ACTA NEUROBIOL. EXP. 1981, 41: 447–466

LIGHT LEVEL INDUCED REORGANIZATION OF CAT'S LATERAL GENICULATE NUCLEUS RECEPTIVE FIELDS: A SPATIOTEMPORAL STUDY

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Key words: lateral geniculate nucleus, receptive fields, adaptation

Abstract. The spatiotemporal organization of receptive fields (RF) of the cat's lateral geniculate cells was investigated under several scotopic and mesopic light adaptation levels, using stationary and moving light stimuli. A given adaptation level was reached by changing of either the diffuse background or the adapting central spot intensity. Both methods gave the same qualitative results. The RFs were prominently reorganized after dark adaptation. Under such conditions, the central response area was enlarged and the classic excitatory and inhibitory surrounds were hardly visible in most cases. A minimum light level was needed for developing classic surrounds. Both inhibitory and excitatory surrounds changed their spatial positions simultaneously at higher light adaptation levels. ON- and OFF-center cells changed their spatiotemporal organization similarly, thus indicating similar underlying mechanisms.

INTRODUCTION

Since the first Hubel and Wiesel experiments (4) LGN-cells receptive fields (RF) and their role in the visual information processing have been studied extensively. Both extra (3, 8, 10, 15–17) and intracelullar (13, 14) recordings in cats have confirmed that, similarly to the retinal RFs, the receptive fields of the LGN neurons have a concentric center-anta-

gonistic surround organization. Although similar also in diameter, they differ in some functional aspects from those of ganglion cells. They exhibit a more pronounced center-surround antagonism (8, 10) which was found not to disappear completely during dark adaptation. Quantitatively different results were obtained by different authors (10, 16). Some authors (3, 8, 10) have described additional excitatory and/or inhibitory surrounds beyond the classic one whereas others (14, 15) have not confirmed those findings.

As a consequence, two hypotheses were put forward: that the LGN receptive field surround is build up by retinal RF centers or by their surrounds (4, 10, 15). Recurrent inhibitory interneuron wiring was further postulated, to explain the qualitative differences between the retinal and geniculate RF's (1, 8, 13). All these findings should be further investigated to examine the role of the lateral geniculate nucleus in visual analysis. The aim of these experiments was to reexamine the present knowledge about the LGN-cells receptive fields. The level of light adaptation (background luminance) was used as a parameter influencing the spatiotemporal organization (15) of the RFs with the aim to shed some light on the underlying neuronal mechanisms.

METHODS

Preparation. Experiments were done on 19 adult cats ranging in weight from 2.0 to 3.3 kg. Pretrigeminal transection was performed under ether anesthesia. A small window in the skull and dura was made above the LGN and the cortex was covered with warm agar. The animals were then immobilized with flaxedil (60 mg/h, given intravenously) and artificial respiration with room air was applied (rate 19/min). The stroke volume was adjusted during an experiment to keep a tidal CO_2 between 3.5–4%. Temperature was maintained automatically at 38°C. In prolonged experiments, an injection of 0.9% NaCl with 5% dextrose fluid mixture was given.

In most experiments the expected progression of RF locations and the changes of the ocular dominance of the consecutive neurons (12) made histological confirmation unnecessary. Histological examinations were performed in ambiguous cases only.

Optics and recording. Pupils were fully dilated and nictitating membranes were retracted using a combination of 1% atropine sulfate and 10% phenylephrine. Corneas were protected by +1D contact lenses. This lense power was found to be an average refractory correction needed to focus on a perimeter-like (60° sphere sector) screen, 70 cm in front of the cats eyes.

Hubel-type tungsten microelectrodes were used. A 5–20 μm uncovered tip with a sharp-ended lacquer border allowed a long lasting uni- and multiunit recordings with excellent resolution.

Stimulation and data processing. The stimulus was a small bar of light, subtending 0.5° × 1°, with a luminance of 5 cd/m². It was switched on and off by a galvanometer-driven shutter placed at the focal plane of the light source. A mirror attached to another galvanometer was used to deflect the stimulus bar to discrete positions along the axis of the receptive field. The center of the mirror was placed close to the cat's head and the eye was concentric with the screen. Both galvanometers were controlled by specially constructed electronic generators.

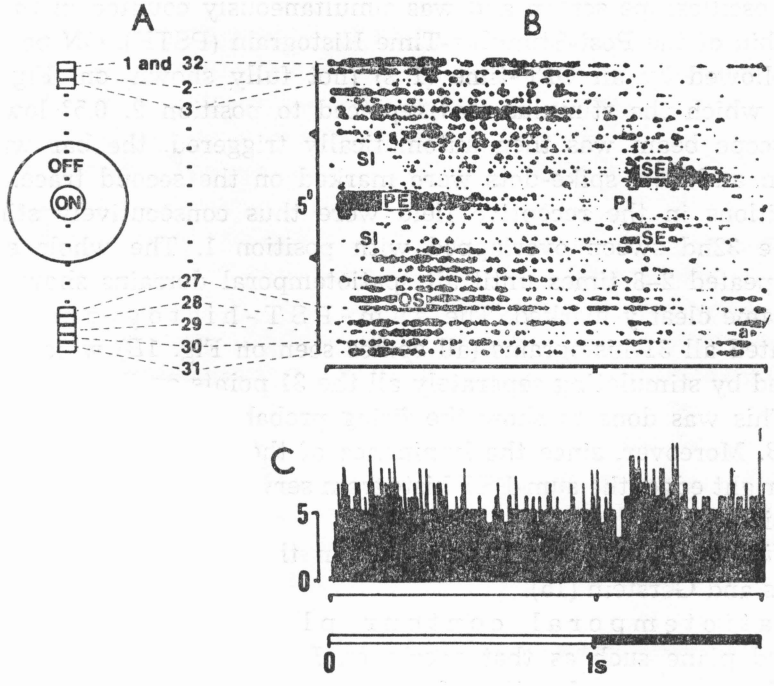

Fig. 1. *A*, an outline of a classical ON-center LGN receptive field (RF) and 31 points of stimulation by a 1°×0.5° bar of light (5 cd/m²) along the RF axis. *B*, a spontaneous contour plane of the field shown in *A*. It represents 31 responses for dual stimulations of the appropriate points on the RF axis (two repetitions of the stimulus in each point, four in the uppermost line). Dark and white domains on the plane: PE, primary excitatory; PI, primary inhibitory; SI, secondary inhibitory; SE secondary excitatory; OS, tertiary; *a*, artifact. Further explanation in the text. Vertical scale on left: calibration in degrees of visual angle. *C*, sum-PST-histogram represents numbers of spikes from all responses integrated in space. Same time axis as in *B*; white bar, stimulus ON; dark bar, stimulus OFF. 2 ms bin width. Vertical scale on left: number of spikes per bin.

