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SPATIOTEMPORAL ORGANIZATION OF THE RECEPTIVE FIELDS OF RETINAL GANGLION CELLS IN THE CAT: A PHENOMENOLOGICAL MODEL

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Abstract. The reorganization of ganglion cell receptive fields (RFs) with different levels of light adaptation was investigated by means of spontaneous contour planes (SCPs). The SCP shows the spatiotemporal characteristics of the cell responses to a small bar of light switched on and off at 31 separate points along the RF horizontal axis. We assume a radial symmetry of RFs. A mathematical function describing the SCPs and their light level induced changes was found. Its form suggests that three mechanisms (central, surround and phasic) are required to account for RF organization of both homogeneous and heterogeneous retinal ganglion cells. The phasic component is probably identical with the nonlinear mechanism described by other authors. Responses to moving stimuli were also investigated and correlated with the spatiotemporal organization of the RF.

INTRODUCTION

One of the most complete descriptions of the spatiotemporal properties of the visual neuron receptive field (RF) is the contour plane (CP), a method introduced some time ago by Stevens and Gerstein (26). Contour planes have recently been used to analyze the RF properties of both retinal and lateral geniculate neurons (4, 23, 28 - 30). A very extensive examination of the RFs of different types of retinal ganglion

cells was given by Stein et al. (23), although various features of CPs were only qualitatively analyzed in their study. Here, we have tried to go one step further by describing the characteristics of the CPs mathematically. It has been necessary to vary the RF organization to obtain the parameters of the mathematical function. In a previous paper (28) changes of the background luminance were shown to be useful for this purpose. This procedure was, therefore, applied in the present experiments.

Several morphologically and functionally distinct groups have been recognized among retinal ganglion cells i.e. X, Y and W cells. We have restricted our investigation to units belonging to the X and Y categories. These cell types were shown by Stevens and Gerstein (26) to correspond to their heterogeneous/homogeneous classification of RFs. In the following, we shall use their terminology which is naturally connected with the characteristics of RFs as revealed by the CP method. Our intention was that the mathematical description of the RFs be sufficiently complete to account for the basic differences in organization of hetero- and homogeneous RFs.

METHODS

Experiments were performed on 10 adult cats weighing 2.2 - 3.7 kg. The experimental procedure including surgery, visual stimulation, recording and data analysis as well as definitions of specific terms used, have been described in detail before (28). In brief, a pretrigeminal brain stem transection was performed under ether anesthesia which was subsequently discontinued. The animals were paralysed with Flaxedil and artificially ventilated. The pupils were fully dilated and the nictitating membranes contracted by the application of an atropine/neosynephrine mixture and the corneas were protected by +1D contact lenses.

The stimulus used was a small vertical bar of light ($0.5° \times 1°$) of 5 cd/m^2 luminance projected onto a concave perimeter-like screen. This stimulus was switched on and off consecutively for periods of 1 s, at different neighboring points along the horizontal axis as described below. It could be also moved (velocity 2 - 5 degrees of visual angle per second) left and right along the same axis to study the appropriate responses of the cell by means of regular post-stimulus-time histograms. Different light adaptation levels were achieved by means of another light bar ($0.5° \times 4°$) placed vertically in the center of the RF; its luminance was varied from 0 to 22 cd/m^2. This method allows for

light adaptation of the cell without changes in the stimulus contrast for all stimulation points except for the central one overlapping with the adapting light bar (15, 28). A homogeneous diffuse background was used in several cases as a control adapting stimulus. The spatiotemporal arrangement of the RFs remained basically the same with either method. At least 3 min of adaptation was allowed for each luminance level (20 min in the case of complete dark adaptation) before the recording began. A dim background of 0.05 cd/m^2 was switched on routinely at all levels except where complete dark adaptation was investigated, when the screen luminance was less than 0.005 cd/m^2.

