicker responses in humans (Kelly, 1966). For relatively low spatial frequencies the responses to sinewave gratings moving in the preferred direction consist of a periodic pattern of separate response-peaks (Fig. 9a and b). In the range of high spatial frequencies, a permanently high level of inhibitory activity prevents the generation of these peaks (Fig. 9c and d). Responses in the null direction are small and increase slowly with decreasing spatial frequency. Although these properties remain to be tested physiologically, it is worthwhile to note that some of the direction-selective ganglion cells recorded by Oyster (1968) responded to moving black-white gratings with periodic discharges.

Fig. 9. Responses of the detector to moving sinewave gratings. (a) shows the luminance at the right-hand subunit's center as a function of time for a sinewave period of 380 d.u. and a velocity of 3 v.u. Due to the delay and leaky integrator in the lateral pathway, the inhibitory signal is temporally shifted with respect to the excitatory events. This shift results in a partial transmission of excitatory information to the final output stage (b). In (c) and (d) the total response is plotted as a function of the sinewave period for the preferred and null direction, respectively. Detector parameters: $s = 15$ d.u.; $d = 12$ t.u. Stimulus parameters: background luminance 100, modulation depth 1.0, velocity 3 v.u.

4. DISCUSSION

It was shown that the bilocal Barlow–Levick type of detector model of Figs 1 and 2 satisfies most physiological requirements. Only experiments revealing a spatial decay of inhibition cannot be mimicked without adding more subunits. The detailed simulations of the bilocal model clarified several aspects of the direction-selective mechanism that are easily overlooked in paper-and-pencil analysis. For instance, it could be inferred from the shape of velocity tuning curves that short-range interactions are most important in the mechanism of direction selectivity. The bilocal model is sufficient for most purposes, even though it seems clear that there are many more than two subunits in the RF of retinal direction-selective ganglion cells. A physiologically plausible multiple-subunit model with a distance-dependent inhibition by subunits was also simulated. It was found that a high spatial resolution of direction selectivity (Barlow & Levick, 1965; Michael, 1968) can be achieved even if the subunits have relatively large, overlapping receptive fields.

Barlow and Levick's veto-gate model, although designed for the retina, shares a number of features with cortical direction-selective cells, e.g. velocity-tuning (Maunsell & Van Essen, 1983), and a spatial decay of inhibition (Goodwin, Henry & Bishop, 1975; Ganz & Felder 1984). However, there are also important differences between the behaviour of a bilocal Barlow–Levick detector, such as the one of Figs 1 and 2, and most classes of direction-selective cells in the cortex. Schiller, Finlay and Volman (1976) described six types of S (simple) cells, showing various modes of edge sensitivity and direction selectivity. Only the S1-type can readily be simulated by the type of Barlow–Levick detector that has been developed for the retina. It is not possible either to mimick the responses of cortical cell types S2–S6 with the present model or with networks consisting of uniform chains of this unit. Instead, one would need more than two interacting elements with different edge-sensitivities (Ruff, Rauschecker & Palm, 1987). Even though the responses of CX (complex) cells to moving bars can be mimicked quite well by our present version of the Barlow–Levick detector, the model fails the moving random-dot test. Hammond and MacKay (1975) showed that CX cells respond vigorously to moving random-dot patterns, whereas the Barlow–Levick model does not. The vertebrate visual system is known to con-

tain velocity band-pass, band-reject, low-pass, high-pass units (e.g. Orban, Kennedy & Maes, 1981), so we suspect that the Barlow–Levick detector, the Reichardt detector, and probably several other types of bilocal and multi-local detectors can all play a role.

Several predictions follow from the present model which can be tested experimentally. In addition to the physiological experiments reported so far it would be useful to study responses of direction-selective cells to moving random-dot patterns and to moving sinewave gratings. To the former type of stimulus we would predict a very small response irrespective of the direction of motion, and to the latter type a direction-selective response which—in the preferred direction—is strongly dependent on spatial frequency. Furthermore, it was argued above in connection with Fig. 1, that one should keep in mind the different ways in which apparent movement and real movement might stimulate a network model. Only a battery of tests make it possible to discriminate between the presented type of Barlow–Levick detector and various other models, or to reliably estimate parameter values.

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