The diffuse background luminance was varied between 0 to 5 cd/m² by changing the DC voltage supplied to the special bulb. Different light adaptation levels could be also achieved by changing the DC voltage in a projector illuminating the central part of the receptive field with a $0.5° \times 2°$ bar of light. In this case, a low-level diffuse background light was also switched on, to eliminate the influence of scattered light.

Each receptive field was initially plotted using a handheld projector; the central axis of the stimulus projector (position "16" on Fig. 1*A*) was moved to the center of this field. The analysis started at the uppermost position "1" (Fig. 1*A*). The bar was switched on synchronously with the start of the first trace on a storage oscilloscope (Fig. 1*B*) and with the start of the digital analyser ANOPS (Fig. 1*C*). Each spike marked a dot on the oscilloscope screen and was simultaneously counted in the appropriate bin of the Post-Stimulus-Time Histogram (PSTH). ON period (1 s) was followed by an OFF-time (1 s) (not fully shown on Fig. 1*B, C*) during which the stimulus was replaced to position 2, 0.5° lower. The oscilloscope beam was then automatically triggered, the bar was switched on and new spike-dots were marked on the second trace. All the 31 positions in the receptive field were thus consecutively stimulated and the 32nd sweep overlapped with position 1. The whole sequence was repeated 2–8 times until all spatiotemporal domains shown in Fig. 1*B* became clearly marked. The sum-PST-histogram in Fig. 1*C* integrated all 31 histograms (all spikes seen on Fig. 1*B*) which could be obtained by stimulating separately all the 31 points on the receptive field axis. This was done to show the firing probability changes not seen on Fig. 1*B*. Moreover, since the luminance of the scope diminished slightly at the right edge, the sum-PST histogram served as a control of the firing probability.

Definitions. The terminology used in this study was adapted from Stevens and Gerstein (15).

Spatiotemporal contour plane is an experimentally obtained plane such as that shown on Fig. 1*B*. It exhibits changes in firing frequency as a function of space and time.

Spontaneous contour plane is a plane recorded at the "spontaneous firing level". It was achieved by choosing such number of repetitions that black dots representing spontaneously occuring spikes and white intervals between them were evenly distributed on a scope trace refering to the points outside the RF. The spontaneous contour plane was a basic plane studied in this and in the accompanying paper.

Domain is an area of a contour plane encompassing both a region of space and a period of time; it is used to describe a portion of the contour plane. "White holes" (areas devoid of dots) or rarely dotted

regions of a spontaneous contour plane represent domains which contain fewer spikes than would be expected during spontaneous firing. The heavily dotted regions where the dots may fuse to produce a solid black area represent domains which contain a greater number of spikes than would be expected during spontaneous firing.

Typical domains for an ON-center cell are labelled in Fig. 1*B*; PE, SE, PI, SI, OS.

Primary excitatory (PE) domain appears as a solid black region of the spontaneous contour plane. It is the strongest excitatory domain which always corresponds to the classic excitatory center response.

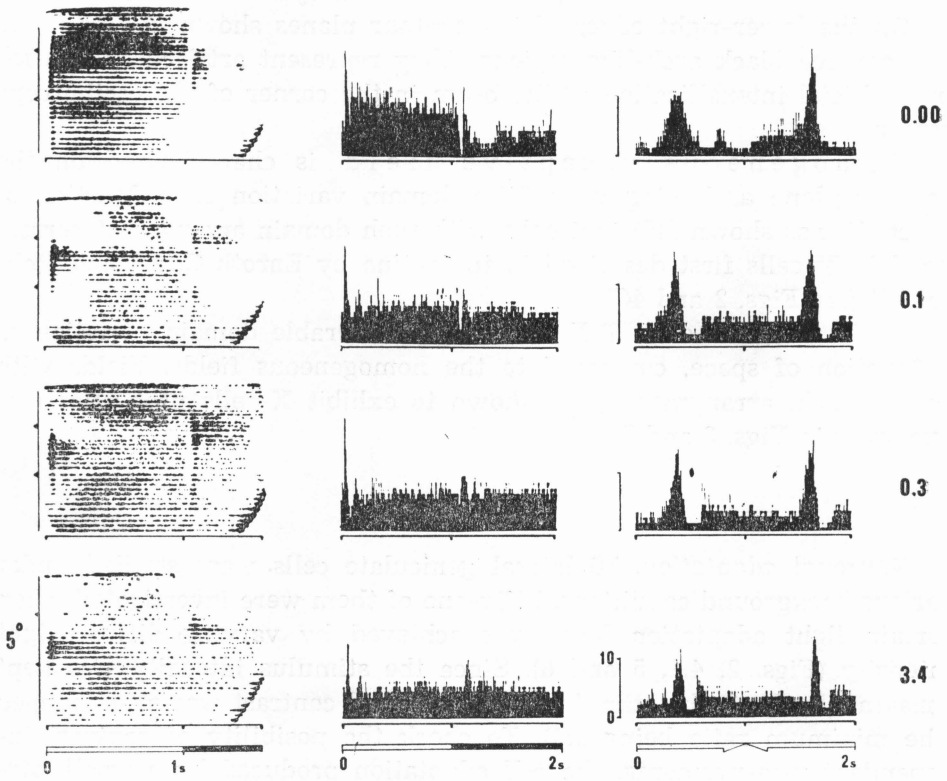

Fig. 2. Analysis of an ON-center homogeneous RF at different light adaptation levels. Diffuse background luminances in cd/m² are indicated on the right side. Bar stimulus: intensity 5 cd/m². 1°×0.5°. Left column, changes of spatiotemporal RF organization as analyzed by means of spontaneous contour planes. 4 repetitions of the stationary stimulus in each point. Middle column, sum-PST-histograms of appropriate contour planes. Right column, PST-histograms of spike responses to the same stimulus moving across the cell's RF axis. 32 repetitions, both directions.