The spike activity of retinal ganglion cells was recorded with tungsten electrodes inserted into the optic tract. The spatiotemporal firing patterns were analyzed in terms of contour planes (CPs) (28). A CP is a two-dimensional picture of cell responses evoked by "simultaneous" cyclic stimulation of 31 separate points along the RF axis by the testing bar. These points were separated by 0.5°, so that they were opposed but not overlapping. The 16th covered the central point of the RF. Only the horizontal axis was investigated, assuming the radial symmetry of ganglion cell RFs. The cell responses were displayed on the screen of a storage oscilloscope, each not representing one spike. One of the contour planes: a spontaneous contour plane (SCP) was obtained by superimposing several sweeps at each position, until the dots representing spikes occurring spontaneously, for stimulus positions outside the RF, covered about 50% of their traces. The spontaneous firing rate was then represented by "gray" trace sectors, while the excitation and inhibition showed up as darker or lighter sectors, respectively. These sectors of the neighboring traces formed characteristic domains. We adopted the description of these domains from the Stevens and Gerstein paper (26): see Fig. 1. The primary excitatory (PE) domain describes the spatiotemporal characteristics of the center response; the secondary excitatory (SE) domain refers to an opposite type excitatory surround; the secondary inhibitory (SI) domain can be considered a result of activation of the inhibitory surround; and the primary inhibitory (PI) domain corresponds to the centrally induced inhibitory domain evoked by light OFF in an ON-center cell and light ON for an OFF-center cell. The PST-sum-histograms, as shown in the middle columns of Figs. 1 and 2 integrate all 31 space-different histograms into one, thus containing all responses evoked from different stimulation points.

Consecutive stimulation of neighboring points, as applied in most cases, may result in an artificial deformation and assymetry of the contour planes. In order to avoid such effects, a different sequence of

stimulation (every-third point instead of every consecutive one) was used in later experiments as follows: 1, 4, 7, 10, 13, 16, 19, 22, 25, 28, 31, 2, 5, 8, 11, 14, 17, 20, 23, 26, 29, 3, 6, 9, 12, 15, 18, 21, 24, 27, 30, where numbers denote positions on the screen.

RESULTS

Experimental

Forty one cells were studied at various levels of adapting luminance. Twenty seven of them were fully investigated with all the tests described in the Methods section. Fourteen from among the 27 were classified as heterogeneous ON-center, 3 as heterogenous OFF-center, 4 as homogeneous ON-center and 6 as homogeneous OFF-center units. These data were sufficient to estimate the parameters which account for the RF domains as investigated by our SCP method. All of them resembled the respective domains from examples of contour planes presented by Stein et al. (23). It was found that the spontaneous contour planes (SCPs) of the OFF-center cells were mirror-like images of the SCPs of the ON-center units within a given class (homo- or heterogeneous), i.e. the OFF-center cell was inhibited in the same spatiotemporal area where the ON-center cell was excited and vice versa. This finding is in a good agreement with the results of other authors (4, 23, 26). In following we show only examples of RFs of ON-center cells, since our light stimulus was more adequate for such fields.

Typical examples of the SCPs of a heterogeneous ON-center ganglion cell at various levels of light adaptation are shown in Fig. 1 (left column). All domains, as classified by Stevens and Gerstein (26), are clearly seen. A striking rearrangement of the SCP can be observed with changes in the level of adapting luminance. For the dark adapted cell (top row) the stimulus-ON part of the SCP consists of one wide (over 10° of visual angle) PE domain (see Fig. 1 and Methods section for the abbreviations used). An equally wide, PI domain occurs in the stimulus-OFF part of the SPC. Both PE and PI domains taper to the right, becoming narrower with time. There was an additional excitatory domain inside the PI domain in nearly half of the units examined. This excitatory domain was always centrally placed, a few degrees wide, and of short duration. This domain, induced by light OFF is presumably a prolongation of the PE domain onto the stimulus-OFF part of the SPC, and was originally called the "tab of excitation" (26). After adaptation to a low, scotopic luminance this excitation was abolished (Fig. 1, second row, 0.12 cd/m^2). Simultaneously, the PE and PI domains were reduced abruptly in width and length.

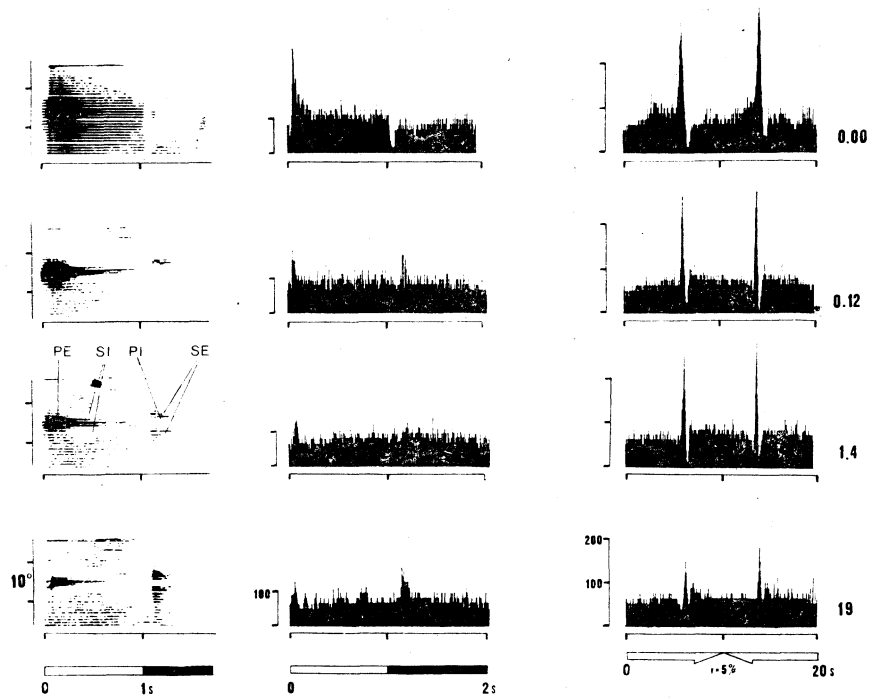

Fig. 1. Analysis of ON-center heterogeneous RF at different light adaptation levels. Numbers to the right show luminance of the vertical adapting bar ($0.5° \times 4°$) in cd/m². Underlying diffuse background intensity was 0.12 cd/m² except in the top row, where it was 0.00 cd/m². Stimulus: vertical $0.5° \times 1°$ bar of light of 5 cd/m² intensity. Left column, spontaneous contour planes (SCPs) produced from two repetitions of the stimulus at each point on the horizontal RF asis. 10° of visual angle marked on vertical axes to the left. Middle column, corresponding PST- sum-histograms. Abscissa in all three columns, time; white and black stripes under the columns represent stimulus-ON and -OFF time, respectively. Right column, PSTHs showing the responses to horizontally moving stimulus (8 repetitions) passing through the RF center; stimulus directions and velocity (v) are marked under the column. The firing rate in spikes/s, counted in 2 ms bins, are marked on vertical axes for all histograms. The SCP domains are indicated by arrows in the left column, third row; PE, primary excitatory; PI, primary inhibitory; SE, secondary excitatory; SI, secondary inhibitory.

The secondary domains, SI and SE, appear in the stimulus-ON and stimulus-OFF parts respectively, surrounding the primary domains. In the mesopic and photopic light adaptation levels (Fig. 1, two lower rows, 1.4 and 19 cd/m²) the primary domains do not change much, the only difference beeing a small reduction in the spatial dimension. The secondary domains grow, broadening towards both the periphery and the center of the RF, so that they now occupy the positions taken up by the primary domains at lower luminance levels.

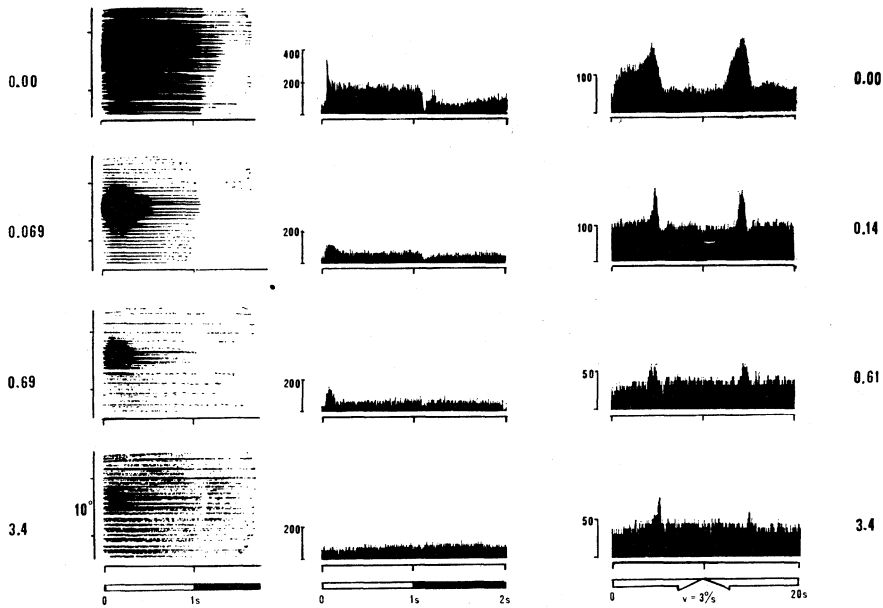

Fig. 2. ON-center homogeneous RF. Numbers to the left and right show diffuse background luminances in cd/m² during consecutive investigations by flashing (SCPs) and moving (PSTHs) bar, respectively. Right column, PSTHs of responses to moving stimulus (16 repetitions). Other parameters are as in Fig. 1.