Secondary excitatory (SE) domain is the second strongest excitatory domain. It appears as a heavily dotted region of the contour plane and corresponds to the classic excitatory surround.

Primary inhibitory (PI) domain appears as white "hole" on a spontaneous contour plane. It is the strongest inhibitory domain.

Secondary inhibitory (SI) domain appears as a white, sparsely dotted region on a spontaneous contour plane. It is the second strongest inhibitory domain and corresponds to the classic inhibitory surround.

Tertiary domain is a weak excitatory or inhibitory domain which generally follows one of the four domain types described above. For example, the excitatory domain on Fig. 1*B* which probably corresponds to the outer surround (OS) as described by Hammond (3).

On the lower-right edges of the contour planes shown in this paper one can see black arch-like regions. They represent artifacts (a) caused by artificial intensification of the beam in the corner of the oscilloscope screen.

Homogeneous receptive field is characterized on the contour plane as having very little domain variation as a function of space. It was shown (15) that cells with such domain arrangment correspond to Y cells first described in the retina by Enroth-Cugel and Robson (2) (see Figs. 2 and 4*C*).

Heterogeneous RF shows a considerable domain variation as a function of space, compared to the homogeneous fields. Fields with such domain arrangment were shown to exhibit X-cells properties (see examples in Figs. 3 and 5).

RESULTS

Neuronal adaptation. 76 lateral geniculate cells were studied under various background conditions. Fifty-one of them were investigated when certain light adaptation level was achieved by varying diffuse light intensity (Figs. 2, 4*A*, 5 and 6). Since the stimulus intensity was kept constant (5 cd/m^2) the stimulus-to-background contrast was also changed (the minimum ratio being 1.5). To check the posibility of contrast independent measurements, the cell adaptation produced by a small, steady light spot in the RF center was tested, as was done before for retinal cells (11). Twenty-five neurons were analysed when a small bar of light (0.5° × 2° to 3°) of varying intensity was used to adapt the receptive field center. Low intensity diffuse background was also used to minimize the light scatter. In the latter case, only the central point of the space axis of the contour plane was investigated under different

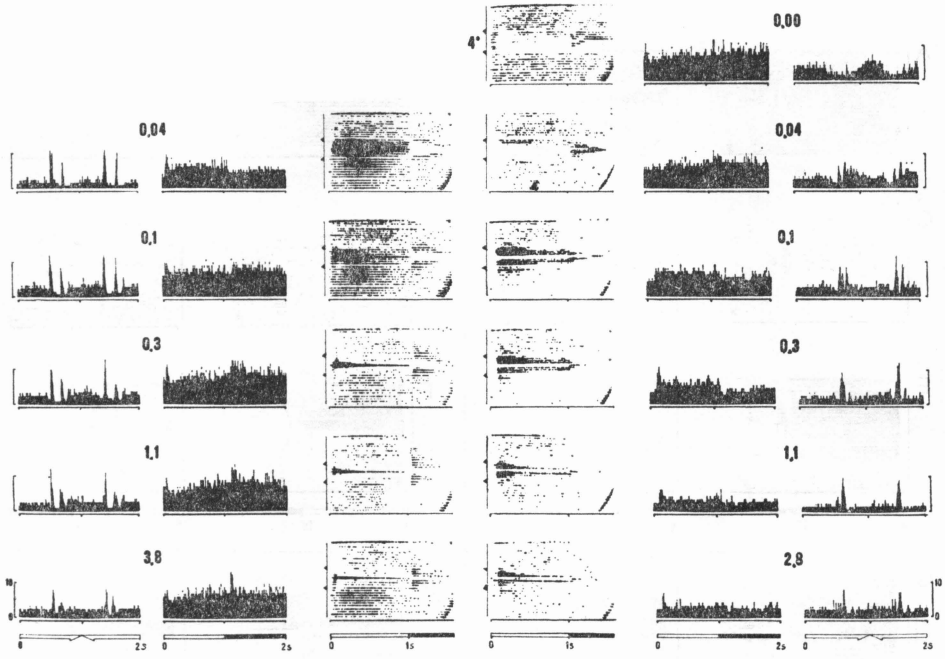

Fig. 3. Analysis of heterogeneous RFs of two neurons at different light adaptation levels (numbers in rows show luminance of adapting 0.5°×3° bar in cd/m²). The neurons were registered 100 μm apart. The stimulated axes of both fields overlapped in the visual field. Left three columns: responses of an ON-center cell (moving bar response, PST-sum-histograms and appropriate contour planes). Right three columns (mirror-image arrangement with respect to the lef): responses of an OFF-center cell. Spontaneous contour planes in two middle columns show reciprocal domains arrangement. See text for details. 32 repetitions for moving bar responses, 6 repetitions for contour planes. Stimulus intensity — 5 cd/m²; stimulus size 0.5°×1°.

contrast conditions, when the testing bar (also 0.5° wide) was switched on overlapping the adapting one. All other points of the RF axis were tested with the same contrast conditions in light adaptation levels (Figs. 3 and 4C).

No qualitative differences in contour planes arrangement have been noticed for a given cell using either method of adaptation. All main domains had similar spatiotemporal extensions when a given adaptation state was achieved, either by diffuse light or by a small spot in receptive field center. It was not true under the condition of strong (more than 4 cd/m²) adapting light: the RF secondary domains were smaller when first method of adaptation (diffuse light) was used. This could be explained, however, to be a result of contrast changes.