The typical spatiotemporal arrangement of a homogeneous ON-center receptive field, and the influence of light adaptation on it can be seen in Fig. 2. There are several features by which the SCP of a homogeneous cell differs from that of a heterogeneous one. A detailed examination of all investigated cells showed that the primary domains of homogeneous cells were wider but shorter in time. Measurements of width (x) and length (t) of the PE domains were made for 27 cells. Differences between homo- and heterogeneous domains were investigated statistically using Student t-test for difference in the distributions of the quotient $q = x/t$. Statistically significant differences between these groups were found for both ON-center ($14.9 \pm 6.3°/s$ vs. $5.8 \pm 4.6°/s$, respectively, $P < 0.001$) and OFF-center cells ($10.9 \pm 5.5°/s$ vs. $3.7 \pm 3.8°/s$, $P < 0.01$). Assuming linear changes of q (with log intensity units), this quotient was found to be statistically independent on the adaptation level within the group of 27 cells tested. Thus the responses of homogeneous cells appear to be more phasic than those of heterogeneous type. The most apparent difference, however, is that the primary do-

mains cover the entire width of the homogeneous RF at all luminance levels. The secondary inhibitory domains are less visible and the SE domains are very weak and present only at mesopic and photopic levels. Both SI and SE domains, if present, overlap spatially with the periphery of the primary ones but are delayed in time. This means that, for some peripheral positions of the stimulus (e.g. Fig. 2, second row, 5° apart from the central point), the cell is first excited and then inhibited.

With light adaptation there is a rearrangement of the homogeneous RFs similar to that for the heterogeneous one. This rearrangement consists of a decrease of the PE and PI domains when the RF is adapted to higher light intensities.

The responses of the hetero- and homogeneous ON-center cells to the same light stimulus moving horizontally along the RF axis with a speed of 3 - 5°/s are shown in the right hand columns of Figs. 1 and 2. There are no significant differences between the responses to the bar moving from the left to the right or in the opposite direction. The response of the cell with a dark adapted RF (as shown in Fig. 1) consists of two phases: a strong excitation followed by a strong inhibition. At higher luminance levels two additional phases appear: a weak inhibition preceding the first excitatory phase and a weak excitation following the inhibitory phase. All of these four phases are outlined in Fig. 4*A*. These additional phases gradually increased in amplitude with adaptation to higher luminances. There was a parallel decrease in the amplitudes of the original excitatory and inhibitory phases. These observations agree with the mentioned changes in the secondary domains of the SCPs (see Discussion).

The remarkable difference can be seen when examining the responses of homogeneous type ganglion cells to a moving stimulus (Fig. 2). Although the direction of changes of consecutive phases are similar, they are much less readable, especially with respect to the inhibitory phases. This is in accordance with their weaker SI domains and their partial spatial overlap with the PE domains.

Theoretical

Mathematical description of the SCP. The concentric organization of the ganglion cell RF, characterized first by Kuffler (14), was afterwards described by Rodieck and Stone (20). Their model assumed two retinal mechanisms: an excitatory one and an inhibitory one, with a common center point and a radial symmetry. The ON-center cell is, in that

model, excited by the central mechanism and inhibited by the surround mechanism, while the OFF-center cell, on the contrary, is inhibited by the central and excited by the surround one. The cell's response may be, therefore, expressed as a sum:

(1) $$v = v_1 + v_2$$

where v_1, v_2 are, respectively, the center and surround components of the total response v. The signs of v_1 and v_2 are then opposite:

(2) $$v_1 v_2 < 0.$$

The influences of both mechanisms decrease with the distance from the central point of the RF according to a Gaussian function (18):

(3) $$v_i = a_i e^{-(r/b_i)^2}$$

where a_i — amplitude, b_i — space constant, r — the stimulus distance from the central point, $i = 1$ or 2, indicates central or surround component, respectively.

The surround space constant b is greater than the central one, while the surround amplitude a should be smaller than the central one (20).

(4) $$b_2 > b_1$$

(5) $$|a_2| < |a_1|$$

Relation (2) implies that:

(6) $$a_1 a_2 < 0.$$

Equation (3) does not involve the time dependence of the response. We assumed that such dependence was a product of two processes: a growth of the response, which may result from temporal summation of inputs and a subsequent decline, possibly caused by the electrical properties of the cell membrane and/or exhaustion of the synaptic transmitter substance. We have attempted to describe these processes by exponential functions. The function of a single mechanism was then expressed by the formula:

(7) $$v_i = a_i e^{-(r/b_i)^2} (1 - e^{-t/\tau^+ i}) e^{-t/\tau_i^-}$$

where t — time counted from the stimulus onset, τ_i^+, τ_i^- — time constants, τ_i^+ might correspond to the latency and τ_i^- might simulate tonic or phasic properties when its value is large or small, respectively. $(1 - e^{-t/\tau_i^+})$ and e^{-t/τ_i^-} factors refer to the above mentioned processes.

According to the Rodieck and Stone's model (20) the latency of the surround mechanism was assumed to be longer than that of the central one. The ON-OFF responses found by Hartline (10) could thus be explained in terms of this model. Accordingly, we assumed that:

(8) $$\tau_1^+ < \tau_2^+$$

Substituting (7) into (1) we obtained a function which was expected to approximate the response planes (the three-dimensional view of the CP) obtained by Stein et al. (23) and corresponding SCPs. By testing this functions numerically, it was found that it could roughly appro-

ximate the heterogeneous contour plane, but did not fit the homogeneous one at all. For a better fit we assumed, therefore, the existence of a third mechanism, acting simultaneously with the two discussed above. This third mechanism was introduced to account for the early part of the SCP, which is phasic and widely extended in space. The existance of such a mechanism has also been suggested by other authors (6, 27). We assumed that the third mechanism had the same shape as function (7), but with parameters which should satisfy the relations:

(9) $$\tau_3^+ \approx \tau_3^- \ll \tau_1^-$$

because it is phasic and

(10) $$b_3 > b_2$$

because of its large spatial extent. The combined function is now expressed by the formula:

(11) $$v = \sum_{i=1}^{3} a_i \bar{e}^{(rb/i)^2} (1 - \bar{e}^{t/\tau_i^+}) \bar{e}^{t/\tau_i^-}$$

The spatiotemporal points (r, t) for which the function has positive or negative values correspond to the excitatory or inhibitory domains respectively.

Function (11) was tested using a computer for several sets of parameter values and two such sets (Table I) were found to provide a good fit to the stimulus-ON parts of the experimental SCPs of ON-center cells. One of these sets corresponds to the homogeneous RF, and the other to the heterogeneous one. Some maps of the function using other

TABLE I

Two sets of parameters of the function (12) (see text), approximating the experimental spontaneous contour planes of the homo- and heterogeneous ON-center RFs. Graphic presentation in Fig. 3. Units: a, s^{-1}; b, °; τ, ms

Type of RF		Homogeneous	Heterogeneous
central mechanism	a_1	800	800
	b_1	2.25	1.5
	τ_1^-	300	500
	τ_1^+	250	400
surround mechanism	a_2	dependent on adaptation level	
	b_2	4	4
	τ_2^-	550	750
	τ_2^+	420	600
phasic mechanism	a_3	1500	600
	b_3	10	10
	τ_3^-	20	20
	τ_3^+	20	20

values, differing by a few percentage points from these, also resembled the SCPs, although the similarity was less obvious. Victor and Shapley (27) assumed a third, phasic mechanism only for Y-cells (with homogeneous RFs) but the analysis of the SCPs obtained in this study and suggestions of other authors (e.g. 3) indicate that such a phasic mechanism may also be important for heterogeneous RFs. The values of the third mechanism amplitude a_3, should be, however, considerably smaller for heterogeneous than for homogeneous RFs as shown in Table I.

The response to switching the stimulus off was assumed to be described by the same function (11) but with reversed amplitude signs. In addition we assumed that in the stimulus-OFF part of the SCP the