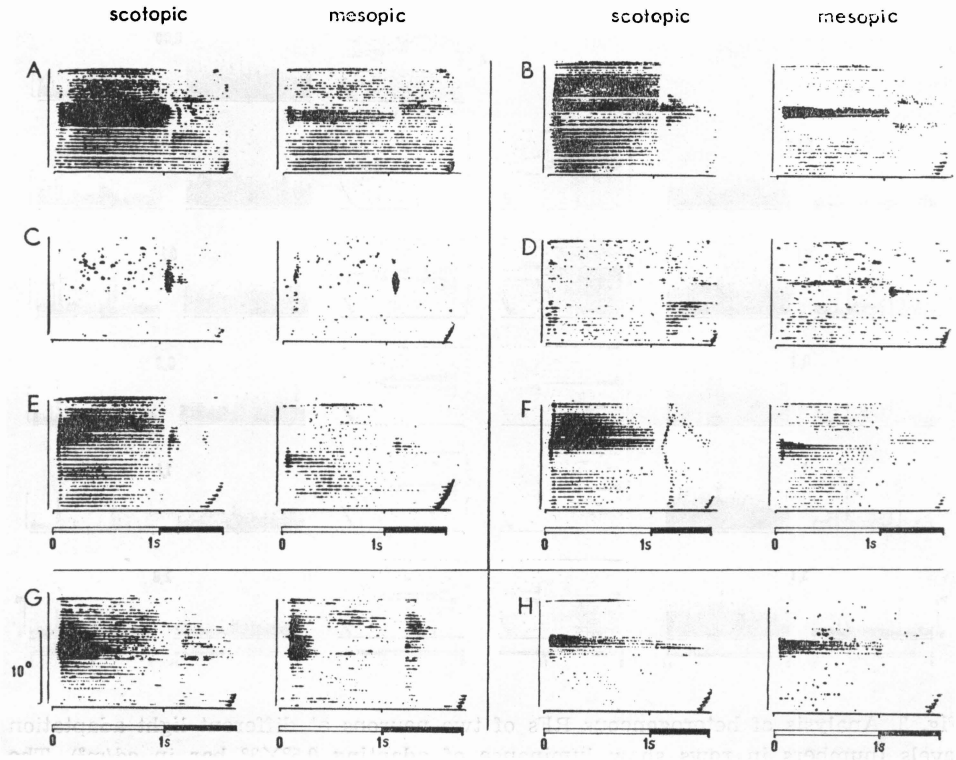

Fig. 4. Examples of RFs reorganizations of 8 LGN cells in two ranges of light adaptation: scotopic and mesopic. *A, B,* heterogeneous ON; *E, F,* homogeneous ON; *C,* homogeneous OFF; *D,* heterogeneous OFF; *G, H,* ON/OFF type cells. Stimulus intensity 5 cd/m²; stimulus size 0.5°×1°. Background intensities for scotopic conditions: *A,* 0.07 cd/m²; *C,* 0.1 cd/m² *B, D, E, F, G, H,* 0.00 cd/m². 4 or 6 repetitions for different contour planes.

Three minutes of adaptation time were allowed for any light intensity level. Time courses of adaptation were not studied in detail but it was noted that qualitative rearrangment of contour plane was often finished during the first 1/2 to 1 min. No further changes were noted in any of the fields with adaptation times longer than 3 min. This was not true, however, for the case of dark adaptation (background light intensity level 0.00 cd/m²). Although the basic rearrangment of the domains had taken place during first 2-10 min, their spatiotemporal extent could be still changing in some cases up to 15 min. Therefore at least 20 min of adaptation was allowed for any cell investigated in the dark. The dispersion of adaptation time courses had nothing to do with the physiological state of an animal since different properties were exhibited by neighboring cells. These data are in a good agreement with the

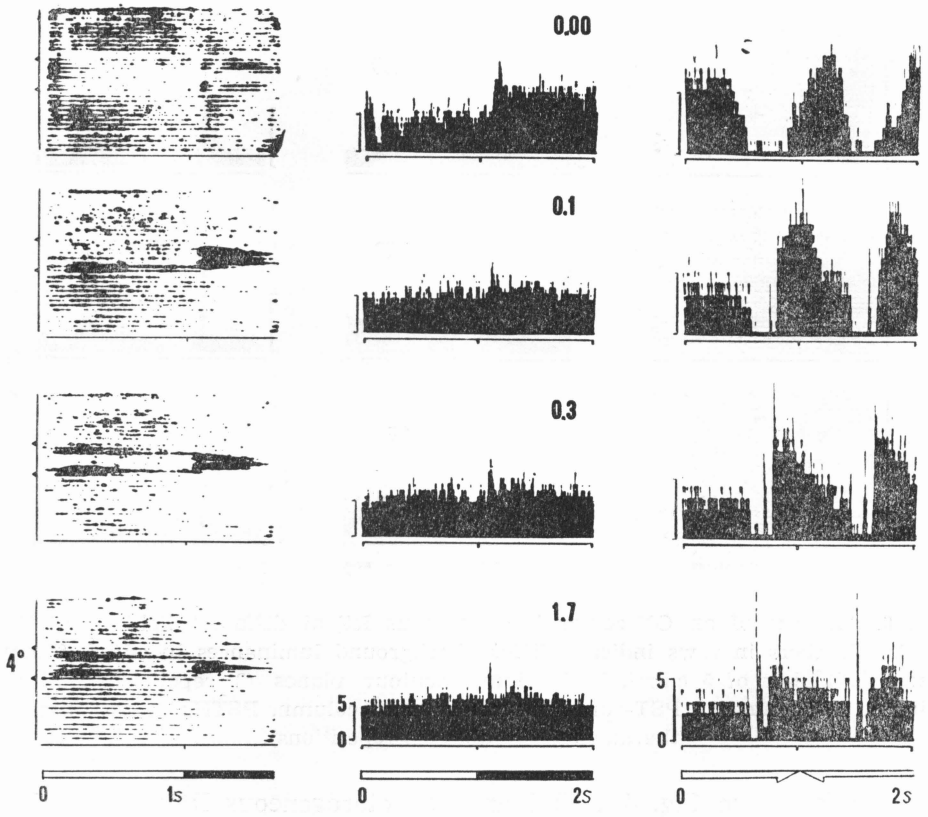

Fig. 5. Analysis of an OFF-center heterogeneous RF at different light adaptation levels. Numbers indicate diffuse background intensity levels in cd/m² for appropriate rows. Stimulus: 0.5°×1° bar of 5 cd/m² luminance. Left column, contour planes (4 repetitions); middle column, corresponding PST-sum-histograms; right column, PSTHs of responses to the moving stimulus (64 repetitions).

results of Virsu et al. (16), who analyzed the time courses of the PST response stabilization for a centrally located stimulus.