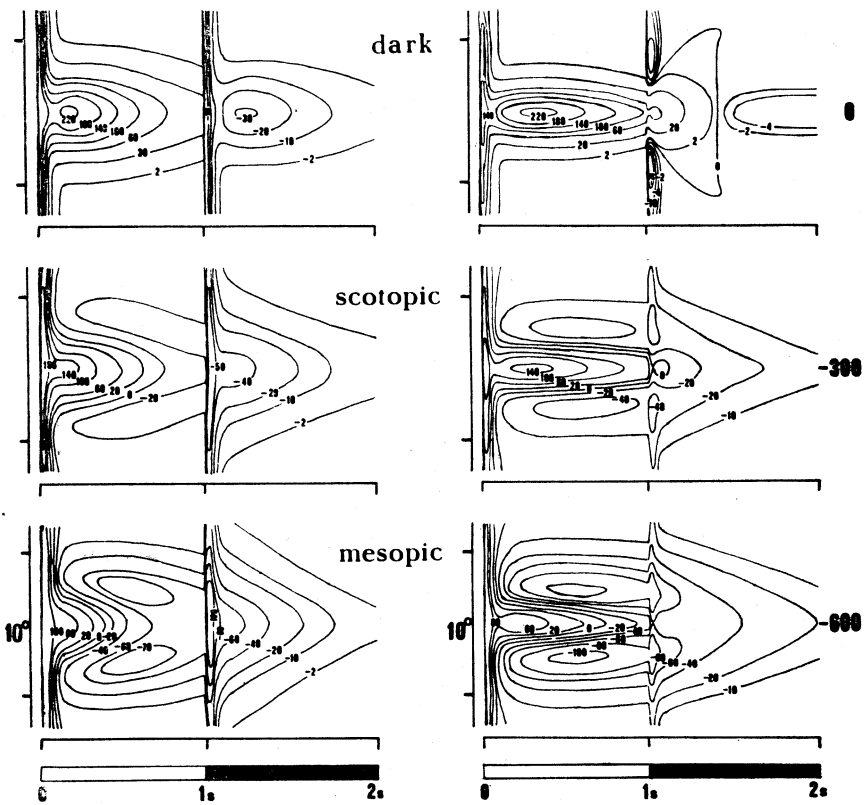

Fig. 3. Two series of maps of the function (13) simulating contour planes for parameters values as listed in Table I. Left column, homogeneous RF; right column, heterogeneous RF. 10° of visual angle is marked on the vertical (spatial) axes. Horizontal axes, time. White and black stripes, stimulus-ON and -OFF time, respectively. Numbers to the right show values of the variable parameter a_2, simulating various light adaptation levels. Further explanations in text.

response to switching the stimulus off overlapped temporally with the prolonged, decaying ON-time activity of the cell. The function describing the stimulus-OFF part of the SCP was then:

(12) $$v_{off}(t) = v(t) - v(t - t_{on})$$

where t — time counted from the preceding switching the stimulus on, t_{on} — stimulus-ON duration, equal to 1s in our experiments, $v(t)$ — function (11).

A still better fit could be achieved by multiplying the second component by a constant $k < 1$. This might result from the fact that switching a light bar off is not a specific stimulus for ON-center cells. We assumed a value of $k = 0.2$. The total function for both parts of the SCP was now expressed as:

(13) $$v_{tot}(t) = v(t) - kv(t - t_{on});$$
$$k = \begin{cases} 0 & \text{for } t \leqslant t_{on} \\ 0.2 & \text{for } t > t_{on} \end{cases}$$

Light adaptation. Barlow et al. (1) described the disappearance of the antagonistic surround in the dark adapted ganglion cell RF. Rodieck and Stone (20) confirmed that result and tried to explain it in terms of their model, assuming an increase in the sensitivity of the surround mechanisms and a constant sensitivity of the central mechanism with a rise in the adapting luminance level. Maffei et al. (15) came to the same conclusion, but other authors (7 - 9) have suggested that the sensitivity of both mechanism are dependent on the adaptation level.

Light adaptation was found to shorten the duration of the response to stimulation of the whole receptive field in comparison to central stimulation (2, 21, 31). Our method of spatiotemporal analysis takes into account both spatial and temporal changes. We could also describe, therefore, the spatial shift of the center-surround border which was not discovered before applying the SCP method (compare also (28) for the lateral geniculate cells).

Taking into account the conclusions of Rodieck and Stone (20) and Maffei et al. (15), we obtained two families of functions, simulating the SCPs at various luminance levels, by changing the value of one parameter only; i.e. the surround component amplitude a_2. The maps of these function families are shown in Fig. 3. The top row shows the approximation of the SCPs of the dark adapted homo- and heterogeneous RFs, and the middle and bottom rows correspond to the scotopic and mesopic light adaptation states, respectively.

The obtained theoretical SCP series gave a satisfactory fit with the experimental data, proving that described model might be considered as an approximate description of spatiotemporal characteristic of ganglion cells receptive fields.