Receptive field organization as a function of luminance. The rearrangement of spatiotemporal RF-organization of different types of LGN cells is shown in Figs. 2 to 6. Many of the contour planes shown on these figures exhibit considerable asymmetry of domains. In Fig. 2 the upper flank of the widely spread PE domain (top row contour plane, background 0.00 cd/m²) is much stronger than the lower one. When the adapting light intensity is raised (0.1, 0.3, 3.4 cd/m²) the secondary domains visible above the RF center (SI during ON-time and SE during OFF-time of the stimulus) are also better expressed than the ones below it. For ON-center cells, this asymmetry is better expressed among the homo-

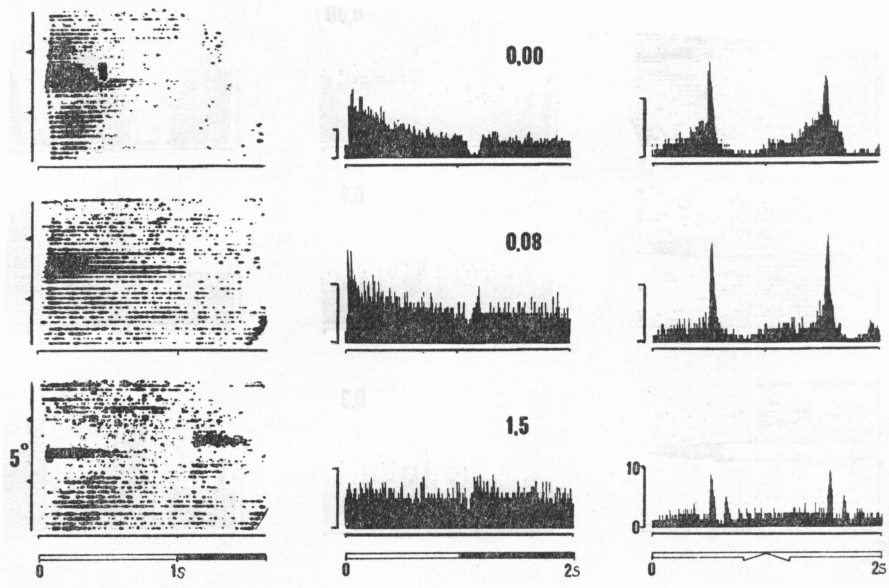

Fig. 6. Analysis of an ON-center heterogeneous RF at different light adaptation levels. Numbers in rows indicate diffuse background luminances in cd/m². Stimulus: 0.5°×1° bar of 5 cd/m². Left column, contour planes (2 repetitions); middle column, corresponding PST-sum-histograms; right column, PSTHs of responses to the moving stimulus (32 repetitions).

geneous (compare Fig. 4*E*, *F*) than the heterogeneous RFs (Fig. 3 left hand columns and Fig. 4*A*, *B*) in which it can be observed only for secondary domains. The same feature can be seen in the OFF-center cells (Figs. 4*D* and 5).

The above described asymmetry seems to be partially related to the non-random method of stimulation used (see method, Fig. 1). Although a one-second duration of the ON and OFF periods was used in this experiment, it is clearly seen that the inhibitory and/or excitatory responses evoked by switching the stimulus on or off last much longer than 1 s and influence the subsequent response pattern. Another possibility, especially at scotopic adaptation levels, is that the testing bar switched on for a second in the RF center, partially light-adapts the field, evoking a changed response from the following point of the RF axis. These complications can be avoided by using a spatially-randomized stimulation (Wróbel and Gerstein, unpublished results).

Apart of the asymmetry factor, other prominent changes in the RF organization can be followed. In Fig. 2 the contour planes obtained at four background intensity levels are shown for a homogeneous ON-cen-

ter cell. It can be seen that after changing the adaptation state from dark (top row, 0.00 cd/m^2) to a very low luminance (second row, 0.1 cd/m^2) the PE domain of the presented RF is strongly reduced. Parallely, the PST sum-histogram in the second column loses its tonic ON component. That was also noted by Jakiela et al. (5) in the scotopic range of light adaptation for retinal genglion cells. The spatial extent of the PE is further reduced at higher background levels. Note, that the spatial position of the PE under mesopic adaptation corresponds to the place from where the responses with the shortest latencies were obtained in the dark (top contour plane).

No inhibitory domains can be seen in the ON-time half of the contour plane of the dark adapted cell of Fig. 2, except for a narrow stripe of postexcitatory inhibition immediately following the first phasic response. This short inhibitory period is also evident in the respective PST-histogram on the right. Widely spread SI domains appear around the PE domain (second row contour plane) at the 0.1 cd/m^2 adapting level. At a still higher background luminance (0.3 cd/m^2 — third row) the SI domains unite in the RF center after the first 200 ms of PE domain, cutting down its tonic part. Large excitatory tertiary domains follow SI on the flanks of the field. The development of SI on the fourth contour plane row (3.4 cd/m^2) is not so clear, most probably due to a smaller stimulus-to-background contrast. The number of impulses in the whole investigated area during the ON-time is, however, further diminished, as seen on the PST sum-histogram to the right.

The unitary SE domain is seen in the dark-adapted state of the RF shown in Fig. 2 (first row contour plane OFF-time); moreover, its shortest latency corresponds to the center of the field (compare also Fig. 4 *B*, *F*). This is different than the SE domains organization at all other light levels where the classic surround SE domains are seen. This different, dark induced SE domain is surrounded by a large PI domain which is also well visible in the neighboring PST-histogram. Light adaptation (second row, 0.1 cd/m^2) changes the organization of the OFF-period of the contour plane. The PI domain appears in the central region of the field. Simultaneously the SE domain is separated into two surrounding regions, spatially overlapping upon the SI domains preceeding them in time. This spatial overlap remains also at higher background intensities, although both the SI and the corresponding SE domain are closer to the RF center. The PI domain can be seen on these contour planes (0.3 and 3.4 cd/m^2) as a white stripe following the termination of the stimulus. Its duration is, however, interrupted by a thin stripe of excitation connecting the two SE domains.