DISCUSSION

We have attempted to find a theoretical model to describe spontaneous contour planes: the result of spatiotemporal analysis of ganglion cell receptive fields. Considering three mechanisms underlying the cell activity we were able to construct a function with numerical values which fitted experimentally obtained SCPs satisfactorily. Additionally, we have analysed this function dynamically by changing the parameter of the inhibitory mechanism, which was previously postulated to be responsible for reorganization of RFs with changes in light adaptation level (1, 15, 21, 31). A satisfactory fit between theoretical and experimental data was also obtained with such a procedure. The experimentally found changes in the RF organization at various luminance levels (i.e. the space, time and strength decline of the PE domain, adequate increase of the SI domain and even the central, additional excitatory domain found within the PI domain in darkness) were thus accounted for by a simple mathematical function. We conclude, therefore, that our phenomenological model might be considered to be a reliable description of the real retinal processing. It has, however, the following shortcomings: (i) The SCP stimulus-OFF part of the light adapted heterogeneous RF is not approximated well. The SE domains are partly covered by the PI domain. (ii) The prolongation of excitation onto the stimulus-OFF time in darkness is not clearly marked for the homogeneous RFs. (iii) All three mechanisms are expressed, for simplicity, by the same shape formulas (7), although a different functions could probably give a closer approximation. This hope is based on the assumption that different mechanisms are associated with the contributions of different parts of the neural network (see below). (iv) The dependence of the phasic mechanism sensitivity on the adapting light intensity, visible on some of the PST-sum-histograms, is not represented in our model.

General remarks on RF network organization. The relation between the physiology of ganglion cell receptive fields and the retinal cell connections remain speculative although attempts have been made to find such relations with respect to the spatial extent of RF (3, 17, 25). The results of such attempts are not quite convincing because of the difficulties in establishing the borders of RF centers (e.g. 17), which depend on the dynamic balance between excitation and inhibition. The SCP method used in this experiment is the most sensitive procedure for evaluating both the spatial and time extent of RF domains. Despite this, our present limited knowledge of the retinal elements, presynaptic to ganglion cell, allows for only a crude assigment of particular mechanisms to their anatomical correlates.

Kolb (12) has estimated from anatomical studies that α-cells receive 80% of their input through amacrine cells and only 20% by direct synapses from bipolar cells, whereas β-cells have mainly bipolar input (70% bipolar 30% amacrine). Table I shows the same proportion for our calculated parameters a_1 and a_3. In partial agreement with these data Ikeda and Sheardown (11) postulated from their transmitter studies that "sustained" and "transient" ganglion cells receive their excitatory input via bipolar and bipolar-amacrine pathways, respectively.

Recent investigations (for review see (25)) have supplied a reasonable amount of data about the dendritic tree diameters of several types of retinal cells. To compare the ratios of calculated space parameters b (Table I), we have assumed that the dendritic tree of α-ganglion cell corresponds roughly to the extent of the central mechanism (17). On the other hand, the diameter of the β-cell dendritic tree is clearly smaller (about three times) than its receptive field center (5, 6, 17). We suggest that convergence of several bipolar cells might explain the rather big b_1 parameter as obtained for the heterogeneous cell type. This has to be taken into account in further speculations upon the relation of b_2 and b_3 parameters with anatomical values of other retinal elements. It was postulated previously (18) that a contribution from AII-type amacrine cells might explain the two-fold enlargement of the RF center for β-cells in the scotopically adapted retina. We have observed also a similar increase of the heterogeneous RF center under scotopic compared to mesopic conditions. A possible contribution of AII amacrine cells to this effect needs further physiological clarification especially since the observed enlargement was not phasic.

The most likely element transmitting the phasic mechanism would be one of the wide-field amacrine cells, since their dendritic tree diameters can be several times larger than the ganglion cell dendritic tree, whether α- or β-type. The A22 and A19 type of amacrines described by Kolb et al. (13) might be possible candidates since they are supposed to be excitatory. One could also assume that many small-field amacrines may converge to give a similar spatial extent to the phasic mechanism. The connection of the phasic mechanism with the amacrine cells has been considered before (11, 23, 27). Their transient responses correlate well with the short time constants obtained in our model.