The above-described features of reorganization of homogeneous RF

can be similarly observed in heterogeneous receptive fields (Fig. 3, first 3 columns). The third column of Fig. 3 shows the contour planes obtained at a different level of light adaptation. The PE domain of the top contour plane, 3° wide at the background intensity of 0.04 cd/m² is getting narrower at higher backgrounds down to 0.5° at 3.8 cd/m². Simultaneously, the SI domains appear on the flanks of the PE domain and enlarge spatially at its expense.

Similar relationships can be observed in the OFF part of the contour planes shown in the third column of Fig. 3. The PI domain spatially overlaps the proceeding wide PE domain at the 0.04 cd/m² adaptation level (top contour plane). The PI domain becomes narrower with increasing level of light intensity adaptation (lower contour planes). The SE domains surrounding the PI domain move simultaneously toward the spatial RF center reflecting the same direction of changes of SI domains. A shortening of latencies of SE domains is notable at higher adaptation levels. The SI domains seem to extend more laterally than the SE domains, similarly to the homogenous RF previously described.

Let us briefly investigate the rearrangment of the OFF center cells shown in Fig. 3 (last three columns) and Fig. 5. It is interesting to compare the two top contour planes in both figures. The SE domains (in these cases — ON surrounds of OFF center RFs) show up at higher adaptation levels at the flanks of the same spatial positions where PI domain was observed in dark adaptation.

The presented reorganization of receptive fields following a change of background intensity is characteristic for that specific factor. Our own unpublished results point out that other factors, e.g. barbiturate anesthesia, can reorganize receptive fields in a quite different manner.

Controls. Particular attention must be paid to the problem of stray light, the effect of which could influence the obtained data. It was shown that light adapted RFs exhibit similar changes whether studied in steady or variable stimulus-to-background contrast. It proves indirectly that stray light does not play a crucial role for reorganization observed in the light adapted receptive fields. To reduce the effect of stimulus "halo" a low intensity background light was applied at all levels of light adaptation. The control experiment was performed separately on a field adapted by centrally positioned low intensity bar. The contour planes of that field were recorded with and without the diffuse background light. Both planes showed the same spatiotemporal distribution of domains, proving that "halo" of the stimuli did not have any effect upon the peripheral organization of the light adapted RFs.

The qualitatively different organization of the dark adapted RFs might be, however, due to the stimulus projector imperfections. Other

control experiment was done to check this possibility. Luminance of the stimulus "halo" was measured at the distance of 0.5° and 1.5° from the normally illuminated bar (5 cd/m²). RF was than replotted twice using bars with the obtained levels of luminance. The first contour plane showed only narrow and weak PE domain in the RF center. The lower intensity stimulus did not evoke any response. Thus the scattered light effect can be limited to approximately 1.5° dispersion of the PE border.

Reciprocal organization of domains in ON and OFF-center receptive fields. Figure 3 shows the reorganization of two heterogeneous receptive fields. ON and OFF-center found on the same electrode track, 100 μm apart. Both RFs covered the same spatial area on the retina, so that the stimulation axis (see method) did not have to be changed in-between the two analyses. First three columns (responses to movement, PST-sum-histograms and contour planes) show the ON-center cell responses, and the last three columns, arranged in a reciprocal sequence, were obtained during the analysis of an OFF-center cell. Coressponding contour planes of the middle columns can thus be compared with regard to their spatiotemporal organization. It is easily seen that both sets of contour planes look basically like mirror images. The spatio-temporal area covered by PE domain of ON-center cell is reduced at high light-adaptation levels (third column); so does the corresponding area of the PI domain of the OFF center cell (fourth column). The same is basically true for the PI domain of the ON-center cell (OFF time period of contour planes in the third column) and for the PE domain of the OFF-center cell (OFF center response in the fourth column).

Many similarities can be seen also in the spatiotemporal organization of the SI domains of the ON-center cell and the SE domain of the OFF-center cell, although the SI domains seem to cover wider spatial areas (Fig. 3, higher light-intensity levels).

Six examples of RFs, investigated at scotopic and mesopic adaptation levels are shown in Fig. 4 *A–F*. These cells were recorded in the upper two layers of the LGN in different animals. Two of them exhibit heterogeneous ON (Fig. 4*A*, *B*) and two homogeneous ON (Fig. 4*E*, *F*) type of RF organization. The remaining pairs are heterogeneous OFF (Fig. 4*D*) and homogeneous OFF (Fig. 4*C*) receptive field types. They were gathered in one figure to show the reciprocal correspondence of the organization of the RF domain in ON and OFF-center fields (both stimulated by light).

Comparing the PI domains on contour planes of Fig. 4*A* and PE domain on contour planes in Fig. 4*C* one can note their spatiotemporal overlap including oscillatory reproduction in scotopic conditions. Developing of SI domain in mesopic light level observed in Fig. 4*A* also

corresponds to the appearance of SE domain in Fig. 4C. On the other hand, the latency of the first oscillatory response of PE domain in Fig. 4C is comparable with that of the first inhibitory stripe in Fig. 4E elicited by the cassation of the stimulus.

More similarities can be found between the organization characteristic of receptive fields of the same type. The ON center heterogeneous RF shown in Fig. 4B exhibits a large PE domain and is elongated from the central region of the field into arrow-like SE domain during the OFF-portion of the plane. The scotopically adapted RF of OFF-center heterogeneous cell in Fig. 4D looks very similar. Large PI domain on the ON portion of the contour plane is elongated into arrow-like inhibition hollowing out the hole in PE domain expected in this place in an OFF-center field. Such tabs of excitation (Fig. 4B) or inhibition (Fig. 4D) elongating light evoked primary domains into OFF period of the contour plane, were previously reported by Stevens and Gerstein (15).

A prominent reorganization of the fields in Fig. 4B, D can be observed when they are adapted to the mesopic light level. The PE (Fig. 4B) and PI (Fig. 4D) domains are strongly reduced in size by the secondary domains of opposite signs. The PI (Fig. 4B) and PE (Fig. 4D) show up in the central region of the fields on OFF-part of the apropriate contour planes. These reorganizations take place, correspondingly, so that the two contour planes taken at mesopic light condition look again like mirror images (Fig. 4B, D).

A detailed inspection of other corresponding features in between the presented set of contour planes is left to the reader.

Examination of Figs. 3 and 4 leads to the conclusion that the ON and OFF-center cells (some times subdivided into two subsystems: B and D) have similar, although reciprocally arranged, receptive field organizations at different background levels. Some observed differences found between homogeneous and heterogeneous receptive fields should be underlined, however.

ON-OFF type receptive fields. Figure 3 shows also examples of investigations of cells found from time to time among typical geniculate neurons. They were not included in the sample of neurons discussed in this paper since they did not have a classical RF organization of the LGN relay cells.

In Fig. 3G contour planes of a cell found in the A1 layer of LGN close to the medial interlaminal nucleus are shown. Dark adapted RF of this cell exhibits some center-surround organization. This is changed at the mesopic adaptation level: a prominent OFF domain appears with a center shifted in space from the biggest ON-response. Such organiza-

tion reminds one of the nonconcentric ON-OFF type of the receptive field.

The RF shown on Fig. 3*H* exhibits properties of the cell found in the lower part of A1 layer in the lateral part of LGN. The contour plane in the dark consists only of PE domain prolonged by an extensive excitation during OFF period. The OFF response is abolished at the mesopic adaptation level but none of the secondary domains suggesting concentric organization appears.

The types of fields similar to that shown on Fig. 4*G, H* were reported previously (1, 15). Dubin and Cleland (1) suggest that they may represent interneuronal receptive fields. The examples presented here may be functionally related in many ways to the typical concentrically organized receptive fields described above (Fig. 4*A–F*. See also accompanying paper, 18).

Responses to moving stimuli at various levels of light adaptation. The same bar (0.5° × 1°) as used for contour plane analysis was moved along the investigated axis of RF with a speed of 60°/s. Some homogeneous ON receptive fields with weak SE domains show simple, predictable patterns of movement responses. They consist (Fig. 2) of excitation as the stimulus moved into the RF centre followed by inhibition when it left it, followed by some (if any) excitatory response. The central excitatory-to-inhibitory transition is gradually faster at higher background luminance levels (0.00 to 3.4 cd/m²) and the inhibitory period shortens.

In other homogeneous and most heterogeneous ON-center fields this pattern becomes complicated by an appearance of the second excitatory peak inside the postcentrally evoked inhibition (Fig. 6 and 3, left column). This peak appears, as a rule, simultaneously with the appearance of the SE domain (compare Fig. 6, 1.5 cd/m²) at higher background levels. The time period between both excitatory peaks obtained during one direction of movement remains constant in all scotopic levels of background illumination. It diminishes slightly at higher intensities (Fig. 3, 3.8 cd/m²). This feature follows simultaneous diminution of spatiotemporal extent of PI domain, and shortaning of latency of SE domains which was presented in previous sections.

Two examples of heterogeneous OFF receptive fields stimulated by same moving light bar are presented in Figs. 3 (most right column) and 5. More spontaneously active and therefore more demonstrative was the cell shown in Fig. 5. The large inhibition seen on PST histogram reflects wide PI domain of the contour plane (upper-most row, 0.00 cd/m²). This inhibition is limited at its right side in higher light adaptation levels when SE domain appear (0.1–1.7 cd/m²). Small excitatory peak might be

seen on the rising phase of inhibitory period of the uppermost movement histogram. It strenghthens and moves toward the middle of inhibitory period with increasing background level.

Spatiotemporal extent of the PE and PI domains seen on contour planes (left column of Fig. 5) changes correspondingly to shifts in the position of the central excitatory peak. In the dark PI domain exceeds the ON period and holes out the PE domain with long tab of inhibition. This tab shortens at higher light adaptation levels and disappears at 1.7 cd/m^2.

Thus, the patterns of PST histogram for moving stimuli should be analyzed on the basis of both spatial and temporal characteristics of responses to stationary stimuli.

DISCUSSION

Background-induced RF changes. The main results of this experiment show a prominent reorganization of the LGN-cell RF after dark adaptation. It was not possible to study this phenomenon directly, neither by two (center/periphery) stimuli method (10, 16) nor by obtaining the area summation curves (3, 4, 16, 17), we therefore decided to analyze the LGN receptive fields with contour planes.

As mentioned in the methods section, classical names of spatial areas of an RF can be adapted with some approximation to compare other autors' findings with our spatiotemporal data: the PE domain describes spatiotemporal characteristics of the center response; SE domains refer to an opposite type excitatory surround; the SI domains can be considered a result of activation of the inhibitory surround; and the PI domain partially corresponds to the centrally-induced reciprocal inhibition (13). The last term will be discussed further in the accompanying paper (18).

The greatest change in the receptive field of the LGN cell observed in this experiment concerns the extent of the central responses of the dark-adapted RF. The PE domain of an ON-center cell is much wider in the scotopic than in the mesopic range (although 1.5° dispersion of that domain in dark adapted state, may result form "halo" of the stimulus — see the Controls section). It is due to the SI domains which develop at higher light adaptation levels in spatial positions occupied by the PE domain in darkness. Similarly, the SE domains of the OFF-center cells develop at higher background levels on the flanks of the PI domain. In both cases a stimulation of the same point of the retina can evoke either an excitation or an inhibition, depending on the adaptation state.

It appears further that a certain minimal light-adaptation level is necessary for developing prominent classic excitatory and inhibitory sur-

rounds. When well dark-adapted, all OFF-center and many ON-center receptive fields do not appear to have clear excitatory surrounds (Fig. 5 and 6). Some ON-center cells exhibit a centrally placed SE domain instead (Fig. 4*B, E, F*). Also the secondary inhibitory domains under scotopic conditions (Fig. 4*A, B, E, F*) differ in their spatiotemporal extent from those observed in corresponding RFs in the light adapted state. Classic inhibitory surround appears in ON-center RFs shown in Figs. 2 and 3 only when adapted to 0.1 cd/m^2 or higher levels.