Concerning the surround mechanism Ikeda and Sheardown (11) have proposed separate interneurons for the ON and OFF-pathways (GABA and glycine accumulating amacrines) but either type supplying both α- and β-ganglion cells. The identified glycine containing amacrines, however, possess much smaller diameter of dendritic trees than GABA containing amacrines (25). Additionally, our study and data of Stein

at al. (23) show that the inhibitory domains of ON- and OFF-cells within the homogeneous or heterogeneous RF classes resemble each other but are qualitatively different between the classes. In general, the heterogeneous RF inhibitory surrounds are more tonic than those of homogeneous ones, as also indicated by the values of τ_2^- parameter in Table I. On the bases of the $b_1 : b_2$ ratio we propose that a limited number of GABA-ergic amacrines (11, 13) may produce the surround mechanism of homogeneous cells, although some contribution of horizontal cells (24) might also be suggested considering the rather big time constants for the surround mechanism. The best fit with our parameter b_2 for heterogeneous type cell is given by horizontal cells as has been proposed by Sterling (25). The amacrine-mediated inhibitory input might play only a minor role in organization of such fields.

Moving stimuli. According to the cinematograph principle, a bar moving through the RF can be considered as a number of bars flashed consecutively in neighboring positions. The spot appears in the first position, remains there for a short time interval and then disappears, as it is switched on in a second position. After an equally short next interval it disappears again and then reappears in the third position, and so on. A response to a moving stimulus should then consist of consecutive, overlapping responses to a spot flashing on and off along the RF axis. The response pattern to a single bar switching off in any position and its switching on at the same time in the next one could be deduced from the form of the SCP as a sum of the stimulus-OFF part of the post-stimulus-time histogram (PSTH) for one position and the stimulus-ON part of the next PSTH (22).

Considering this approach, it seems reasonable to associate the four phases of the movement response, described in the Results with the particular SCP domains. The outline of this association for an ON-center heterogeneous cell is shown in Fig. 4. The first phase, a weak inhibition is caused by the stimulus appearing in the RF surround and it corresponds to the SI domain. The second, a strong excitation, results from the appearance of the stimulus in the RF center and is intensified by its simultaneous disappearance from the surround, corresponding to the PE and SE domains. Two other phases of the movement response pattern can be attributed to the remaining SCP domains analogously. All four phases of the response to the moving stimulus are more obvious for cells with heterogeneous RFs. In parallel, the secondary domains of stimulus-ON parts of the SCPs are also better visible for this type of field. We believe, however, that the basic association described above is also valid for cells with homogeneous RFs.

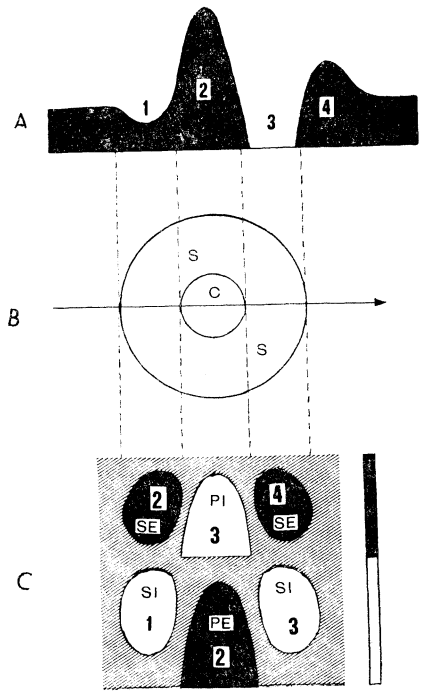

Fig. 4. A qualitative model of the response of an ON-center, heterogeneous cell to a moving stimulus, based on comparisons with contour plane and on the cinematograph principle of operation. The phases of the response (indicated by numbers, 1 - 4) relate to contour plane domains. *A*, Outline of the PSTH of response to moving stimulus. *B*, Outline of the RF; S, surround; C. center; arrow indicates the stimulus trajectory. *C*, Outline of contour plane; horizontal axis, space; vertical axis, time, white and black stripes to the right, stimulus-ON and -OFF paris, respectively; white and black areas, inhibitory and excitatory domains, respectively; numbers assign particular phases to the appropriate domains.

We have presented a qualitative model in which only the central and surround mechanisms are taken into acount. The contribution of the phasic mechanism, probably more important for homogeneous RFs was neglected here. One can expect that the influence of the phasic mechanism might become more significant with stimulus movement faster than used in our experiments.

The adaptation level induced changes in intensity of the particular phases, the growth of phases 1 and 4, and the diminution of phases 2 and 3 can be also represented by this model, since the domains ascribed to them change in a similar way.

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