The above presented data are in agreement with the finding (10, 16) that the inhibition persists in the RFs of LGN cells after dark adaptation. But simultaneously these data show that the spatiotemporal extent of the inhibitory influences is much different in light adapted than in dark adapted LGN RFs which contributes to the hypothesis of two different inhibitory processes in the LGN cells as discussed below.

Present experiments do not support the conclusion by Maffei and Fiorentini (10) that classic surround responses persist under scotopic conditions. It was shown, with increasing light-adaptation level that spatial position of both SE and SI domains move towards the center of the field. Thus the peripheral spot or annulus located in a fixed position cannot evoke a representative surround response. Secondly, as underlined in the Results section, the adaptation time and the time between consecutive stimulations play crucial roles for the intensity of the cell response in darkness. Frequent stimulation of the region close to the RF center can readapt the cell (compare Fig. 4F).

Neuronal adaptation. It was shown by Maffei et al. (11) that the antagonistic surround response disappears in ganglion cells after local darkening within the field center, and that, on the contrary, a light spot in the center enhances this response. It was further confirmed (6) that the antagonistic surround effect can be abolished in a few seconds after switching off the light within the field center in both ON and OFF-center cells. These findings showed that a neurophysiological mechanism induced from the RF center determines the surround effect of the lateral activation in ganglion cells. From our experiment it appears that the LGN receptive field can be also quickly reorganized by a local light spot placed within the field center. It was shown, however, similarly to the data of Virsu et al. (16), that a much longer time (up to 20 min) is required for a complete dark adaptation.

Moving stimuli. Lee et al. (7) have recently reported the responses of heterogeneous LGN cells to moving stimuli at various background levels. They did not find a strong relationship between the complex response patterns and the surround organization of the receptive fields. The above presented results seem to point out to such a relationship

with respect to the spatiotemporal organization of the excitatory and inhibitory field domains, especially for the heterogeneous RFs. This, however, needs a further investigation.

Receptive field organization of the LGN cells. Three models of the LGN cell receptive field organization were put forward (Fig. 7). In the so-called "zone" model (Fig. 7*A*) the opposite type retinal RF centers

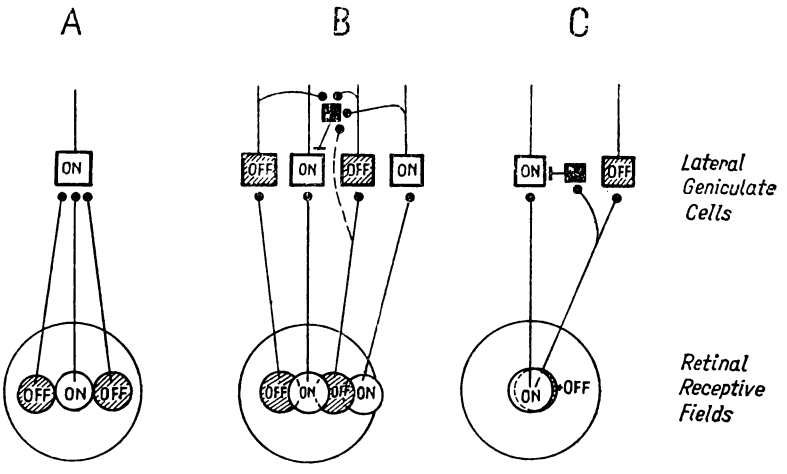

Fig. 7. Three models of a receptive field of a LGN neuron: *A*, "zone" (3, 10); *B*, "pool" (8, 13, 17); *C*, "reciprocal" (15). Small circles represent retinal RF centers. Large circle, the periphery of the ON-center retinal ganglion cell from which the LGN cell receives its main input. LGN relay cells are drawn as large squares. Each LGN neuron can receive fibers from several ganglion cells of fully overlapping RFs of the same center response type (8, 15), thus a line showing a retinogeniculate connection may represent more than one input. The OFF retinal fields and the corresponding LGN cells are shadowed. Small black squares, inhibitory interneurons. The dashed line connection in *B* is an alternative to the recurrent interneuron inputs (13, 17).

are assumed to strengthen the periphery effect of a given LGN cell receiving its major input from a ganglion cell of the same type (3, 10). The "pool" model assumes that many relay cells of different types excite interneurons which in turn deepen the LGN-cell surround in an additional "suppresive" field. Partial overlap of all retinal RFs of both types is postulated in this model as shown in Fig. 7*B* (13, 17). The third model suggest that only several opposite type ganglion cells afferents contrast "reciprocally" the basic organization of main input via an interneuron (15). Such organization requires an almost full overlap of both types of the retinal receptive fields (Fig. 7*C*).

"Zone" model cannot explain simply the results obtained in this experiment: narrowing of the central response area at higher background levels; simultaneous change of spatial position of SE and SI domains with different adaptation levels, integration of the "surround" SE domains in the central region of the RF in darkness.

The mirror-image changes of domains of the ON- and OFF-center receptive fields would support the hypothesis of reciprocally arranged inhibitory connections. On the other hand, a wider spatial extension of the inhibitory than of the excitatory domains of the receptive fields investigated, seems to confirm the pool model. We have recently found (Wróbel and Gerstein, unpublished results) that, in many LGN RFs, the inhibitory pool might be the deepest in the field center coextensively with a strongest central excitatory response.

According to our recent results (in preparation) and those published by others, about 10–20% of LGN neurons do not, although they possess classis RF organization, respond to stimulation of areas 17 and 18 (1) nor are labeled by their afferents (9), and can therefore be interneurons. It is not excluded that such neurons were also recorded among the sample presented here. In addition ON-OFF type neurons were found, just above the nucleus and in the lowest parts of its layers. Similar RF type was postulated for the other type of interneurons (1). The possible role of such cells for the models of receptive field formation of a LGN neuron is presented in the accompyining paper (18).

I thank Miss D. Stumpło and Mrs. B. Stachelska for splendid technical assistane; Mr. W. Gawor for photography; Dr. R. Tarnecki and Dr. M. Kossut for reading this manuscript and helpful suggestions.

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Accepted 23 May 1981